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The Potential Value of the Mid-Abdominal Musculature and Nervous System in the Reconstruction of Interordinal Relationships in Lower Neoptera

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> ## Abstract

The mid-abdominal musculature and its innervation are compared for several lower neopteran "orders"; data on Embioptera and Mantophasmatodea are presented for the first time. For the sclerotisations, the musculature, and the nervous system of the mid-abdomen general descriptions are given, and general aspects of homologisation in these elements are explained; for the lateral muscles the distinction of three groups innervated by the T-, B-, or C-nerves is confirmed. Differences in the musculature and nervous system of the lower neopteran lineages are discussed and evaluated with regard to their phylogenetic implications. Conditions in Ephemeroptera, Megaloptera, and Zygentoma are partly included in the discussion. Several characters were found to be informative on interordinal relationships. Plecoptera have features probably plesiomorphic at the neopteran level: the origin of nerve A in front of the ganglion and the innervation of intrasegmental lateral muscles by nerve A; this may support the monophyly of a taxon comprising all other Neoptera. The hyperneural muscle found in many Dictyoptera also appears as a uniquely plesiomorphic structure (at the pterygotan level). The co-occurrence of two specific lateral muscles supplied by nerve B as well as certain subdivisions in the lateral muscles may support a clade Phasmatodea + Embioptera. We also point to character systems that appear informative on the internal phylogeny of order-level taxa, such as the relationships between nerves T and M in Plecoptera, the ventral musculature in Ensifera, the dorsal musculature in Dermaptera, and details of the hyperneural muscle in Dictyoptera. Besides the very low number of taxa studied so far, major problems still persistent in the use of mid-abdominal characters for phylogenetic work are (1) the insufficient knowledge on topographic homologies for the lateral cuticular areas of the mid-abdomen; (2) lacking knowledge on the neuronal structural level of the mid-abdominal nervous system; (3) difficulties in the homologisation of muscles and nerves between Pterygota and the apterygote Archaeognatha and Zygentoma, which are partly due to the presence of a system of non-cuticular tendons in the latter and limit outgroup comparison for Pterygota.

> ## Key words

Abdomen, musculature, innervation, homology, Pterygota, Neoptera, Embioptera, Mantophasmatodea.

1.   Introduction

Much work has been done in recent years attempting to resolve the phylogenetic relationships among the principal lineages of the Pterygota. Some contributions are based on morphological data, either on the isolated study of some specific character system (e.g., Pass et al. 2006: circulatory system; Haas & Kukalová-Peck 2001: wing structure), on the discussion of the morphological characters currently available (e.g., Willmann 2003, 2005; Grimaldi & Engel 2005; Klass in press), or on the analysis of large character matrices (Beutel & Gorb 2001, 2006). Other papers focused on the analysis of molecular data, using different sets of genes and analytical approaches, and partly incorporating morphological data as well (Terry & Whiting 2005; Kjer 2004; Kjer et al. 2006; Cameron et al. 2006a,b). The phylogenetic results of these con-

tributions are highly contradictory because no grouping of two or more of the major pterygotan lineages is supported consistently. Solely the monophyly of the Neoptera is generally accepted.

Accordingly, the phylogenetic tree of KRISTENSEN (1991: fig. 5.5) still seems to be the most adequate representation of our knowledge on pterygotan phylogeny. Therein the relationships between Ephemeroptera, Odonata, and Neoptera are considered unresolved, and the base of Neoptera is shown as a polytomy composed of 10 principal lineages: the Plecoptera, Embioptera, Notoptera (= Grylloblattodea), Phasmatodea, Orthoptera, Dermaptera, Dictyoptera, Zoraptera, Acercaria (= hemipteroid orders) and Endopterygota (= Holometabola). In 2002 the Mantophasmatodea have been added to this polytomy, representing the 11th lineage (KLASS et al. 2002, 2003).

While several morphological character systems were in the focus of some recent studies, such as the spermatozoa (JAMIESON et al. 1999; DALLAI et al. 2003), circulatory system (PASS 2000; HERTEL & PASS 2002; PASS et al. 2006), wing base and venation (HAAS & KUKALOVÁ-PECK 2001; HÖRNSCHEMEYER 1998, 2002), and female genitalia (KLASS 1998, 2001a, 2003), it is evident from a survey of the morphological literature that the knowledge on many other character systems is still much too limited for their consequent use in the discussion of pterygotan relationships or incorporation into character matrices. This applies to most parts of the musculature and its innervation, including the segments of the middle part of the abdomen, which are in the focus of this contribution.

The abdominal musculature in insects fulfills a variety of tasks. It is responsible for all movements of the abdomen, e.g., during egglaying or for respiration (ventilation of the tracheal system). In some taxa there are highly specialised functions such as bending the abdomen anteriad over the head (Dermaptera: for grasping prey; Phasmatodea: *Sceptrophasma*: during egglaying) or stabilising the particularly long abdomen (e.g., Phasmatodea).

The various abdominal segments and their musculature show differences due to the association with the thorax or genitalia, and three groups of segments can be distinguished: **(1)** The segments of the mid-abdomen, which lie in between the two following groups, are most generalised with regard to their musculature. **(2)** The anteriormost segments – the 1st and, to a lesser extent, the 2nd or even the 3rd – show peculiarities depending on their close functional relationship to the thorax and on their partial reduction in many taxa; reduction is particularly true for segment 1. **(3)** In the posteriormost segments (postabdomen) the musculature is ± strongly specialised for genitalic functions or for moving the cerci; the most anterior segment showing such specialisation is usually the 7th or 8th in the

female and the 9th in the male. However, the extent to which these segments differ from the mid-abdomen depends strongly on the extent of differentiation of the external genitalia. The mid-abdomen thus comprises abdominal segments 2–7 as a maximum, or only 4–6, depending on the number of modified anterior and posterior segments.

There are a number of contributions where the musculature of the mid-abdominal segments is described in detail for some taxon (or taxa), though the quality of the descriptions varies strongly. In only a few studies, however, the arrangement of the abdominal nerves and their relationships to the muscles have been included.

Concerning the lower Neoptera (excluding the Acercaria and Endopterygota), the literature shows a strong focus on the two suborders of Orthoptera. For **Caelifera** the abdominal musculature of *Paratettix cucullatus* (Tetrigidae = Acrydiidae) and *Melanoplus bivittatus* (Acrididae) is described in the extensive work of FORD (1923), who altogether included representatives from several lower neopteran orders as well as Ephemeroptera and Odonata. SNODGRASS (1935) described the abdominal musculature of *Dissosteira carolina* (Acrididae), ALBRECHT (1953) described that of *Locusta migratoria* (Acrididae), and COVELO DE ZOLESSI (1968) described that of *Cephalocoema albrechti* (Proscopiidae). BLACKITH & BLACKITH (1967) studied the muscles and nerves in Morabinae (Eumastacidae), while STEINMANN (1965) in his study of *Acrotylus insubricus* (Acrididae) and SCHMITT (1954), treating *Dissosteira*, considered only the nervous system. For **Ensifera** the description of the abdominal musculature of a number of species is included in FORD´s (1923) work (Gryllidae: *Nemobius fasciatus*, *Gryllus assimilis*; Gryllotalpidae: *Gryllotalpa hexadactyla*; Tettigoniidae: *Ceutophilus lapidicola*, *Cyphoderris monstrosa*, *Neoconocephalus ensiger*, *Conocephalus fasciatus*, *Scudderia furcata*). DU PORTE (1920) described the musculature of *Gryllus assimilis*, while SCHMITT (1954) treats the nervous system of the same species (as "*Acheta*"). SCHMITT (1964) provides data on the nerves of some tettigoniid species for which the muscles had been studied by FORD (1923).

For **Dictyoptera**, FORD (1923) gave descriptions of the musculature in the blattarians *Blaberus atropos* (Blaberidae) and *Parcoblatta pennsylvanica* (Blattellidae) and in the mantodean *Stagmomantis carolina* (Mantidae), while SCHMITT (1954) provided data on the nerves in the cockroach *Periplaneta americana* (Blattidae). SHANKLAND´s (1965) description of abdominal muscles and nerves in *Periplaneta americana* is the most elaborate of all the older contributions. LAGRECA & RAINONE (1949) and LEVEREAULT (1938) treated the abdominal muscles of *Mantis religiosa* and *Stagmomantis carolina*, respectively, and KERRY & MILL (1987) studied the muscles and nerves of *Hier-*

odula membranacea (all Mantidae). More recently the mid-abdominal musculature and its innervation was investigated in detail for two representatives of Dictyoptera, *Sphodromantis viridis* (Mantidae) and *Periplaneta americana* (KLASS 1999; including comprehensive comparison with SHANKLAND´s 1965 and KERRY & MILL´s 1987 data). This is also the first comparative approach including both muscles and nerves, and intraspecific variation is also extensively considered. KLASS (2000) described the abdominal muscles of the primitive isopteran *Mastotermes* (Mastotermitidae).

Data on the abdominal muscles of **Phasmatodea** are available from the study of MAKI (1935) on *Megacrania tsudai*, and information on the muscles and nerves is given in MARQUARDT (1939) for *Carausius morosus*. Most recently the mid-abdomen of several phasmatodean species was described and discussed in KLUG (2005) and KLUG & BRADLER (2006), including the muscles and nerves. This also included *Timema nevadense* (Timematidae) and *Agathemera crassa*, which represent the most basal branches within Phasmatodea.

For adult **Plecoptera**, data are provided by FORD (1923) on *Perla* sp. (Perlidae), by SCHMITT (1963) on *Pteronarcys californica* (Pteronarcyidae; also including data on the nymph) and by ZWICK (1973) mainly on *Eusthenia* sp. (Eustheniidae). In addition, KNOX (1965) studied the nymphal muscles and nerves of *Acroneuria* sp. (Perlidae). Regarding **Notoptera**, WALKER (1943) studied in detail the abdominal musculature of *Grylloblatta*, but there are no data on the nervous system. Data on **Dermaptera** have been sparse and contradictory, based on FORD´s (1923) and POPHAM´s (1959) studies of the musculature of *Forficula auricularia* (Forficulidae). KLASS (2001a) provided more detailed information on the muscles in the epizoic dermapteran *Hemimerus vosseleri* (Hemimeridae), including also some data on the nerves and a discussion of FORD´s and POPHAM´s results. There are not any data yet in the literature on the mid-abdominal muscles and nerves in **Embioptera** and **Mantophasmatodea**.

There are also a few contributions on the abdomen of **Acercaria** and **Endopterygota** where both muscles and nerves are included. MAKI´s (1936) treatment of *Chauliodes formosana* (Megaloptera) is most important, because the morphology of this taxon is very generalised. Other detailed work is available for Coleoptera: HOLSTE (1910) on the *Dytiscus* imago (Dytiscidae), and JÖSTING (1942) on the *Tenebrio* larva (Tenebrionidae). For **Ephemeroptera** there is, besides the fairly superficial treatment of *Hexagenia bilineata* in FORD (1923), a comprehensive study of the muscles and nerves of *Povilla adusta* (BIRKET-SMITH 1971). ASAHINA (1954) describes the abdominal musculature of a number of representatives of **Odonata**, but there are no data on the nerves of this group.

For the **apterygote Insecta**, BIRKET-SMITH (1974) provided a detailed study of abdominal muscles and nerves in the archaeognathan *Petrobius lohmanderi* and the zygentoman *Lepisma saccharina*. BITSCH (1973) described the abdominal muscles in the archaeognathan *Trigoniophthalmus alternatus*. However, both the musculature and the nervous system are difficult to compare between apterygote Insecta (especially Archaeognatha) and the pterygotan representatives studied because of widely unclear muscle and nerve homologies. This is due to the presence of a system of tendons (consisting of connective tissue) in the apterygote taxa, on which many of the abdominal muscles are inserted. In the Pterygota such tendons were lost and all muscle insertions are immediately located on the cuticular body wall. Since each of the ventral tendons is attached to the body wall at several positions, a comparison of insertion areas between apterygote Insecta and Pterygota is often ambiguous (see KLASS 2001a: 295ff and figs. 37, 38). Another reason impeding homology hypotheses is that the sets of muscles innervated by the various main nerves of a segment are quite different from the sets of muscles targeted by the single nerves in Pterygota. Axons seem to be bundled into nerves according to fairly different patterns. Consequently, major rearrangements of the abdominal musculature and nervous system must have occurred in the stem lineage of Pterygota.

The musculature and nervous system of the mid-abdominal segments are relatively simple as compared to the thoracic segments. Yet it is evident from the previous literature (see KLASS 1999: 34ff) that they are still complex enough, and also variable enough among high-rank subgroups of Neoptera, for being a rich source of characters potentially informative on phylogenetic relationships among the principal neopteran lineages.

The present work gives an overview over the muscle and nerve arrangement of mid-abdominal segments in the Lower Neoptera. Our survey and discussion is based on the literature and own studies as summarised in Table 1. Data on the mid-abdominal anatomy of Embioptera and Mantophasmatodea are presented here for the first time, though they still are quite fragmentary. Muscle arrangement and nerve topography of mid-abdominal segments are evaluated for characters that appear useful for plylogenetic analysis in lower Neoptera.

2.   Material and Methods

Material. For the investigation of abdominal musculature and innervation specimens fixed in alcohol or in Bouin's solution, or freshly killed specimens were

used; the material is listed in Tab. 1; in the text, the respective species are referred to by their generic name. In addition, data from the literature are considered to a large extent, and references for relevant contributions are also included in Tab. 1. Ephemeroptera and occasionally Zygentoma (mainly according to Birket-Smith 1971, 1974) are referred to as outgroup taxa. *Chauliodes* (according to Maki 1936) is included in the comparisons as a particularly suitable generalised endopterygotan 'exemplar'.

Dissection. The pregenital abdominal segments of all specimens were opened laterally and dissected in isopropanol or ethanol. For better identification of fine nerve branches, muscles and nerves were stained using Coomassie brilliant blue (however, in alcohol-preserved specimens the fine rami of nerves could not always be detected). Such staining lasted for about one hour in freshly killed specimens. Dissections were done under a stereo microscope, with magnifications between 10x and 176x. The angle of light was varied to optimize contrast.

Illustrations. All figures show the right side of the body in an internal view. The dorsal body wall and the ventral body wall were bent to lie in the same plane. Consequently, as compared to the longitudinal muscles, the lateral muscles appear longer than in the natural condition. However, the topographical relations among all muscles and nerves are preserved in the view chosen here.

From bottom to top the coxosternum with the ventral nerve cord and ventral muscles, pleural membrane overlain by lateral muscles, and the tergum with dorsal muscles can be seen in each figure. The internal ventral longitudinal muscles are shaded in a dark grey, the external ventral longitudinal muscles are shaded in pink. The lateral muscles innervated by nerve T are green, those innervated by nerve B are blue, those innervated by nerve C are yellow. Sclerotised parts of the body wall are shaded in light grey (weaker sclerotisations in a paler grey).

Terminology. The terminology of muscles and nerves is modified after Klass (1999). Muscles are briefly designated by arabic numerals. Major nerve branches are termed with upper case letters. In the illustrations, only those nerve branches are depicted that innervate muscles. Terms for muscles and nerves used in the previous literature are supplemented by an asterisk (*).

Abbreviations

1, 2 …	numbers of muscles
A	dorsal nerve (main branch)
B	lateral nerve (main branch)
C	ventral nerve (main branch)
G	ganglion
M	median nerve
T	transverse nerve
est	eusternite
lst	laterosternite
ltg	laterotergite
pl	pleurite
mT–A	mesal anastomosis between nerves T and A
lT–A	lateral anastomosis between nerves T and A
T–A	anastomosis between nerves T and A
A–B	anastomosis between nerves A and B
B–C	anastomosis between nerves B and C
C–T	anastomosis between nerves C and T

3.　Survey of components of mid-abdominal segments

3.1.　The mid-abdominal exoskeleton and sclerites

The exoskeleton is essentially comprised of a dorsal tergite and a ventral coxosternite, and on each side a pleural membrane in between. Most important is the occurrence of smaller sclerites in the lateral parts of a segment, which can be isolated lateral parts of the tergite (laterotergites) or of the coxosternite (laterosternites), or formations of the pleural membrane (pleurites). In addition, paratergites are lateral parts of the tergite set off from the main part by a distinct fold. While the pattern of mid-abdominal sclerites is of primary importance for the interpretation of mid-abdominal muscles, homologies across taxa are not always clear for the smaller lateral sclerites. The termini "paratergal" or "laterotergal" used for different insects do not always address homologous structures (Klass 1999); in this paper the description of muscle insertions as "tergal" refers to the tergum including paratergal sclerotisations. The spiracles are important, but not unambiguous landmarks in the attempt to homologise sclerites.

In Archaeognatha and Zygentoma only a tergite and a coxosternite are present, the latter still showing the primary subdivision into a median eusternite and lateral coxites in Archaeognatha and some Zygentoma (Bitsch 1973: **stVI*** and **cxtVI*** in fig. 2). The spiracles are located in the pleural membrane in Zygentoma (e.g., Rousset 1973; Birket-Smith 1974: 36), but on the lowest parts of the tergites in Archaeognatha (e.g., Bitsch 1973: fig. 1B); this sheds doubt on the positional conservation of the spiracles and their reliability as landmarks for homologisation.

Among the lower Neoptera, the Dermaptera (Klass 2001a: fig. 1; Giles 1963: 122, 133), Pleco-

ptera (Zwick 1973, 1980: 53), and Phasmatodea (Beier 1968: 18f) have retained this pattern of coxosternite, tergite, and pleural membrane without any smaller sclerites. Exceptions are some tiny sclerites immediately associated with the spiracles, and a small sclerotised tendon in Dermaptera (Klass 2001a: **lt*** in fig. 1). Dermaptera and Phasmatodea have the spiracles in the pleural membrane. The spiracles of Plecoptera lie immediately below the tergum in the pleura.

Dictyoptera also have undivided coxosternites and tergites, without pleural sclerites. In Blattaria and Mantodea the lateral parts of the tergite are set off from the main parts by a fold and are called paratergites; to these some lateral muscles are attached (Klass 1999). *Mastotermes* lacks a fold separating tergal s.str. and paratergal areas (Klass 2000).

Many Ensifera show a subdivision of the coxosterna into a median part and paired lateral parts; the latter are usually further subdivided (e.g., Beier 1972: 68; Ford 1923). Often the median part is called "eusternite", and the lateral parts "laterosternites". This subdivision is likely secondary and probably does not reflect the primary components, eusternite and coxites, of apterygote Insecta, and the ensiferan "eusternite" is thus probably not a true eusternite. The subdivision is present in Tettigoniidae, Anostostomatidae, Gryllacrididae, Stenopelmatidae, and many Rhaphidophoridae (Desutter-Grandcolas 2003), while some Rhaphidophoridae (*Macropathus*: Richards 1955; *Troglophilus*: Fig. 8) lack it. In addition, Ensifera frequently have small sclerites in the pleural membrane (pleurites), lateral to the coxosternite (Ford 1923; Ander 1939). The spiracles are located on the lower parts of the tergites (Beier 1972: 68).

Conditions in Caelifera vary strongly (Snodgrass 1935: fig. 2). The division into "eu- and laterosternites" can be present or absent, and the same is true for discrete pleurites and laterotergites. The spiracles are variously located on the lower part of the tergite, or on the laterotergite if present, or in the pleural membrane.

Embioptera regularly have two sclerites between coxosternite and tergite (*Antipaluria*: Fig. 3), the upper, spiracle-bearing laterotergite **ltg** and the lower pleurite **pl**, both of which may be further subdivided (e.g., Ross 2000: figs. 37, 38).

Patches of weak sclerotisation between coxosternite and tergite also occur in Notoptera and Mantophasmatodea (in the posterior portion of the pleura near the coxosternite in *Tyrannophasma*: Fig. 4; K.-D. Klass pers. observation), but these are not well documented and can hardly be distinguished from the surrounding pleural membrane; in both taxa spiracles are located in the pleural membrane.

3.2. Muscles of the mid-abdomen

The muscles potentially occurring in Neoptera are listed in Tab. 2. The mid-abdominal segments of Neoptera contain several groups of muscles: The dorsal muscles have a longitudinal course and connect successive tergites. The ventral muscles also have a longitudinal course and connect successive coxosternites. The lateral muscles have a vertical course and connect tergites and coxosternites of the same or of successive segments, though one of the insertions can be on the pleural membrane or smaller sclerites located therein. Spiracle muscles (**13**, **14**) connect different parts of a spiracle with each other, with the coxosternite, or with lateral parts of the tergite. Dorsal transverse muscles (alary muscles **15**) extend from anterolateral areas of a tergite to the heart. The ventral side includes some further muscular structures of very different kind that are often comprised as the "ventral transverse muscles". Only dorsal, ventral, and lateral muscles, and the ventral transverse muscles are considerd here (see Klass 2000 for a discussion of spiracle muscles).

In the dorsal muscles, two groups can be distinguished in most lower Neoptera according to positional criteria: The internal dorsal muscles (**10**) typically extend from one segmental border (or the area shortly behind it) to the next (borders as defined by the antecostae if present) and have a straight course. The external dorsal muscles (**11**, **12**) extend from a more central or posterior part of the tergite to the segmental border or intertergal membrane behind and usually have an oblique course. Both the internal and external dorsal muscles are usually subdivided into several bundles.

In the ventral muscles there is a similar distinction of two groups according to positional criteria: The internal ventral muscles (**7**) usually extend from one segmental border (or the area shortly behind it) to the next and have a straight course. The external ventral muscles (**8**, **9**) extend from a more central or posterior part of the coxosternite to the segmental border or intersternal membrane behind and usually have an oblique course. Both the internal and external ventral muscles are usually subdivided into several bundles.

The lateral muscles include those that connect elements of the same segment (intrasegmental lateral muscles **1**, **2**, **3**, **16**, **17**, **18**, **22**, **23**). They run from the tergite to the coxosternite, or they connect the tergite or the coxosternite with the membrane or small sclerites of the pleural area. These muscles can be split into several or even numerous individual bundles, and they may form groups according to different levels of insertion on the tergite or coxosternite. The posterior part of a segment may include lateral muscles running to sclerites of the succeeding segment (intersegmental lateral muscles **4**, **5**, **6**, **19**; considering the "secondary segmentation" defined by the sclerites); these may

either be ascending from the coxosternite to the tergite of the successive segment (**4**, **5**), or descending from the tergite to the coxosternite of the successive segment (**6**, **19**), though either the upper or the lower insertion can be on the pleural membrane.

The ventral transverse muscles in the widest sense comprise several different structures that with very few exceptions do not co-occur in a taxon. The first are true transverse muscles that connect the left and right parts of a coxosternite and are shaped as a ± compact bundle (**20**). The second type is a delicate sheet of muscle fibres and connective tissue that continues throughout most segments of the abdomen (and often thorax) and is attached to the coxosternites in at least one point per segment and side (ventral diaphragm). The third kind of structure is the hyperneural muscle of Blattaria and Isoptera (**16*** in Klass 1999), which consists of a pair of longitudinal bundles running along the abdominal CNS and is attached to the body wall only in the metathorax and abdominal segments 2 and 9, at its anterior and posterior ends.

3.3. Nerves of the mid-abdomen

Each abdominal segment possesses a neuromere, which either forms a ganglion of its own or is fused with neighbouring segmental neuromeres to form a compound ganglion. Concerning the fusion of ganglia, there is much variation among the Lower Neoptera (Nesbitt 1941), which surely also includes much parallel evolution. A ganglion or neuromere can be located within its own segment or can be placed ± far anterior to it, occasionally several segments ahead (Klass 1999: **4G** in fig. 2). Successive ganglia are interconnected by the paired connectives and usually by an unpaired, delicate median nerve **M** between them.

Each neuromere usually sends off four pairs of nerves: the dorsal nerve **A**, the two ventral nerves **B** and **C** (**B** also called lateral nerve), and the transverse nerve **T**. However, two or more of these nerves can leave the neuromere jointly, having a common stem; which nerves have a common stem varies among taxa but can also vary between individuals of a species or between different segments of an individual (e.g., Klass 1999).

Nerve **T** usually arises from the median nerve shortly in front of a ganglion. At or near their origin from nerve **M** the **T**-nerves are usually somewhat swollen to form perisympathetic organs (surveyed in Grillot 1983). Nerve **T** continues laterally in the anterior part of the segment to innervate anterior lateral muscles and the spiracle muscles, and perhaps the alary muscles.

Nerve **A** arises from its ganglion or from the connectives in front of it. It runs laterad and innervates the internal ventral muscles. Further laterally it ascends

dorsad and gives off branches into the internal and external dorsal muscles, and eventually it terminates into the lateral heart nerve **H**, which runs alongside the heart on both sides. In the pleural and dorsal areas nerve **A** gives origin to branches that ramify over the lateral and dorsal body wall.

Nerves **B** and **C** arise from their ganglion and most frequently have a common stem. Nerve **B** gives rise to several branches that ramify upon the ventral body wall, and then innervates lateral muscles near the middle of the segment. Nerve **C** sends branches into the external ventral muscles and, further laterally, may additionally innervate posterior lateral muscles.

For some Neoptera a paramedian nerve **P** has been reported that runs longitudinally in the ventrolateral part of the abdomen, crossing many segments (Klass 1999 for *Periplaneta*; Maki 1936 for *Chauliodes*; Schmitt 1954), closely associated to the ventral diaphragm if present, and interconnecting successive **T**-nerves. Such a nerve may be present in many taxa but is easily overlooked because its fine fibres are usually embedded in surrounding tissue.

The major segmental nerves **T**, **A**, **B**, and **C** are variously interconnected by anastomoses. There is most frequently an anastomosis between nerves **T** and **A** (anastomosis **T–A**), or even two of them (the mesally located **mT–A**, and the lateral **lT–A**). Further anastomoses can connect nerves **A** and **B** (**A–B**), nerves **B** and **C** (**B–C**), and nerve **C** with nerve **T** of the following segment (**C–T**), all being located in the ventrolateral part of a segment. Anastomoses can consist of one or more nerve strands traversing from one nerve to another, but they can as well be represented by a spatially limited fusion of the two nerves (alternatives also observed as individual variations in *Periplaneta*; Klass 1999).

The insect abdomen contains several types of stretch receptors that are connected with the nervous system (e.g., Osborne & Finlayson 1962; Finlayson & Lowenstein 1958; Shankland 1965; Klass 1999). We do not include these structures here, but note that they constitute a character system worthwhile further exploration and comparison among neopteran lineages.

4. Homology of components of mid-abdominal segments

4.1. Basis for homology hypotheses

Topographic homology is the first step of homologising and relates to hypotheses on the correspondence (by evolutionary origin) of body parts in different taxa (Klass 2001b: 230f). In the following the innervation

by certain nerve branches is used as one criterion in homologising muscles, and having specific muscles as targets is used as one criterion in homologising nerve branches. We emphasize that this is not circular. Rather, the entire structural pattern formed by the skeletomuscular and nervous systems (and further elements if available) of a segment is compared among taxa, and homologies are hypothesised following parsimony as a rule. This means those homologies are accepted that require the lowest extent of structural transformation to be assumed. This basically corresponds with the procedures in the alignment of DNA sequences – with the major difference, however, that in morphology the extent of transformation can rarely be objectively measured and be treated numerically.

4.2. Homology of muscles

In many cases the position of a muscle (i.e., the location of its attachments) is sufficiently specific for homologising muscles between taxa, but innervation is often necessary to distinguish muscles with similar position.

In the dorsal muscles, following positional criteria, straight muscles attaching far anteriorly on the tergite are considered internal dorsals, oblique muscles attaching far posteriorly on the tergite are considered external dorsals. The innervation pattern cannot contribute to the distinction of specific dorsal muscles. The dorsal muscles are all innervated by branches from the dorsal nerve **A**, and at least in *Periplaneta* and *Sphodromantis* much individual variation was found regarding the arrangement of the various nerve branches that innervate the external and the internal dorsal muscles (KLASS 1999: figs. 10–21). Therefore, when positional criteria are ambiguous, the same applies to statements of topographic homology of dorsal muscles.

In the ventral muscles, positional criteria similarly suggest that straight muscles attaching far anteriorly on the coxosternite are internal ventrals, oblique muscles attaching far posteriorly on the coxosternite are external ventrals. However, innervation can contribute a further criterion, as the internal ventrals are innervated by branches of nerve **A**, and the external ones by branches of nerve **C**. Innervation is here considered conclusive evidence on homology in cases of ambiguous positional criteria.

The lateral muscles are a particularly diverse group that includes many homology problems. Positional criteria are essential for homology hypotheses. The primary distinction is between intrasegmental lateral muscles, ascending intersegmental ones, and descending intersegmental ones (Tab. 2). Within these three categories, muscles connecting the tergite and coxosternite can be distinguished from those having one

attachment in the membrane or on small sclerites in between, and muscles may be more specifically homologised based on this criterion. The location in the anterior or more posterior part of the segment is another poor criterion for homology of particular intrasegmental lateral muscles. However, these positional criteria are more difficult at closer inspection. One basic problem concerns the distinction between intra- and intersegmental in cases where one insertion (or both) is on membrane close to the segmental border, while the exact course of this border cannot be determined; on the tergite the antecosta usually provides a useful landmark, but there is rarely such a clear structure in the pleural region. Another basic problem is that for cuticular areas in the lateral wall of the abdomen – between the margins of the main coxosternal and tergal sclerite plates – the topographic homologies among higher taxa are widely unresolved. Insufficient knowledge on the course of the borders between the coxosternal, pleural, and tergal territories is a major aspect of this problem. Related questions are whether smaller sclerites in the lateral abdominal wall of certain taxa are split off lateral parts of the coxosternum or tergum, or truly pleural sclerites. Or, whether in specific taxa membraneous parts of the "pleura" may rather be desclerotised lateral parts of the tergal or coxosternal territory (muscle insertions then only apparently being located in the "pleural membrane"). A taxon particularly problematic in this regard is *Gryllus* (Fig. 7, with several small sclerites and muscle attachments in the pleural region). These problems have the effect that the comparative topographic interpretation of attachment sites of lateral muscles is often ambiguous. As explained above, additional landmarks such as the spiracles are also of questionable reliability.

Most importantly, the lateral muscles can additionally be specified according to their innervation via nerve **T**, nerve **B**, or nerve **C**. The muscles are here called **T**-muscles (**2**, **3**, **19**, and **22**), **B**-muscles (**1**, **16**, and **23**), and **C**-muscles (**4**, **5**, **6**, 17, and **18**). This provides a highly valuable criterion for muscle homologies in Neoptera. Nonetheless, it must not be forgotten that there are anastomoses between these nerves, and innervation through different nerves in different taxa may thus actually be accomplished by homologous axons. Positional criteria and innervation correlate to some extent: **T**-muscles are usually located in the anterior part of their segment, **B**-muscles in the middle part, and **C**-muscles in the posterior part (though with exceptions). **T**- and **B**-muscles are usually intrasegmental, whereas **C**-muscles are mostly intersegmental (with the exception of muscles **17** and **18** of Phasmatodea).

Nonetheless, even after a combined consideration of cuticular structures, muscles, and nerves some cases of muscle homology will remain ambiguous. Conse-

quently, also in the present paper the resolution of homologies for lateral muscles will be limited (Tab. 2 must also be seen with this limitation).

4.3. Homology of nerves

The main nerves and their branches and anastomoses are bundles of axons, and homologous axons might well be included in different nerves in different taxa, or pass from one nerve to another via an anastomosis. Consequently, homologising nerves and their branches is necessarily superficial, and respective statements must be seen with this limitation. A more detailed view of homologies in the nervous system needs consideration of all single axons and the location and connections of their cell bodies in the CNS, which is not within the scope of this contribution.

The four main segmental nerves **A**, **B**, **C**, and **T** can topographically be recognised regarding their target regions, i.e., certain muscles or parts of the body wall, and anastomoses (according to the description in 3.2.). Sᴄʜᴍɪᴛᴛ (1962, 1963, 1964, 1965) discussed the homology of nerves **A**, **B**, **C**, **T** and the anastomoses for members of Caelifera, Ensifera, Blattaria, Phasmatodea, Plecoptera, and a megalopteran. Kʟᴀss (1999) discussed nerve homologies in Dictyoptera and other Neoptera. With a few exceptions the single main nerves are morphologically distinct and have similar sets of targets throughout the lower neopterans studied, which are evident from chapter 4.2. on muscle homologies. However, the sets of anastomoses differ greatly among taxa.

5. Structural differences among lower neopteran taxa

5.1. Roots of main nerves

Usually in Pterygota the main nerves **A**, **B**, and **C** arise from the ganglion of the segment they supply, or more rarely from the connectives behind the ganglion. In Plecoptera, however, nerve **A** originates from the CNS *in front* of the ganglion (Fig. 9), either from the connective, or even from the posterior face of the preceding ganglion (depending on the segment). This has been interpreted as an origin *behind* (or on the hind part of) the neuromere of the corresponding segment (though with some additional complications in the different hypotheses proposed by Sᴄʜᴍɪᴛᴛ 1963 and Kɴᴏx 1965, and by Zᴡɪᴄᴋ 1973). However, the relations between the various nerves and their anastomoses and targets clearly show that the former interpretation is

much more likely. Accordingly, earlier assignations of ganglia to segments in Plecoptera must also be revised (e.g., the neuromere/ganglion of abdomen 4 in Zᴡɪᴄᴋ 1973 is actually the neuromere/ganglion of abdomen 3). An origin of the dorsal nerve far in front of its ganglion is also found in Zygentoma and Chilopoda (Bɪʀᴋᴇᴛ-Sᴍɪᴛʜ 1974; Rɪʟʟɪɴɢ 1968; Hᴇᴄᴋᴍᴀɴɴ & Kᴜᴛsᴄʜ 1995) and may represent a plesiomorphic condition.

Among the Neoptera that have the root of nerve **A** on the con-segmental ganglion, nerve **A** originates separately from nerves **B** and **C** in the phasmatodean *Timema* (Fig. 1), the orthopterans *Locusta* (Fig. 5), *Dissosteira* (Sᴄʜᴍɪᴛᴛ 1954), *Gryllus* (Sᴄʜᴍɪᴛᴛ 1954; Fig. 7), and *Troglophilus* (Fig. 8), the dermapterans *Hemimerus* (Kʟᴀss 2001a) and *Labidura* (Klass unpubl. observations), and the mantophasmatodean *Hemilobophasma* (not depicted). In contrast, nerve **A** has a common stem with nerves **B** and **C** in the phasmatodeans *Sceptrophasma* (Fig. 2), *Carausius* (Mᴀʀ-ǫᴜᴀʀᴅᴛ 1939), and *Diapheromera* (Sᴄʜᴍɪᴛᴛ 1954), and in the mantodeans *Sphodromantis* (Kʟᴀss 1999) and *Hierodula* (Kᴇʀʀʏ & Mɪʟʟ 1987). In *Periplaneta*, *Antipaluria* (Fig. 3), and *Tyrannophasma* (Fig. 4: only the common stem of nerves is shown, **A** and **B**+**C** arise separately from **G4**) the character was found to vary among segments and, as observed in *Periplaneta*, among specimens (for *Periplaneta* see Kʟᴀss 1999: figs. 22–28, also Sᴄʜᴍɪᴛᴛ 1954 and Sʜᴀɴᴋʟᴀɴᴅ 1965). The latter cases indicate that the character is too variable for phylogenetic work on high-rank taxa.

The transverse nerve **T** usually arises from the median nerve **M** in a position anterior to the ganglion (Figs. 1–2; 5–8). Most often the right and left nerves originate at the same level, but the origins can also be asymmetrical. Asymmetry was consistently found in *Hemilobophasma* but also occurs in *Ephemera* (Fig. 10) and *Sphodromantis* (Kʟᴀss 1999: fig. 2). Considering the intraspecific variation in different insects (see also Gʀɪʟʟᴏᴛ 1983), this character cannot be considered to be of much phylogenetic value.

For Plecoptera some interesting variation with regard to the median nerve **M** and the origins of the **T**-nerves is evidenced by the data in the literature (Kɴᴏx 1965; Sᴄʜᴍɪᴛᴛ 1963; Zᴡɪᴄᴋ 1973): Nerve **M** is usually divided into a right and a left strand for some distance in between two ganglia (Zᴡɪᴄᴋ 1973: fig. 26), and the two strands may additionally be attached to the connectives and the anterior face of the ganglion behind. The nerves **T** (**Q*** in Zwick 1973) have separate origins on the right and left strands of **M**, and seem to originate from the connective or anterior part of a ganglion if the strands of **M** are attached to these parts. In the latter case nerves **T** can seemingly co-originate with nerves **A** and be coalesced with them for some distance, thereby appearing as a basal branch of nerve **A** (Kɴᴏx 1965: **TN*** in fig. 1). In *Perlodes* (Fig. 9) an

undivided **M** is visible between the connectives up to the anterior face of ganglion **G3**, while in the segments behind half-strands of **M** are likely attached to the connectives, which seemingly give rise to the nerves **T**. These variations might be of interest for phylogeny reconstruction within Plecoptera.

5.2. Arrangement of main nerves and their major branches

Usually in Neoptera there is a clear separation of nerves **A**, **B**, and **C**, and the nerves have specific targets as described in chapter 3.3. However, two lower neopteran taxa are exceptional: In Plecoptera nerve **B** is absent and its components integrated into nerves **A** and **C**. In Ensifera nerves **B** and **C** are physically fused.

The case of Plecoptera is particularly interesting, as there is a basic similarity to conditions in Zygentoma and Ephemeroptera. The muscle and nerve arrangements in Zygentoma (and Archaeognatha) as described by BIRKET-SMITH (1974) differ strongly from the pattern typical for Neoptera. However, Zygentoma, Ephemeroptera (*Povilla* in BIRKET-SMITH 1971; *Ephemera* in Fig. 10), and Plecoptera (SCHMITT 1963; KNOX 1965; ZWICK 1973; Fig. 9) share the feature that one or more intrasegmental lateral muscles are innervated by the dorsal nerve, i.e. the nerve that otherwise supplies the internal dorsal muscles. On the other hand, there is no nerve **B** evident to supply lateral muscles of this kind, as is the case in other Neoptera. The sensory innervation of the ventral body wall in at least Plecoptera and probably Zygentoma is accomplished by branches of the ventral nerve (KNOX 1965; see KLASS 1999: 36; no clear data on Ephemeroptera), hence along the same pathway as in other Neoptera. This indicates that in Plecoptera a discrete nerve **B** is absent, and its responsibilities, and thus probably its axons, are distributed to nerve **A** (innervation of lateral muscles) and nerve **C** (innervation of ventral body wall). The comparison with Zygentoma and Ephemeroptera suggests that the pattern in Plecoptera is plesiomorphic for Neoptera (KLASS 1999: 36). The shift of this responsibility (and probably the related axons) to the ventral nerve and the resulting existence of a nerve **B** appears to be an apomorphy supporting the monophyly of all Neoptera under exclusion of Plecoptera.

On the other hand, the condition that the branch supplying the respective lateral muscles originates from nerve **A**, as in Zygentoma, Ephemeroptera, and Plecoptera, has also been found in some of the Phasmatodea studied by KLUG & BRADLER (2006; *Sungaya*, *Sceptrophasma*; **B*** in figs. 8, 10 therein); the case of *Sceptrophasma* is illustrated in Fig. 2. In addition, in our present study of the embiopteran *Antipaluria* we found the same condition in one of two examined segments (Fig. 3, **G4**), while the other segment showed the typical neopteran condition (Fig. 3, **G5**). However, in *Sceptrophasma* the sensory branch to the ventral wall (the other constituent of nerve **B**) has a common origin with the nerve supplying the lateral muscles, contrasting the plecopteran pattern (branch not known in *Antipaluria*).

In all investigated members of Ensifera, nerves **B** and **C** together constitute one major ventral nerve which supplies all the targets supplied by branches of **B** and **C** in other Neoptera (SCHMITT 1954, 1964; KLASS 1999: 36; Figs. 6–8). This is a potential autapomorphy of the group. Nonetheless, since nerves **B** and **C** frequently have a common stem, this is a relatively simple transformation.

The topographic relation between the main branch of the dorsal nerve **A** and the internal ventral muscles **7** varies among the neopteran taxa (see also KLASS 1999: 38). Nerve **A** passes the muscles internally in the studied Orthoptera (*Dissosteira*, *Locusta*, *Neoconocephalus*, *Tettigonia*, *Troglophilus*, *Gryllus*; SCHMITT 1954, 1964; Figs. 5–8) and in *Sphodromantis* (KLASS 1999), as it also does in the coleopteran *Dytiscus* (HOLSTE 1910) and the megalopteran *Chauliodes* (MAKI 1936). In contrast, nerve **A** passes the muscles externally in *Timema* (Fig. 1), *Antipaluria* (Fig. 3), *Periplaneta* (KLASS 1999), *Tyrannophasma* (Fig. 4), and in the dermapterans *Hemimerus* (KLASS 2001a) and *Labidura* (K.-D. Klass unpubl. observations). In different plecopterans, nerve **A** either passes the muscles internally (e.g., *Perlodes*: Fig. 9), or externally, or penetrates the muscles (ZWICK 1973: fig. 27; KNOX 1965). In *Ephemera*, nerve **A** also penetrates the internal ventral muscle (Fig. 10). The polarity of this character ist best considered unresolved, and it should also be noted that segmental variation occurs (KLASS 1999: 38). Phasmatodea other than *Timema* cannot be assessed due to the lack of muscles **7** (see below).

5.3. Anastomoses between main nerves

For the anastomoses it is easy to claim presence when during a dissection they are found to be represented by a distinct nerve branch. However, it is difficult to claim their absence, as an anastomosis can well consist of several very delicate strands that might additionally be located inside dense tissue (e.g., a muscle) and thus can be very difficult to trace. This must be kept in mind in the following – also in cases where a species seems to show intraspecific variation in the presence of an anastomosis. The occurrence of anastomoses is also discussed in KLASS (1999: 39f). Our sampled Mantophasmatodea and Embioptera material did not allow for a study of the anastomoses.

An anastomosis **A–B** (connecting nerves **A** and **B**) is only known from the mantodeans *Sphodromantis* and *Hierodula* (KLASS 1999: tab. 1; KERRY & MILL 1987). This is apparently an apomorphy (KLASS 1999) and could be tested for its informativeness regarding mantodean phylogeny.

An anastomosis **B–C** was found in the dictyopteran *Periplaneta* (KLASS 1999) and the phasmatodean *Sceptrophasma* (Fig. 2; KLUG & BRADLER 2006: fig. 9) but not in any other neopteran, including other Phasmatodea. It may thus have evolved independently in *Periplaneta* and *Sceptrophasma*. This character cannot be assessed in Ensifera because **B** and **C** are not separated, and in Plecoptera due to the absence of a discrete nerve **B**.

An anastomosis **C–T** has been reported for *Periplaneta* (KLASS 1999), for the orthopterans *Dissosteira* (SCHMITT 1954), *Neoconocephalus* (SCHMITT 1964), *Tettigonia* (Fig. 6), and *Gryllus* (SCHMITT 1954; Fig. 7), for the phasmatodean *Carausius* (MARQUARDT 1939), for the plecopteran *Eusthenia* (ZWICK 1973: fig. 26), and for the megalopteran *Chauliodes* (MAKI 1936). Occasionally, it was also found in *Ephemera* (Fig. 10) and the mantodean *Hierodula* (females only; KERRY & MILL 1987; see KLASS 1999: 39). Among other phasmatodeans, this anastomosis was neither found in *Timema*, *Agathemera*, and *Sceptrophasma* (KLUG & BRADLER 2006), nor in *Diapheromera* (SCHMITT 1954). It is also absent in *Sphodromantis* and was not observed in the plecopteran *Acroneuria* (KNOX 1965). Most likely this anastomosis belongs to the ground plan of Pterygota and may have become lost (or too delicate for observation) several times independently (KLASS 1999).

Anastomosis **lT–A** is also widely distributed, present in all studied Caelifera and Ensifera (Figs. 5–8; SCHMITT 1954, 1963, 1964: the line connecting points "A" and "B" in his illustrations), in the dictyopterans *Periplaneta*, *Sphodromantis*, and *Hierodula* (KLASS 1999; KERRY & MILL 1987), in the phasmatodeans *Carausius* (MARQUARDT 1939), *Agathemera*, and *Ramulus* (KLUG & BRADLER 2006: figs. 3, 9; not detected in the other Phasmatodea studied therein), in the dermapteran *Labidura* (K.-D. Klass unpublished observation), in all plecopterans studied (SCHMITT 1963; KNOX 1965; ZWICK 1973: fig. 26), and it also occurs in *Chauliodes* (MAKI 1936: **Ia2i*** in fig. 58). **lT–A** may frequently be present as several fine nerve branches embedded in the fat body and thus probably difficult to find in certain taxa. Among the lower Neoptera a mesal anastomosis **mT–A** has so far only been reported for Dictyoptera, where it is realised in different ways including segmental variation (KLASS 1999: 39, **mT–A** and **lT–A** in, e.g., figs. 1, 2). It is probably also present in *Chauliodes* (MAKI 1936: **Tnp*** and its mesal connection with root of nerve **I*** in fig. 58). The occur-

rence of two anastomoses between nerves **T** and **A** reminds of a pattern in Zygentoma (BIRKET-SMITH 1974: e.g., fig. 23): the anastomoses **RM*** (mesal) and **RL*** (lateral) connecting the nerves **IA*** and **IP***, which concerning their targets resemble nerves **A** and **T** in Neoptera. Accordingly, the presence of **mT–A** and **lT–A** may be plesiomorphic for Neoptera, and perhaps part of these may just have been overlooked so far in neopterans other than Dictyoptera and *Chauliodes*.

5.4. Dorsal muscles

The dorsal muscles cannot provide much phylogenetic information. Most Lower Neoptera have a wide sheet of long internal dorsal muscles (**10**; often divided into several parallel bundles) and one or several bundles of differently orientated short external dorsal muscles (**11**, **12**). The subdivisions in both groups are not distinctive enough and there is too much variation at a low systematic level as to homologise subsets of the external or internal muscles across, and often within, neopteran orders. In addition, because all dorsal muscles are supplied by nerve **A**, it is often difficult to distinguish external from internal ones if these are somewhat untypical. The branching pattern of nerve **A** upon the dorsal muscles cannot help in the analysis of muscle homologies, because for *Periplaneta* and *Sphodromantis* it has been demonstrated to show much intraspecific variation (KLASS 1999: figs. 10–21). The distinction between muscles **11** and **12** is useful within Dictyoptera (KLASS 1999) but can hardly be transferred to any other taxa.

Yet, on closer inspection there might be some features characterising "orders" or subgroups thereof. The dermapteran *Hemimerus* has several very distinctive bundles of dorsal muscles that are attached far anteriorly to the tergite and show various orientations (muscles **11*–15*** in KLASS 2001a: fig. 2). This includes the division of the internal dorsals into at least two parts (**11***, **13***) that are distinctly angled against each other. The latter character was also found in *Labidura* (K.-D. Klass unpublished observations) and *Forficula* (FORD 1923: fig. 17) and might be an autapomorphy of Dermaptera.

The extension of the internal dorsal (and ventral) muscles to the anterior varies strongly. In, for instance, *Antipaluria* (Fig. 3; see also VERHOEFF 1904: fig. 28), *Tyrannophasma* (Fig. 4), *Periplaneta* (KLASS 1999: fig. 3), and Plecoptera (ZWICK 1973: fig. 20) the anterior insertions are on the anterior segmental border and thus in touch with the posterior insertions of their counterparts in the preceding segment. In many other taxa, such as Mantodea (KLASS 1999: fig. 4) and Caelifera (Fig. 5; SNODGRASS 1935: fig. 8), the anterior insertions are far more posteriorly, with large gaps in

between muscles of successive segments. In the taxa representing the former case, part of the fibres may appear to span several segments, as observed during dissection by removal of single fibres. However, in a microscopical examination of an embiopteran Verhoeff (1904: fig. 27) found that fibres do not continue across segmental borders. For Plecoptera Zwick (1980: 54) reported that some inner fibres of the internal dorsal muscles continue over several segments, but no microscopical examination is mentioned. If fibres actually continue across segmental borders, these cases might be reminiscences of conditions reported for the zygentoman *Thermobia*, where some of the dorsal muscles are bi- or trisegmental (Rousset 1973: **dlm1c,d*** on p. 65).

Phasmatodea apart from the basal genera *Timema* and *Agathemera* have only fairly short dorsal muscles. Klug & Bradler (2006) tentatively interpret the longer, inner ones of these as shortened internal dorsal muscles (**16***, **17*** in figs. 4–10 therein). This may appear justified since beneath these muscles other, still shorter muscles are present that vary in direction (external dorsal muscles). On the other hand, all these phasmatodean muscles might well be external dorsal muscles, as it is known from other taxa that the various groups of external dorsals can also be of distinctly different lengths (e.g. dictyopterans in Klass 1999: figs. 3, 4: muscles **11*** versus **12***). Anyway, either a distinct shortening of the internal dorsal muscles or a loss of these muscles is a potential autapomorphy of a taxon comprising most Phasmatodea, the Neophasmatidae (Klug & Bradler 2006).

Among the studied Orthoptera, all Caelifera (e.g., Snodgrass 1935: fig. 8; Ford 1923: fig. 6) as well as Gryllotalpidae (Ford 1923: fig. 24) and Rhaphidophoridae (Fig. 8) among Ensifera show a clear distinction between internal and external dorsal muscles, the latter inserting far posteriorly on the tergite and being distinctly oblique. In constrast, in Tettigoniidae and Gryllidae (Ford 1923; Figs. 6, 7) only internal dorsal muscles seem to be present, which in Gryllidae form two distinct length classes, a long one in the mesal part and a short one in the lateral part of the tergum (Du Porte 1920: fig. 32; Ford 1923: figs. 13, 14; Fig. 7). Nonetheless, clearcut conclusions are difficult, as short lateral portions of the "internal muscles" cannot be excluded to be straightened external muscles.

These few examples show that the dorsal muscles may contain phylogenetic information, and further comparative studies in, e.g., Dermaptera appear worthwhile. Further conclusions must surely be based on much larger taxon samples than currently available, and the innervation of all dorsal muscles by nerve **A** will surely remain a problem. So far there is not yet a single character known that may be informative at the superordinal level.

5.5. Ventral muscles

The ventral muscles do not provide much phylogenetic information either. Most Lower Neoptera have a wide sheet of long internal ventral muscles (**7**; often divided into several parallel bundles) and one or several bundles of differently orientated short external ventral muscles (**8**, **9**). The subdivisions in both groups are usually not distinctive enough and there is too much variation as to homologise subsets of the external or internal muscles across, and partly within neopteran orders. In contrast to the dorsal muscles, however, internal and external ventral muscles can be distinguished by their innervation through nerves **A** or **C**. The distinction between a lateral external muscle **8** and a mesal muscle **9**, defined for Dictyoptera (Klass 1999), may also be useful for some other taxa.

In Phasmatodea the most basal genus *Timema* has retained the plesiomorphic condition with both groups of ventral muscles being present (Fig. 1). In the remaining Phasmatodea (Euphasmatodea), only ventral muscles innervated by nerve **C** are present (Fig. 2), which thus appear to be external ones throughout. This is probably an autapomorphy of Euphasmatodea. In some euphasmatodean taxa portions of the external ventrals have lengthened to span almost the entire segment, thus appearing like internal ventrals (Klug & Bradler 2006).

A lengthening of the external ventral muscles (**8** or **9**) was also found in the two dermapterans studied, *Hemimerus* (Klass 2001a: **10*** in fig. 2) and *Labidura* (K.-D. Klass unpublished observations), where these muscles insert anteriorly almost at the same level as the internal ventrals **7**; for both taxa the innervation by nerve **C** has been confirmed.

Some noteworthy differentiations occur in the Orthoptera. In some Tettigoniidae, which have the coxosternum divided into an inwardly sunken "eusternite" and less strongly sclerotised laterosternites, oblique muscles insert on the infolding between the eu- and laterosternite (**8** and **9** in Fig. 6; **mos***, **los*** in Ford 1923: fig. 11 and Schmitt 1964: fig. 1), one extending laterally, and one mesally towards the following coxosternum. These muscles are considered external ventral muscles as they are in the right position and are innervated by the ventral nerve composed of nerves **B** and **C**. In addition, a highly peculiar muscle connects the lateral margins of the eusternite and laterosternite (**24** in Fig. 6). Ford (1923: 233, secondary transverse sternal muscle) considers it the mesal portion of a lateral muscle that has gained an intermediate attachment upon the lateral margin of the laterosternite (Ford 1923: figs. 11, 12; Schmitt 1964: fig. 1). Muscle **24** is also innervated by branches of nerve **B+C**. It may be a lateral muscle of the **B**- or **C**-group. On the lateral part of the laterosternite, a longitudinal muscle spans

the entire segment, which is innervated by a branch of nerve **A** (**7** in Fig. 6; SCHMITT 1964: fig. 1); this is clearly the internal ventral muscle. The sternal region and its muscles surely provide characters useful for phylogenetic work in Ensifera.

In the caeliferans, a short lateral part of muscle **7** connects the middle of the coxosternite with the anterior apodeme of the following coxosternite (Fig. 5; FORD 1923: fig. 6; SNODGRASS 1935: muscle **173***; COVELO DE ZOLESSI 1968: muscle **155a***). It is also innervated by a branch of nerve **A** and thus categorized as an internal ventral. Apparently the lateral part of the internal ventral muscle attached to the area of origin of the apodeme became shorter and more oblique with the elongation of the apodeme, and detached from the main part of muscle **7**.

5.6. Lateral muscles

In the following the innervation by nerves **T**, **B**, or **C** is one major criterion for the grouping of lateral muscles. Of course, for taxa where data on mid-abdominal nerve topography are fragmentary or absent, the categorization of muscles is ± tentative; this especially concerns Notoptera, Mantophasmatodea, and Embioptera, and to some extent Dermaptera.

5.6.1. Intrasegmental lateral muscles. Muscles **1** (often with differently placed parts **a** and **b**), **16**, and **23** (**a** and **b** in *Gryllus*) are supplied by nerve **B**. Muscle **1a** connects the tergite and coxosternite, muscle **1b** connects more lateral parts of the tergite (or the laterotergite) and coxosternite. Muscle **16** is tergo-pleural, and muscle **23** is pleuro-coxosternal. These intrasegmental **B**-muscles, some of which are present in all insect orders for which the innervation is known, are best discussed together, because there are many transitions.

In the dictyopteran *Periplaneta* (KLASS 1999: **1*** in fig. 3) and the ensiferans *Neoconocephalus* (SCHMITT 1964: **stg***) and *Tettigonia* (Fig. 6) only one bundle is present, which complies with the criteria for muscle **1**; the same is true for *Troglophilus* (muscle **1** in Fig. 8), where, however, the innervation of this muscle is unknown.

Sphodromantis (KLASS 1999: **1a,b*** in fig. 4) has a longer anteromesal (**1a**) and a shorter posterolateral (**1b**) bundle, which are both clearly tergo-coxosternal and thus both considered part of muscle **1**.

Tyrannophasma and *Grylloblatta* have a tergo-coxosternal muscle in the middle of the segment (**1** in Fig. 4; **154*** in WALKER 1943: fig. 8), a pleural-coxosternal muscle in front of it (**23** in Fig. 4; **153*** in WALKER 1943: fig. 8), and a tergo-pleural muscle behind it (**16** in Fig. 4; **155*** in WALKER 1943: fig. 8); the nerve supply in *Grylloblatta* and that of the posterior bundle

(**16**) in *Tyrannophasma* is unknown. In these two taxa the shorter posterior muscles **16** are ventrally either inserted on a weak marginal part of the coxosternite (*Tyrannophasma*) or clearly on the pleural membrane (*Grylloblatta*). Thus, the muscle in *Tyrannophasma* approaches the condition of muscle **1b** in *Sphodromantis*, and its interpretation as **1b** or **16** is ambiguous (here classified as muscle **16**). This indicates that the muscles **1b** (tergo-coxosternal) and **16** (tergo-pleural) are possibly homologous in some taxa, and variations in the ventral attachment sites may be due to a desclerotisation of lateral parts of the coxosternal area.

Gryllus (Fig. 7) also shows a pattern resembling that in *Grylloblatta*: There is a strong, distinctly tergo-coxosternal muscle (**1**), a small pleuro-coxosternal muscle in front of it (**23a**), and a small tergo-pleural muscle external to it (**16**, nerve supply unknown); in addition, however, there is a second pleuro-coxosternal muscle (**23b**) external to muscle **1** and in line with muscle **16**.

In *Perlodes* (Fig. 9) there are a longer posteromesal (**1a**?) and two shorter anterolateral (**1b**?) bundles of muscle **1**. The anteroposterior succession of the shorter and longer muscles is reversed as compared to *Tyrannophasma* and *Grylloblatta*; as in these, the bundles **1b** could as well be interpreted as representing muscle **16**.

The dermapterans *Hemimerus* (KLASS 2001a: fig. 2) and *Labidura* (K.-D. Klass unpublished observations) both have one strong coxosternal muscle **1a** supplied by nerve **B** (**1*** in KLASS 2001a: fig. 2). Otherwise, *Labidura* has only one additional muscle external to muscle **1a**, which is clearly tergo-pleural and **B**-innervated, and thus evidently muscle **16**. *Hemimerus* has four smaller muscles external to muscle **1a** (**2***, **3***, **4***, **5*** in KLASS 2001a: fig. 2), which are partly tergo-coxosternal (representing the **1b** type) and partly tergo-pleural (representing muscle **16**); for none of these muscles, however, the innervation has been observed.

All Phasmatodea including *Timema* have long, internal tergo-coxosternal muscles **1a**, shorter, external coxosternal muscles **1b**, and still shorter tergo-pleural muscles **16** (Figs. 1, 2; FORD 1923; MAKI 1935; MARQUARDT 1939; KLUG & BRADLER 2006); all these muscles occur along most of the segment and are subdivided into several to numerous individual bundles. This pattern is in two ways conclusive on muscle homologies among neopteran lineages: First, the co-occurrence of muscles **1a** and **16** in this taxon shows that these are distinct groups of muscles probably not homologous across all taxa. Second, the extension of all three types of muscles (**1a**, **1b**, **16**) along much of the segment may indicate that muscles **1a** and **1b/16** can be homologous between Plecoptera on the one hand and *Grylloblatta* and *Tyrannophasma* on the other despite their reversed positions.

In the embiopteran *Antipaluria* (Fig. 3) we found three longer, mesal muscle **1** bundles having the dorsal insertion on the tergite (**1a**; innervation unknown for the most anterior bundle), and two shorter, lateral muscle **1** bundles inserted on the laterotergite (**1b**). In addition, there is a single muscle connecting the laterotergite and pleurite, which is best considered a homologue of muscle **16** in Phasmatodea (though its innervation is unknown). The subdivision of both muscles **1a** and **1b** into parallel bundles as well as the co-occurrence of muscles **1b** and **16** constitute noteworthy similarities to Phasmatodea.

Caelifera are particularly interesting regarding muscle **1**, and some earlier hypotheses need revision based on our new data. The acridids *Melanoplus*, *Dissosteira*, and *Locusta* have three discrete bundles (Ford 1923: **stg***, **ssm***, **tsm*** in fig. 6; Schmitt 1954: **li2***, **le2***, **le3*** in plt. 1; Snodgrass 1935: **176***, **178***, **179*** in fig. 10; Albrecht 1953: **176***, **178***, **179*** in fig. 77; **1a**, **1b**, **1c** in Fig. 5): A large internally located bundle (**1a**) inserts fairly high on the tergite and has a vertical course; two externally located bundles (**1b**, **1c**) insert on lower parts of the tergite, have opposite oblique courses, and thus cross each other. Klass (1999) interpreted the bundle **1a** (Fig. 5) as belonging to the **T**-muscle **2** (**2a*** in Klass 1999: fig. 42); this was based on the data in Schmitt (1954: plt. 2 fig. 1), who indicates an innervation by nerve **T** for bundle **1a** (**li2*** therein). However, we found that this bundle is in contact with nerve **T** of the *following* segment, while lateral muscles of the **T**-group in other taxa are supplied by **T** of the *same* segment. In other words, muscles **2a*** and **2b*** in Klass (1999: fig. 42) receive branches from nerves **T** of two different segments. In addition, the supply by nerve **T** has also become questionable, because the branch supplying the muscle bundle in question (**1a** in Fig. 5) is closely associated with the anastomosis connecting nerve **T** with nerve **B+C** of the preceding segment (Fig. 5). Bundle **1a** is thus best considered as a lateral muscle of the **B**-group, i.e. part of muscle **1**. In morabine (Blackith & Blackith 1967: fig. 9) and proscopiid Caelifera (*Cephalocoema* in Covelo de Zolessi 1968) all parts of muscle **1** seem to be dissolved into a number of delicate bundles. As in the two latter taxa the innervation is unknown and additional peculiarities are found in the pattern of the lateral muscles, further conclusions cannot be drawn at present; mutually crossing fibre-groups such as bundles **1b** and **1c** in acidids are apparently absent. The variation in the courses and subdivisions of subsets of muscle **1** is likely to provide useful characters for phylogenetic work in Caelifera. The increase in muscle **1** bundles probably evolved independently in the slender, elongated Morabinae, Proscopiidae, and Phasmatodea.

The only intrasegmental **C**-muscles so far known occur in some Phasmatodea: muscles **17** and **18** in Fig. 2. They lie in the most posterior region of the segment and correspond with the **B**-muscles **1b** and **16** of the larger anterior part of the segment. They were detected in *Sceptrophasma* (Fig. 2), *Carausius* (muscles **el3 t-st***, **l3 t-p*** of Marquardt 1939), and *Ramulus* (Klug & Bradler 2006) and may have been overlooked so far in *Timema* using the alcohol material at hand. They – or their supply by nerve **C** – would represent an autapomorphy of Phasmatodea or Euphasmatodea.

Three further intrasegmental lateral muscles are innervated by nerve **T**: muscles **2**, **3**, and **22**. All are ventrally attached to the coxosternite, but they differ with regard to the level of their dorsal insertion. Muscle **22** has it on the pleural membrane. Muscles **2** and **3** have it on the tergite, and they have been defined in Dictyoptera based on their tergal s.str. (**2**) resp. paratergal (**3**) insertions (Klass 1999). Since the corresponding sclerite areas cannot be clearly identified in other Pterygota, this distinction cannot be unambiguously transferred to other taxa. Tentatively, however, the same distinction is here applied to **T**-muscles inserted on the tergite far laterally resp. further mesally, or on the tergite proper resp. the spiracle-bearing laterotergite.

T-muscles showing the specifications of muscle **2** are present in the Phasmatodea *Timema* (Fig. 1), *Sceptrophasma* (Fig. 2), *Carausius* (muscles **el1***, **il1***, **t-st*** of Marquardt 1939), *Sungaya*, and *Ramulus* (Klug & Bradler 2006), the Dictyoptera *Periplaneta* and *Sphodromantis* (two bundles **a** and **b** in Klass 1999), the dermapterans *Hemimerus* (muscle **6*** in Klass 2001a: fig. 2) and *Labidura* (K.-D. Klass unpublished observations), and in Caelifera (*Locusta*: Fig. 5; **li1*** of *Dissosteira* in Schmitt 1954; **ptg*** of *Melanoplus* in Ford 1923). Muscle **2** is found also in Ensifera (*Tettigonia*: Fig. 6; *Gryllus*: Fig. 7; *Troglophilus*: Fig. 8; **ptg***, **stg*** of *Ceuthophilus*, *Cyphoderris*, *Neoconocephalus*, *Conocephalus*, and *Nemobius* in Ford 1923; **2TS*** of *Macropathus* in Richards 1955); it is located rather far posteriorly. Despite lacking data on the innervation, a far anterior muscle of *Grylloblatta* is also best interpreted as muscle **2** (**162*** in Walker 1943: fig. 8).

T-muscles with far lateral tergal (or para-, or laterotergal) insertions, here categorised as muscles **3**, are present in Phasmatodea (*Timema*: Fig.1; *Sceptrophasma*: Fig. 2; Klug & Bradler 2006), in the dictyopterans *Periplaneta* and *Mastotermes* (Klass 1999, 2000; degenerated thin strands in both), Caelifera (Fig. 5; muscle **le1*** in Schmitt 1954), the dermapterans *Hemimerus* (muscle **7*** in Klass 2001a: fig. 2) and *Labidura* (K.-D. Klass unpublished observations). For the muscles in Dermaptera, however, the innervation is unknown; as in Caelifera the ventral insertion is on a coxosternal apodeme.

An intrasegmental **T**-muscle **22** connecting the pleura and the lateral margin of the coxosternite in the anterior part of the segment (Figs. 6–8) is present in most Ensifera, but not in other taxa. In *Gryllus* its upper insertion is located on an anterior pleural sclerite and immediately below the ventral insertion of muscle **19**. It is unclear if these muscles could have shifted their origin from the paratergite to the pleura, being homologous with muscle **3** of other taxa. Since the upper insertion is fairly remote from the tergal region in all Ensifera, it is treated here as an extra muscle, **22**.

The muscle termed **3** in Fig. 3 of *Antipaluria*, connecting the laterotergite and coxosternite in the anterior part of the segment, is difficult to interpret due to lacking innervation data. The interpretation as muscle **3** (due to its very low tergal insertion) is quite likely, but it is also conceivable that it is another, far anterior bundle of muscle **1b** (if supplied by nerve **B**).

In *Tyrannophasma*, a very slender, far anterior muscle (# in Fig. 4) connects an upper and a lower part of the pleura, the dorsal insertion being on a fold very close to the spiracle (innervation unknown). It does not seem to insert on the spiracle, but this possibility cannot be completely excluded (in *Mantophasma* the spiracle muscle has a similar position and ends ventrally at the coxosternite; K.-D. Klass personal observation).

5.6.2. Intersegmental lateral muscles. Muscles **4** and **5** are ascending intersegmentals, both supplied by nerve **C**. They have been defined in Dictyoptera based on the different levels of their dorsal attachments on the tergite or paratergite. While the corresponding tergal areas cannot be clearly identified in other taxa, the level of the dorsal attachment can be tentatively used to categorize muscles as **4** or **5**. Muscles **6**, supplied by nerve **C**, and **19**, supplied by nerve **T**, are both descending intersegmentals. According to the data in BIRKET-SMITH (1974), no potentially corresponding intersegmental lateral muscles occur in *Lepisma*.

The descending **C**-Muscle **6** runs from a tergite to the coxosternite or pleura of the following segment. It is present in *Sceptrophasma* (Fig. 2) and *Carausius* (muscle **il3 t-st*** in MARQUARDT 1939) among Phasmatodea, in Dictyoptera (muscle **6*** in KLASS 1999, 2000), in Plecoptera (Fig. 9), and in *Chauliodes* (MAKI 1936: muscle **243*** supplied by **C**-branch **Vd3***).

The descending **T**-Muscle **19** was so far only found in *Gryllus*; it runs from the posterolateral corner of a tergite to an anterior pleural sclerite of the following segment (Fig. 7; muscle **100*** in DU PORTE 1920 for *Gryllus assimilis*; not depicted in FORD 1923). SCHMITT (1954: plt. 2 fig. 2, as "*Acheta*") reports the same innervation of this muscle. It should be noted that *Gryllus* is among those taxa that have an anastomosis **C–T** shortly mesal to where nerve **T** supplies muscle **19**. It

is thus conceivable that muscle **19** is actually innervated by axons that have crossed from nerve **C** to **T** via **C–T**, and that it is a **C**-muscle homologous with muscle **6**.

A muscle showing positional correspondence with both **6** and **19**, dorsally inserted on the tergite, but with unknown innervation, was found in *Antipaluria* (**6** in Fig. 3; ventral insertion coxosternal) and in nymphs of Odonata (FORD 1923). Both *Grylloblatta* (**151*** in WALKER 1943; **itm*** in FORD 1923) and *Tyrannophasma* (**6** in Fig. 4) possess an intersegmental muscle from the lowest part of the intertergal membrane to the pleural membrane next to the anterolateral corner of the coxosternite of the following segment; regarding the relationships to the anterior tergal margin (antecosta!) and a vertical fold in the pleural area, the muscles likely cross the segmental border (data on *Grylloblatta* based on re-investigation by K.-D. Klass). We consider all these muscles as **6** or **19**; a clearer identification must await data on the nerve supply. Descending intersegmentals have so far not been reported for Caelifera, Ensifera other than *Gryllus*, and Dermaptera.

A descending intersegmental tergo-coxosternal muscle resembling **6** also occurs in *Ephemera* (* in Fig. 10). However, this muscle is supplied by a branch of nerve **A** (which in ephemeropterans also includes branches that belong to nerve **B** in most Neoptera, see 5.2.). Homologisation with muscle **6** is thus ambiguous: the muscle in *Ephemera* may either be a muscle **6** whose innervating axons run along a different pathway than in Neoptera; or it is a dorsal muscle whose posterior insertion has shifted to the coxosternite.

The ascending **C**-muscles **4** and **5** insert ventrally on the coxosternite and dorsally on the tergal (**5**) or paratergal to pleural (**4**) region of the following segment. Such muscles are present in Dictyoptera (**4*, 5*** in *Periplaneta* and *Sphodromantis*: KLASS 1999: figs. 3, 4; **4*, 5*** in *Mastotermes*: KLASS 2000, innervation unknown), *Hemimerus* (**8*** in KLASS 2001a, a muscle **4**; absent in *Labidura*), and *Antipaluria* (**5** in Fig. 3). MARQUARDT (1939) described one slender bundle in *Carausius* with similar course, but this muscle has not been found in any other phasmid yet (KLUG & BRADLER 2006). In *Tyrannophasma* we found a small muscle in the posterior part of segment 5 that ascends from a weakly sclerotised area beside the coxosternite to a vertical fold in the pleura, which seems to form the anterior rim of the following segment (Fig. 4). It thus shows positional correspondence with muscle **4** and could be a homologue; its innervation is unknown. No such muscle has been reported for *Grylloblatta*.

5.7. Ventral transverse muscles, ventral diaphragm, and hyperneural muscle

Three very different ventral structures of the abdomen are here included: (1) compact segmental transverse muscles, (2) delicate sheets composed of muscle fibres and connective tissue and extending through many segments (ventral diaphragmata), and (3) the hyperneural muscles with their longitudinal muscle fibres and chiasmata, which also continue through most of the abdomen.

A hyperneural muscle has only been reported for Blattaria and Isoptera (Shankland 1965: fig. 6; Klass 1999: figs. 1, 3; Klass 2000: figs. 19, 23). It extends, dorsal to the nerve cord, from its anterior attachments on the metathoracic furca and laterally on abdominal coxosternum 2 to its posterior attachments on the frontal margin of coxosternum 9. Throughout the mid-abdomen it is composed of a left and a right group of muscle fibres (see Shankland 1965: fig. 6 for the modified anterior part). The fibres of each side are embedded collectively in connective tissue, and in each segment the left and right parts are connected by a transverse bridge of connective tissue. Via these bridges in *Periplaneta* and *Mastotermes* a few mesal fibres cross from the one to the other side (chiasmata), while in *Polyphaga aegyptiaca* no fibres were observed within the bridges, which thus are purely tendinous plates. Lateral and chiasmatic muscle fibres appear to continue throughout the length of the muscle, but at least in *Polyphaga* mesal fibres end in the areas of the transverse bridges, thus being segmental (K.-D. Klass unpubl. observ.). The hyperneural muscle is innervated by nerve rami that are best considered branches of nerve **A** (Klass 1999: 12f, 40). Especially the hyperneural muscle of *Polyphaga* is reminiscent of conditions in Zygentoma, where longitudinal ventral muscles interconnect tendinous plates in the middle of each segment (Birket-Smith 1974; Klass 2001a: fig. 37: plates **ES*** and muscles **VL***). As compared to the pattern in Zygentoma the hyperneural muscles are simplified: no further muscles are attached to the tendinous plates (many additional muscles in Zygentoma), and there are no extensions of the tendinous plates that go to the cuticular body wall (3 pairs of such extensions in Zygentoma). Altogether, the hyperneural muscles appear to be vestiges of the ventral muscle-tendon-system of Zygentoma (and other arthropods; see Boudreaux 1979). If this homology is true, the *Polyphaga* type of the segmental transverse bridges should be plesiomorphic (without chiasmatic fibres).

Among the Orthoptera, the ensiferans *Tettigonia*, *Cyphoderris*, *Ceutophilus*, *Scudderia*, *Conocephalus*, *Neoconocephalus* (Tettigoniidae), *Gryllus*, *Oecanthus* (Gryllidae), *Troglophilus*, and *Macropathus* (Rhaphidophoridae) have one compact ventral trans-verse muscle in the anterior part of each segment, which is attached to the anterolateral part of the coxosternum (**20** in Figs. 6–8; Ford 1923; Richards 1955; Schmitt 1964). The muscle is innervated by a branch of nerve **A**.

In the caeliferans *Melanoplus*, *Locusta*, *Dissosteira* (Acrididae), and *Paratettix* (Tetrigidae = Acrydiidae), in Caelifera-Morabinae (Eumastacidae), as well as in the ensiferan *Gryllotalpa* (Gryllotalpidae) a delicate sheet-like ventral diaphragm with fine, mainly transverse, and partly interwoven muscle fibres embedded in connective tissue is present; it continues through most of the abdomen (Ford 1923: "webby type" of ventral transverse muscle; Schmitt 1954: plt. 3 fig. 1; Snodgrass 1935: 33f, fig. 15C; Albrecht 1953; Blackith & Blackith 1967). For the Proscopiidae (Caelifera) no ventral diaphragm is reported (Covelo de Zolessi 1968). In *Gryllotalpa* the segmental attachments are limited to the anterolateral corners of each coxosternite, as for the ventral transverse muscles of other Ensifera. In the caeliferans the diaphragm has multiple insertions (or a long insertion area) along the lateral part of each coxosternum. Most notably, in the caeliferans the posteriormost fibres of each segment are intersegmental, connecting the one side of a coxosternum with the opposite side of the following one (in *Gryllotalpa* this character is difficult to assess due to a fairly irregular fibre pattern). Morabinae are peculiar in that there seems to be a series of ca. 10 discrete bundles per segment rather than a continuous sheet as in Acrididae (Blackith & Blackith 1967: fig. 9). In the studied Acrididae the ventral diaphragm is probably innervated by branches of the paramedian nerve (see chapter 3.3.), which is closely associated with the diaphragm (Schmitt 1954). In the other taxa including *Gryllotalpa* the innervation is unknown.

Nemobius (Gryllidae) shows an interesting mixture of ensiferan and caeliferan conditions (Ford 1923: fig. 14). Besides a typical compact transverse muscle there is an additional portion forming a ventral diaphragm. As in all Ensifera, the attachments of both structures are limited to the anterolateral part of the coxosternum, but as in (most?) Caelifera the diaphragm portion includes, besides intrasegmental traversing fibres, intersegmental crossing fibres (compare Ford 1923: fig. 14 and Blackith & Blackith 1967: fig. 9).

In the other lower neopteran lineages structures as here in question are either absent, or reports are very limited and/or conflicting. Mantophasmatodea have a continuous, delicate ventral diaphragm (Klass et al. 2002), but structural details have remained unknown; the structure could not be studied in the ethanol-preserved material available for this study. For a notopteran Richards (1964) reports a ventral diaphragm, though without much detail. However, there is no mention of such an element for *Grylloblatta* in

WALKER (1943), FORD (1923: 230) claims absence, and K.-D. Klass neither found any traces of it in an unpublished study of the female abdomen. In Phasmatodea none of the muscular structures here considered has been found in a study of 8 representatives (including *Timema*) and survey of all relevant literature (KLUG & BRADLER 2006). Also for Mantodea there are no reports of such structures in the literature (LEVEREAULT 1938; KERRY & MILL 1987), and *Sphodromantis* clearly lacks any such elements (KLASS 1999). Complete absence is probably also true for the only studied embiopteran (*Antipaluria*, Fig. 3). Likewise, for the Plecoptera and Dermaptera no such structures have been reported in relevant studies (Fig. 9; KLASS 2001a: tab. 1; POPHAM 1959; KNOX 1965; SCHMITT 1963); FORD (1923), who generally considers such muscles, did not find them in either taxon, nor was anything found in the dermapteran *Hemimerus* (Klass 2001a: fig. 2). However, in a preliminary unpublished study of the dermapteran *Labidura*, K.-D. Klass observed a delicate, apparently muscular strand traversing between the anterolateral corners of a mid-abdominal coxosternite, the transverse nerve running along it dorsally. This reminds of the ventral transverse muscles in Ensifera.

Odonata have a delicate, sheet-like ventral diaphragm that continues throughout most of the abdomen. It consists of muscular fibres embedded in connective tissue and has many perforations. In the zygopteran *Calopteryx* (K.-D. Klass unpubl. observations) there are two pairs of insertions per mid-abdominal segment, located on two pairs of lateral coxosternal apodemes. From there muscular fibres fan out mesally, and concentrated bundles of fibres along the flanks of the diaphragm connect successive apodemes. The median part of the diaphragm contains fibres of mostly transverse or oblique courses. RICHARDS (1964: figs. 9, 32, tab. 1) also reports the diaphragm for a zygopteran. FORD´s illustration (1923: **ts*** in fig. 18) for a teneral libellulid complies with the findings in *Calopteryx*, except that the transverse fibres appear to continue from the left to the right apodemes. In anisopteran nymphs the ventral diaphragm has highly specialised components (ASAHINA 1954: plt. 70). Altogether, the muscular pattern and the insertions of the diaphragm in Odonata are quite different from Caelifera.

Megaloptera (*Chauliodes* in MAKI 1936: fig. 58; *Sialis* in SELMAN 1965: 521, figs. 38, 39) have a diaphragm very similar to that in Odonata. Two pairs of lateral insertions are present per segment (as for **239*** and **240*** in MAKI 1936: fig. 58), which are probably – contra MAKI´s (1936: 181f) segmental assignment – both located in the anteriormost part of a segment (i.e. **240*** inserts on the anterior border of a segment rather than on the posterior part of the preceding segment). The details shown in SELMAN (1965: figs. 38, 39) also comply closely with conditions in *Calopteryx*: Muscle

fibres arise in dense bundles from the insertions and spread into the diaphragm; the insertions of successive segments (area around **e*** in SELMAN´s fig. 38) are probably also connected by continuous longitudinal fibres along the lateral margin of the diaphragm. Conditions in other Endopterygota are described, for instance, in RICHARDS (1964) and KRISTENSEN & NIELSEN (1980).

The muscular structures considered in this chapter are extremely problematic with regard to topographic homology, character transformation, and parallel evolution. All these structures might be homologous to some extent, perhaps derived from a subset of the ventral muscle-tendon system of Archaeognatha and Zygentoma, which then evidently represents the plesiomorphic condition in Insecta (KLASS 2000: 256). In the Pterygota, the hyperneural muscle of Blattaria and Isoptera is structurally closest to this basic type, especially regarding conditions in *Polyphaga*. The possibly close anagenetic correlation between compact coxosternal transverse muscles and sheetlike diaphragms is indicated by the intermediate structure found in the gryllid *Nemobius* (FORD 1923: fig. 14), by ANDO's (1962: 122) report for the odonatan *Epiophlebia* of an origin of the diaphragm from narrow intersegmental mesodermal anlagen, and by RICHARDS´ (1964: 18, 23, 24) finding of compact transverse muscles in the larva of *Sialis*, contrasting with the diaphragm of the imago. The relationships between diaphragms and transverse muscles on the one hand and the ventral muscle-tendon systems and hyperneural muscles on the other, however, are less clear. In the attempt to reconstruct the ground plan of Pterygota the odonatan-megalopteran similarities would compete with the zygentoman-blattarian similarities. Alternatively, the former similarities could be interpreted as apomorphic, then supporting odonatan-endopterygotan relationships. Phylogenetic implications are thus ambiguous.

6. Phylogenetic implications

6.1. Interordinal relationships in lower Neoptera

Archaeognatha and Zygentoma have a system of tendons made from connective tissue to which many muscles are attached with one or both insertions (BITSCH 1973; BIRKET-SMITH 1974). As similar tendinous structures are found in most non-insect (= non-ectognathan) Hexapoda and Arthropoda (BOUDREAUX 1979), this equipment is surely plesiomorphic. The abdominal musculature is very different in Archaeognatha and Zygentoma, and, moreover, due to the insertion of many muscles on tendons, only part of the muscles can be convincingly homologised between

these taxa and Pterygota. Archaeognatha and Zygentoma also differ strongly in their pattern of nerve topography. Pterygota are very different from both, though in many aspects more similar to Zygentoma than Archaeognatha. Comparing the arrangement of muscles and nerves between these three lineages is beyond the scope of the present contribution but would otherwise be an interesting issue. Herein we only included Zygentoma to an extent that we can use the data on it as outgroup comparison for characters that are variable in Pterygota and Neoptera.

The system of tendons is almost completely absent in the abdomen of Pterygota, and this is a potential autapomorphy of this taxon. The segmental transverse bridges in the hyperneural muscle of Blattaria and Isoptera – especially those in *Polyphaga*, which are made only of connective tissue – are the only evident vestige of this tendon system. This character would support a position of the Dictyoptera as the sister group of all remaining Neoptera (KLASS in press) or even Pterygota. However, no trace of the hyperneural muscle has been found in the Mantodea studied so far. It would be of great interest to examine whether this structure is present or absent in the basal mantodean taxa *Mantoida* and *Chaeteessa*.

The homology and evolution of the ventral transverse muscles and diaphragms are highly uncertain. Nonetheless, the extensive similarity of this structure between Odonata and Megaloptera may be taken as support for an unconventional relationship between Odonata and Endopterygota, contradicting the monophyly of Neoptera. A detailed comparative study of the ventral transverse muscles and diaphragms together with their innervation in a dense taxon sample across the Pterygota would surely provide phylogenetic information, but a high degree of homplasy may also be expected.

Beside Dictyoptera, the Plecoptera also show two conditions that appear (almost) uniquely plesiomorphic among the (Lower) Neoptera: (1) Most importantly, there is an intrasegmental lateral muscle supplied by a branch of nerve **A**, like in Zygentoma and Ephemeroptera. In the remaining Neoptera this branch has likely become associated with the ventral nerve, where it forms, together with the sensory nerve branch supplying the ventral body wall, a new major nerve **B**. Some of the studied Phasmatodea also show the condition as found in Plecoptera (but with a different position of the ventral sensory branch); however, since this does not apply to the basal taxa *Timema* and *Agathemera*, this appears as a reversal within Phasmatodea. The case of the embiopteran *Antipaluria*, where a plecopteran-like condition was found in one of two studied segments, should also be kept in mind. (2) The origin in Plecoptera of the dorsal nerve **A** from parts of the CNS far in front of the ganglion of its own segment corresponds with conditions in Zygentoma but not Ephemeroptera; it may appear as a plesiomorphy unique within the Neoptera, but the interpretation is ambiguous. These two characters contradict ZOMPRO's (2004) hypothesis of a close relationship between Phasmatodea and Plecoptera. On the other hand, they comply with the findings of BEUTEL & GORB (2006), though therein the dichotomy between Plecoptera and the remaining Neoptera is based on the lack of ligaments inside the stipes ("stipital transverse muscle") in the latter group.

Some remarkable similarities in the lateral muscles may rather indicate a phasmatodean-embiopteran relationship: Only in these two taxa short external tergo-coxosternal **B**-muscles (**1b**) co-occur with tergo-pleural **B**-muscles (**16**). In addition, the tergo-coxosternal muscles **1a** and **1b** are each divided into several discrete parallel bundles.

Mantophasmatodea was described as a new insect order by KLASS et al. (2002). TILGNER (2002) suggested these insects to be aberrant orthopterans – a view contradicted by KLASS (2002). Morphological and molecular data support a relationship of Mantophasmatodea either to Notoptera (TERRY & WHITING 2005: nuclear genes in fig. 12A; KJER et al. 2006; BEUTEL & GORB 2006; tentatively in BAUM et al. 2007), or to Phasmatodea (CAMERON et al. 2006a,b: mitochondrial genes; KLASS et al. 2002, 2003: vomer/vomeroid behind male genitalia), or to Dictyoptera (KLASS et al. 2003: right part of male genitalia; PASS et al. 2006: double-walled antenna vessels), or to Dictyoptera + Orthoptera (DALLAI et al. 2003: connecting bands in spermatozoan flagellum), but a more isolated position of this group is also conceivable (see review in KLASS in press). The contradictory evidence on the phylogenetic position of Mantophasmatodea clearly justifies the high taxonomic rank of this group (as one of 11 lineages in an unresolved basal neopteran polytomy). The present study cannot contribute much significant evidence to this particular problem. There is some basic similarity between *Tyrannophasma* (Fig. 4) and *Grylloblatta* (WALKER 1943) in the mid-abdominal lateral musculature. The anteroposterior succession of a pleuro-coxosternal, a tergo-coxosternal, and a tergo-pleural lateral muscle is quite striking, but the ensiferan *Gryllus* shows a very similar pattern. Specific apomorphic conditions shared by Notoptera and Mantophasmatodea are presently not evident. A closer study of the nervous system in both taxa is likely to improve the evidence.

6.2. Implications at order-level and below

Some of the structural elements and characters discussed in this paper may confirm the monophyly of

some order-level taxa or may be useful in the reconstruction of the internal phylogeny of these taxa.

With regard to **Phasmatodea** the implications from several characters were already discussed in Klug & Bradler (2006). The strong division of some lateral muscles into several bundles each (**1a**, **1b**, **16**), distributed along the segment, is perhaps an autapomorphy of Phasmatodea (see also Kristensen 1975), while a weaker subdivision of muscles **1a** and **1b** may be an autapomorphy of a clade Phasmatodea + Embioptera. It should be noted that similar subdivisions also occur in some Caelifera with elongated abdomina, as reported for Morabinae and the proscopiid *Cephalocoema*. Such a modification may support ventilation in the elongated abdomen (see Runhaar 1982). The loss of the internal ventral muscles **7** supports the monophyly of Euphasmatodea, and a strong shortening (or perhaps complete loss) of the internal dorsal muscles **10** supports a taxon Neophasmatidae (Euphasmatodea under exclusion of *Agathemera*).

Examples for characters potentially relevant in **Dictyoptera** are the condition of the transverse bridges in the hyperneural muscle (with or without crossing muscle fibers), the general presence of the hyperneural muscles, and the presence of the anastomoses **A–B** (so far only in two mantodeans) and **B–C** (so far only in *Periplaneta*).

A strong differentiation of the dorsal musculature appears to be typical for **Dermaptera**. In particular, there is a division of the internal dorsal muscles **10** into at least two portions that are distinctly angled against each other. This might be correlated with the anterodorsal bending of the abdomen accomplished by earwigs when grasping prey. The distinct differences between the very few dermapterans studied so far indicate that the musculature will provide many additional characters informative on dermapteran phylogeny. The varying differentiation of the dorsal muscles and the lateral muscles of the **B**-group, and the presence of ascending intersegmental lateral muscles are examples.

An interesting character complex in **Plecoptera** is the lengthwise division of the median nerve in certain segments and the attachment of the halfstrands to the connectives. A survey of the muscle data known so far indicates that there are also many differences with regard to the lateral musculature.

In **Orthoptera** the possession of one compact ventral transverse muscle per segment may support the monophyly of Ensifera (possibly as a paedomorphic feature, and perhaps under exclusion of Gryllotalpidae). Furthermore, the various ensiferans show much structural diversity both in their ventral muscles ("secondary ventral transverse muscle" **24**, specific arrangement of external ventral muscles **8** and **9**) and in their lateral muscles. Much of the diversity in the ventral musculature is probably correlated with the subdivision

of the coxosternal region into eu- and laterosternites, which likewise can be used as a character for phylogenetic analysis within Ensifera (Desutter-Grandcolas 2003). In the Caelifera the lateral muscles, mainly the bundles of muscle **1**, might provide useful characters.

7.   Outlook

The musculature and nerve topography of the mid-abdomen surely include many characters potentially useful for phylogenetic work. This applies to the inter-"ordinal" relationships of insects as well as to intra-"ordinal" relationships in all order-level taxa (with the possible exception of the fairly uniform Notoptera and Mantophasmatodea). As is the case with many morphological character systems, however, detailed and coherent studies for large taxon samples are still required before well-founded conclusions can be drawn or characters can be entered into data matrices for cladistic analyses. A denser taxon sample will surely make hypotheses on topographic, primary, and secondary homology more reliable, and reveal homoplasies. Otherwise, there are four major problems or tasks that should be considered in forthcoming comparative studies of mid-abdominal anatomy.

(1) Regarding the comparison of mid-abdominal anatomy among high-rank pterygotan or neopteran taxa, there are problems with the topographic homologies of cuticular areas in the lateral wall of the mid-abdomen, including the location of the borders between the coxosternal, pleural, and tergal territories. In some taxa it is questionable whether sclerites in the "pleural" region are true pleural sclerites or isolated lateral parts of the coxosternum or tergum, or whether a muscle attachment in the "pleural region" is truly pleural or rather located on desclerotised lateral parts of the tergal or coxosternal territory. The topographic interpretation of attachment sites of lateral muscles is thus often ambiguous. Additional landmarks such as the spiracles are also of questionable reliability. Even in a combined assessment of cuticular structures, muscles, and nerves, as done above, many issues remain unclarified. This complex problem can perhaps be resolved by using a much denser taxon sample, but some points will likely remain doubtful due to evolutionary gaps between the extant taxa.

(2) A second problem in the attempt to resolve topographic homologies is that the consideration of nerve topography is necessarily superficial. Among neopteran lineages it is frequently conserved enough as to allow clear statements on the homology of nerve branches, and in this way it can yield characters of its own. However, many questions will remain open without knowledge on the cellular level of the ner-

vous system. This concerns homologisation of single neurons according to their location and interrelations in the CNS and the peripheral targets of their axons, as well as the pattern of their bundling into nerves. The anatomical concept of what is called a "nerve" may be altogether inadequate for comparing neuronal networks in different insects. Neurons can be made visible using special stainings and confocal laser scanning microscropy. These methods allow an insight into the neuronal inventory of a nerve branch. Such investigations are at the beginning but may provide new insights into neuronal networks that will also help in the exploration of the character system mid-abdomen.

(**3**) Yet another problem concerns outgroup comparison for Pterygota and Neoptera. Zygentoma and Archaeognatha have a mid-abdominal musculature that is strikingly different from that in Pterygota, mainly due to the presence of a system of tendons and the insertion of many muscles on such tendons. Strong differences in the pattern of nerve topography add to this. This situation constitutes fundamental problems in the analysis of topographic homologies between the primarily wingless insects and the Pterygota, and thus in the outgroup comparison for Pterygota. Detailed studies of the mid-abdominal muscles and nerves in various subgroups of (mainly) Zygentoma and extensive comparisons with a selection of pterygotan exemplars are urgently needed; consideration of the neuronal level might help in the identification of homologous muscles.

(**4**) Changes in the musculature and sclerotisations seem to occur frequently during nymphal development (see KLUG 2005 for Phasmatodea; KLASS 1999 for Blattaria); they are especially striking in Odonata (WHEDON 1929). Then, inclusion of data from the nymphs is important for comparative studies on adult structure, because evolutionary changes in the adults may be due to paedomorphosis; this is indicated by KLASS' (2001a) results on the female abdomen in Dermaptera, may apply to thoracic morphology in the frequent cases of wing reduction in lower Neoptera, and may likewise concern the mid-abdomen. Consideration of the nymphal musculature may also provide important evidence on the interpretation of cuticular areas (see (1) above). Furthermore, it is important to compare males and females in study taxa, as exemplified in KLUG & BRADLER (2006). For future studies it is thus recommendable to include data from both sexes and the nymphs.

Comparative anatomical work on the insect mid-abdomen is thus only at its beginning, and to reach a sufficient coverage of both anatomical details and taxa will need considerable effort. Even for the relatively "simple" mid-abdominal character system (as compared to the pterothorax) a meaningful treatment that allows to include characters into data matrices for phylogenetic analyses is a tremendous task.

8.   Acknowledgements

9.   References

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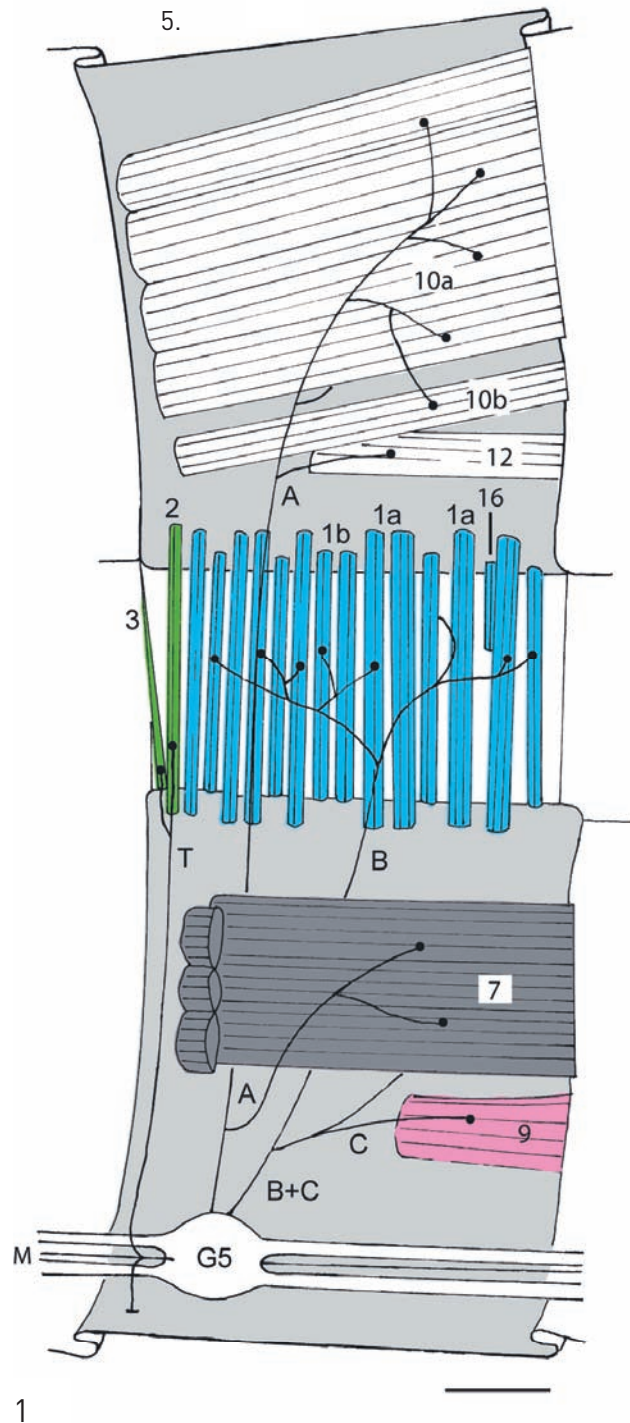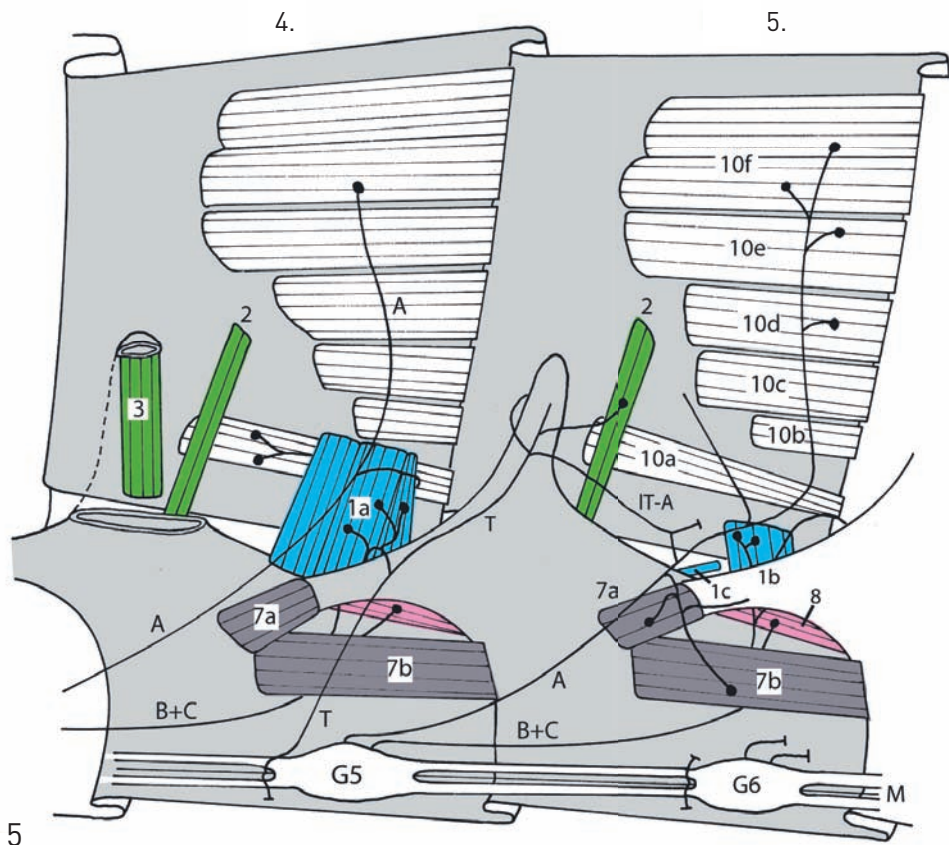

Figs. 1–3. Mid-abdominal musculature with innervation, sclerotised parts gray. From bottom to top in each figure: coxosternite with ventral nerve cord and ventral muscles, pleural membrane with lateral muscles, tergite with dorsal muscles. Orientation: ← anterior, → posterior, ↑ mid-dorsal, ↓ mid-ventral. **1**: Abdominal segment 5 of *Timema nevadense*, female; scale bar: 0.2 mm **2**: Abdominal segment 5 of *Sceptrophasma hispidula*, female; scale bar: 1 mm. **3**: Abdominal segments 4 and 5 of *Antipaluria caribbeana*, female; scale bar: 0.2 mm.
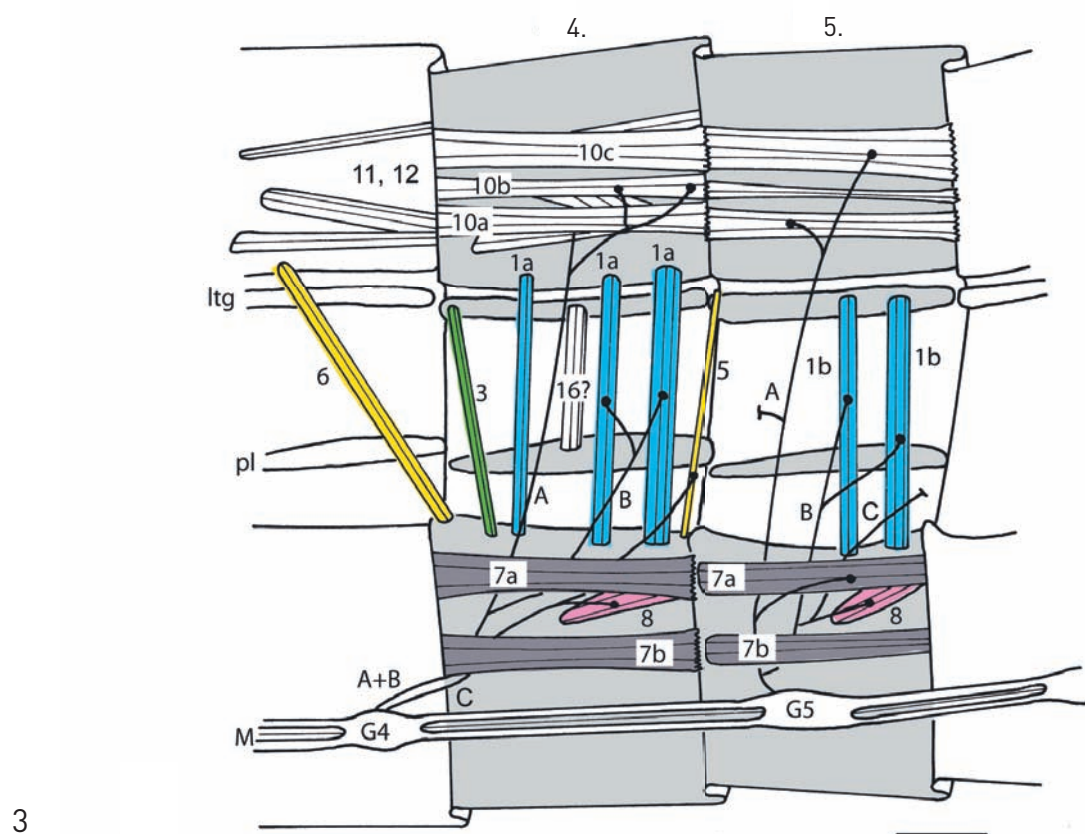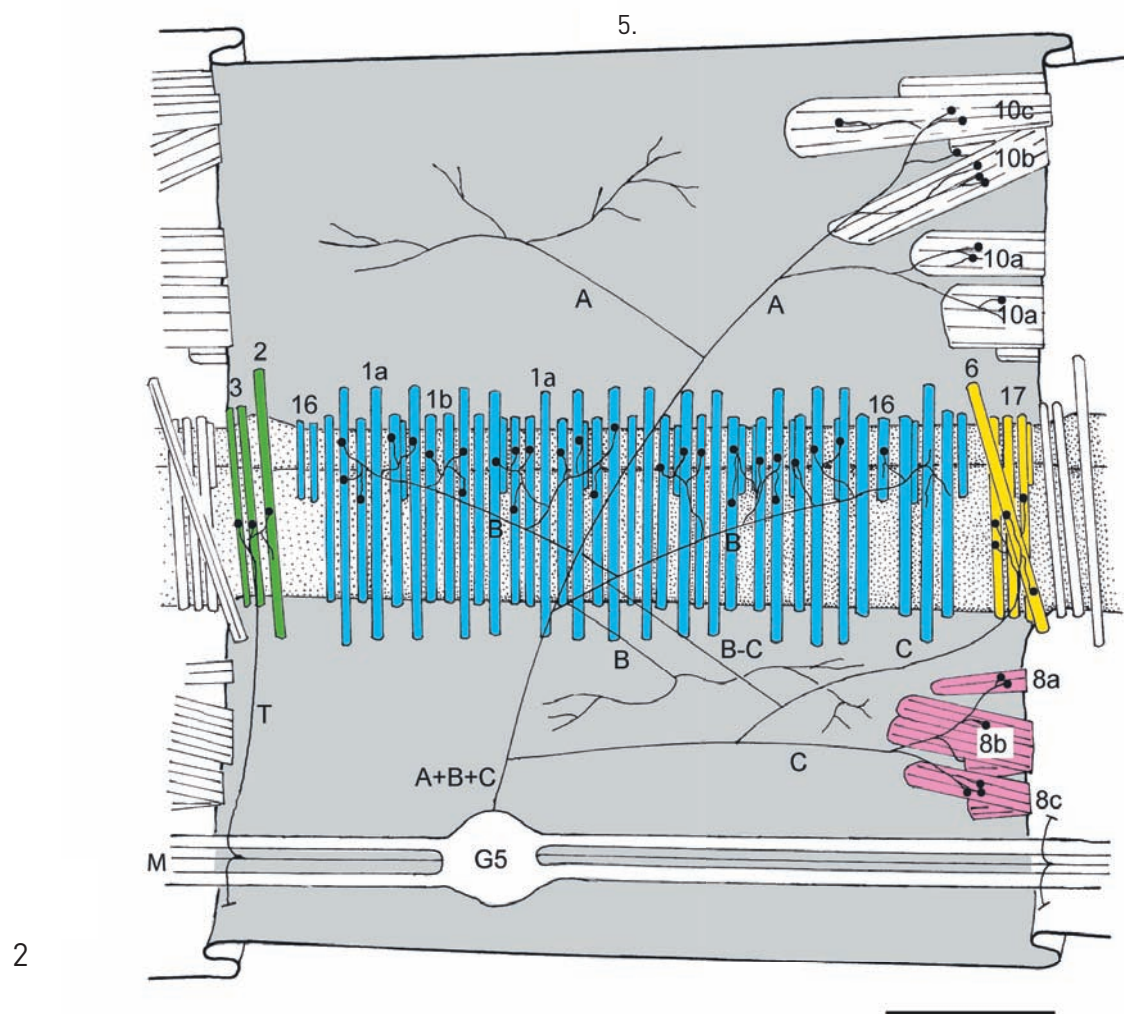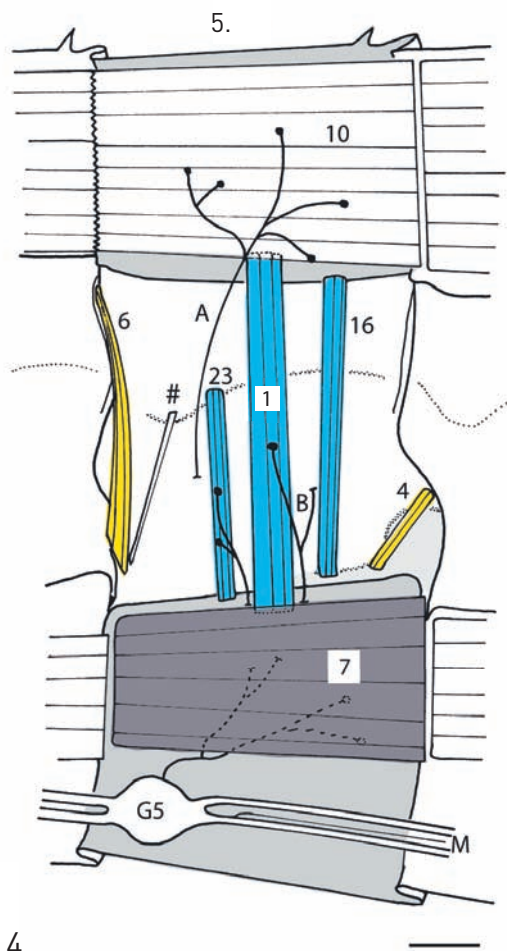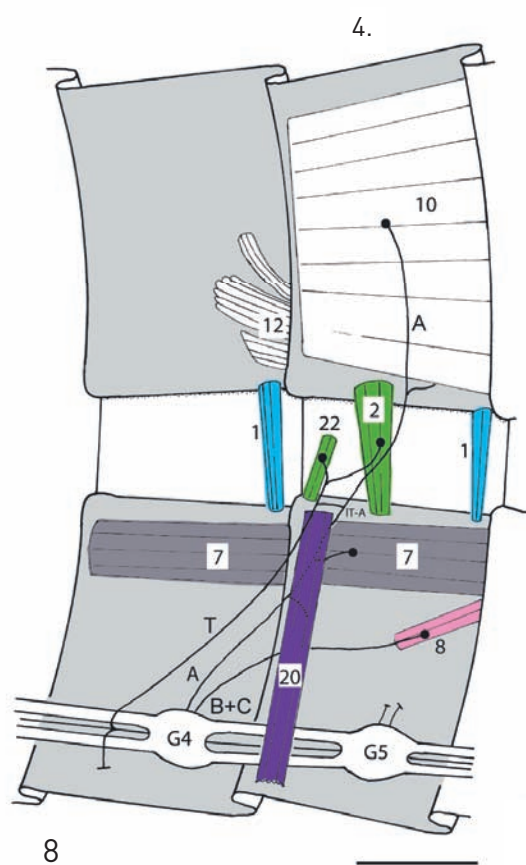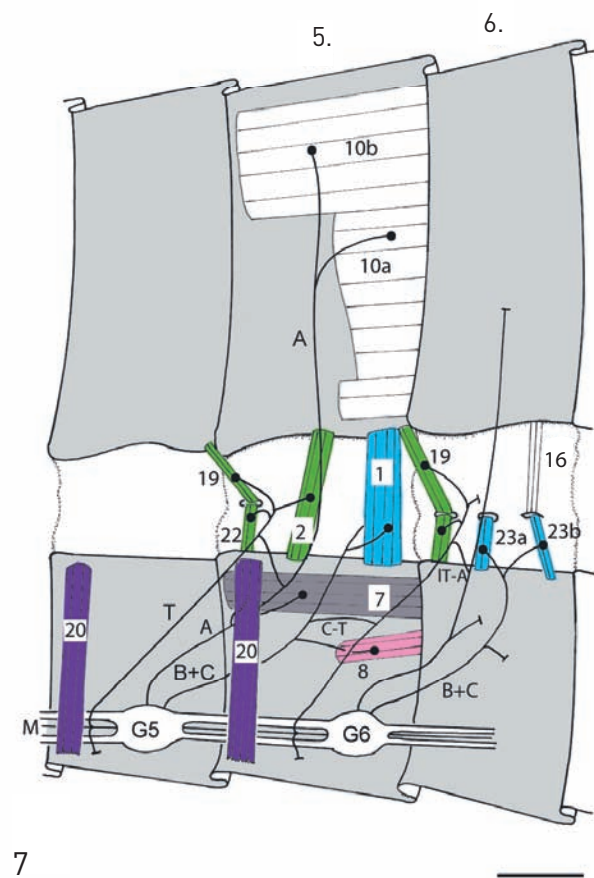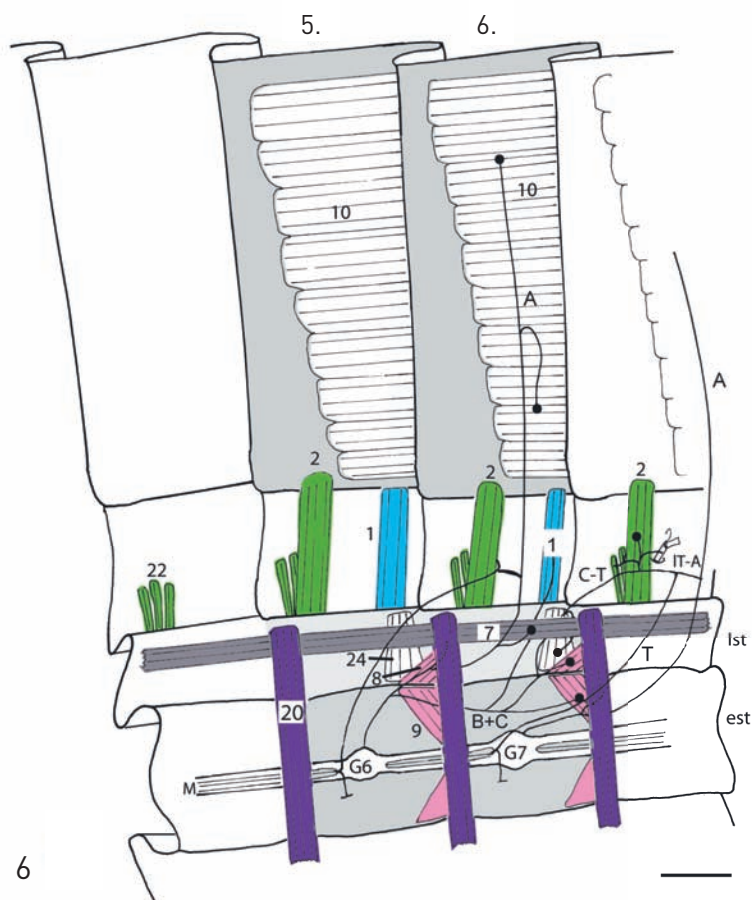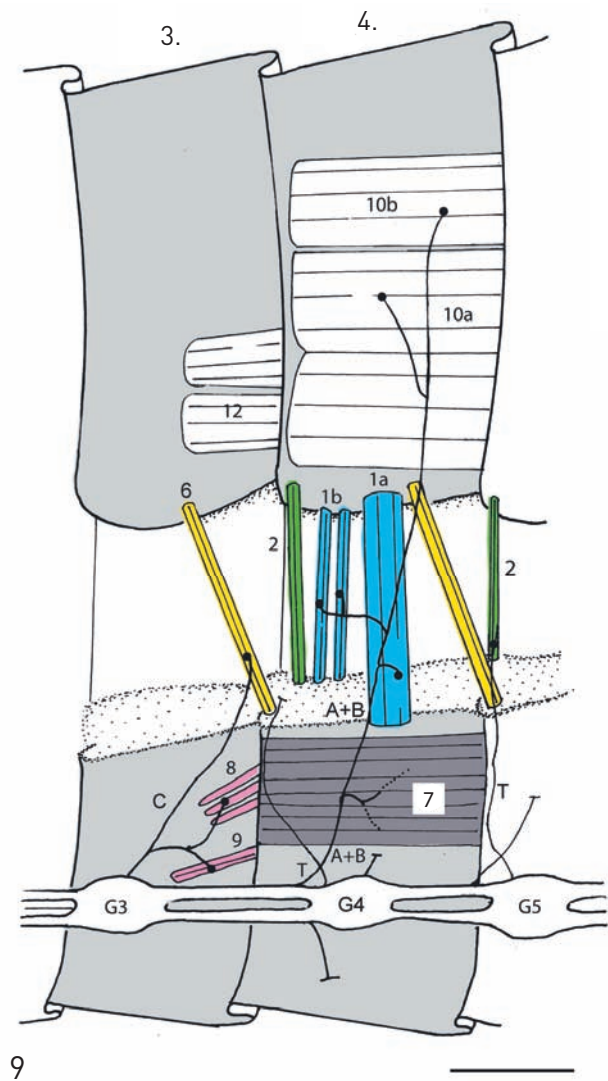
Figs. 4–8. Mid-abdominal musculature with innervation, sclerotised parts gray. From bottom to top in each figure: coxosternite with ventral nerve cord and ventral muscles, pleural membrane with lateral muscles, tergite with dorsal muscles. Orientation: ← anterior, → posterior, ↑ mid-dorsal, ↓ mid-ventral. **4**: Abdominal segment 5 of *Tyrannophasma gladiatior*, female; # delicate muscle fiber; scale bar: 0.2 mm. **5**: Abdominal segments 4 and 5 of *Locusta migratoria*, male; scale bar: 2 mm. **6**: Abdominal segments 5 and 6 of *Tettigonia viridissima*, male; scale bar: 1 mm. **7**: Abdominal segments 4 to 6 of *Gryllus bimaculatus*, male; in segment 6, the external lateral muscles can be seen; scale bar: 0.5 mm. **8**: Abdominal segments 3 and 4 of *Troglophilus neglectus*, female; scale bar: 0.5 mm.

Figs. 9, 10. Mid-abdominal musculature with innervation, sclerotised parts gray. From bottom to top in each figure: coxosternite with ventral nerve cord and ventral muscles, pleural membrane with lateral muscles, tergite with dorsal muscles. Orientation: ← anterior, → posterior, ↑ mid-dorsal, ↓ mid-ventral. **9**: Abdominal segments 3 and 4 of *Perlodes microcephala*, male; in segment 3 the external ventral muscles are depicted; scale bar: 1 mm. **10**: Abdominal segments 2 and 3 of *Ephemera danica*, female; in segment 3 the external dorsal, lateral and ventral muscles are shown. * lateral muscle of ambiguous interpretation; scale bar: 0.5 mm.
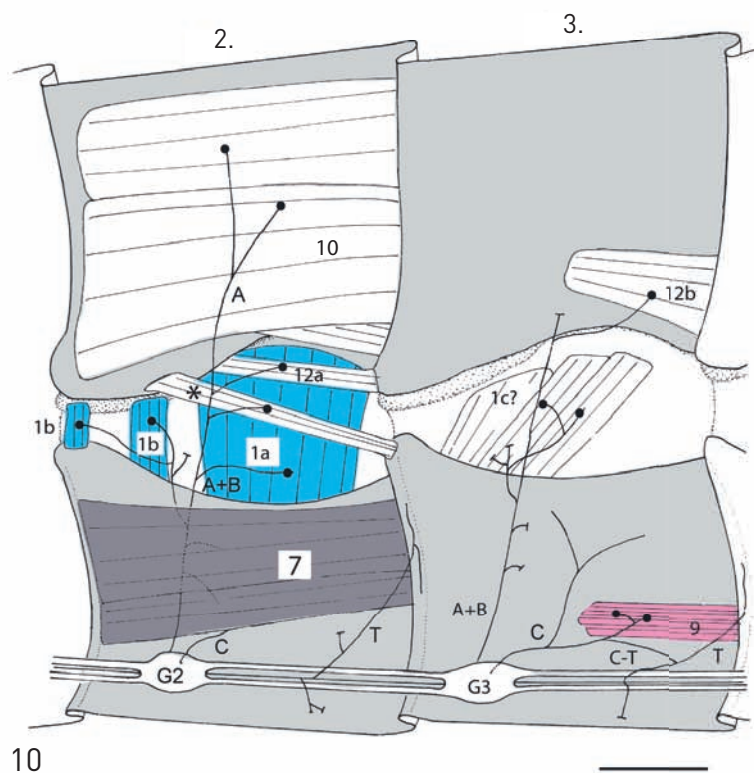
Tab. 1. List of species studied in this work and in previous contributions. The fixation method is given as far as known (specimens studied in this paper and in previous papers by the authors): Alc = alcohol fixed specimens; Bn = specimens fixed in Bouin's solution; F = fresh material.

Higher taxon	Species	Fixation method	Literature data
Ephemeroptera	*Ephemera danica* Müller, 1764	Alc, Bn	
	Ephoron virgo (Olivier, 1791)	Alc, Bn	
	Povilla adusta Navas, 1912	—	Muscles + nerves: Birket-Smith 1971
Plecoptera	*Perlodes microcephala* (Pictet, 1833)	Alc	
	Eusthenia sp.	—	Muscles + nerves (sparse data): Zwick 1973, 1980
	Perla sp.	—	Muscles: Ford 1923
	Pteronarcys californica Newport	—	Muscles + nerves: Schmitt 1963
	Acroneuria sp. (nymph)	—	Muscles + nerves: Knox 1965
Embioptera	*Antipaluria caribbeana* Ross, 1987	Alc	
Mantophasmatodea	*Hemilobophasma montaguense* Klass, Picker, Damgaard, van Noort & Tojo, 2003	Alc	
	Tyrannophasma gladiator Zompro, 2003	Alc	
Phasmatodea	*Timema nevadense* Strohecker, 1966	Alc	Muscles + nerves: Klug & Bradler 2006
	Sceptrophasma hispidula (Wood-Mason, 1873)	F	Muscles + nerves: Klug & Bradler 2006
	Abrosoma festinatum Brock & Seow-Choen, 1995	F	Muscles + nerves: Klug & Bradler 2006
	Phyllium celebicum DeHaan, 1842	F	Muscles + nerves: Klug & Bradler 2006
	Agathemera crassa (Blanchard, 1851)	Alc	Muscles + nerves: Klug & Bradler 2006
	Sungaya inexpectata Zompro, 1996	F	Muscles + nerves: Klug & Bradler 2006
	Haaniella dehaanii (Westwood, 1859)	F	Muscles + nerves: Klug & Bradler 2006
	Ramulus thaii Hausleithner, 1985	F	Muscles + nerves: Klug & Bradler 2006
	Lopaphus sphalerus (Redtenbacher, 1908)	Alc, Bn	Muscles + nerves: Klug & Bradler 2006
	Phaenopharos khaoyaiensis Zompro, 1999	F	Muscles + nerves: Klug & Bradler 2006
	Carausius morosus (Sinéty, 1901)	—	Muscles + nerves: Marquardt 1939
	Megacrania tsudai (Shiraki, 1932)	—	Muscles: Maki 1935
Ensifera	*Gryllus bimaculatus* (de Geer, 1773)	F	
	Gryllus (Acheta) assimilis Fabricius, 1775	—	Muscles: Du Porte 1920, Ford 1923; nerves: Schmitt 1954
	Nemobius fasciatus (de Geer, 1773)	—	Muscles: Ford 1923
	Gryllotalpa hexadactyla Perty, 1832	—	Muscles: Ford 1923
	Tettigonia viridissima (Linnaeus, 1758)	Bn, F	
	Neoconocephalus ensiger Harris, 1841	—	Muscles: Ford 1923
	Neoconocephalus exiliscanorus (Davis, 1905)	—	Muscles + nerves: Schmitt 1964
	Troglophilus neglectus Krauss, 1879	Alc, Bn	
	Macropathus filifer Walker, 1869	—	Muscles: Richards 1955
Caelifera	*Locusta migratoria* (Linnaeus, 1758)	Alc, F	Muscles: Albrecht 1953
	Dissosteira carolina (Linnaeus, 1758)	—	Muscles: Snodgrass 1935; nerves: Schmitt 1954
	Acrotylus insubricus (Scopoli, 1786)	—	Nerves: Steinmann 1965
	Melanoplus bivittatus (Say)	—	Muscles: Ford 1923
	Paratettix cucullatus (Burmeister)	—	Muscles: Ford 1923
	Morabinae spp.	—	Muscles: Blackith & Blackith 1967
	Cephalocoema albrechti Zolessi, 1968	—	Muscles: Covelo de Zolessi 1968
Mantodea	*Sphodromantis viridis* (Forskål, 1775)	F	Muscles + nerves: Klass 1999
	Hierodula membranacea (Burmeister)	—	Muscles + nerves: Kerry & Mill 1987
	Stagmomantis carolina (Johansson, 1763)	—	Muscles: Ford 1923, Levereault 1938
	Mantis religiosa (Linnaeus, 1758)	—	Muscles: LaGreca & Rainone 1949
Blattaria	*Periplaneta americana* (Linnaeus, 1758)	F	Muscles + nerves: Shankland 1965, Klass 1999; nerves: Schmitt 1954, 1962
	Parcoblatta pennsylvanica (de Geer)	—	Muscles: Ford 1923
	Blaberus atropos (Stoll, 1813)	—	Muscles: Ford 1923
Isoptera	*Mastotermes darwiniensis* Froggatt, 1896	F	Muscles: Klass 2000
Dermaptera	*Hemimerus vosseleri* Rehn & Rehn, 1935	Alc	Muscles + nerves: Klass 2001
	Forficula auricularia Linnaeus, 1758	—	Muscles: Ford 1923, Popham 1959
Notoptera	*Grylloblatta campodeiformis* Walker, 1914	—	Muscles: Ford 1923, Walker 1943
Megaloptera	*Chauliodes formosanus* Petersen	—	Muscles + nerves: Maki 1936

Tab. 2. List of muscles of mid-abdominal segments in Lower Neoptera, with their characteristics and preliminary identification in taxa. Numbering of muscles expanded from KLASS (1999), spiracle muscles (13, 14 in KLASS 1999 not included). Occurrence: ++ in all studied representatives of taxon; +− only in some studied representatives of taxon; − in none of the studied representatives of taxon; muscles shaded dark gray: innervation known; light gray: innervation unknown; 0 unknown due to lacking studies or insufficient detail of studies; ?: homologisation of muscle doubtful; (!): no compact transversal muscle in *Gryllotalpa*. Abbreviations: Di Dictyoptera; Ph Phasmatodea; En Ensifera; Ca Caelifera; De Dermaptera; Em Embioptera; Np Notoptera; Mp Mantophasmatodea. See KLASS (1999: 40) on innervation of alary muscle 15.

No.	Group	Reach	Innerv.	Position	Di	Ph	En	Ca	De	Em	Np	Mp
1	lateral	intrasegmental	B	tergo-coxosternal / paratergo-coxosternal	++	++	++	++	++	++	++	++
16	lateral	intrasegmental	B	paratergo-pleural	−	++	+−	−	++	++	++	++
23	lateral	intrasegmental	B	pleuro-coxosternal	−	−	+−	−	−	−	++	++
2	lateral	intrasegmental	T	tergo-coxosternal	++	++	++	++	++	++?	++	−
3	lateral	intrasegmental	T	paratergo-coxosternal	+−	++	++	++	++	−	−	−
22	lateral	intrasegmental	T	pleuro-coxosternal	−	−	++	−	−	−	−	0
17	lateral	intrasegmental	C	paratergo-coxosternal	−	+−	−	−	−	−	−	−
18	lateral	intrasegmental	C	paratergo-pleural	−	+−	−	−	−	−	−	−
4	lateral	intersegmental asc.	C	paratergo-coxosternal	++	−	−	−	+−	−	−	++?
5	lateral	intersegmental asc.	C	tergo-coxosternal	++	−	−	−	−	++	−	−
6	lateral	intersegmental desc.	C	tergo-coxosternal / tergo-pleural	++	+−	−	−	−	++	++?	++?
19	lateral	intersegmental desc.	T	(para)tergo-pleural	−	−	+−	−	−	−	−	−
7	ventral longitudinal	intersegmental	A	internal, coxosterno-coxosternal	++	+−	++	++	++	++	++	++
8	ventral longitudinal	intersegmental	C	external lateral, coxosterno-coxosternal	++	+−	+−	++	++	++	++	0
9	ventral longitudinal	intersegmental	C	external mesal, coxosterno-coxosternal	++	−	+−	−	−	−	−	−
24	ventral transverse	intrasegmental	B or C	eusterno-laterosternal	−	−	+−	−	−	−	−	−
20	ventral transverse	intrasegmental	A	coxosterno-coxosternal	−	−	++(!)	−	−	−	−	−
21	ventral	intersegmental	A	hyperneural muscle	+−	−	−	−	−	−	−	−
10	dorsal longitudinal	intersegmental	A	internal, tergo-tergal	++	++	++	++	++	++	++	++
11	dorsal longitudinal	intersegmental	A	external mesal, tergo-tergal	++	++	+−	+−	++	+−	++	0
12	dorsal longitudinal	intersegmental	A	external lateral, tergo-tergal	++	++	++	++	++	++	++	0
15	dorsal transverse	intrasegmental	A+T?	from tergum to heart (alary muscle)	++	++	++	++	++	++	++	0