

## The pregenital abdominal musculature in phasmids and its implications for the basal phylogeny of Phasmatodea (Insecta: Polyneoptera)

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### Abstract

Recently several conflicting hypotheses concerning the basal phylogenetic relationships within the Phasmatodea (stick and leaf insects) have emerged. In previous studies, musculature of the abdomen proved to be quite informative for identifying basal taxa among Phasmatodea and led to conclusions regarding the basal splitting events within the group. However, this character complex was not studied thoroughly for a representative number of species, and usually muscle innervation was omitted. In the present study the musculature and nerve topography of mid-abdominal segments in both sexes of seven phasmid species are described and compared in detail for the first time including all putative basal taxa, e.g. members of *Timema*, *Agathemera*, Phylliinae, Aschiphasmatinae and Heteropteryginae. The ground pattern of the muscle and nerve arrangement of mid-abdominal segments, i.e. of those not modified due to association with the thorax or genitalia, is reconstructed. In *Timema*, the inner ventral longitudinal muscles are present, whereas they are lost in all remaining Phasmatodea (Euphasmatodea). The ventral longitudinal muscles in the abdomen of *Agathemera*, which span the whole length of each segment, do not represent the plesiomorphic condition as previously assumed, but might be a result of secondary elongation of the external ventral longitudinal muscles. Sexual dimorphism, common within the Phasmatodea, also applies to the muscle arrangement in the abdomen of some species. Only in the females of *Haaniella dehaanii* (Heteropteryginae) and *Phyllium celebicum* (Phylliinae) the ventral external longitudinal muscles are elongated and span the length of the whole segment, possibly as a result of convergent evolution.

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**Keywords:** Phasmatodea; *Timema*; *Agathemera*; Abdominal morphology; Muscle innervation; Phylogeny

### Introduction

Phasmatodea (stick and leaf insects) comprises about 3000 described species of mainly tropical and subtropical insects. Its monophyly seems to be well supported by molecular data (Wheeler et al. 2001; Whiting et al. 2003) as well as by a number of morphological characters such as a pair of prothoracic repellent glands (Hennig 1969, 1994; Kristensen 1975, 1991; Ax 1999; Tilgner 2002; Bradler 2003; Whiting et al. 2003; Willmann 2003a,

*Abbreviations:* A, dorsal nerve (main branch); B, lateral nerve (main branch); C, ventral nerve (main branch); DLM, dorsal longitudinal muscle; eL, outer tergo-sternal musculature; G, ganglion; iL, inner tergo-sternal musculature; T, transversal nerve; tp, tergo-pleural musculature; VLM, ventral longitudinal muscle; 1, ..., 21, muscle numbers

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2004), the venation pattern of the hindwing (Ragge 1955; Bradler 2003; Willmann 2003b), pear-shaped secretory appendices on the posterior part of the mesenteron (Marshall and Severin 1906; Kristensen 1975, 1991; Hennig 1994; Ax 1999; Tilgner et al. 1999; Bradler 2003), the splitting of the lateral dorsoventral musculature into isolated muscle fibres (Ford 1923; Kristensen 1975; Saure 1988; Bradler 2003), the absence of mitochondria in spermatozoa (Baccetti 1987; Jamieson 1987; Kristensen 1991; Ax 1999; Whiting et al. 2003), and the male vomer (Bradler 1999, 2003; Tilgner et al. 1999; Whiting et al. 2003; Willmann 2003a, b). The position of the Nearctic *Timema* as the sister group to the remaining Phasmatodea, the Euphasmatodea, seems to be uncontroversial and is supported by numerous morphological and molecular studies (Kristensen 1975; Wheeler 1998; Tilgner et al. 1999; Wheeler et al. 2001; Tilgner 2002; Whiting et al. 2003; Wheeler et al. 2004; Bradler et al. 2003). Zompro (2004), on the other hand, placed *Timema* outside the Phasmatodea, as sister group to the Embioptera, based on several symplesiomorphic characters.

In recent years, conflicting hypotheses concerning the basal relationships within the Euphasmatodea have emerged (Bradler 1999, 2000, 2003; Tilgner 2002; Whiting et al. 2003; Zompro 2004; for summary see Bradler et al. 2003). Authors using molecular data place wingless members of the Nearctic and Neotropical Diapheromerinae as the most basal lineages of extant Euphasmatodea, which leads to the striking conclusion that the ancestral phasmid lacked wings and that wings originated de novo in several subordinate taxa (Whiting et al. 2003; see also Bradler et al. 2003). These controversial results have been debated since (Trueman et al. 2004; Whiting and Whiting 2004; Willmann 2004; Zompro 2004; Grimaldi and Engel 2005). In fact, Diapheromerinae are in many aspects highly derived stick insects that had not been regarded as a basal side branch before. In this group, the abdomen is elongated with longitudinal muscles distinctly shortened and restricted to the posterior part of each segment (Ford 1923), a condition considered as the usual case for Phasmatodea (Beier 1968; Saure 1988). Kristensen (1975) pointed to some features in *Timema* indicating that its non-lengthened segments represent a primitive condition: in the abdomen, the longitudinal muscles span the entire segment. Bradler (2001) observed the same character state in the species-poor phasmid taxon *Agathemera* from South America, suggesting *Agathemera* as the most basal branch within Euphasmatodea. This hypothesis was rejected by Tilgner (2002) who performed a cladistic analysis of the Phasmatodea based on morphological structures of the adult female and egg capsule. Tilgner (2002) presented evidence that the Aschiphasmatinae form the most basal lineage of extant euphasmatodeans (followed by *Agathemera*), but muscle

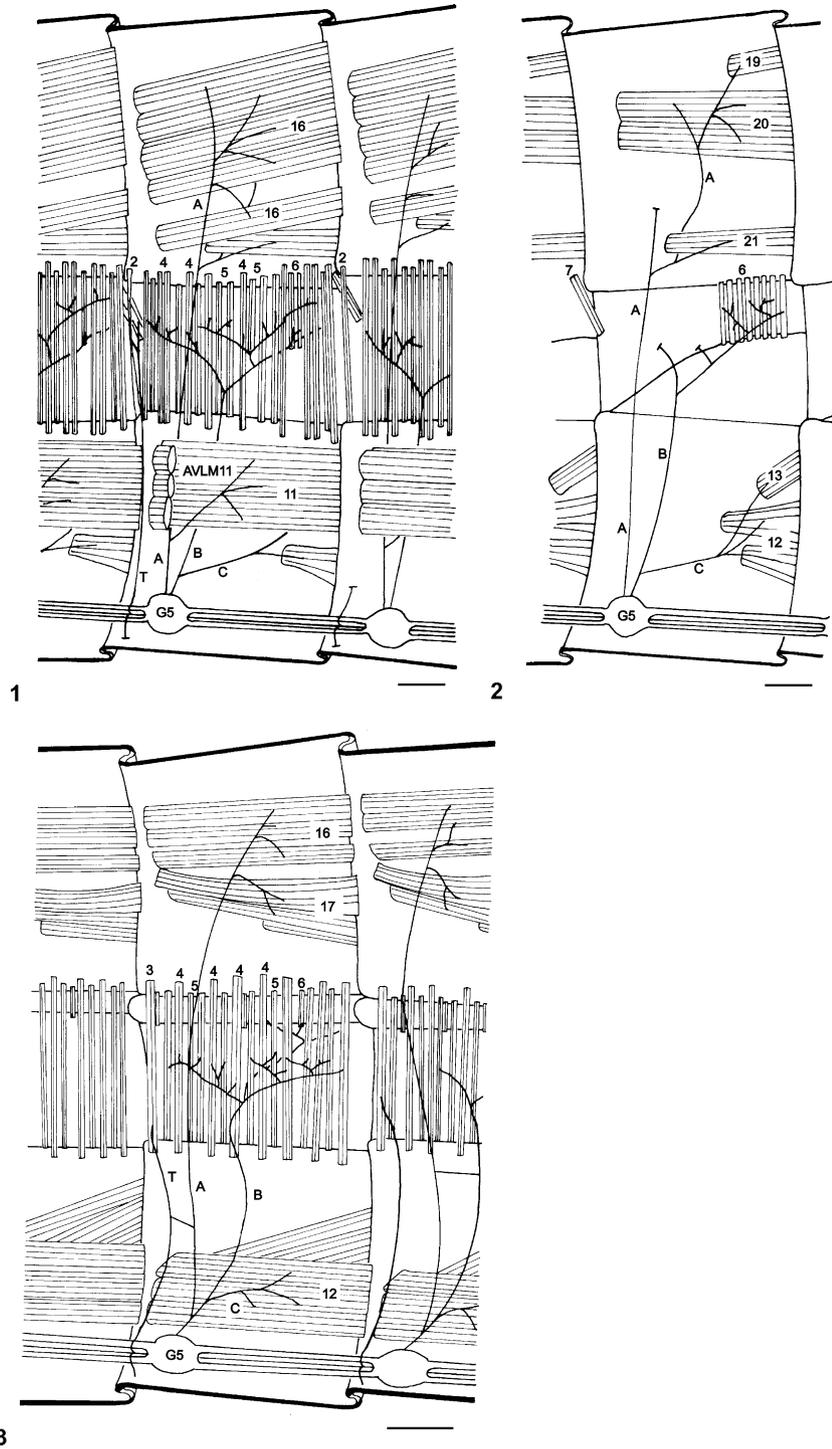
anatomy of the abdomen was not included in this analysis. Bradler et al. (2003: Fig. 2) re-examined this character complex for *Abrosoma festinatum*, a Malayan member of the Aschiphasmatinae. The apomorphic condition was found to be present: the longitudinal muscles of *Abrosoma* do not span the entire length of an abdominal segment but are restricted to its posterior part, at least on the ventral side. This is likely due to loss, not shortening, of the internal longitudinal muscles, as previously assumed by Klass (1999).

Obviously, comparative investigations into the muscle arrangement in the abdomen of stick insects are a neglected area of phasmid research that is crucial for understanding the early evolution within the group. Beyond this, a reconstruction of the ground-pattern of this character complex might also contribute to phylogenetic analyses of inter-ordinal relationships among lower Neoptera (see Klass 1999).

Numerous workers have contributed results on the external morphology of Phasmatodea (Ragge 1955; Bauchhenß 1971; Kristensen 1975; Bradler 1999, 2000, 2001; Tilgner et al. 1999; Tilgner 2002). Descriptions of the internal anatomy are rare; especially the musculature is scarcely described in detail. The thoracic and abdominal musculature of the Indian stick insect, *Carausius morosus*, was described by Jeziorski (1918) and Marquardt (1939). Ford (1923) compared the musculature of abdominal segment III of the North American stick insect *Diapheromera femorata* with that of other Neoptera. Maki (1935) exhaustively described the complete musculature of *Megacrania tsudai*. Having compared the musculature of abdominal segments IV and V of five phasmatodeans, Saure (1988) is the only previous author to have pursued a comparative approach.

The nervous system of the third abdominal segment of *D. femorata* was described by Schmitt (1954). Marquardt (1939) has provided the only description of the musculature of *C. morosus* that includes its innervation. Nerves and muscles in the pregenital segments of two dictyopterans, the mantid *Sphodromantis viridis* and the cockroach *Periplaneta americana* were depicted in detail by Klass (1999), revealing new characters useful for phylogenetic analyses. With the exception of this latter study no comparative analysis of both structures with regard to lower Neopteran phylogeny has been undertaken.

Here, the musculature and nerve topography of 'general' mid-abdominal segments, i.e. those metameres not modified due to their close association with the thorax or genital structures, are investigated in seven species. The study includes *Timema* and Euphasmatodean taxa discussed as putatively basal by previous workers, such as *Agathemera* (Bradler 2003; Zompro 2004), Aschiphasmatinae (Tilgner 2002) and *Phyllium* (Zompro 2004). The results are compared with data



**Fig. 1–3.** Internal (Figs. 1 and 3) or external (Fig. 2) layers of musculature with innervation. (1, 2) *Timema nevadense*, female; (3) *Agathemera* sp., male. From bottom to top in each figure: sternum with ventral nerve cord and ventral muscles, pleural membrane with lateral muscles, vertically arranged (Fig. 1: muscles nos. 2, 4–6; Fig. 2: muscles nos. 6,7; Fig. 3: muscles nos. 3–6), tergum with dorsal muscles. Orientation: ← anterior; → posterior; ↓ ventromedian; ↑ dorsomedian. Scale bars: Figs. 1 and 2 = 0.2 mm; Fig. 3 = 1 mm.

from the literature. Thus, this character complex is surveyed here for the first time for a broad assortment of representatives (14 out of the 19 traditional subfamilies recognized by Günther 1953). Besides placing *Timema*

and *Agathemera* at the base of Phasmatodea and Euphasmatodea, respectively, we follow the classification of Günther (1953) who was the only contributor considering phylogenetic systematics by searching

for monophyletic groups within the Phasmatodea (“geschlossene Gruppe” [...] “apomorpher Komplex”; Günther 1953, p. 551). Subsequent classifications (Bradley and Galil 1977; Kevan 1977, 1982; Zompro 2003, 2004) dramatically changed Günther’s arrangement without presenting new evidence, and did not stay within the methodical framework of phylogenetic systematics. Zompro (2003, 2004), e.g., established new clades explicitly based on plesiomorphic characters. Hence, these latter classifications are not considered as well founded (Key 1991; Bradler et al. 2003; Grimaldi and Engel 2005).

## Material and methods

### Species examined (\* = literature data only)

Timematinae: *Timema nevadense* Strohecker, 1966; Aschiphasmatinae: *A. festinatum* Brock & Seow-Choen, 1995; Phylliinae: *Phyllium celebicum* de Haan, 1842; *Agathemera crassa* (Blanchard, 1851); Heteropteryginae: *Sungaya inexpectata* Zompro, 1996, *Haaniella dehaanii* (Westwood, 1859), *Heteropteryx dilatata* (Parkinson, 1798)\*; Tropidoderinae: *Extatosoma tiaratum* (Macleay, 1826)\*; Phasmatinae: *Ramulus thaii* (Hausleithner, 1985); Eurycanthinae: *Eurycantha calcarata* Lucas, 1870\*; Platycraninae: *Megacrania tsudai* Shiraki, 1932\*; Cladomorphinae: *Aplopus cytherea* Westwood, 1859\*; Necrosciinae: *Lopaphus sphalerus* (Redtenbacher, 1908), *Phaenopharos khaoyaiensis* Zompro, 1999; Pachymorphinae: *Sceptrophasma hispidula* (Wood-Mason, 1873); Lonchodinae: *C. morosus* (Sinéty, 1901)\*; Heteronemiinae: *D. femorata* (Say, 1824)\*.

In the following, these species are mostly referred to by their generic names only.

### Dissection

Freshly killed specimens or, in cases of rare material, specimens preserved in 70% ethanol were used for preparation. Abdominal segments II–VII were isolated, opened laterally or dorsally, and pinned out in a dissecting tray with 70% isopropanol. This turns muscles and nerves whitish and hardens them, so that they are not destroyed when the fat body and tracheae are removed. Isopropanol fixation was carried out for 2 or 3 days. For better identification, muscles and nerves were stained for about 1 h using methylene blue or Coomassie brilliant blue, respectively. Dissections were made under a stereomicroscope, at magnifications between 10× and 176×. Varying the angle of light improved the contrast.

Cross-sections and longitudinal sections of some specimens were used to check the identity of small muscles and nerves under a light microscope.

## Terminology

The terminology of nerves and muscles was modified after Klass (1999). The main nerve branches are termed with upper-case letters. Fine ramifications are not denoted by numbers and lower-case letters, as Klass (1999) did, but the upper-case letter is followed by an abbreviation for the muscle innervated by this nerve branch and ramus. Nerves either supply muscles or ramify on the body wall. Here, only nerve branches that innervate muscles are described, in order to focus on structures considered to be relevant for phylogeny reconstruction.

Muscles are denoted by numbers. The dorsal and ventral longitudinal muscles are numbered from median to lateral, the lateral muscle groups from anterior to posterior. For example, ADLM1 denotes the nerve branch that innervates dorsal longitudinal muscle no. 1; the same format is used to name other nerves and their muscles.

The main objectives of this terminology are to reflect the connection of muscles and their innervation, and to avoid redundant terms. The descriptions and designations of the nerves are purely topographical. Hence, what is called a ‘nerve’ here is not identical to an axon and its course.

## Illustrations

For preparation purposes, usually the abdomen was opened laterally and pinned out. Hence the tergum, pleura and sternum were stretched in one plane. Consequently, the lateral muscles and the nerve branches appear longer in the figures than they are in nature. Nevertheless, the relative positions of muscles and their innervation represent the natural condition.

All figures show the right-hand side of the fifth segment.

## Results

### Descriptions

#### General aspects of the nervous system

Roots of main nerves. Nerves A and B+C arise separately from the ganglion in *Timema* (Figs. 1, 2). In all other phasmids investigated, A, B and C have a short common stem. In segments III–VI separate ganglia are present. Ganglia II and III are fused or closely attached to the ganglion of the metathorax; the posterior ganglia are merged. The free ganglia of segments III–VI usually lie near the anterior rim of the corresponding segment. The ganglion belonging to segment II is located in the posterior region of the preceding segment. The median

nerve lies between the connectives. It is often closely attached to one of the connectives, thus not easily visible. The transversal nerve (T) arises from the median nerve anterior to the ganglion of the corresponding segment. It runs laterad to some lateral muscles in the anterior portion of the corresponding segment and to a delicate intersegmental muscle present in some species. The transversal nerve (T) often passes along the anterior rim of the sternum, e.g. in *Timema* (Fig. 1), *Phyllium* (Fig. 6) and *Sungaya* (Fig. 8).

**Anastomoses.** The main nerve branches may be connected by a short branch, an anastomosis. Since only the topography is shown, it is not possible to decide if axons of topographically distinct nerve branches pass through the anastomosis. However, it is obvious that presence/absence of anastomoses is subject to individual variation.

The following anastomoses are present: B-C in *Ramulus* and *Sceptrophasma* (Figs. 9 and 10); C-T in *Carausius* (Marquardt 1939), A-B and T-A in some individuals of *Agathemera* (Fig. 3). There might be anastomoses in other species as well, but due to the paucity of material for some species this could not be verified.

#### *Timema nevadense*

The numbers refer to the muscles as depicted in Figs. 1 and 2. The two insertion points of the muscles are given.

**Lateral muscles.** 2: arises from anterior edge of tergum – anterior edge of sternum of same segment; a delicate bundle ventrally attached to cuticular rim of sternum; innervated by transversal nerve (T). 4: tergum, laterally – sternum, laterally, intrasegmental; several slender bundles scattered along lateral region of segment. 5: tergum, laterally external to 4 – lateral rim of sternum; several slender bundles distributed as in no. 4. 6: tergum, laterally external to 4-fold in pleural membrane; small slender bundles distributed over posterior half of segment. Muscles 4, 5 and 6 innervated by B. 7: posterior edge of tergum – anterior portion of pleural membrane; largest bundle of lateral musculature, one intersegmental bundle; innervated by nerve T. This muscle is present in *Timema* only.

**Ventral longitudinal muscles.** 11: sternum, anteriorly – following sternum, anteriorly; a strong, compact bundle consisting of two layers; innervated by a branch of nerve A, and only present in *Timema*. 12: posterior quarter of sternum – anterior rim of following sternum; muscle consists of two separate bundles that broaden near rim of following sternum. Median bundle next to ventral nerve cord shorter than other one. Muscles 12 and 13 innervated by C. 13: posterior fifth of sternum – anterior rim of following sternum; a small, oblique bundle.

#### Dorsal longitudinal muscles

16: tergum, anteriorly – following tergum, anteriorly; consists of two bundles, a broad median one and a very slender one more laterally. 19: posterior fifth of tergum – anterior rim of following tergum; a small, slightly oblique bundle. 20: anterior portion of tergum – anterior rim of following tergum, a large bundle, slightly oblique. 21: anterior half of tergum – anterior rim of following tergum; a rather slender bundle. All dorsal longitudinal muscles innervated by dorsal nerve (A).

**Nerve A.** Arises from ganglion and runs laterad external to muscle 11. Medially from muscle no. 11 it ramifies to this inner ventral muscle (Ramus AVL11; Fig. 1); this ramus located between the two layers of muscle 11. This condition is unique to *Timema*; in other Phasmatodea this ramus and muscle 11 are not present. Main ramus passes medially from the lateral muscles and ramifies in the dorsal muscles. One ramus (ADLM21) innervates most lateral muscle 21 (Figs. 1 and 2), the other ramus branching off ADLM21 passes externally to muscles 16 and 21 and ramifies into muscles 19 and 20 (Fig. 2).

**Nerve B.** Has common stem with nerve C, runs laterad externally to muscle 11 (Fig. 1) and ramifies on the lateral muscles. Ramifies into two branches; right-side branch disappears externally to muscle bundles 4 and 5 in posterior region of segment and supplies muscle bundles 6 (Fig. 2). From right branch of B several rami arise that innervate muscle bundles 4 and 5 (Fig. 1). Left branch of nerve B ramifies on anterior portions of muscle bundles 4 and 5 (Fig. 1).

**Nerve C.** Arises from nerve B and runs laterad to the external ventral longitudinal muscles where it ramifies on muscles 13 and 14.

**Nerve T.** Arises from median nerve and passes along anterior rim of sternum. Innervates lateral muscles 2 and 7 (Fig. 1).

#### Muscles and nerves of Euphasmatodea

**Lateral muscles.** 1: posterior rim of tergum – anterior rim of following sternum; often inserts on beginning of intersegmental membrane; a very delicate bundle, hidden in intersegmental membrane; innervated by transversal nerve T; present in *Phyllium* and *Sungaya*, probably absent in other species. 2: anterior edge of tergum – anterior edge of sternum of same segment; arises on pleura in some taxa (e.g. in *Ramulus*; Fig. 9); occasionally consists of two to three bundles (e.g. *Sceptrophasma*; Fig. 10); a delicate bundle, innervated by nerve T; present in all species except *Agathemera*. 3: anterior rim of tergum – anterior rim of sternum of same segment; innervated by T; always a slim bundle. 4:

tergum, laterally – sternum, laterally; an intrasegmental muscle consisting of many bundles distributed along lateral body region; innervated by lateral nerve B; present in all phasmids. In many forms, especially elongated slender ones (e.g. *Ramulus*, *Sceptrophasma*; Figs. 9 and 10) these bundles are delicate. In *Phyllium* they tend to have a concave form (Fig. 6). Some stouter forms (e.g. *Sungaya*; Fig. 8) possess rather strong bundles. 5: tergum, laterally – lateral margin of sternite; external to 4; innervated by B; present in all phasmids; divided in several bundles as in no. 4; condition of bundles in different morphs as in 4.

6: tergum, external to 4 – hypopleurite, if sclerotization present. If pleura not sclerotized, muscle bundles attached to a fold in pleural membrane; innervated by B. Several more or less delicate bundles distributed along pleural region of segment. They are the most tightly packed lateral muscles. 8: posterior margin of tergum – anterior margin of following sternum; innervated by ventral nerve C; a delicate intersegmental bundle present in *Phyllium*, *Ramulus*, *Sceptrophasma* and *Carausius* (Figs. 6, 9 and 10; for *Carausius* see Marquardt 1939 and Saure 1988).

9: tergum, laterally – lateral margin of sternum, like no. 5; a portion of slender muscle bundles located in posterior region of segment; in contrast to 5 innervated by ventral nerve C; present in *Ramulus*, *Sceptrophasma* and *Carausius* (Figs. 9 and 10; for *Carausius* see Marquardt 1939). 10: tergo-pleural muscle bundles like no. 6, but in posterior region of segment; external to 9;

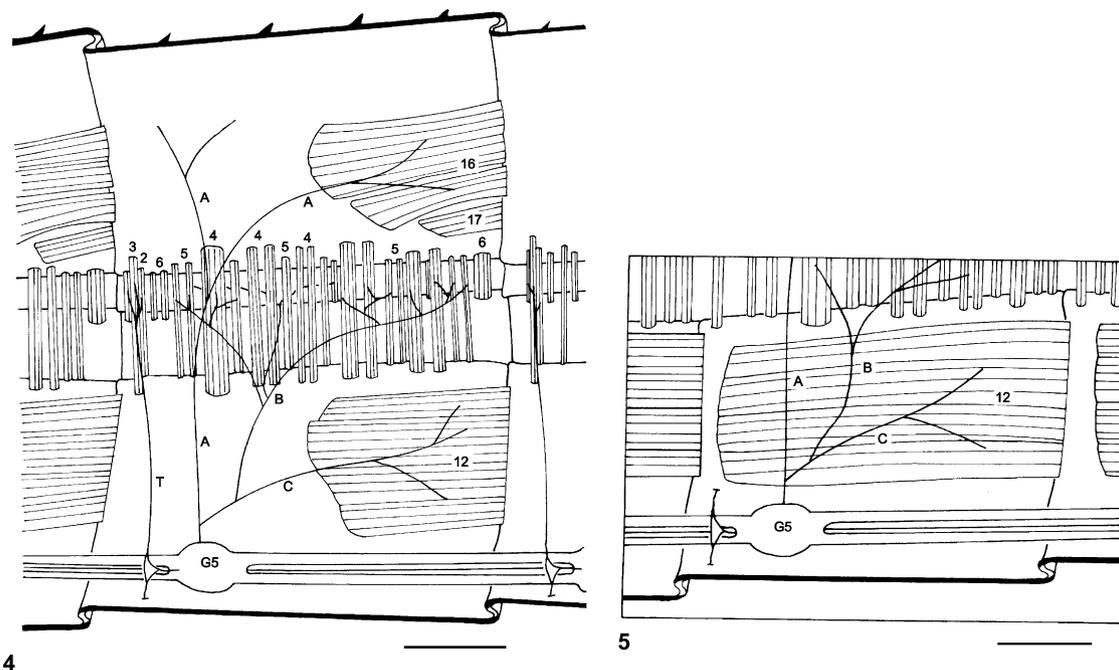
innervated by nerve C, present in *Carausius* (Marquardt 1939).

Ventral longitudinal muscles. 12: sternum, anteriorly – following sternum, anteriorly in *Agathemera* (Fig. 3), female *Haaniella* (Fig. 5), female *Phyllium* (Fig. 6). In male *Haaniella* (Fig. 4), male *Phyllium* (Fig. 7) and remaining Euphasmatodea, muscle does not span entire segment (Figs. 8–10); innervated by ventral nerve C.

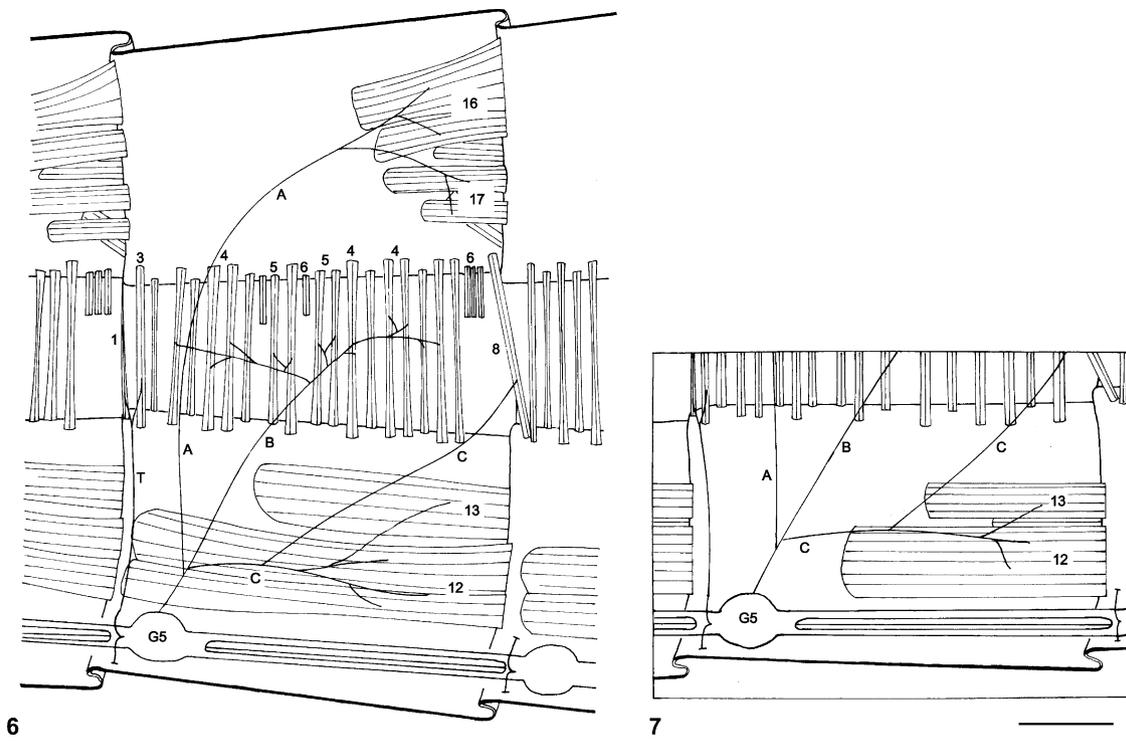
13: Lateral to 12, not spanning entire segment, neither in female *Phyllium* nor in other phasmids where it is present (Figs. 6, 8 and 10); innervated by C.

Underneath these muscles there is another layer consisting of several (2–3) muscles with variable direction and size. All these are innervated by branches of nerve C, too. No homology hypothesis can be presented here. As these muscles do not bear characters relevant to the phylogenetic considerations at hand, they are not illustrated here.

Dorsal longitudinal muscles. 16: tergum, anteriorly – following tergum, anteriorly in *Agathemera* (Fig. 3). In all other Euphasmatodea, muscle does not span entire segment. 17: laterally to 16, in *Agathemera* spanning entire segment (Fig. 3); in other phasmids shorter. 18: most laterally located, present in *Sungaya* and *Carausius* (Fig. 8; for *Carausius* see Marquardt 1939; Saure 1988: D3). External to these muscles a layer of external dorsal longitudinal muscles that is not elucidated more precisely here, for same reason as with



**Fig. 4, 5.** *Haaniella dehaanii*, musculature with innervation. (4) Male, internal layers of musculature; from bottom to top: sternum with ventral nerve cord and ventral muscles, pleural membrane with lateral muscles nos. 2–6, tergum with dorsal muscles. (5) Female, ventral musculature. Orientation: ← anterior; → posterior; ↓ ventromedian; ↑ dorsomedian. Scale bars: 1 mm.



**Fig. 6, 7.** *Phyllium celebicum*, musculature with innervation. (6) Female, internal layers of musculature; from bottom to top: sternum with ventral nerve cord and ventral muscles, pleural membrane with lateral muscles nos. 3–6, tergum with dorsal muscles. (7) Male, ventral musculature. Orientation: ← anterior; → posterior; ↓ ventromedian; ↑ dorsomedian. Scale bars: 1 mm.

ventral muscles. All dorsal longitudinal muscles innervated by dorsal nerve A.

## Discussion

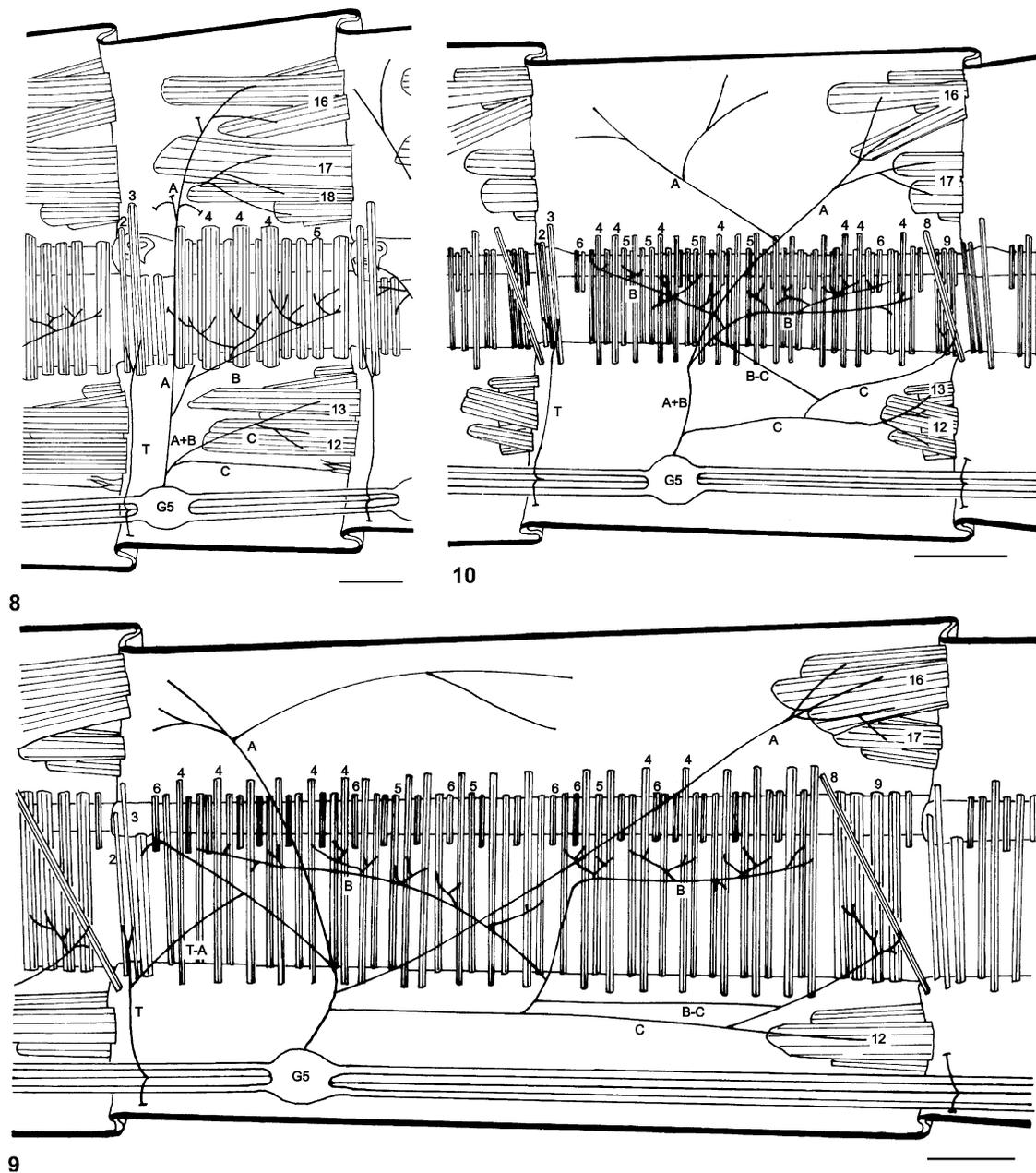
### Absence of muscles or neuronal structures, variation

It is possible that some delicate muscles such as nos. 1, 2 or 3 that are recorded as absent in *Timema* or *Agathemera* were not detected by the authors due to the suboptimally preserved material available for examination. Another muscle not mentioned so far is the transverse muscle or alary muscle in the dorsal diaphragm; it originates from the anterior rim of the tergum or from the antecosta and inserts at the heart (Maki 1935; Marquardt 1939; Nutting 1951; Saure 1988). Its delicate fibres are embedded in tissue. It is expected to be present in all Phasmatodea, but often not detected in alcohol-preserved material, e.g. of *Timema* or *Agathemera*. Similar problems concern the nervous system, especially small nerve branches. The branches of nerve C which innervate external lateral muscles in *Carausius* (Marquardt 1939) were not found in some other species. It is possible that more anastomoses are present, e.g. in *Timema*, *Haaniella* or *Phyllium*.

The specific characteristics (compactness, direction) of muscles vary in the respective segments of different species. Individual variation of muscles (differences between individuals of the same species) seems to be lower than individual variation in the branching pattern of the nerves. The branches of main nerves that innervate the longitudinal muscles often show such variation. Segmental variation (differences between segments of the same individual) is mainly related to the nerve cord and roots of the main nerve branches. The relative positions of the ganglia can vary slightly, although no hyperneuronal muscle moving them is present. Either the ganglia can slightly be moved passively, or the differences are an artefactual result of preparations. The length of the common stem of nerves A, B and C varies, too. Anastomoses can vary in a single individual as well, as shown in *Agathemera* (Fig. 3).

### Outgroup

In order to decide which of two different character states in phasmid anatomy is apomorphic for Phasmatodea or Euphasmatodea, an outgroup comparison using different orders was required. However, previous contributions to the character complex studied here with few exceptions deal with either the musculature or the nervous system alone and do not provide the necessary



**Fig. 8–10.** Internal layers of musculature with innervation in females of (8) *Sungaya inexpectata*, (9) *Ramulus thaii*, (10) *Sceptrophasma hispidula*. From bottom to top in each figure: sternum with ventral nerve cord and ventral muscles, pleural membrane with lateral muscles, tergum with dorsal muscles. Orientation: ← anterior; → posterior; ↓ ventromedian; ↑ dorsomedian. Scale bars: 1 mm.

information. Schmitt (1963) and Zwick (1973) described both muscles and innervation of the abdomen in Plecoptera. The anatomy of the dermapteran abdomen was described by Klass (2001). Klass (1999) also compared extensively the pregenital abdominal musculature and innervation of two members of Dictyoptera, a mantid and a cockroach. Kerry and Mill (1987) treated muscles and nerves of a mantid. Walker (1943) described the abdomen of a grylloblattid. Du Porte (1920) and Ford (1923) provided musculature data on

Ensifera, whereas works of Schmitt (1954, 1964) dealt with the nerves of Ensifera. Snodgrass (1935) described the musculature of the abdomen of the grasshopper *Dissosteira carolina* (Caelifera). Schmitt (1954) examined the nerves of the same species. The most comprehensive work on the pregenital abdomen published so far is the study on the mantid *S. viridis* and the blattid *P. americana* by Klass (1999), which includes an outline of this character complex for lower Neoptera in general. The Dictyoptera are generally not regarded as

closely related to the Phasmatodea, with the exception of Beutel and Gorb (2001). More often, Orthoptera (Saltatoria) or Embioptera are proposed as the adelphotaxon of Phasmatodea (Rähle 1970; Kristensen 1975, 1981, 1991; Flook et al. 1999; Wheeler et al. 2001; Whiting et al. 2003; Willmann 2003a, b, 2004). Nevertheless, the published information on the dictyopteran abdomen is sufficient to polarize the characters in the examined phasmid taxa, as both groups belong to the Polyneoptera (Martynov 1925; Willmann 2003a, 2004; Grimaldi and Engel 2005), as do the other groups mentioned in this context. A homologisation of the structures under consideration was undertaken by Klass (1999). Furthermore, for Embioptera information on abdominal anatomy is rather fragmentary. An exhaustive comparison of this character complex among neopteran taxa, which will hopefully elucidate possible sister groups of the Phasmatodea, has yet to emerge, but one of us (Klug) is currently focusing on this task.

### Ground pattern of a pregenital abdominal segment of Phasmatodea

Muscle and innervation data combined are presented here for the presumably most basal phasmid, *Timema*. It is thus possible to reconstruct a ground pattern for the pregenital abdomen of Phasmatodea.

The main nerve branches are homologous throughout Polyneoptera (Schmitt 1954, 1962, 1963, 1964, 1965; Klass 1999).

In *Timema*, the dorsal nerve A arises separately from the ganglion (Figs. 1, 2). This was also observed in other Neoptera, e.g. the locust *Dissosteira* (Schmitt 1954), the earwig *Hemimerus* (Klass 2001) and *Periplaneta* (in segment VI, Klass 1999). In the other Phasmatodea (i.e. the Euphasmatodea) the three main nerves have a common stem. This is also the case in *Sphodromantis* (Klass 1999). For many other outgroups no data are available. It is thus not easy to decide whether or not the common stem A+B+C is an apomorphy of Euphasmatodea.

If the neuronal network were investigated on the axonal level, the topographical description and interpretation of the nervous system of a segment would be inadequate. Because of the common main-nerve stem in Euphasmatodea it is possible that neurons running in branch ADLM11 of *Timema* are integrated in branch C innervating the ventral longitudinal muscles in Euphasmatodea. However, loss of the inner ventral longitudinal muscles in *Timema* seems obvious, as can be seen in Figs. 3–10. The main nerve branches disappear externally to the sheets of muscle 11. In *Agathemera*, female *Haaniella* and female *Phyllium* (Figs. 3, 5 and 6) the nerves run internally to the elongated muscles. This is strong topographical evidence for loss of the inner

ventral muscles. Nevertheless, nerve homology still remains tentative (Marquardt 1939; Klass 1999); further research must clarify this finding by investigating the innervation on the axonal level.

The inner dorsal and ventral longitudinal muscles span the entire segment in *Timema* (Fig. 1). This is also true for the polyneopteran outgroup taxa (Verhoeff 1904; Ford 1923; Snodgrass 1935; Walker 1943; Schmitt 1954, 1964; Klass 1999, 2000, 2001). In Mantodea, the longitudinal musculature spans approximately two thirds of the segment (Kerry and Mill 1987; Klass 1999). In *Timema* the inner layer of ventral longitudinal muscles is innervated by a branch of nerve A. The outer, shorter layer is innervated by nerve C. This is the plesiomorphic condition, because in other Neoptera for which data are available the inner ventral muscles are innervated by A as well (Schmitt 1954, 1963, 1964; Klass 1999). This is also the case in Coleoptera (Jöosting 1942: larva) and Megaloptera (Maki 1936). All Phasmatodea have several sheets of longitudinal muscles (Ford 1923; Maki 1936; Marquardt 1939; Saure 1988). In *Timema* the long inner ventral, A-innervated muscles are still present. In the remaining Phasmatodea, all ventral longitudinal muscles are innervated only by the ventral nerve (C). Consequently, the loss of the inner ventral longitudinal muscles must be regarded as an autapomorphy of the Euphasmatodea (Fig. 11: character dot = cd 2).

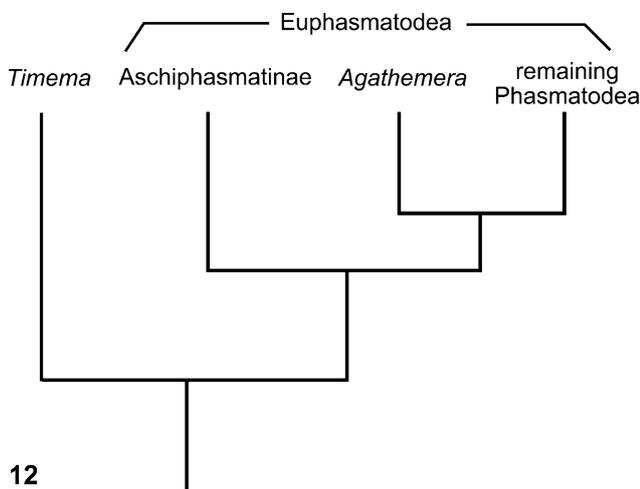
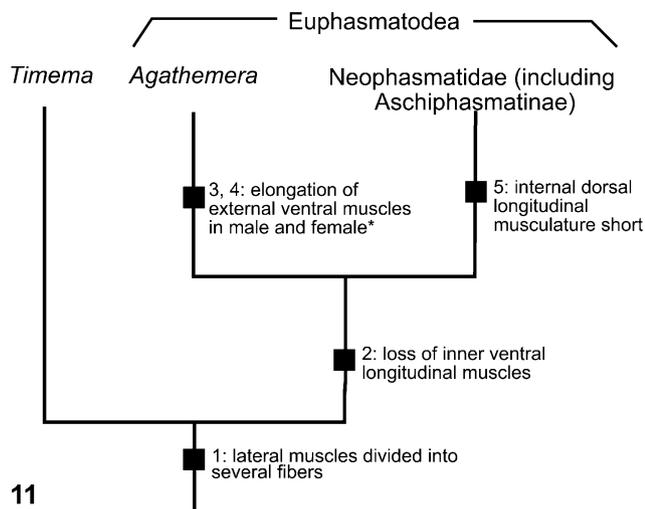
All dorsal longitudinal muscles of *Timema* are supplied by the dorsal nerve (A), as they are in the other Polyneoptera (Schmitt 1954; Klass 1999) and all Euphasmatodea. Thus, nerve A is not of phylogenetic significance in our context. Homology assumptions for the dorsal muscle sheets cannot be made (Klass 1999).

In *Timema* and the Euphasmatodea the lateral musculature which is divided into slender bundles is distributed along the segment. In all outgroup taxa only few lateral bundles are present (Ford 1923; Walker 1943; Schmitt 1954; Zwick 1973; Klass 1999, 2001). The different parts of the lateral musculature can be distinguished by their innervation. Some muscles in the anterior region of the segment are innervated by the transverse nerve (T), while most of the remaining lateral muscles are supplied by the lateral nerve (B) and ventral nerve (C). The lateral muscles are divided in several bundles which can be classified in groups corresponding to their innervation (Fig. 11: cd 1).

Furthermore, in the ground pattern of Phasmatodea the inner ventral longitudinal muscles are present.

### Muscle homologies

In the lateral musculature several groups can be distinguished, not only by their position (Saure 1988) but also by their innervation (Klass 1999). These groups



**Fig. 11, 12.** Basal relationships within Phasmatodea. (11) Present hypothesis according to new characters of musculature; \* = convergently elongated in females of *Phyllium* and *Haaniella dehaanii*. (12) Alternative hypothesis of Tilgner (2002), with Aschiphasmatinae as the most basal Euphasmatodea.

of muscles are also present in the outgroup taxa. They can be homologized even with those muscles of the Phasmatodea which are divided into several fibers, based on their innervation (Klass 1999). Reliable homology assumptions can be reached only when both muscle position and innervation are considered. Especially in Phasmatodea there are several muscle bundles, e.g. intrasegmental inner tergo-sternal muscles 3 and 4 (iL intra in Table 1) or external tergo-sternal muscles 5 and 9 (Table 1: eL intra), that can be distinguished easily by their innervation (Table 1). Sometimes there seem to be small gaps between muscle portions, as in *Carausius* (Marquardt 1939), *Extatosoma* (Saure 1988) or *Sceptrorhina* (Fig. 10). Table 1 shows homologous muscles of Phasmatodea and other Polyneoptera.

Muscle no. 2 may be present in *Agathemera* and *Phyllium* but has not been found yet. The same is true for muscle 3 of *Timema*. These two muscles build the T-muscle group in all insects under consideration. The B-muscle group consists of three muscles in Phasmatodea (nos. 4, 5, 6) plus one in the outgroup. It was difficult to decide whether muscles 8 and 9 were present, for the reason mentioned above. In *Timema*, an additional intersegmental tergo-leural, T-innervated muscle is present. This muscle was not found in any other phasmid nor in the outgroup and is interpreted as an autapomorphy of *Timema*.

In the ground pattern of Phasmatodea different lateral muscles are present which are divided into several fibers. This is a strong argument for the position of *Timema* within the Phasmatodea, which clearly contradicts the view of Zompro (2004) that *Timema* is more closely related to the Embioptera and Plecoptera.

### Basal relationships within Phasmatodea and conflicting hypotheses

The abdominal musculature and innervation provides some useful characters for phylogenetic analysis of the basal Phasmatodea. Table 2 lists the character codings for all species examined or scored from the literature.

In the longitudinal musculature, the ventral sheets in *Timema* and the outgroup representatives can be distinguished by their innervation. They consist of long internal ventral muscles innervated by the dorsal nerve (A) and short external ventral muscles innervated by the ventral nerve (C) (Klass 1999). However, both sexes of *Agathemera*, the females of *Haaniella* and *Phyllium* possess long ventral muscles that are innervated by C. Hence, the long ventral muscles in *Timema* on the one hand and in *Agathemera* and in females of *Phyllium* and *Haaniella* on the other hand cannot be considered to be homologous. This contrasts with earlier hypotheses about the phasmatodean muscle arrangement. We assume that the long ventral muscles innervated by A are lost in Euphasmatodea (Table 2: character 2; Fig. 11). All ventral longitudinal muscles of Euphasmatodea are externals, because they are innervated by nerve C. The external ventral longitudinal muscles consist of at least two layers in Phasmatodea (Saure 1988).

The loss of the inner ventral longitudinal muscles (Table 2: character 2) is an apomorphy of Euphasmatodea (Fig. 11: cd 2).

Consequently, the condition of the ventral longitudinal musculature in *Agathemera* represents a derived state. These muscles are interpreted as secondarily elongated in both sexes (Fig. 11: cd 3, 4). According to molecular data *Agathemera* is not at the base of the Euphasmatodea (Whiting et al. 2003). Thus the

**Table 1.** Muscles of a pregenital abdominal segment in Phasmatodea

No.	Position	Innervation	Present in								Outgroup					
			<i>Tim.</i>	<i>Agath.</i>	<i>Haan.</i>	<i>Phyll.</i>	<i>Sung.</i>	<i>Scep.</i>	<i>Ram.</i>	<i>Car.</i>	<i>Per.</i>	<i>Sph.</i>	<i>Dis.</i>	<i>Neo.</i>	<i>Hem.</i>	
2	eL Intra	T	+	?	+	?	+	+	+	+	+	2a	2a	li2	?	?
3	iL Intra	T	?	+	+	+	+	+	+	+	+	2b	2b	li1	?	6?
4	iL Intra	B	+	+	+	+	+	+	+	+	+	1	1a, b	le2, le3	stg?	1?
5	eL Intra	B	+	+	+	+	+	+	+	+	+	–	–	–	?	?
6	tp Intra	B	+	+	+	+	+	+	+	+	+	–	–	–	?	?
8	iL Inter	C	?	?	–	+	–	+	+	+	+	6	6	–	?	?
9	eL Intra post.	C	?	?	?	?	–	+	+	+	+	–	–	–	?	?
11	Inner VLM	A	+	–	–	–	–	–	–	–	–	7a, b	7	?	?	9

Potential muscle homologies for Phasmatodea and Dictyoptera.

Information on *Periplaneta* (Per.) and *Sphodromantis* (Sph.) as given in Klass (1999).

Abbreviations: *Agath.* – *Agathemera*, *Car.* – *Carausius*, *Dis.* – *Dissosteira*, *Haan.* – *Haaniella*, *Hem.* – *Hemimerus*, *Neo.* – *Neoconocephalus*, No. – muscle number, *Phyll.* – *Phyllium*, *Ram.* – *Ramulus*, *Sung.* – *Sungaya*, *Tim.* – *Timema*.

Question marks show uncertain status of muscle.

**Table 2.** Coding of characters for Phasmatodea and outgroup

Character	1: Lateral muscles few (0); many isolated fibers (1)	2: Internal VLM present (0); absent (1)	3: External VLM ♂ short (0); long (1)	4: External VLM ♀ short (0); long (1)	5: Internal DLM long (0); short (1)
Taxon					
<i>Timema</i>	1	0	0	0	0
<i>Agathemera</i>	1	1	1	1	0
<i>Haaniella</i>	1	1	0	1	1
<i>Phyllium</i>	1	1	0	12:1; 13:0	1
<i>Sungaya</i>	1	1	–	0	1
<i>Sceptrophasma</i>	1	1	0	0	1
<i>Ramulus</i>	1	1	0	0	1
<i>Carausius</i>	1	1	0	0	1
<i>Abrosoma</i>	1	1	0	0	1
<i>Lopaphus</i>	1	1	0	0	1
<i>Phaenopharos</i>	1	1	–	0	1
<i>Eurycantha</i>	1	1	0	0	1
<i>Periplaneta</i>	0	0	0	0	0
<i>Sphodromantis</i>	0	0	0	?	0
<i>Dissosteira</i>	0	0	0	0	0
<i>Neoconocephalus</i>	0	0	0	0	0
<i>Hemimerus</i>	0	0	?	?	0

0 – plesiomorphic; 1 – apomorphic; ? – no data available.

*Sungaya* and *Phaenopharos* are parthenogenetic.

previously assumed basal position of *Agathemera* (Bradler 2000, 2003; Bradler et al. 2003; Zompro 2004) receives less support.

On the other hand, *Agathemera* is devoid of any characters that could be interpreted as synapomorphies with any other subordinate phasmid lineage (including the Pseudophasmatinae, to which *Agathemera* has traditionally been assigned; Bradler 2000); it is also considered rather basal by Tilgner (2002). *Agathemera*'s non-lengthened thoracic and abdominal segments might nevertheless represent the primary Euphasmatodean

condition, as the dorsal longitudinal muscles of the abdomen are similar to those in *Timema*, not shortened. Shortening occurs in all remaining Euphasmatodea.

The dorsal muscles are innervated by the dorsal nerve (A) in all phasmids. In Polyneoptera and insects in general, the dorsal abdominal muscles usually span the whole segment. This is the plesiomorphic condition. Therefore, similarly long muscles in *Timema* and *Agathemera* have been supposed as being homologous. The long dorsal muscles in *Agathemera*, however, may be derived instead, like the elongated ventral ones,

because in all other phasmids the dorsal longitudinal muscles are short. However, this cannot be stated with certainty as all dorsal muscles are supplied by the same nerve. If the long dorsal muscles of *Agathemera* are plesiomorphic, this could support the basal position of *Agathemera*, which appears as primarily stout-bodied with the segments not elongated.

The function of the long ventral longitudinal muscles, which obviously have replaced the lost inner ventral muscles in *Agathemera*, is not understood; further investigations are necessary to clarify the position of *Agathemera*. According to Tilgner (2002); Fig. 12 the Aschiphasmatinae form the basal lineage within the Euphasmatodea. This has not been checked by us, since members of the Aschiphasmatinae have not been included in any molecular analysis. In Aschiphasmatinae, only the short external ventral muscles are present.

The assumption that Euphasmatodea is monophyletic is well supported by several characters: the fusion of the metanotum and the first abdominal tergum, the reduced furca in the prothorax, the hard-shelled egg with an external micropylar plate (Clark Sellick 1998; Tilgner et al. 1999; Bradler 2003; Bradler et al. 2003) and, as shown in the present paper, the loss of the inner ventral longitudinal musculature. Monophyly is also supported by molecular data (Wheeler et al. 2001; Whiting et al. 2003).

### Apomorphies and sexual dimorphism

It appears necessary to always study both sexes of each species, because in certain taxa distinct sexual dimorphism in the length of the external ventral longitudinal musculature exists. Females of *Haaniella* possess a C-innervated ventral longitudinal muscle (12) that spans the entire length of the segment (Fig. 5). In the male the muscle is short, spanning only about half of the segment (Fig. 4). The dorsal longitudinal muscles are short in both sexes. In all other Heteropteryginae, e.g. in *Sungaya* (Fig. 8) and *Heteropteryx* (Saure 1988), both the ventral and dorsal muscles are short.

The female of *Haaniella*, therefore, shows the apomorphic state of character 4 (Table 2).

The secondary elongation of the ventral longitudinal muscles appears to be an autapomorphy of *Haaniella*, and obviously has evolved independently from that in *Agathemera*, because no evidence, neither morphological nor molecular, supports an *Agathemera* + *Haaniella* clade (Tilgner 2002; Whiting et al. 2003), whereas *Haaniella* does share some convincing synapomorphies with *Heteropteryx*. The females of both taxa possess a tibial organ located in the hind wing that is used for defensive stridulation (Carlberg 1989), as well as a beak-shaped secondary ovipositor that is dorsally formed by the elongated epiproct (lamina supraanalis) (Bradler

2002). In addition, molecular data strongly support a close relationship between *Haaniella* and *Heteropteryx* (Whiting et al. 2003).

A similar sexual dimorphism is present in *Phyllium*, the leaf insect. In females the median ventral longitudinal muscle (12) spans the entire segment, whereas the lateral ventral muscle (13) is short. The dorsal longitudinal muscles are short (Fig. 6). In males, both ventral muscles are short (Fig. 7). In all other examined Phasmatodea, both the dorsal and ventral longitudinal muscles are short.

Functional aspects of the anatomy of the abdominal musculature must be taken into consideration to explain this finding. Females of *Haaniella* have a secondary ovipositor to place their eggs into the substrate. Thus one can surmise that a ventral muscle sheet is secondarily elongated, as the ability to shorten a muscle generally depends on its length (Saure 1988). *Eurycantha* and *Sungaya*, e.g., also have a secondary ovipositor, because they place their eggs into the substrate. However, their ventral longitudinal muscles are short. Long ventral muscles might be advantageous for flexion of the abdomen. Apparently, no functional necessity exists that could explain the evolution of long ventral externals. In *Phyllium* the median ventral longitudinal muscles are even secondarily elongated, but no secondary ovipositor is present. Phylliinae simply drop their eggs, as do the majority of stick insects. The function or advantage of one ventral muscle spanning the entire segment in *Phyllium* remains unclear.

*Agathemera* and other basal Phasmatodea, e.g. the Aschiphasmatinae, Heteropteryginae and Phylliinae, require further study. Beyond this, any detailed account of the diversification of the numerous higher Euphasmatodeans is outside the scope of the present contribution. There is still a great need for additional morphological and molecular evidence bearing on this issue.

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