

Phylogenetic Relationships of the Orders of Hexapoda: Contributions from the Circulatory Organs for a Morphological Data Matrix

GÜNTHER PASS*, BARBARA-AMINA GEREKEN-KRENN, MONIKA MERL,
JOHN PLANT, NIKOLAUS U. SZUCSICH & MARKUS TÖGEL

Department of Evolutionary Biology, University of Vienna,
Althanstraße 14, 1090 Vienna, Austria
[guenther.pass@univie.ac.at; barbara-amina.gereben@univie.ac.at;
Moni_Merl@yahoo.com; john.plant@aon.at; nikola.szucsich@univie.ac.at;
toegel@biologie.uni-osnabrueck.de]

* Corresponding author

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> Abstract

Discussions of phylogenetic studies based on morphological data focus mainly on results of the cladistic analysis while selection and evaluation of characters themselves are often underrepresented. Our paper seeks to address this with a survey of characters of the circulatory organs to contribute to the analysis of phylogenetic relationships of hexapod orders. The survey is based on examination of literature and includes, in addition, numerous unpublished data. Of 38 variable traits of the dorsal vessel and the various accessory circulatory organs, we selected 11 which are potentially informative at supraordinal level. They are critically discussed and coded as characters for use in comprehensive future cladistic analyses employing greater sets of morphological data. It must be stated that many features of circulatory organs for higher systematic categories are still based on one or few species for most orders of hexapods; this deficiency is due to the great methodological effort required to investigate internal organs. In general, circulatory organs of hexapods are simply organized making it difficult to discriminate homology from convergence. In addition to phylogeny, general aspects of the evolution of the circulatory system are outlined. In an appendix we provide comprehensive information on the traits, characters and the species in which they occur.

> Key words

Insecta, circulatory system, accessory pulsatile organs, morphology, phylogeny, cladistic analysis, organ evolution.

1. Introduction

Reconstruction of insect phylogeny has indeed progressed over the past decades. Most extant orders of Hexapoda are well-supported as monophyletic groups (KRISTENSEN 1997; AX 1999; GRIMALDI & ENGEL 2005). Yet despite intensive efforts at molecular and morphological levels many supraordinal relationships remain unsettled (e.g. KRISTENSEN 1991; WHITING et al. 1997; BITSCH & BITSCH 1998; EDGEcombe et al. 2000; BEUTEL & GORB 2001; WHEELER et al. 2001; HOVMÖLLER et al. 2002; BITSCH & BITSCH 2004; BITSCH et al. 2004; GIRIBET et al. 2004; KJER 2004; LUAN et al. 2005; TERRY & WHITING 2005; BEUTEL & GORB 2006; KJER et al. 2006; CAMERON et al. 2006). This is also evident from the contradictory results presented in the listed publications.

The contributions from morphologists to phylogenetic analyses are in general plagued by several shortcomings. Since it is hardly possible for one person to collect sufficient original data from the various organ systems for cladistic analyses, morphologists must extract data to a great extent from the literature. Yet reliance on such data is problematic in several respects. Review papers and general textbooks tend to over-simplify and ignore the full range of variation, and primary literature is usually not focused on phylogeny. Those who have not acquired proficiency in an area of morphological research will inevitably find it difficult to compare literature data especially when the scope of studies, their level of accuracy and range of observation vary considerably. A specific difficulty

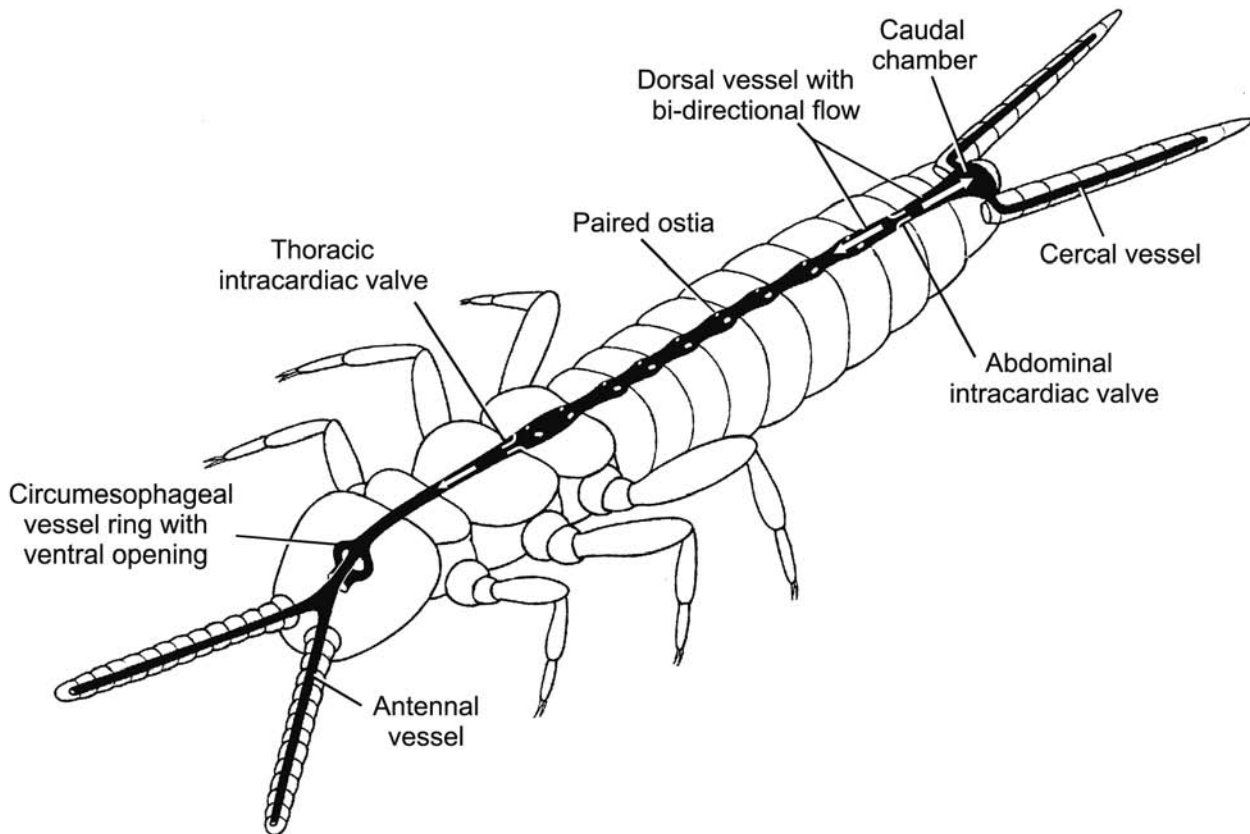


Fig. 1. Circulatory organs in *Campodea* (Diplura) illustrating the probable plesiomorphic condition for Hexapoda (modified after GEREBEN-KRENN & PASS 1999). Arrows indicate direction of hemolymph flow.

in morphological analyses has been the assessment of homology, a task which often requires broad experience in a particular field. Another problem is that the taxon sample is often meager and generalized statements intended to apply to a higher systematic category are formulated on the basis of only one or very few investigated species. These insufficiencies may lead to fallacious character matrices, biased data analyses and consequently uncertain phylogenetic interpretations. Our approach is intended to partially remedy this. In this paper we evaluate the circulatory organs of hexapods – our research topic for many years – and seek to provide a morphological character set suitable for incorporation into cladistic analyses. This was achieved by a thorough search for morphological variation of the organ system. From this survey we identified distinguishing traits, some of which were appropriate for character coding because they appeared to be informative at the supraordinal level. To show the full extent of data on which hypotheses of particular characters are based we provide an extensive appendix that lists the traits and characters, the species investigated, and all references. We thereby hope to fill in the gap between morphological raw data and the phylogenetic analysis of that data.

As a brief reminder, the circulatory system in insects is classed as open, and hemolymph circulates freely among the internal organs (Figs. 1, 2). The main component of the circulatory organs is the dorsal vessel (*heart*), which functions as the central pumping organ and extends throughout the whole body from head to the tip of the abdomen. Little appreciated is that most insects possess additional circulatory organs, such as diaphragms, which regulate the flow of hemolymph in the body cavity, and autonomous pumps (*auxiliary hearts*), which ensure circulation in the various body appendages (Fig. 2) (reviews on hexapod circulatory system: JONES 1977; MILLER 1985; PASS 1998, 2000; WASSERTHAL 1998; HERTEL & PASS 2002).

Few anatomical features of the circulatory system have been previously employed in cladistic analyses of arthropods and hexapods (BITSCH & BITSCH 1998, 2004; EDGEcombe et al. 2000; BEUTEL & GORB 2001, 2006; WHEELER et al. 2001; GIRIBET et al. 2004). Based on literature data and many unpublished results from our laboratory we present additional characters, make proposals for their coding and discuss their phylogenetic value. Further we outline general aspects of the evolution of the circulatory organs relevant for a deeper understanding of the topic.

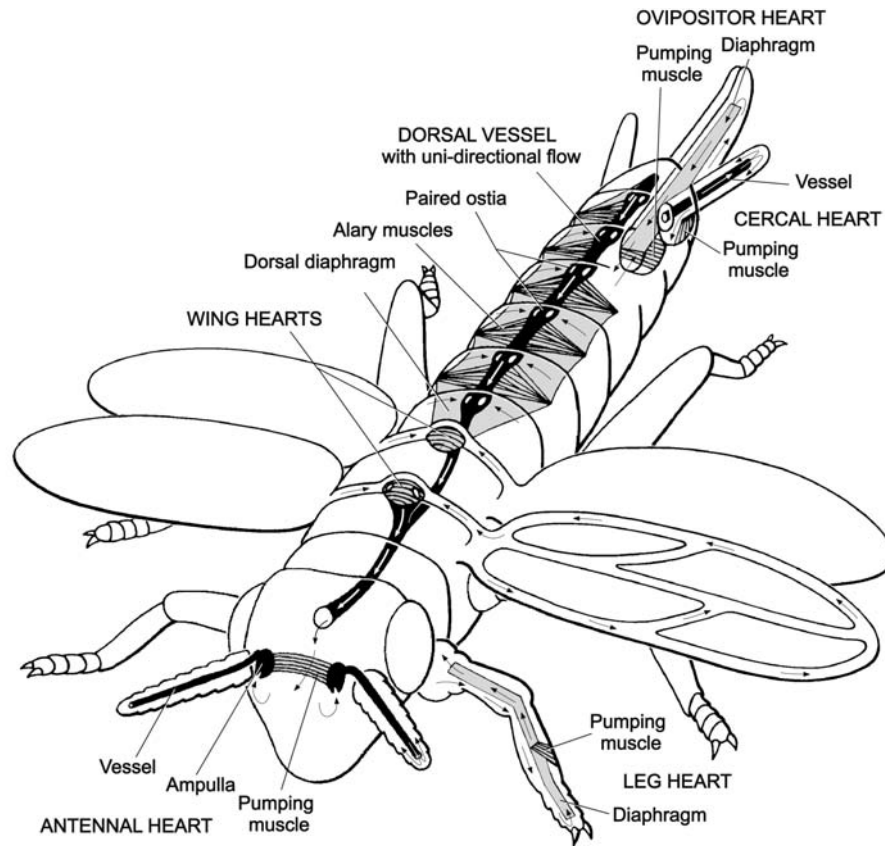


Fig. 2. A generalized pterygote insect showing dorsal vessel and associated structures, as well as a maximum set of auxiliary hearts (ventral diaphragm not shown) (modified after PASS 2000). Arrows indicate direction of hemolymph flow.

2. Material and methods

Character selection and coding. Primary literature was examined for accurate descriptions of morphological variation of the circulatory organs of hexapods and combined with unpublished data from our laboratory. We attempted to consider all traits regardless of their phylogenetic implications, and selected only those traits for character coding which were sufficiently investigated to permit comparison across hexapod orders. Characters were defined for which discrete character states could be delineated that are relatively constant at ordinal level and that contain only a moderate degree of variation at the supraordinal level. Furthermore, the states of a character were defined as homologous variables within the framework of a transformational hypothesis (e.g. DE PINNA 1991; BROWER & SCHAWAROCH 1996; HAWKINS et al. 1997; CARINE & SCOTLAND 1999; JENNER 2002). For a few traits, character construction would result in a character state distribution that is clearly in conflict with all known phylogenetic hypotheses. These traits are described and discussed but excluded from character construction to avoid the introduction of noise into phylogenetic analyses. The plesiomorphic condition

and polarity of characters were usually determined with some degree of confidence by consideration of the condition in myriapods and crustacean outgroups; exceptions are discussed in the text.

Hexapod orders which could not be assigned to any state of a particular character, because the surrounding character complex is absent (e.g. wing circulatory organs in wingless taxa), were scored as inapplicable, although many standard cladistic software programs treat the inapplicable condition as missing data (see LEE & BRYANT 1999; STRONG & LIPSCOMB 1999). Scoring inapplicability as missing data withholds valuable information from the reader, while scoring such data with its own state may introduce a strong bias into the data set. Also we avoided coding the secondary absence of a character as a separate state, because this would introduce disputable presumptions on character evolution and phylogenetic relationships into an analysis.

Morphological studies. Original investigations presented in this paper are based on analysis of serial semi-thin and TEM sections. The procedure for preparing semi-thin sections followed PERNSTICH et al. (2003). To investigate with TEM, specimens were

fixed initially in Karnovsky solution, subsequently transferred to Karnovsky solution with 1% Tannin and postfixed in 1% aqueous osmiumtetroxide. Dehydration and embedding as described in PERNSTICH et al. (2003). Ultra-thin sections were stained with uranyl acetate and lead citrate.

3. Results

The following sections describe the anatomical *traits* of the dorsal vessel and the accessory circulatory organs of hexapods without regard to possible phylogenetic implications. Thereafter *characters* are selected which represent potential synapomorphies at the supraordinal level. Traits and characters are marked by bold numbers in text and Appendix. Within the respective sections proposals are given for the coding of characters. Names of the investigated species pertinent to the traits and characters throughout the insect orders can be found in the Appendix.

3.1. Dorsal vessel and associated structures

Almost all insects possess a dorsal vessel; it may be absent only in very minute species (e.g. the chalcidid wasp *Encarsia formosa*: Krenn & Pass unpubl. data; Coleoptera-Ptiliidae: Polilov pers. comm.). In most papers dealing with the dorsal vessel only its general course and the location of ostia are described; very little information has been published on the condition in the head, on vessel suspension and the alary muscles. Detailed descriptions exist for one or a few species of Archaeognatha (BÄR 1912), Ephemeroptera (MEYER 1931), Blattaria, Mantodea, Isoptera, Phasmatodea, Orthoptera, Dermaptera, Plecoptera, Embioptera, Grylloblattodea, Zoraptera (NUTTING 1951; Orthoptera also in BAYER 1968), Phthiraptera (FULMEK 1917), Hemiptera (HINKS 1966), Megaloptera (SELMAN 1965), Hymenoptera (FREUDENSTEIN 1928), Coleoptera (KUHL 1924) and Diptera (JONES 1954; CURTIS et al. 1999). Aside from the study of NUTTING (1951) extensive comparative investigations on the dorsal vessel and its associated structures are still lacking.

3.1.1. Vessel morphology. The dorsal vessel is a muscular tube formed by two rows of opposing (left and right) crescent-shaped cells, which interlock at their dorsal and ventral margins (WASSERTHAL 1999; BODMER & FRASCH 1999). The vessel lumen is lined by a basal lamina, and the outer surface is coated by the *adventitia*, a sheath which consists of collagen fibers, elastic filaments and fibroblasts (FRANÇOIS

2003). The shape of the dorsal vessel is not uniform along its course through the body. In general, the portion of the dorsal vessel, which contains the ostia, has a thicker muscular wall and is traditionally distinguished as the *heart*, while a portion anterior of it has a thinner wall, lacks ostia and is referred to as the *aorta* (IMMS 1970). Accordingly, the length of the aorta depends on the distribution of ostia (**trait 1**). The diameter of the dorsal vessel lumen (**trait 2**) is more or less constant throughout the whole length, or it is enlarged either in the anterior or posterior abdominal region. Additionally, local enlargements form ampullae or diverticula in the pterothoracic region (see wing circulatory organs) or segmental enlargements (*heart chambers*) (**trait 3**). Only some Diptera possess prothoracic enlargements, whereby the aorta dilates to form a bulb-like sinus or sac with a single sphincter-like opening in the ventral wall (JONES 1954). Likewise correlated with the wing circulatory organs is the course of the dorsal vessel through the thorax (**trait 4**). In some taxa the vessel runs straight through the center of the thorax; in others it is dorsally arched and may adjoin the wing circulatory organs. In addition, in some Hymenoptera the portion of the dorsal vessel lying in the first abdominal segment forms a series of loops (**trait 5**) (FREUDENSTEIN 1928; WILLE 1958).

Differences between larval instars and adults regarding number and position of ostia, as well as length and course of the dorsal vessel occur in some insects (JONES 1977).

3.1.2. Alary muscles, dorsal vessel suspension and dorsal diaphragm. Along its entire length, attachment of the dorsal vessel is achieved by fine suspending strands of elastic connective tissue (**trait 6**) which connect to the integument, fat body, and other organs as well (JONES 1977). Alary muscles (**trait 7**), by contrast, are always segmentally arranged pairs of muscles which are mainly found in the region of the heart. Usually, they spread fan-shaped from their insertion points at the anterior margin of the tergites to the dorsal vessel. Their mode of attachment to the dorsal vessel varies (**trait 8**). In the region where alary muscles are present, the dorsal connective tissue strands may be lacking and the dorsal vessel is directly attached to the tergal cuticle.

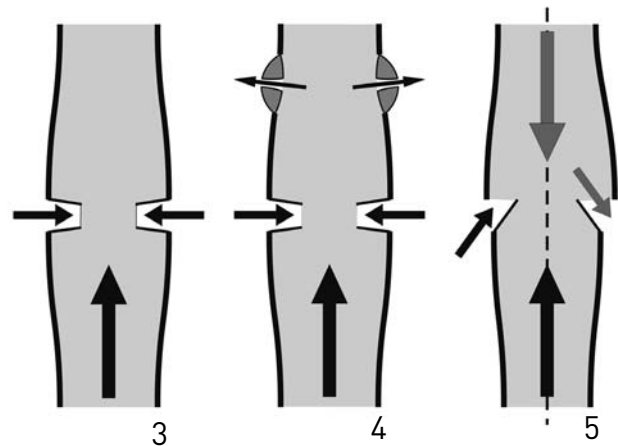
The *dorsal diaphragm* (**traits 9–10**), consisting of connective tissue (LOCKE 1998), and the alary muscles separate the pericardial sinus from the perivisceral sinus. The dorsal diaphragm is either developed as a single membrane, a continuous double membrane, a single membrane with an additional membrane in abdominal segments bearing excurrent ostia, or it is reduced to various extents.

3.1.3. Anterior end of dorsal vessel. The dorsal vessel enters the head capsule through the narrow neck and passes either beneath the brain close to the esophagus up to the front of the brain or ends in the region just behind the brain. In some hexapods the anterior end of the dorsal vessel is connected directly to the antennal vessels or indirectly via a frontal sac (see antennal circulatory organs). In all other cases the dorsal vessel opens anteriorly either into the sinus in front of the brain or into the channel-like space between the ventral side of the brain and the esophagus. Some species of Hymenoptera and Diptera deserve special mention (**trait 11**). In *Apis mellifera* (Hymenoptera) the dorsal vessel is enlarged behind the brain and completely envelops the esophagus; the suspension muscles of the esophagus cross the aortic wall through openings that also permit exit of hemolymph to the brain (FREUDENSTEIN 1928). In *Calliphora erythrocephala* (Diptera), the dorsal vessel extends only as far as the neck region, where it is perforated forming an excurrent opening. This opening is associated with a pulsatile organ consisting of cuticle, muscles and tracheal air sacs; its contractions are coordinated with those of the dorsal vessel (WASSERTHAL 1999).

3.1.4. Circumesophageal vessel ring. In species from almost all apterygotan orders, a pair of vessels laterally branch off the dorsal vessel immediately posterior of the brain, and encircle the esophagus forming the *circumesophageal vessel ring* (Fig. 1). Ventrally, a short anteriorly directed vessel opens like a funnel into the hemocoel of the head capsule. Hemolymph discharged through this opening supplies the ventral head region. The lateral vessels and ring formation are absent in all examined Pterygota (**trait 12: char 1**).

Character 1. Head vascular system, 0: containing a *circumesophageal vessel ring* branching off the dorsal vessel posterior of the brain – *Diplura*, *Collembola*, *Archaeognatha*, *Zygentoma*. **1:** containing no *circumesophageal vessel ring* branching off the dorsal vessel posterior of the brain – all Pterygota. **Missing data:** *Protura*.

3.1.5. Ostia. The lateral passage of hemolymph through the heart wall is mediated by minute openings each created by two special cardiomyocytes. In hexapods, two basic kinds of ostia are discernible according to the anatomy of the valve. One kind, *ostia with lips*, is characterized by the lip-like extension of the ostia-forming cardiomyocytes that project into the vessel lumen and thereby function as a valve (**trait 13: char 2**). In almost all hexapods, both the anterior and the posterior cardiomyocytes are developed as lips. The paired lips enclose the aperture and prevent



Figs. 3–5. Diagrams of a segmental portion of dorsal vessel illustrating various kinds of ostia. Arrows indicate direction of hemolymph flow. **3:** Incurrent ostia with paired lips. **4:** Incurrent ostia plus excurrent ostia. **5:** Two-way ostia with a single (posterior) lip; left side: incurrent flow during anterograde phase, right side: excurrent flow during anterograde phase, gray arrows indicate flow during retrograde phase.

outflow of hemolymph independent of the direction of the contraction waves across the dorsal vessel. Thus, they are generally referred to as *incurrent ostia* (Figs. 3, 4, 6). In some Neuroptera and some Diptera, only the anterior lip is developed in the most posterior pair of ostia, which are located at the terminal end of the dorsal vessel. These ostia, too, function as incurrent ostia since just one lip suffices to close the opening. In Ephemeroptera, pocket valves (**trait 14**) in the anterior portion of the dorsal vessel are characterized by reduction of the posterior lips and the openings. The anterior lips are enlarged and their anterior orientation prevents backflow of hemolymph during diastole (MEYER 1931). By contrast, in Lepidoptera (WASSERTHAL 1980, 1981, 1998; Tögel & Pass unpubl. data) and Trichoptera (Tögel & Pass unpubl. data) so-called *two-way ostia* occur which always lack the anterior lip (Figs. 5, 7). This anatomical construction prevents the outflow of hemolymph during anterograde beating phases and enables it during retrograde beating phases (heartbeat reversal). One exception to this is a Trichoptera species in which the posterior-most ostia are located at a terminal position and have paired lips (Tögel & Pass unpubl. data).

A comparative investigation on the posterior portion of the dorsal vessel in Holometabola (Tögel & Pass unpubl. data) reveals that the position of the lipped ostia differs considerably. The opposing ostia either are distinctly separate from each other, or meet along the dorsal midline, or meet along the dorsal and ventral midlines; when ostia meet their posterior lips are attached to each other (**trait 15**).

The segmental occurrence of lipped ostia varies in Hexapoda, as well (Tab. 1) (**trait 16**). The maximum

Tab. 1. Occurrence and number of ostia and segmental vessels in lower Pterygota (compiled after SCHWERMER 1914; MEYER 1931; NUTTING 1951; KRENN & PASS 1994/95; Merl & Pass unpubl.). Question marks indicate that taxa were not investigated or that their investigation predated discovery of excurrent ostia and segmental vessels. Segment numbers are indicated by Roman numerals. See Appendix for taxa investigated for each order.

	Number of Ostia						Segmental vessels	
	Incurrent paired		Excurrent paired		Excurrent unpaired			
	Thorax	Abdomen	Thorax	Abdomen	Thorax	Abdomen	Thorax	Abdomen
Ephemeroptera	0–1	1–4	?	?	?	?	?	?
Odonata	0–2 _{II,III}	2	?	?	?	?	?	?
Dermaptera	1–2	9	0	0 or 4 _{II,V}	0	0	0	0
Mantophasmatodea	2	9	?	?	0	0	?	?
Plecoptera	2	9	0	0	1 _{II}	0	0	0
Embioptera	2	9	0	0	2 _{II,III}	1 _I	0	0
Phasmatodea	0	9	1 _{III}	2 _{I,II}	0	0	0	0
Grylloblattodea	2	9	0	0	2 _{II,III}	6 _{I-IV}	0	0
Orthoptera	2–3	9	1–2 _{II,III}	0–5 _{I-V}	0	0	0	0
Mantodea	3	9	0	4 _{III-VI}	0	0	0	0 or 4 _{III-VI}
Blattaria	3	9	2 _{II,III}	4 _{III-VI}	0	0	2 _{II,III}	4 _{III-VI}
Isoptera	2	9	0	0	0	0	0	0

number of pairs is twelve (Mantodea, Blattaria, some Orthoptera), with each segment from the prothorax to the ninth abdominal segment bearing a pair of ostia. The minimum of one pair is found in larvae of Odonata at the posterior end of the dorsal vessel (WIGGLESWORTH 1955).

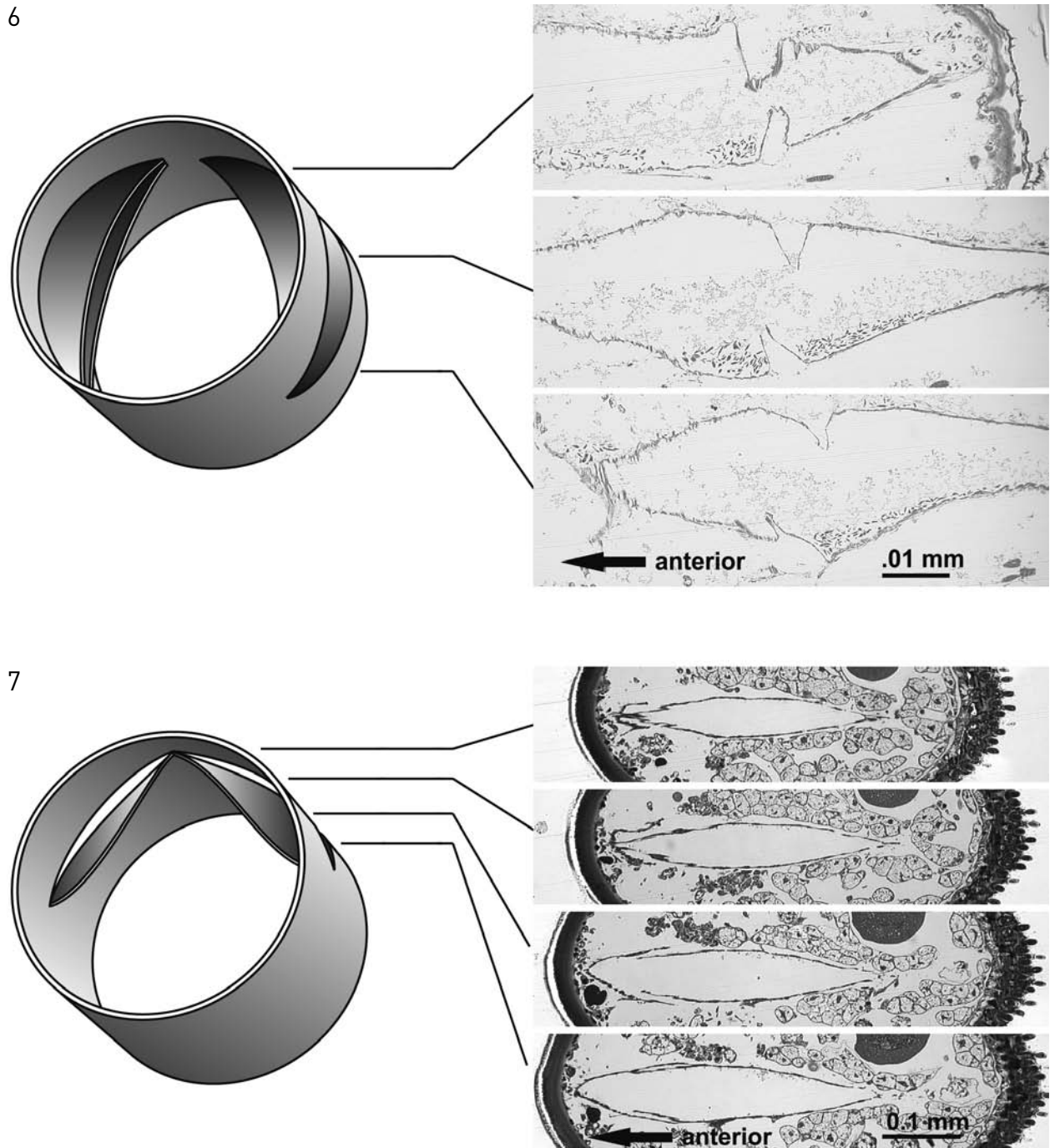
Character 2. Ostia with lips, 0: anterior and posterior lips present (incurrent ostia) – all orders except those with state (1). **1:** only posterior lip present (two-way ostia) – Trichoptera, Lepidoptera.

The second kind of ostia are *excurrent ostia* (**trait 17: char 3**) (Fig. 4). In contrast to incurrent or two-way ostia, they lack lips but instead have a valve consisting of unusual muscle cells (MILLER 1985; Merl & Pass unpubl. data). These cells unlike typical muscle cells are plasma-rich and contain very few myofibrils which extend in all directions (Fig. 12). Additionally, annulate lamellae occur in these cells suggesting high metabolic activity (Fig. 13). The anatomical construction of valved excurrent ostia ensures that the hemolymph flows only out of the dorsal vessel. The ostia open independently and out-of-phase with the contractions of the dorsal vessel (MILLER 1985). Excurrent ostia always occur additionally to the incurrent ostia within a particular segment. They have either paired or unpaired (ventrally located) openings (**trait 18: char 4**). NUTTING (1951) mentioned in his comprehensive paper that he found six unpaired excurrent ostia in *Zygentoma*. BARNHART

(1961) and recent re-investigations (Gereben-Krenn & Pass unpubl. data) could not confirm the existence of any excurrent ostia in *Zygentoma*. Regarding the number and distribution of paired or unpaired excurrent ostia along the dorsal vessel there is considerable variation at the ordinal level (Tab. 1) (**traits 19–21**). Even the mode of hemolymph discharge into the abdominal hemocoel varies widely (**traits 22–23**). The excurrent ostia open either above the dorsal diaphragm (when present) or below it, or they open into the space between the two layers of the diaphragm (and hemolymph is channeled into the abdominal viscera), or they open into blind diverticula (the so-called *phagocytic organs* of the abdomen), or into the segmental vessels (NUTTING 1951).

Character 3. Dorsal vessel, 0: containing only ostia with lips – all orders except those with state (1). **1:** containing in addition ostia without lips (excurrent ostia) – Dermaptera, Grylloblattodea, Plecoptera, Embioptera, Phasmatodea, Orthoptera, Mantodea, Blattaria.

Character 4. Position and number of excurrent ostia within a segment, 0: ventro-lateral and one pair – Dermaptera, Grylloblattodea, Phasmatodea, Orthoptera, Mantodea, Blattaria. **1:** ventro-median and unpaired – Plecoptera, Embioptera. **Inapplicable:** all orders except those with states (0) or (1).



Figs. 6–7. Diagrams of section of dorsal vessel with ostia and corresponding horizontal semi-thin sections. **6:** Incurrent ostia with paired lips of abdominal segment 7, *Tenebrio molitor* (Coleoptera). **7:** Two-way ostia in abdominal segment 8, *Drusus monticola* (Trichoptera); the posterior lips of the opposing ostia meet along the dorsal midline, anterior lip absent.

3.1.6. Segmental vessels. In Blattaria (McINDOO 1939; NUTTING 1951) and some Mantodea (NUTTING 1951), segmentally arranged vessels branch off the dorsal vessel to channel the hemolymph to the lateral body regions (Fig. 8) (**trait 24: char 5**). At the origin of each segmental vessel the dorsal vessel is equipped with an excurrent ostium (Figs. 10–11). The wall of the segmental vessels contains no muscle cells but consists

of connective tissue (Fig. 14) which is continuous with the adventitia of the dorsal vessel (Merl & Pass unpubl. data) (Fig. 9).

Character 5. Vascular system of anterior abdomen, 0: consisting of the dorsal vessel alone – all orders except those with state (1). **1:** consisting of the dorsal vessel and segmental vessels – Mantodea, Blattaria.

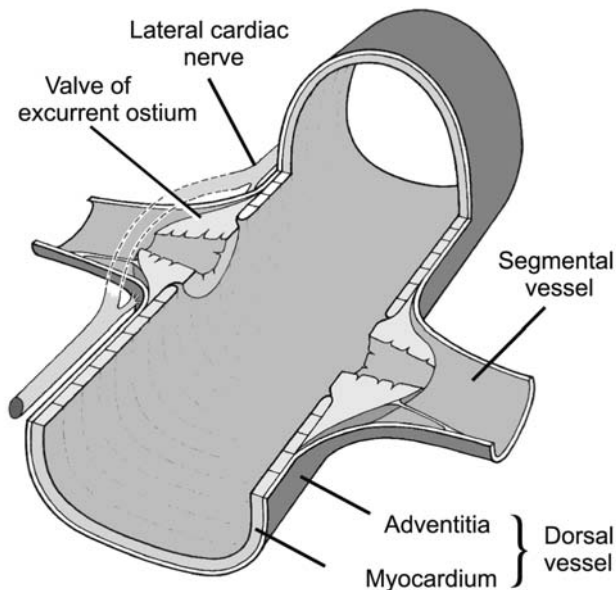


Fig. 8. Dorsal vessel portion with base of segmental vessels in *Periplaneta americana* (Blattaria). Segmental vessels are associated with excurrent ostia (valves shown as open). Segmental vessel wall continuous with the outer connective tissue layer of dorsal vessel (adventitia). Lateral cardiac nerve shown only on left side.

3.1.7. Intracardiac valves and related structures.

These regulate the hemolymph flow inside the dorsal vessel. They occur in the thorax and abdomen. The location of the thoracic intracardiac valve varies (**trait 25**). In Archaeognatha it is in the mesothorax anterior to the first pair of ostia (BÄR 1912), in Diplura (GEREBEN-KRENN & PASS 1999) and some Phasmatodea (OPCZYNSKA-SEMBRATOWA 1936) in the metathorax, likewise anterior to the first pair of ostia; whereas in Embioptera it is between the incurrent ostia and the unpaired excurrent ostium of the metathorax (NUTTING 1951). The presence of an abdominal intracardiac valve (**trait 26: char 6**) as in Diplura (Fig. 1), Archaeognatha (Fig. 24), Zygentoma and Ephemeroptera (Fig. 25) (GEREBEN-KRENN & PASS 1999, 2000) is conditional for the bi-directional flow of hemolymph in the dorsal vessel, i.e., hemolymph can be pumped at the same time anteriorly toward the head and posteriorly toward the rear end (GEREBEN-KRENN & PASS 2000; Ephemeroptera: CREUTZBURG 1885; DRENKELFORT 1910; MEYER 1931).

In Diptera, various structures project from the heart wall into the dorsal vessel lumen and probably function as valves, such as muscle pillars, large spongy cells (**trait 27**), or cellular pads between adjacent ostia in larvae (POPOVICI-BAZANOSANU 1905; WETTINGER 1927) and adults (DEMEREK 1950; WASSERTHAL 1999; Tögel & Pass unpubl. data).

Character 6. Dorsal vessel in abdomen, 0: containing an intracardiac valve – *Diplura*, *Archaeognatha*,

Zygentoma, *Ephemeroptera*. **1:** without intracardiac valve – all orders except those with state (0).

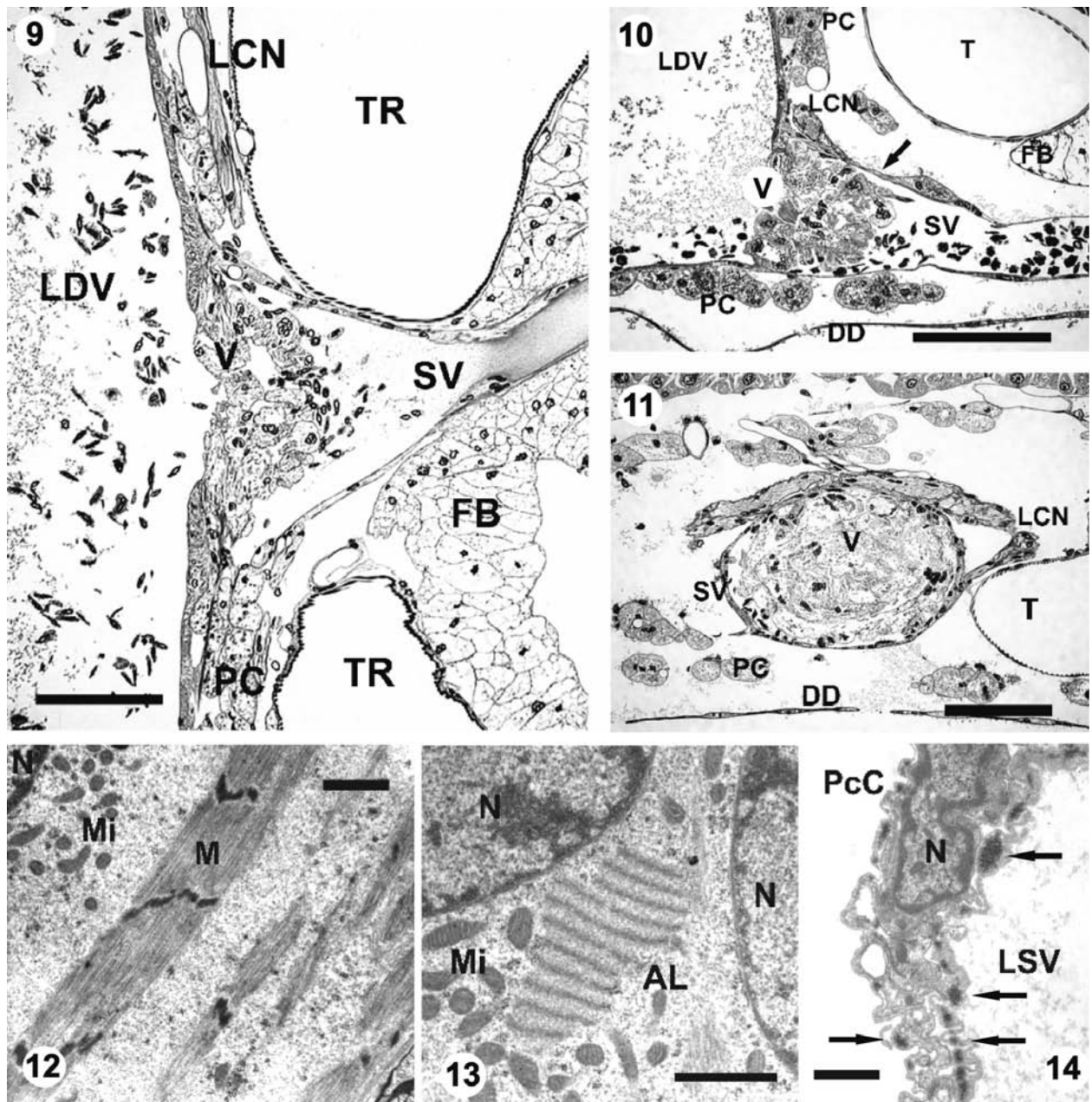
3.1.8. Region posterior to the abdominal intracardiac valve.

In basal Hexapoda, the region of the dorsal vessel posterior to the abdominal intracardiac valve is variously modified (**trait 28**). In Diplura, the region is enlarged and termed the *caudal chamber*. In Archaeognatha, the region is designated the *caudal tube*; it is characterized by an enlarged muscle layer and a rather narrow lumen. In *Zygentoma*, the wall of this region, although hardly thicker than the anterior part, is widened to form a *caudal pulsatile ampulla* (ROUSSET 1974; GEREBEN-KRENN & PASS 2000). In Ephemeroptera, the region forms a pear-shaped caudal pulsatile ampulla (Fig. 25) (ZIMMERMANN 1884; CREUTZBURG 1885; POPOVICI-BAZANOSANU 1905; DRENKELFORT 1910; MEYER 1931; GEREBEN-KRENN & PASS 2000). The ampulla is functionally independent of the anterior part of the dorsal vessel and contracts at a very different frequency (MEYER 1931). A small structure, termed the *spherical body*, is located between the end of the caudal pulsatile ampulla and the base of the terminal filament vessel and probably functions as a valve (Fig. 25) (GEREBEN-KRENN & PASS 2000).

In Diplura, Archaeognatha and *Zygentoma*, the posterior end of the dorsal vessel opens into the vessels of the terminal filament and cerci (**trait 29**). In Collembola (BÄR 1912; FRISH 1978) and Protura (FRANÇOIS 2003) the posterior end of the dorsal vessel is closed. This condition occurs likewise in almost all Pterygota. In Megaloptera, some Neuroptera, some Trichoptera, and some lower Diptera the last pair of ostia is terminally positioned. A posteriorly open dorsal vessel is found only in a few Holometabola: Raphidioptera (Tögel & Pass unpubl. data), some Coleoptera (WASSERTHAL 1982), and some Diptera (SNODGRASS 1935; WIGGLESWORTH 1955; WASSERTHAL 1982, 1999; ANGIOY et al. 1999; Tögel & Pass unpubl. data).

3.2. Antennal circulatory organs

The antennae are essential body appendages in hexapods, lacking only in Protura. Special organs exist in nearly all insects to supply the antennae with hemolymph. Taxa lacking such organs are generally those with small antennae (imagines of Ephemeroptera and Odonata) or small body size (some Collembola, Phthiraptera, Siphonaptera). In general, the antennal circulatory organs are characterized by an extraordinary morphological diversity. Comparative studies are available for apterygotes and exopterygotes (PASS 1991). However, only single representatives



Figs. 9–14. Segmental vessels and excurrent ostia of *Periplaneta americana* (Blattaria). **9:** Horizontal semi-thin section of dorsal vessel and origin of segmental vessel. Valve of excurrent ostium extends deeply into segmental vessel lumen. Wall of segmental vessel continuous with outer connective tissue layer of dorsal vessel. Bar = 0.1 mm. **10:** Semi-thin cross section of ventrolateral part of dorsal vessel and attached segmental vessel showing excurrent ostium valve at base. Branch of lateral cardiac nerve extends to segmental vessel wall (arrow). Bar = 0.1 mm. **11:** Semi-thin cross section of base of segmental vessel. Ostium valve fills lumen of segmental vessel. Lateral cardiac nerve is located dorsally to segmental vessel and branches anteriorly to segmental vessel sending axons to segmental vessel wall. Bar = 0.1 mm. **12:** TEM section of valve cell with dispersed bundles of myofibrils. Bar = 1 μ m. **13:** TEM section of ostium valve cells with annulate lamellae. Bar = 1 μ m. **14:** TEM cross section of segmental vessel wall. Wall contains no muscle cells and is covered by thick external laminae of collagen fibers (arrows). Bar = 1 μ m. AL = annulate lamellae, DD = dorsal diaphragm, FB = fat body, LCN = lateral cardiac nerve, LDV = lumen of dorsal vessel, LSV = lumen of segmental vessel, M = muscle fibers, Mi = mitochondria, N = nucleus, PC = pericardial cells, PcC = pericardial cavity, SV = segmental vessel, TR = trachea, V = excurrent ostium valve.

from various endopterygotes have been examined (Megaloptera: SELMAN 1965; Coleoptera: PASS 1980; Hymenoptera: FREUDENSTEIN 1928; MATUS & PASS 1999; Lepidoptera: SCHNEIDER & KAISLING 1959; Diptera: CLEMENTS 1956; DUDEL 1977, 1978a,b; numerous orders: Pass unpubl. data).

3.2.1. Antennal vessels. The structure which guides the flow of hemolymph in the antenna is generally a vessel that extends the whole length of the appendage and terminates at the tip with a distal pore. Hemolymph enters the antennae through the vessels and returns to the head capsule in the antennal hemocoel.

The antennal vessels (**trait 30**) are only in Diplura directly connected to the anterior end of the dorsal vessel and are thus termed arteries. In some insects the antennal vessels are connected to a sac-like enlargement (*frontal sac*) in front of the brain (Odonata: PASS 1991; Orthoptera: BAYER 1968; PASS 1991; Megaloptera: SELMAN 1965; Lepidoptera: SCHNEIDER & KAISLING 1959). The antennal vessels in *Zygentoma* have been described as detached from the dorsal vessel (CHAUDONNET 1950; PASS 1991), but reinvestigation shows the existence of a connection via a frontal sac (Gereben-Krenn & Pass unpubl. data). The frontal sacs give rise to additional vessels leading to the optic lobe or to other parts of the head in various taxa. Probably, the frontal sacs are compressed by pharyngeal movements and thus serve as accessory pumps for circulation in antennae. In many Lepidoptera the antennal vessels, which originate from the frontal sac, have an ampullary enlargement at the base, which contains a tissue clod. The tissue clod serves as a valve and may have an endocrine function in addition (GEROULD 1938; EHNBOHM 1948; SCHNEIDER & KAISLING 1959; VONDRAN & WASSERTHAL 1998; WASSERTHAL 2003).

In all other insects the antennal vessels are entirely separate from the dorsal vessel. At the base of the vessels are ampullary enlargements equipped with valved ostia. Hemolymph coming from the frontal sinus enters the antennal vessels through these ostia. In very few taxa, the antennal vessels are replaced by short diaphragms, which enable a countercurrent hemolymph flow by spatial division of the antennal hemocoel (some Collembola, larvae of Ephemeroptera) (**trait 31**).

3.2.2. Antennal vessel wall. The structure and cellular make-up of the antennal vessel wall (**trait 32: char 7**) is uniform in almost all hexapods consisting of thin and simple wall cells. However in Blattaria (Figs. 15–17) (PASS 1985), Mantodea and Mantophasmatodea (Pass in prep.) the proximal part of the antennal vessel is enlarged and forms a glomerule before entering the antenna. Ultrastructural investigation revealed that the wall of this part consists of two tissue layers: an outer cell layer, which lacks specialized organelle equipment, and an inner layer of typical transporting cells with deep invaginations of the basal membrane, numerous mitochondria, and specific cell junctions which are typically in tissues with ionic or osmoregulatory function (Fig. 16) (PASS 1985).

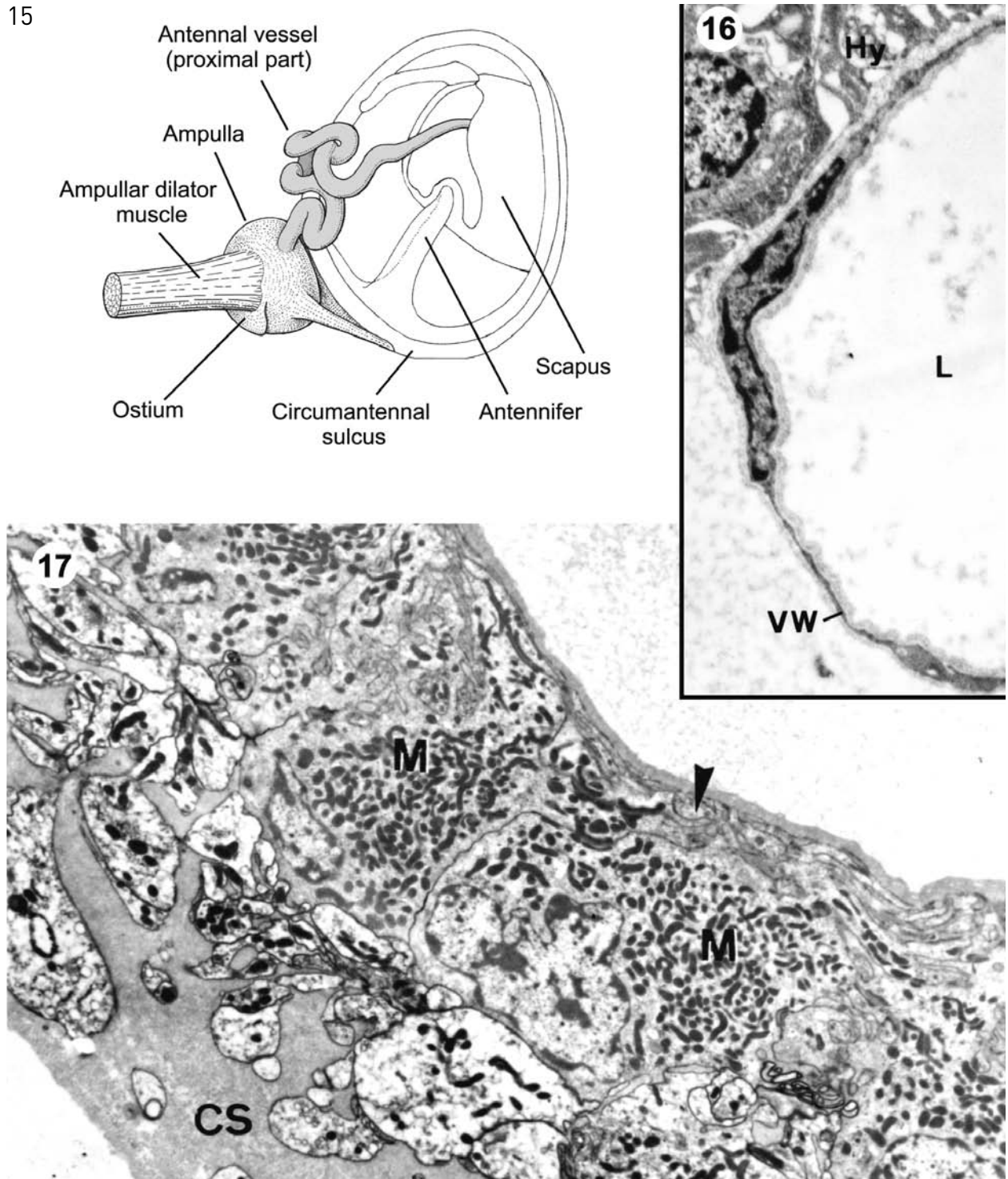
Character 7. Antennal vessel wall, 0: uniform – *Diplura*, *Archaeognatha*, *Zygentoma*, all *Pterygota* except those with state (1). **1:** bipartitioned – *Mantophasmatodea*, *Mantodea*, *Blattaria*. **Inapplicable:** *Protura*, *Collembola*, *Ephemeroptera*, *Odonata*, *Phthiraptera*, *Siphonaptera*, *Strepsiptera*. **Missing data:** *Zoraptera*, *Psocoptera*, *Thysanoptera*.

3.2.3. Ampullary formations and associated pumping muscles. Insects in which the antennal vessels are not adjoined to the dorsal vessel possess either non-pulsatile ampullae or the ampullae are associated with muscles and are therefore pulsatile. The former kind is characteristic for Archaeognatha, some Plecoptera and Grylloblattodea, and the latter for most other insects. The attachment sites of the pumping muscles, which are associated with the ampullae, vary considerably among insects (Fig. 18) (**trait 33: char 8**). In the majority of species, the muscles are attached to the ampulla wall, their contraction causes dilation of the ampullary lumen; following their relaxation the ampulla is compressed due to the elasticity of its wall. The second attachment of these dilator muscles may be the other ampulla (ampullo-ampullary dilator), the pharynx, the frontal cuticle or the anterior end of the aorta. In a few other species, the pumping muscle is not directly attached to the ampulla wall. Contraction of this muscle causes compression of the ampulla lumen while its dilation is effected by the elastic suspension.

Character 8. Antennal ampullae, 0: not connected by a muscle – *Archaeognatha*, *Zygentoma*, all *Pterygota* except those listed below. **1:** connected by an ampullo-ampullary dilator muscle – *Phasmatodea*, *Mantodea*, *Blattaria*, *Isoptera*, *Orthoptera partim*. **Inapplicable:** *Diplura*, *Protura*, *Collembola*, *Ephemeroptera*, *Odonata*, *Phthiraptera*, *Siphonaptera*, *Strepsiptera*. **Missing data:** *Zoraptera*, *Psocoptera*, *Thysanoptera*.

3.3. Leg circulatory organs

Pulsatile organs are described for only few insects (DEBAISIEUX 1936; HANTSCHK 1991); however most insects possess non-pulsatile diaphragms to guide hemolymph flow in the legs (**trait 34: char 9**) (Ephemeroptera: MEYER 1931; Plecoptera: SCHWERMER 1914; Blattaria: BROCHER 1922; Megaloptera: SELMAN 1965; Hymenoptera: FREUDENSTEIN 1928; Diptera: SHANBHAG et al. 1992; comprehensive investigation in species from almost all hexapod orders: Pernstich & Pass unpubl. data). The diaphragms extend the entire length of the leg, terminating shortly before the apex. They effectively partition the leg hemocoel into two sinuses thus enabling a countercurrent flow of hemolymph. In this pattern of circulation, one sinus serves for the efferent flow to the tip and the other sinus for the afferent flow back to the thoracic cavity. In some Ephemeroptera and some Diptera, the leg diaphragm consists of connective tissue only (Fig. 19), whereas in most other insects it is associated with tubular tracheae (Fig. 20) that may be quite voluminous and form the greater part of the leg hemocoel-partitioning structure.



Figs. 15–17. Antennal circulatory organs in *Periplaneta americana* (Blattaria). **15:** Antennal vessel with enlarged proximal part forming a glomerule before entering the antenna (modified after PASS 1985). Arrow indicates flow of hemolymph into opening of ostium. **16:** TEM cross section of distal part of antennal vessel consisting of a single, thin cell layer inside antenna. **17:** TEM cross section of proximal part of antennal vessel consisting of two cell layers; inner layer of transporting cells with basal invaginations (arrow) and numerous mitochondria; outer layer of connective tissue. CS = connective tissue sheath, Hy = hypodermis, L = lumen of antennal vessel, M = mitochondria, VW = vessel wall.

The morphology of the hemocoel-partitioning structure in the legs of Lepidoptera and Trichoptera is different from that described above. It consists entirely of a voluminous tracheal sac which differs from tubular

tracheae by its very thin and irregularly shaped cuticle and by differences in taenidial structure. It resembles the tracheal sacs of the body cavity in that they collapse and expand according to pressure changes. WASSERTHAL

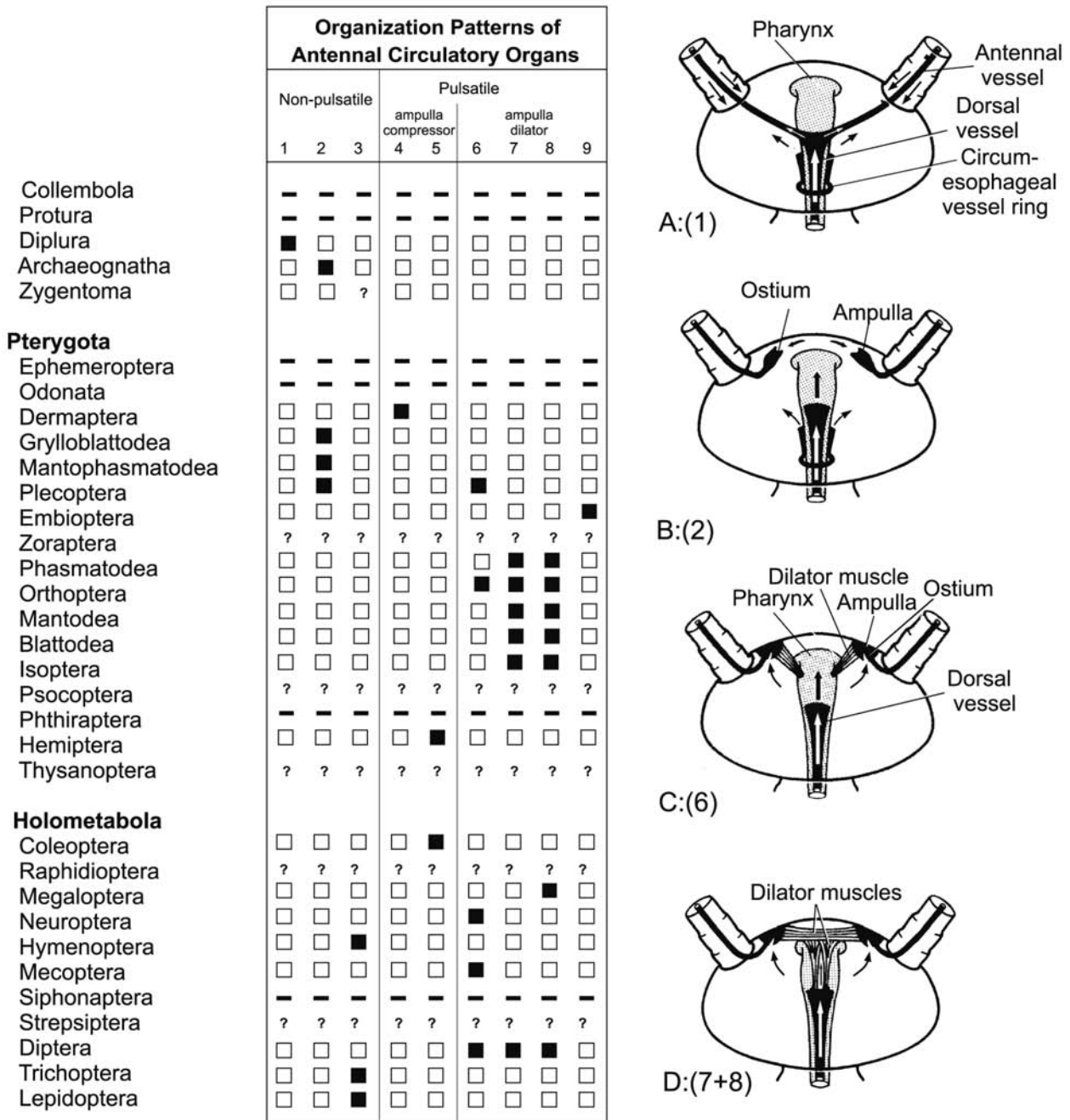
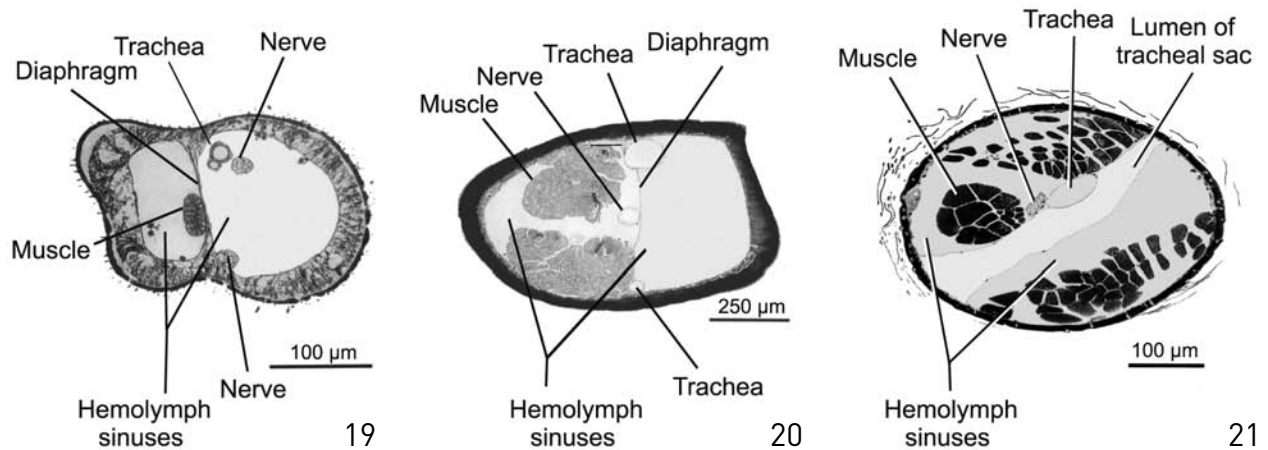


Fig. 18. Antennal circulatory organs and their occurrence in hexapod orders. Numbers 1–9 indicate different patterns of organization. *Non-pulsatile organs*: 1 antennal vessels connected to dorsal vessel; 2 antennal vessel with non-pulsatile ampulla; 3 ampulla or frontal sac indirectly compressed by pharyngeal movements. *Pulsatile organs* are associated with muscles: 4 fronto-pharyngeal compressor; 5 fronto-frontal compressor; 6 ampullo-pharyngeal dilator; 7 ampullo-ampullary dilator; 8 ampullo-aortic dilator; 9 ampullo-frontal dilator. ■ trait present; □ trait absent; – antennal circulatory organs absent; ? not investigated (table modified after PASS 2000). *Right side*: diagrams of heads showing various organizational patterns of antennal circulatory organs (modified after PASS 2000). **A:** *Campodea* (Diplura), **B:** *Machilis* (Archaeognatha), **C:** *Grylotalpa* (Orthoptera), **D:** *Periplaneta* (Blattaria). Numbers in parentheses refer to organization patterns in table. Vessels in solid black, arrows indicate direction of hemolymph flow.

(1982, 1996, 1998) observed changes in the volume of leg tracheal sacs in correlation with periodic heartbeat reversal in some Lepidoptera, thereby indicating their role in hemolymph exchange (Figs. 21–22). An unusual kind of dividing structure is found in the legs of Odonata; in the femur and tibia it is formed by a modified vessel but as it enters the more distal leg

segments it transforms into a longitudinal diaphragm (BROCHER 1917). As mentioned, muscles are generally not associated with the leg hemolymph-partitioning structures, and it remains unclear how the countercurrent flow is generated in these cases. However, in *Locusta* (middle leg only) (HUSTERT 1999) and many Hemiptera



Figs. 19–21. Cross semi-thin sections of legs showing different leg-hemocoel partitioning structures (photos: A. Pernstich). **19:** Tibia with diaphragm in *Ephemera danica* (Ephemeroptera). **20:** Tibia with diaphragm with associated trachea tube in *Periplaneta americana* (Blattaria). **21:** Femur with elastic tracheal sac in *Polyommatus icarus* (Lepidoptera).

(DEBAISEUX 1936; HANTSCHK 1991) muscles are present which are associated with the diaphragms and contract rhythmically, thus forming pulsatile organs. Contractions of the pumping muscles narrow the afferent sinus and, thereby, propel hemolymph toward the thoracic cavity. Simultaneously, the efferent sinus is dilated and hemolymph is drawn from the thorax into the leg.

Leg circulatory organs are completely lacking in basal hexapods, and it is enigmatic how hemolymph exchange is achieved in their appendages.

Character 9. Leg hemocoel, 0: not partitioned – *Diplura*, *Protura*, *Collembola*, *Archaeognatha*, *Zygentoma*, *Embioptera*, *Psocoptera*, *Phthiraptera*, *Thysanoptera*. **1:** partitioned by diaphragm composed of connective tissue and associated tracheal tubes – all *Pterygota* except those with state (2). **2:** partitioned by diaphragm formed by elastic tracheal sac – *Trichoptera*, *Lepidoptera*.

3.4. Wing circulatory organs

The wing veins in insects are tubular channels filled with hemolymph which usually circulates according to a common pattern, i.e., the efferent flow occurs in the anterior veins and the afferent flow in the posterior veins.

The pulsatile organs which enforce circulation through the wing veins are located in the dorsal thorax. They are termed *wing hearts* and consist of a cuticular pumping case and an associated pulsatile apparatus. The scutellum of the wing-bearing segments, an elevation of the tergal cuticle, forms the pumping case. The small hemolymph space beneath the scutellum is connected to the posterior wing veins via tubular

foldings of tergal cuticle; ventrally this space is delimited by the pulsatile apparatus (comparative study of non-Holometabola: KRENN & PASS 1994; Ephemeroptera: MEYER 1931; Odonata: WHEDON 1938; comparative study of Holometabola: KRENN & PASS 1994/95; Mecoptera: KRENN & PASS 1993; Lepidoptera: BROCHER 1919; Hymenoptera: FREUDENSTEIN 1928; Megaloptera: SELMAN 1965; Diptera: THOMSEN 1938).

While the cuticular structures of the wing hearts are relatively uniform in pterygote insects, the associated pulsatile apparatuses differ considerably (**trait 35**) (Fig. 23). In almost all exopterygotes, an enlarged and specifically modified part of the dorsal vessel represents the pulsatile apparatus which is attached to the margin of the scutellum (this configuration is termed *dorsal vessel modification*) (Fig. 23A). Hemolymph exiting the wing veins empties into the small hemolymph space beneath the scutellum and enters the dorsal vessel through its incurrent ostia. In some, the pulsatile apparatus consists of an arched muscular plate (termed *pulsatile diaphragm*) which contracts independently from the dorsal vessel (Fig. 23C). In some Neuroptera, Trichoptera and Lepidoptera the muscle plate is attached posteriorly to the dorsal vessel modification and is thus termed *attached pulsatile diaphragm* (Fig. 23B). Contractions of the muscle cells flatten the diaphragm and hemolymph is drawn out of the wing veins and enters the lumen of the dorsal vessel via its incurrent ostia or empties into the thoracic cavity through a slit-like opening. Usually each winged-segment contains one pulsatile diaphragm (Fig. 23D); in some Lepidoptera and Diptera, however, they are paired and located at the wing bases (Fig. 23E) (KRENN & PASS 1994/95).

It is remarkable that the wing hearts of the mesothorax and metathorax may be entirely different from each other in the same species. In some Coleoptera and

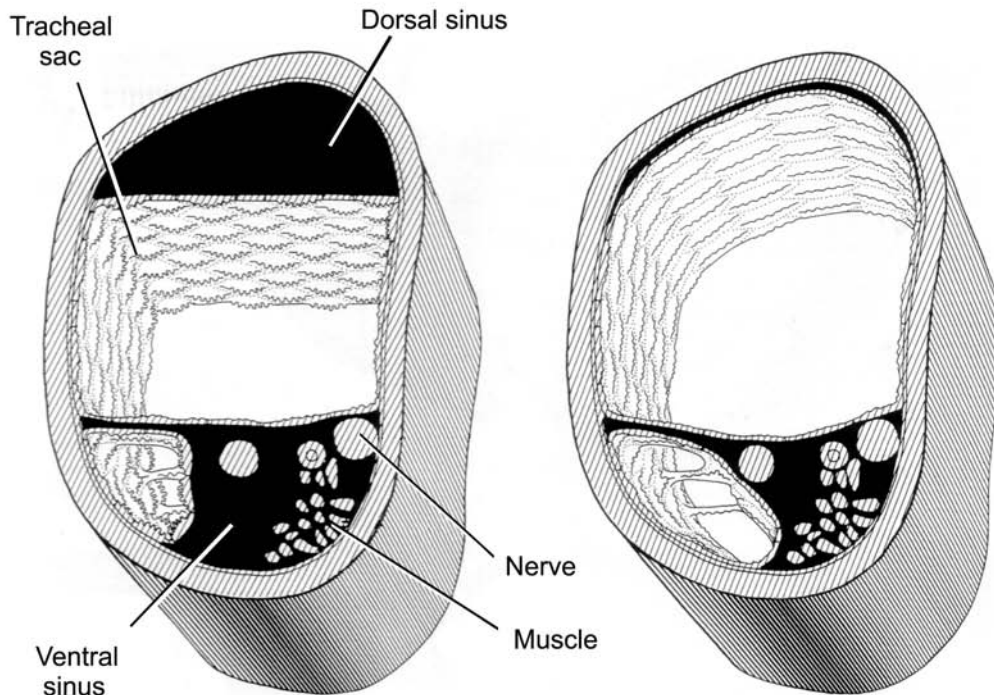


Fig. 22. Diagrams of cross section of tibia in *Deilephila elpenor* (Lepidoptera). Leg hemocoel is divided into two sinuses by an elastic tracheal sac. Hemolymph volume varies according to states of extension of tracheal sac (left: less distended, right: highly distended) (modified after WASSERTHAL 1982).

Lepidoptera, the flow of hemolymph is held to be different. It occurs simultaneously in all wing veins in the same direction and is referred to as *oscillating hemolymph flow*. It is reportedly produced by the concerted action of several factors: changes in the flow direction in the dorsal vessel (heart beat reversal), the intermittent pumping activity of the pulsatile diaphragms in the thorax, and volume changes in abdomen and tracheal system (WASSERTHAL 1996, 1998).

3.5. Circulatory organs of abdominal appendages

The circulatory organs of the various abdominal appendages have received little attention so far. Comparative investigations are available for the cerci and terminal filament only (Diplura: GRASSI 1887; MARTEN 1940; GEREBEN-KRENN & PASS 1999; Archaeognatha: BÄR 1912; BARTH 1963; GEREBEN-KRENN & PASS 2000; Zygentoma: ROUSSET 1974; GEREBEN-KRENN & PASS 2000; Ephemeroptera: MEYER 1931; GEREBEN-KRENN & PASS 2000; Plecoptera: SCHWERMER 1914; PASS 1987). The circulatory organs of these appendages are composed of vessels or diaphragms.

In *Campodea* (Diplura) a pair of cercal vessels (**trait 36: char 10**) is connected to the caudal chamber of the dorsal vessel (Fig. 1). A vessel extends into each cercus and terminates in an opening near the tip of

the appendage. Hemolymph flows through the cercal vessel and returns back to the body cavity via the cercal hemocoel.

In Archaeognatha, *Zygentoma* and Ephemeroptera, the cercal vessels are not directly joined with the dorsal vessel but originate at the transverse septum at the base of the terminal filament (**trait 37**). The vessel of the terminal filament is continuous with the dorsal vessel in Archaeognatha and *Zygentoma*, but in Ephemeroptera the two vessels are separate (Figs. 24–25). All three taxa share the same pattern of hemolymph flow in the cerci and terminal filament.

In Plecoptera, the dorsal vessel is closed posteriorly and the supply of hemolymph to the cerci is achieved differently (Fig. 26). The efferent opening of the cercal vessels is located on the transverse septum at the base of the cerci and the hemolymph flow is effected by an autonomous pump in each anal lobe (*cercal heart*).

In Grylloblattodea, Mantodea and Blattaria, the hemocoel of the cerci is partitioned by a diaphragm (**trait 38: char 11**) which regulates the countercurrent flow (Blattaria: MURRAY 1967; Pass unpubl. data; Grylloblattodea, Mantodea: Hartl & Pass unpubl. data).

Despite the ovipositor of many insects being a long and conspicuous structure, detailed comparative studies on its circulatory organs are lacking. In the cricket, at least, a pulsatile organ is found at the base of the valvulae (PASS 1988).

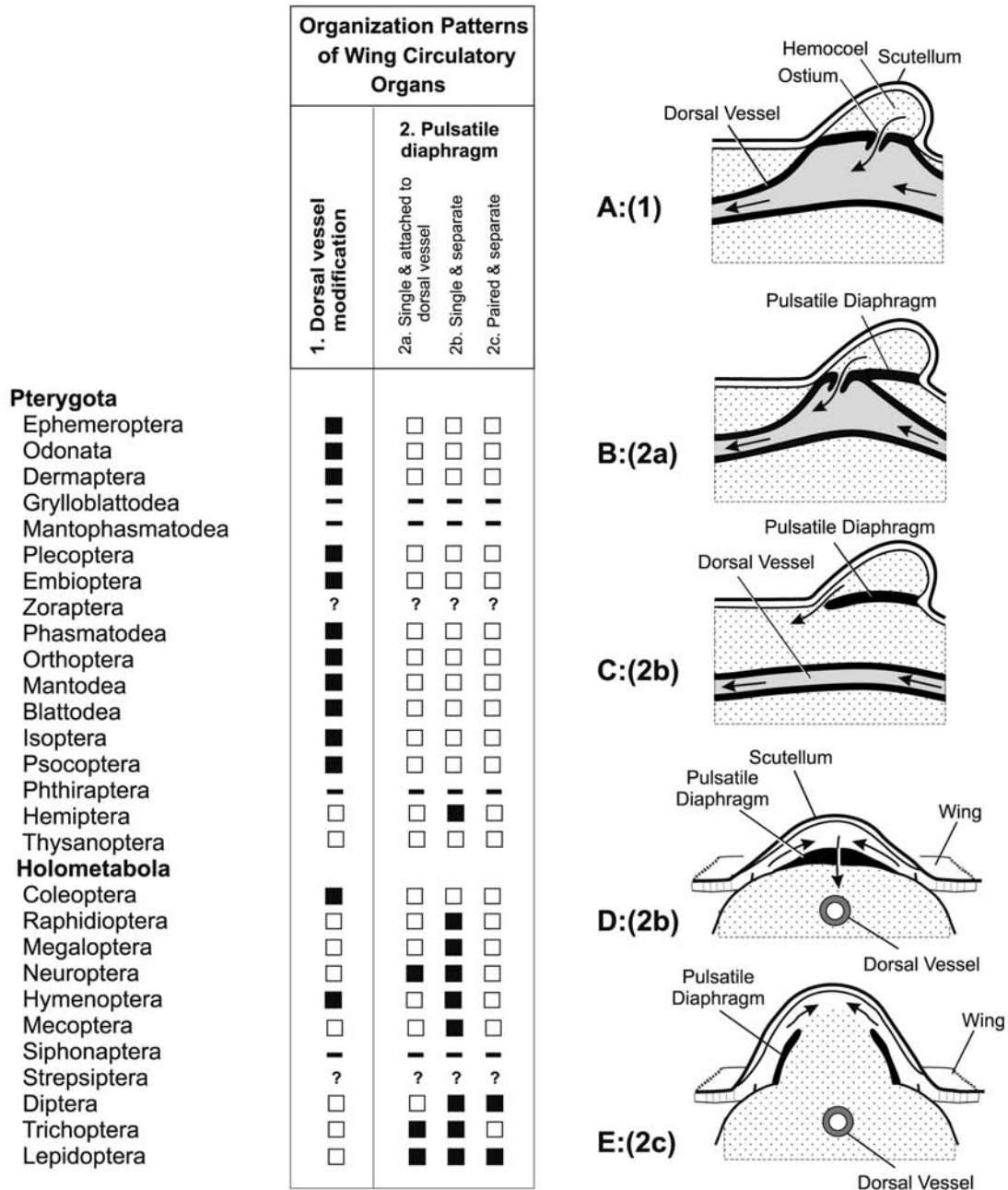


Fig. 23. Wing circulatory organs and their occurrence in insects. ■ trait present; □ absent; - inapplicable (i.e. wingless); ? not investigated (modified after PASS 2000). *Right half:* diagrams of dorsal part of pterothoracic segment showing various organizational patterns of wing circulatory organs (A-C: sagittal, D-E: cross section) (modified after PASS 2000, 1998). Numbers in parentheses refer to organization patterns in table. Arrows indicate direction of hemolymph flow.

Character 10. Cercal vessels, 0: connected to dorsal vessel – *Diplura*. **1:** separate from dorsal vessel – *Archaeognatha*, *Zygentoma*, *Ephemeroptera*, *Plecoptera*. **Inapplicable:** all taxa except those in states (0) and (1).

Character 11. Cercal hemocoel, 0: not partitioned – *Diplura*, *Archaeognatha*, *Zygentoma*, *Ephemeroptera*, *Plecoptera*, *Odonata*, *Mantophasmatodea*, *Embioptera*, *Phasmatodea*, *Orthoptera*, *Isoptera*. **1:** partitioned by diaphragm – *Grylloblattodea*, *Mantodea*, *Blattaria*. **Inapplicable:** all taxa except those in states (0) and (1).

3.6. Ventral diaphragm

Much of the information on the ventral diaphragm is based on the comprehensive work of RICHARDS (1963). The structure is a horizontal membrane situated above the nerve cord and is generally composed of connective tissue and fan-shaped muscles. The connective tissue and muscles vary greatly in attachment sites, overall shape and thickness. Small openings of the diaphragm permit the exchange of hemolymph between the perineural and perivisceral sinuses. Only in *Lepidoptera*

and Trichoptera is the ventral diaphragm directly attached to the nerve cord (KRISTENSEN & NIELSEN 1980). Usually it is located only in the abdomen, but in some taxa it extends into the thorax or even to the base of the head (*Dissosteira*, Orthoptera) (SNODGRASS 1935). The ventral diaphragm may also vary according to the developmental stage.

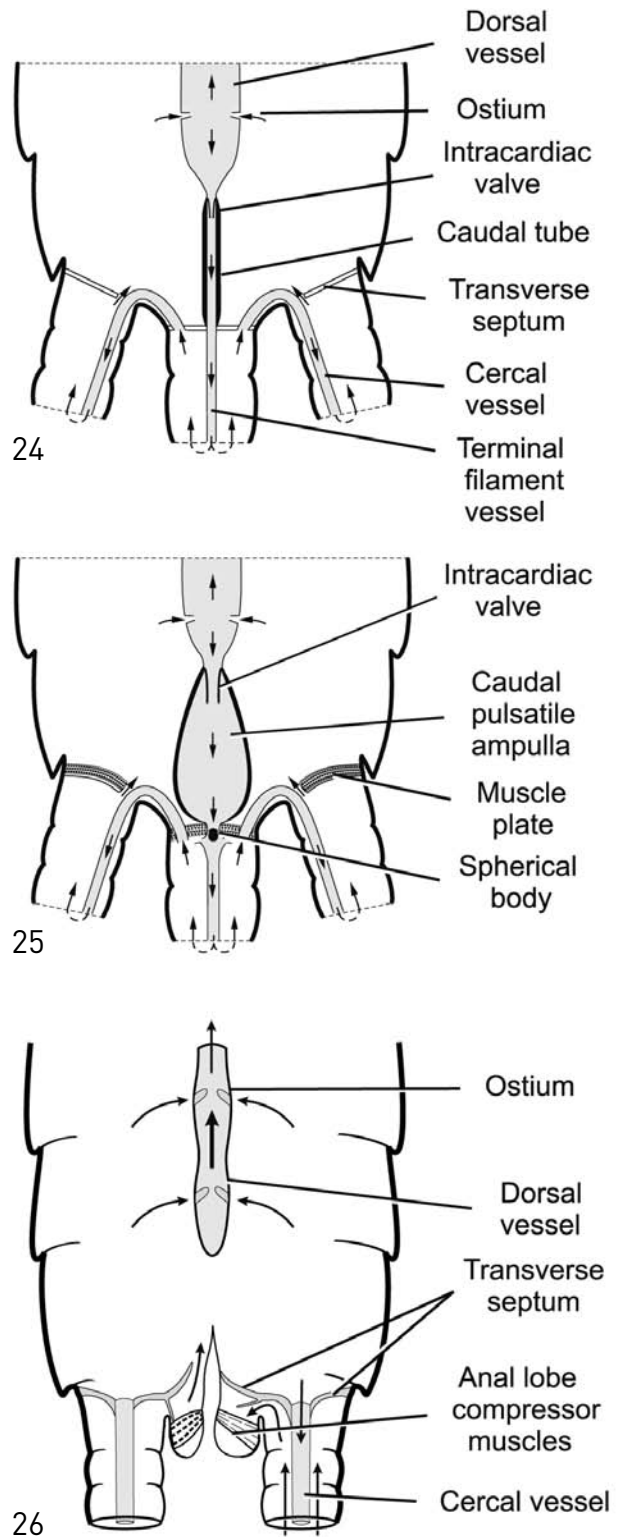
The ventral diaphragm is absent in many taxa, like *Machilis* (Archaeognatha), Campodeidae (Diplura), *Thermobia* (Zygentoma), *Acheta*, other Ensifera (Orthoptera), various genera of Trichoptera and some Lepidoptera (RICHARDS 1963; KRISTENSEN & NIELSEN 1980; KLASS 2001). At least in Ensifera and the respective Trichoptera, transverse muscles are present which pass over the nerve cord (FORD 1923; RICHARDS 1963). Within Dictyoptera, Blattaria and Isoptera possess a so-called hyperneural muscle in the abdomen, which is likewise located above the ventral nerve cord. This hyperneural muscle is composed of a segmental series of unpaired transverse plates of connective tissue, which are connected by longitudinal muscles (KLASS 1999, 2000, pers. comm.).

4. Discussion

In our survey of the circulatory organs of hexapods we aimed to remedy the difficulties faced by phylogeneticists when using characters of this organ system in cladistic analyses. Our study revealed that the greatest impediment to the selection and coding of characters from circulatory organs still lies in the lack of comprehensive comparative investigations. For this reason we excluded traits from character coding on which information was insufficient to permit comparison across hexapod orders (e.g. dorsal vessel suspension, dorsal diaphragm, innervation of the dorsal vessel). Furthermore, traits were excluded if they represent autapomorphies for a single order or a lower taxonomic unit (e.g. dorsal vessel loops, pocket valves), if they contain high intraordinal variability (e.g. length of aorta, presence of incurrent ostia, ventral diaphragm), and if they are evidently convergent developments (e.g. wing hearts). The assessment of the homology of structures continues to present problems, in particular, because circulatory organs are relatively simply organized and contain only few structural elements.

4.1. Dorsal vessel and associated structures

Six characters of the dorsal vessel and its associated structures were selected and coded.



Figs. 24–26. Diagrams of circulatory organs of terminal abdominal appendages (modified after GEREBEN-KRENN & PASS 2000 and PASS 2000). **24:** Archaeognatha: posterior region of dorsal vessel developed as a caudal tube which is connected to terminal filament vessel; cercal vessels originate at transverse septum of terminal filament. **25:** Ephemeroptera: posterior region of dorsal vessel developed as a caudal pulsatile ampulla; terminal filament vessel separate from dorsal vessel; cercal vessels originate from muscular transverse septum. **26:** Plecoptera: posterior region of dorsal vessel closed; cercal vessels originate at transverse septum of cercus, anal lobe with compressor muscles enforce hemolymph flow. Arrows indicate direction of hemolymph flow.

Circumesophageal vessel ring (trait 12: char 1). This structure is characteristic for apterygote orders (Protura have not yet been investigated in this respect). We conclude that the presence of the ring represents the plesiomorphic condition for Hexapoda. It is more parsimonious to consider the similarly shaped circumesophageal vessel ring in Chilopoda (FAHLANDER 1938; RILLING 1968; WIRKNER & PASS 2002) a convergent development. Independent of this question, the loss of the ring is an apomorphy of the Pterygota, as pointed out by KRISTENSEN (1997) and BITSCH & BITSCH (1998).

Ostia with paired lips (trait 13: char 2) are nearly universal in hexapods and probably represent the plesiomorphic condition (Fig. 3, Tab. 1). In Lepidoptera (WASSERTHAL 1982) and Trichoptera (Tögel & Pass unpubl. data) the anterior lip is completely reduced in all ostia (Fig. 5), which thus function as two-way ostia. They are considered to be a potential synapomorphy of Trichoptera and Lepidoptera, further corroborating the well-established taxon Amphiesmenoptera. In one species of Trichoptera, however, the terminally-positioned ostia possess paired lips (Tögel & Pass unpubl. data). This exception may be explained by the specific flow conditions occurring at the terminal end of the dorsal vessel.

Excurrent ostia (trait 17: char 3) are found in several orders of lower Neoptera (some Dermaptera, Grylloblattodea, Plecoptera, Embioptera, Phasmatoidea, some Orthoptera, Mantodea and Blattaria) (Fig. 4). Their segmental appearance may vary, nonetheless excurrent ostia are regarded as homologous structures since they correspond in their ventral location and structure of the valve (NUTTING 1951). Excurrent ostia are considered to belong to the order-level ground patterns of Dermaptera and Orthoptera, although they are absent in some species. At a higher level, excurrent ostia serve as a synapomorphy of Dermaptera, Grylloblattodea, Plecoptera, Embioptera, Phasmatoidea, Orthoptera, and Dictyoptera.

Excurrent ostia – paired or unpaired (trait 18: char 4). The correspondence in the structure of the valves in paired and unpaired excurrent ostia indicates that they are homologous structures (NUTTING 1951) but this has been questioned by KRISTENSEN (1975, 1991). Ultrastructural investigations of the valve cells would be highly desired for clarification of this question. Regardless, following the argumentation of NUTTING (1951) and KRISTENSEN (1991), the single median ostium is a potential synapomorphy of Plecoptera and Embioptera, a clade proposed by e.g. WHEELER et al. (2001).

Segmental vessels (trait 24: char 5) are found only in Blattaria (Figs. 8–14, Tab. 1) and some genera of Mantodea (NUTTING 1951); they most likely represent homologous structures. The base of the segmental vessels is always associated with an excurrent ostium.

We believe that the presence of segmental vessels belongs to the ground pattern of Mantodea. In some species they are lacking probably due to decreased body size (NUTTING 1951).

Although segmental vessels occur in some chelicerates, myriapods, and crustaceans, it is far more parsimonious to assume an independent evolution in the stem lineage of Mantodea and Blattaria than multiple reductions in the remaining hexapods (HERTEL & PASS 2002). The presence of segmental vessels is thus considered a potential synapomorphy of Mantodea and Blattaria, a conclusion which supports the hypothesis of the relationships among Dictyoptera proposed by THORNE & CARPENTER (1992). KRISTENSEN (1975, 1991) alternatively proposed a secondary reduction of segmental vessels in Isoptera, since regressive traits are generally abundant in the latter order. The latter hypothesis is strongly confirmed by all recent phylogenetic analyses based on morphological or molecular data (LO 2003; KLASS 2003; TERRY & WHITING 2005; KLASS & MEIER 2006; KJER et al. 2006), which consistently obtain the Isoptera as a subordinate clade of Blattaria.

Abdominal intracardiac valves (trait 26: char 6) enable the bidirectional hemolymph flow and occur in Diplura, Archaeognatha, Zygentoma and Ephemeroptera. We consider the valves found in these taxa to be homologous structures although they may appear in different segments, since the segmental allocation of internal organs in the posterior most body region is often not consistent. It is unclear if the valves are plesiomorphic for Hexapoda since similarly shaped valves are present in various Crustacea (SIEWING 1956). The loss of valves may be considered a synapomorphy of Odonata and Neoptera, a clade (Metapterygota) which has been previously proposed (KRISTENSEN 1975, 1981, 1991; BEUTEL & GORB 2001, 2006; WHEELER et al. 2001).

Other traits. A vascular connection between the cercal vessel and the posterior end of the dorsal vessel (**trait 29**) is regarded to be the plesiomorphic condition in hexapods. Since trait 29 is dependent on traits 36 (= char 10) and 37 we did not code it as a separate character. Abdominal appendages in Diplura, Archaeognatha, Zygentoma and Ephemeroptera are supplied with hemolymph by vessels which are linked to the dorsal vessel in various ways. In the remaining hexapods, the loss of these connections was accompanied by closure of the posterior end of the dorsal vessel. Presumably, the loss occurred independently in Collembola, Protura and Metapterygota. The posteriorly open dorsal vessel in some orders of Holometabola thus represents a secondary condition, which evolved on multiple occasions.

At present, information is lacking on many aspects of the morphology of the dorsal vessel (**traits 1, 2, 3, 6, 11**) and its course in the body cavity (**traits 4, 5**); hence characters in these structures cannot at present

contribute to the elucidation of hexapod phylogeny. Likewise, several traits of the dorsal vessel may provide useful characters for phylogenetic analyses at intraordinal levels, but comparative investigations are needed to evaluate them, e.g., alary muscles (**trait 7**), dorsal diaphragm (**traits 8, 9, 10**), as well as features of incurrent ostia (**traits 15, 16**) and excurrent ostia (**traits 19–23**).

4.2. Antennal circulatory organs

Some characters of the antennal circulatory organs have been previously used in cladistic analyses (BITSCH & BITSCH 1998; BEUTEL & GORB 2001, 2006; WHEELER et al. 2001; GIRIBET et al. 2004). The organs are re-evaluated in this paper from a phylogenetic point of view.

Antennal vessel wall (trait 32: char 7). The bipartitioned antennal vessels of Mantophasmatodea, Mantodea (Pass in prep.) and Blattaria (PASS 1985) are distinguished by the proximal part being composed of inner and outer cell layers (Figs. 15–17). The outer layer probably corresponds to the wall of the distal portion of the vessel within the antenna; the inner layer consisting of transporting cells represents probably a new acquisition and would be a potential synapomorphy for these taxa. This is consistent with a similar structure of parts of the male genitalia in Dictyoptera and Mantophasmatodea (KLASS et al. 2003). Remarkably, the Grylloblattodea, which have been regarded as the sistergroup of Mantophasmatodea by TERRY & WHITING (2005), possess a uniform single-layered antennal vessel wall (Pass unpubl. data).

Antennal ampulla with ampullo-ampullary dilator muscle (trait 33: char 8). With respect to the muscles of the antennal pulsatile organ the ampullo-ampullary muscle might yield a potential synapomorphy of the Dictyoptera, Phasmatodea and Orthoptera. In some Orthoptera this muscle is not very well developed and consists of only a few fibers which are associated with the frontal sac (BAYER 1968); in *Gryllotalpa* it is completely lacking (PASS 1991). An ampullo-ampullary muscle has been reported from the dipteran *Hemipenthes morio* (DUDEL 1977), but actual reinvestigation could not confirm these findings (Szucsich unpubl. data). Phasmatodea and Dictyoptera have a muscular complex which comprises, in addition to the ampullo-ampullary muscle, a pair of small fan-shaped ampullo-aortic muscles (PASS 1991). This might yield a potential synapomorphy of the Phasmatodea and Dictyoptera (BEUTEL & GORB 2001; GIRIBET et al. 2004, 2005). The assessment of this character, however, is based on few species only and additional data are highly desired.

Other traits. The antennal arteries in Diplura most likely represent the plesiomorphic condition in Hexapoda.

This is substantiated by outgroup comparison with myriapods (Chilopoda: PASS 1991; WIRKNER & PASS 2002; Diplopoda: PASS 1991) and basal Malacostraca (SIEWING 1956). The lack of antennal vessels in some Collembola must then be regarded as secondary; the same holds true for pterygote insects with extremely small antennae (Phthiraptera, Siphonaptera). Antennal vessels connected indirectly to the dorsal vessel by a frontal sac probably represent a derived condition in insects which developed several times independently (**trait 30**).

In insects with detached antennal vessels, the base of the antennal vessel is enlarged to form an ampulla and is equipped with valved ostia. Generally, pumping muscles are associated with the ampullae, but their attachment sites vary and, thus, are difficult to homologize. Several convergencies are clearly apparent, e.g., the fronto-frontal compressor muscle in Hemiptera and Coleoptera (Fig. 18). Some sets of pumping muscles represent autapomorphies of insect orders (e.g. Dermaptera, Embioptera, Coleoptera). In some orders intraordinal variation can be found (Orthoptera, Diptera). The pumping muscles may be originally derived from pharyngeal dilators as deduced from innervation studies in the cockroach *Periplaneta* (PASS et al. 1988).

4.3. Leg circulatory organs

Characters of leg circulatory organs have so far not been included in phylogenetic analyses since the data base is insufficient. The comprehensive study cited in this paper (Pernstich & Pass unpubl. data) enables a preliminary view of the leg circulatory organs from a phylogenetic perspective.

Hemolymph guiding structures (trait 34: char 9). No circulatory organs are identifiable in the legs of apterygotes; this condition is considered plesiomorphic for Hexapoda. Leg diaphragms consisting of connective tissue probably represents an autapomorphy of the Pterygota (Pernstich & Pass unpubl. data). In almost all hexapods, tubular tracheae are associated with the diaphragm. The elastic tracheae in the legs of Trichoptera and Lepidoptera differ distinctly from the above mentioned hemolymph guiding structure. These elastic tracheae are unique in hexapods and serve as a potential autapomorphy for the Amphiesmenoptera (Pernstich & Pass unpubl. data) (Figs. 19–21).

Other traits. Pulsatile organs that ensure the circulation in legs are known only in *Locusta* (HUSTERT 1999) and some Hemiptera (DEBAISIEUX 1936; HANTSCHK 1991). Differences in the anatomy of the leg pulsatile organs in these taxa clearly suggest that they evolved independently. For Hemiptera it could be demonstrated that the pumping muscles were probably recruited

from a skeletal muscle, namely the claw retractor. The muscle attachments vary considerably in the investigated hemipteran species, so that multiple and parallel evolution of the various leg pumping organs has to be assumed for this order (HANTSCHK 1991).

Leg vessels have only been described in dragonflies (BROCHER 1917). Most likely they are not homologous to the leg arteries of other arthropods, since they are distally enlarged and form a diaphragm in the tibia. We conclude that the leg vessels of Odonata represent an autapomorphy.

4.4. Wing circulatory organs

The distribution of the various wing circulatory organs in insect orders (Fig. 23) distinctly shows that the dorsal vessel modification is the plesiomorphic condition in Pterygota (**trait 35**). The occurrence of such dorsal vessel modifications in some Coleoptera and Hymenoptera indicates that the condition may also be plesiomorphic for the Holometabola. Pulsatile diaphragms are derived structures; they clearly developed independently in Hemiptera and several times within Holometabola. Since the parallel-evolved structures appear nearly identical, it was not possible to formulate distinct homologous character states, and we thus excluded them from the list of selected characters. Paired pulsatile diaphragms are obviously derived from unpaired diaphragms and evolved independently in some species of Lepidoptera and Diptera.

The attachment sites, ultrastructure and associated elastic suspending strands indicate that the pulsatile diaphragms are individualized portions of the myocardium. The hypothesis of derivation from the cardiac mesoderm is supported by developmental genetic studies in *Drosophila* (LAWRENCE 1992; SELLIN et al. 2006).

4.5. Cerci and terminal filament circulatory organs

It is debatable whether the hexapod ancestor bore cerci (KRISTENSEN 1991; KUKALOVÁ-PECK 1991; BITSCH 1994; AX 1999). We consider the organization of cercal circulation found in Diplura to represent the plesiomorphic condition of Hexapoda (**trait 36: char 10**) (GEREBEN-KRENN & PASS 1999) or alternatively of a clade formed by Diplura and Ectognatha. Conspicuous cerci are also present in some Polyneoptera. In Plecoptera cercal vessels remain, but in other taxa new hemolymph guiding structures evolved (Figs. 24–26). Among them are cercal diaphragms (**trait 38: char 11**) which occur in Grylloblattodea, Mantodea and Blattaria (but not in the investigated Isoptera) and

may represent a synapomorphy of the three orders. In Plecoptera, a new pulsatile organ evolved at the base of each cercus, and it probably is an autapomorphy for this order (PASS 1987).

The evolutionary origin of the terminal filament in the stem lineage of Ectognatha is an innovation which radically changed the hemolymph circulation in the abdominal appendages. The direct connection between the dorsal and cercal vessels was severed in the stem lineage of Ectognatha. Thus, the separate cercal vessels and the association of the terminal filament vessel with the dorsal vessel (**traits 36, 37**) represent potential apomorphies of Ectognatha. The loss of the terminal filament in basal Pterygota was a key event in the evolution of the circulatory organs of the caudal appendages. The closure of the terminal end of the dorsal vessel and the resulting appearance of unidirectional flow can be regarded as an autapomorphy of the Metapterygota.

4.6. Ventral diaphragm

The high variability of ventral circulatory structures (ventral diaphragm, so-called hyponeural muscle, ventral muscle-tendon-system, etc.) and the scattered distribution of their descriptions in literature prohibit us from constructing plausible characters. A thorough comparison among hexapod orders would be desirable to permit the necessary steps for character construction: hypothesizing homologies to delineate character states, and hypothesizing transformations relating character states to unite alternative states into characters. It may turn out that ventral circulatory structures are phylogenetically informative at the interordinal level. KRISTENSEN & NIELSEN (1980) e.g. consider a ventral diaphragm directly attached to the nerve cord as a potential synapomorphy for Lepidoptera and Trichoptera.

5. Concluding remarks

This paper aimed to bring together the expertise and experience our laboratory has acquired over the years on the circulatory organs of hexapods. As with other internal organs, generalized statements at the order level are usually based only on one or few investigated species. One should, however, remember that collection of data from internal organs is much more time consuming than from external structures, which can often be quickly surveyed and checked in numerous species.

A special objective of this paper was to provide a detailed appendix of the various traits of the circulatory organs. The appendix contains information

at the species level which can be used for cladistic analyses at various higher systematic categories. We selected only those characters which appear to contain phylogenetic value at the supraordinal level. Some traits of the circulatory organs were ultimately not selected because of obvious convergency. We are aware that these decisions are not free of phylogenetic preconceptions. Those who oppose this procedure are free to code further characters by consulting the data in the Appendix. Since many data are scattered and sometimes hidden in the various anatomical monographs and other literature we would greatly appreciate receiving any additional information to the topic. Finally, we hope that specialists from other fields will be encouraged to produce similar evaluations of "their" organ systems, so that a combination of data sets can be analyzed together to help clarify broad phylogenetic relationships in Hexapoda.

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7. References

- ANGIOY, A.M., D. BOASSA & D. DULCIS 1999. Functional morphology of the dorsal vessel in the adult fly *Protophormia terraenovae* (Diptera, Calliphoridae). – *Journal of Morphology* **240**: 15–31.
- AX, P. 1999. Das System der Metazoa II: Ein Lehrbuch der Phylogenetischen Systematik. – Gustav Fischer, Stuttgart. Pp. 5–384.
- BÄR, H. 1912. Beiträge zur Kenntnis der Thysanuren. – *Jenaische Zeitschrift für Naturwissenschaften* **48**: 1–92.
- BARNHART, C.S. 1961. The internal anatomy of the silverfish *Ctenolepisma campbelli* and *Lepisma saccharinum* (Thysanura, Lepismatidae). – *Annals of the Entomological Society of America* **54**: 177–196.
- BARTH, R. 1963. Über das Zirkulationssystem einer Machilide (Thysanura). – *Memorias do Instituto Oswaldo Cruz* **61**: 371–399.
- BAYER, R. 1968. Untersuchungen am Kreislaufsystem der Wanderheuschrecke (*Locusta migratoria migratorioides* R. et F., Orthopteroidea) mit besonderer Berücksichtigung des Blutdruckes. – *Zeitschrift für Vergleichende Physiologie* **58**: 76–155.
- BEUTEL, R.G. & S.N. GORB 2001. Ultrastructure of attachment specializations of hexapods (Arthropoda): Evolutionary patterns inferred from a revised ordinal phylogeny. – *Journal of Zoological Systematics and Evolutionary Research* **39**: 177–207.
- BEUTEL, R.G. & S.N. GORB 2006. A revised interpretation of the evolution of attachment structures in Hexapoda (Arthropoda), with special emphasis on Mantophasmatodea. – *Arthropod Systematics & Phylogeny* **64**: 3–25.
- BITSCH, C. & J. BITSCH 1998. Internal anatomy and phylogenetic relationships among apterygote insect clades (Hexapoda). – *Annales de la Société Entomologique de France (N.S.)* **34**: 339–363.
- BITSCH, C. & J. BITSCH 2004. Phylogenetic relationships of basal hexapods among the mandibulate arthropods: a cladistic analysis based on comparative morphological characters. – *Zoologica Scripta* **33**: 511–550.
- BITSCH, J. 1963. Morphologie céphalique des Machilides (Insecta, Thysanura). – *Annales des Sciences Naturelles Zoologie et Biologie Animale Paris 12/Sér.* **5**: 501–706.
- BITSCH, J. 1994. The morphological groundplan of Hexapoda: critical review of recent concepts. – *Annales de la Société Entomologique de France (N.S.)* **30**: 103–129.
- BITSCH, J., C. BITSCH, T. BOURGOIN & C. D'HAESE 2004. The phylogenetic position of early hexapod lineages: morphological data contradict molecular data. – *Systematic Entomology* **29**: 433–440.
- BODMER, R. & M. FRASCH 1999. Genetic determination of *Drosophila* heart development. Pp. 65–90 in: R.P. HARVEY & N. ROSENTHAL (eds.), *Heart Development*. – Academic Press, San Diego.
- BROCHER, F. 1917. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang, chez les insectes. II Partie. Les larves des odonates. – *Archives de Zoologie Expérimentale et Générale* **56**: 445–490.
- BROCHER, F. 1919. Les organes pulsatiles méso et métatergaux des lépidoptères. – *Archives de Zoologie Expérimentale et Générale* **58**: 149–171.
- BROCHER, F. 1920. Étude expérimentale sur le fonctionnement du vaisseau dorsal et la circulation du sang chez les insectes. III. Le *Sphinx convolvuli*. – *Archives de Zoologie Expérimentale et Générale* **60**: 1–45.
- BROCHER, F. 1922. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang, chez les insectes. V Partie. La *Periplaneta orientalis*. – *Annales de la Société Entomologique de France* **91**: 156–164.
- BROWER, A.V.Z. & V. SCHAWAROCH 1996. Three steps of homology assessment. – *Cladistics* **12**: 265–275.
- CAMERON, S., A.T. BECKENBACH, M. DOWTON & M.F. WHITING 2006. Evidence from mitochondrial genomics on interordinal relationships in insects. – *Arthropod Systematics & Phylogeny* **64**: 27–34.
- CARINE, M.A. & R.W. SCOTLAND 1999. Taxic and transformational homology: Different ways of seeing. – *Cladistics* **15**: 121–129.
- CHAUDONNERET, J. 1950. La morphologie céphalique de *Thermobia domestica* (Packard) (Insecte, Aptérygote, Thysanoure). – *Annales Sciences Naturelles Zoologie et Biologie Animal* **12**: 145–302.
- CHIANG, R.G., J.A. CHIANG & K.G. DAVEY 1990. Morphology of the dorsal vessel in the abdomen of the blood-feeding insect *Rhodnius prolixus*. – *Journal of Morphology* **204**: 9–24.

- CLEMENTS, A.N. 1956. The antennal pulsatile organs of mosquitoes and other Diptera. – *Quarterly Journal of Microscopical Science* **97**: 429–435.
- CREUTZBURG, N. 1885. Über den Kreislauf der Ephemerenlarven. – *Zoologischer Anzeiger* **8**: 246–248.
- CURTIS, N.J., J.M. RINGO & H.B. DOWSE 1999. Morphology of the pupal heart, adult heart, and associated tissues in the fruit fly, *Drosophila melanogaster*. – *Journal of Morphology* **240**: 225–235.
- DEBAISIEUX, P. 1936. Organes pulsatiles des tibias de Noto-nectes. – *Annales de la Société Scientifique de Bruxelles B* **56**: 77–87.
- DEMEREK, M. ed. 1950. *Biology of Drosophila*. – John Wiley & Sons, Inc. – Chapman & Hall, Limited, New York, London. 632 pp.
- DENIS, J.R. 1928. Études sur l'anatomie de la tête de quelques collemboles suivies de considérations sur la morphologie de la tête des insectes. – *Archives de Zoologie Experimentale et Générale* **68**: 1–291.
- DE PINNA, M.C.C. 1991. Concepts and tests of homology in the cladistic paradigm. – *Cladistics* **7**: 317–338.
- DRENKELFORT, H. 1910. Neue Beiträge zur Kenntnis der Biologie und Anatomie von *Siphylurus lacustris* Eaton. – *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* **29**: 527–613.
- DÖNGES, J. 1954. Der Kopf von *Cionus scrophulariae* L. (Curculionidae). – *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* **74**: 1–76.
- DUDEL, H. 1977. Vergleichende funktionsanatomische Untersuchungen über die Antennen der Dipteren. I. Bibiomorpha, Homoeodactyla, Asilomorpha. – *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* **98**: 203–308.
- DUDEL, H. 1978a. Vergleichende funktionsanatomische Untersuchungen über die Antennen der Dipteren. II. Cyclorrhapha (Aschiza and Schizophora-Acalypterae). – *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* **99**: 224–298.
- DUDEL, H. 1978b. Vergleichende funktionsanatomische Untersuchungen über die Antennen der Dipteren. III. Calypterae (I.O. Cyclorrhapha). – *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* **99**: 301–370.
- EDGEcombe, G.D., G.D.F. WILSON, D.J. COLGAN, M.R. GRAY & G. CASSIS 2000. Arthropod cladistics: combined analysis of histone H3 and U2 snRNA sequences and morphology. – *Cladistics* **16**: 155–203.
- EHNBOHM, K. 1948. Studies on the central and sympathetic nervous system and some sense organs in the head of eurypterid insects. – *Opuscula Entomologica Supplementum* **8**, 162 pp.
- FAHLANDER, K. 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoden. – *Zoologische Beiträge aus Uppsala* **17**: 1–148.
- FORD, N. 1923. A comparative study of the abdominal musculature of orthopteroid insects. – *Transactions of the Royal Canadian Institute* **14**: 207–319.
- FRANÇOIS, J. 2003. Ultrastructure du coeur d'*Acerentomon affine* Bagnall (Prot., Acerentomidae). – *Bulletin de la Société Entomologique de France* **108**: 263–264.
- FREUDENSTEIN, K. 1928. Das Herz und das Circulationssystem der Honigbiene (*Apis mellifica* L.). – *Zeitschrift für Wissenschaftliche Zoologie* **132**: 404–475.
- FRISH, A. 1978. Das Herz der Collembola (Insecta) – ein Beitrag zur Anatomie der Collembola. – *Zoologischer Anzeiger* **201**: 177–198.
- FULMEK, L. 1917. Das Rückengefäß der Mallophagen. – *Arbeiten aus dem Zoologischen Institut der Universität Wien und der Zoologischen Station in Triest* **17**: 45–64.
- GEREBEN-KRENN, B.A. & G. PASS 1999. Circulatory organs of Diplura (Hexapoda): The basic design in Hexapoda? – *International Journal of Insect Morphology and Embryology* **28**: 71–79.
- GEREBEN-KRENN, B.A. & G. PASS 2000. Circulatory organs of abdominal appendages in primitive insects (Hexapoda: Archaeognatha, Zygentoma and Ephemeroptera). – *Acta Zoologica (Stockholm)* **81**: 285–292.
- GEROULD, J.H. 1929. Periodic reversal of heart action in the silkworm moth and pupa. – *Journal of Morphology and Physiology* **48**: 385–431.
- GEROULD, J.H. 1938. Structure and action of the heart of *Bombyx mori* and other insects. – *Acta Zoologica* **19**: 297–352.
- GIRIBET, G., G.D. EDGEcombe, J.M. CARPENTER, C.A. D'HAESE & W.C. WHEELER 2004. Is Ellipura monophyletic? A combined analysis of basal hexapod relationships with emphasis on the origin of insects. – *Organisms Diversity & Evolution* **4**: 319–340.
- GIRIBET, G., RICHTER, S., EDGEcombe, G.D. & W.C. WHEELER 2005. The position of crustaceans within Arthropoda – evidence from nine molecular loci and morphology. *In*: S. KOENEMANN & R.A. JENNER (eds.), *Crustacea and Arthropod Relationships*. – *Crustacean Issues* **16**: 307–352.
- GRASSI, B. 1887. Anatomia comparata dei tisanuri e considerazioni generali sull'organizzazione degli insetti. – *Reale Accademia dei Lincei* **4** (ser. 4): 543–611.
- GRIMALDI, D. & M.S. ENGEL 2005. *Evolution of Insects*. – Cambridge University Press, Cambridge. 755 pp.
- HAMILTON, M.A. 1931. The morphology of the water scorpion, *Nepa cinerea* L. (Rhynchota, Heteroptera). – *Proceedings of the Zoological Society of London* **3**: 1067–1136.
- HANTSCHK, A. 1991. Functional morphology of accessory circulatory organs in the legs of Hemiptera. – *International Journal of Insect Morphology and Embryology* **20**: 259–274.
- HAWKINS, J.A., C.E. HUGHES & R.W. SCOTLAND 1997. Primary homology assessment, characters and character states. – *Cladistics* **13**: 275–283.
- HERTEL, W. & G. PASS 2002. An evolutionary treatment of the morphology and physiology of circulatory organs in insects. – *Comparative Biochemistry and Physiology A* **133**: 555–575.
- HINKS, C.F. 1966. The dorsal vessel and associated structures in some Heteroptera. – *Transactions of the Royal Entomological Society of London* **118**: 375–392.
- HÖVMÖLLER, R., T. PAPE & M. KÄLLERSJÖ 2002. The Paleoptera problem: Basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. – *Cladistics* **18**: 313–323.
- HUSTERT, R. 1999. Accessory hemolymph pump in the mesothoracic legs of locusts (*Schistocerca gregaria* FORSKAL) (Orthoptera, Acrididae). – *International Journal of Insect Morphology and Embryology* **28**: 91–96.
- IMMS, A.D. 1970. *A General Textbook of Entomology*. – Methuen, London.

- JENNER, R.A. 2002. Boolean logic and character state identity: Pitfalls of character coding in metazoan cladistics. – *Contributions to Zoology* **71**: <http://dpc.uba.uva.nl/ctz/vol71/nr01/art06>.
- JONES, J.C. 1954. The heart and associated tissues of *Anopheles quadrimaculatus* Say (Diptera: Culicidae). – *Journal of Morphology* **94**: 71–123.
- JONES, J.C. 1977. The Circulatory System of Insects. – Charles C. Thomas, Springfield. 255 pp.
- KHANNA, S. 1964. The circulatory system of *Dysdercus koenigii* (Fabr.) (Hemiptera Pyrrhocoridae). – *Indian Journal of Entomology* **26**: 404–410.
- KINZELBACH, R.K. 1966. Zur Kopfmorphologie der Fächerflügler (Strepsiptera, Insecta). – *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* **84**: 559–684.
- KJER, K.M. 2004. Aligned 18S and insect phylogeny. – *Systematic Biology* **53**: 506–514.
- KJER, K., F.L. CARLE, J. LITMAN & J. WARE 2006. A molecular phylogeny of Insecta. – *Arthropod Systematics & Phylogeny* **64**: 35–44.
- KLASS, K.-D. 1999. The pregenital abdomen of a mantid and a cockroach: musculature and nerve topography, with comparative remarks on other Neoptera (Insecta: Dictyoptera). – *Deutsche Entomologische Zeitschrift* **46**: 3–42.
- KLASS, K.-D. 2000. The male abdomen of the relic termite *Mastotermes darwiniensis* (Insecta: Isoptera: Mastotermitidae). – *Zoologischer Anzeiger* **239**: 231–262.
- KLASS, K.-D. 2001. The female abdomen of the viviparous earwig *Hemimerus vosseleri* (Insecta: Dermaptera: Hemimeridae), with a discussion of the postgenital abdomen of Insecta. – *Zoological Journal of the Linnean Society* **131**: 251–307.
- KLASS, K.-D. 2003. Relationships among the principal lineages of Dictyoptera inferred from morphological data. In: K.-D. KLASS (ed.), *Proceedings of the 1st Dresden Meeting on Insect Phylogeny: “Phylogenetic Relationships within the Insect Orders”* (Dresden, September 19–21, 2003). – *Entomologische Abhandlungen* **61**: 134–137.
- KLASS, K.-D. & R. MEIER 2006. A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. – *Entomologische Abhandlungen* **63**: 3–50.
- KLASS, K.-D., M.D. PICKER, J. DAMGAARD, S. VAN NOORT & K. TOJO 2003. The taxonomy, genitalic morphology, and phylogenetic relationships of southern African Mantophasmatodea. – *Entomologische Abhandlungen* **61**: 3–67.
- KRENN, H.W. & G. PASS 1993. Wing-hearts in Mecoptera (Insecta). – *International Journal of Insect Morphology and Embryology* **22**: 63–76.
- KRENN, H.W. & G. PASS 1994. Morphological diversity and phylogenetic analysis of wing circulatory organs in insects, part I: Non-Holometabola. – *Zoology* **98**: 7–22.
- KRENN, H.W. & G. PASS 1994/95. Morphological diversity and phylogenetic analysis of wing circulatory organs in insects, part II: Holometabola. – *Zoology* **98**: 147–164.
- KRISTENSEN, N.P. 1975. The phylogeny of hexapod “orders”: A critical review of recent accounts. – *Zeitschrift für Zoologische Systematik und Evolutionsforschung* **13**: 1–44.
- KRISTENSEN, N.P. 1981. Phylogeny of insect orders. – *Annual Review of Entomology* **26**: 135–157.
- KRISTENSEN, N.P. 1991. Phylogeny of extant hexapods. Pp. 125–140 in: CISRO (ed.), *The Insects of Australia*. – Melbourne University Press, Carlton, Victoria.
- KRISTENSEN, N.P. 1997. The ground plan and basal diversification of the hexapods. Pp. 281–293 in: R.A. FORTEY & R.H. THOMAS (eds.), *Arthropod Relationships*. – Chapman and Hall, London.
- KRISTENSEN, N.P. & E.S. NIELSEN 1980. The ventral diaphragm of primitive (non-ditrysian) Lepidoptera. A morphological and phylogenetic study. – *Zeitschrift für Zoologische Systematik und Evolutionsforschung* **18**: 123–146.
- KUHL, W. 1924. Der feinere Bau des Zirkulationssystems von *Dytiscus marginalis* L. Rückengefäß, Pericardialseptum und Pericardialgewebe. – *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* **46**: 75–198.
- KUKALOVÁ-PECK J. 1991. Fossil history and the evolution of hexapod structures. Pp. 141–179 in: CISRO (ed.), *The Insects of Australia*. – Melbourne University Press, Carlton, Victoria.
- LAWRENCE, P.A. 1992. *The Making of a Fly*. – Blackwell Scientific Publications, Oxford. 228 pp.
- LEE D.C. & H.N. BRYANT 1999. A reconsideration of the coding of inapplicable characters: Assumptions and problems. – *Cladistics* **15**: 373–378.
- LO, N. 2003. Molecular phylogenetics of Dictyoptera insights into the evolution of termite eusociality and bacterial endosymbiosis in cockroaches. In: K.-D. KLASS (ed.), *Proceedings of the 1st Dresden meeting on insect phylogeny: “Phylogenetic Relationships within the Insect Orders”* (Dresden, September 19–21, 2003). – *Entomologische Abhandlungen* **61**: 137–138.
- LOCKE, M. 1998. Glossary to Parts A, B and C. Pp. 1191–1222 in: F.W. HARRISON & M. LOCKE (eds.), *Microscopic Anatomy of Invertebrates*. Vol. 11C: Insecta. – Wiley-Liss, New York.
- LUAN, Y.X., J.M. MALLATT, R.D. XIE, Y.M. YANG & W.Y. YIN 2005. The phylogenetic positions of three basal-hexapod groups (Protura, Diplura, and Collembola) based on ribosomal RNA gene sequences. – *Molecular Biology and Evolution* **22**: 1579–1592.
- MARQUES, R.M. & F.H. CAETANO 2001. Ultramorphology and histology of dorsal vessel - gastral portion - of *Camponotus rufipes*. – *Sociobiology* **38**: 551–556.
- MARTEN, W. 1940. Zur Kenntnis von *Campodea*. – *Zeitschrift für Morphologie und Ökologie der Tiere* **22**: 1–48.
- MATUS, S. & G. PASS 1999. Antennal circulatory organ of *Apis mellifera* L. (Hymenoptera: Apidae) and other Hymenoptera: Functional morphology and phylogenetic aspects. – *International Journal of Insect Morphology and Embryology* **28**: 97–109.
- MCINDOO, N.E. 1939. Segmental blood vessels of the American cockroach (*Periplaneta americana* (L.)). – *Journal of Morphology* **65**: 323–351.
- MEYER, E. 1931. Über den Blutkreislauf der Ephemeriden. – *Zeitschrift für Morphologie und Ökologie der Tiere* **22**: 1–52.
- MILLER, T.A. 1985. Structure and physiology of the circulatory system. Pp. 289–353 in: G.A. KERKUT & L.I. GILBERT (eds.), *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. – Pergamon Press, Oxford.

- MURRAY, J.A. 1967. Morphology of the cercus in *Blattella germanica* (Blattaria: Pseudomopinae). – Annals of the Entomological Society of America **60**: 10–16.
- NUTTING, W.L. 1951. A comparative anatomical study of the heart and accessory structures of the orthopteroid insects. – Journal of Morphology **89**: 501–597.
- OPOCZYNSKA-SEMBRATOWA, Z. 1936. Recherches sur l'anatomie et l'innervation du coeur de *Carausius morosus* Brunner. – Bulletin International de l'Académie Polonaise des Sciences et des Lettres, Cracow (B) **2**: 411–436, pls. 19, 20.
- PASS, G. 1980. The anatomy and ultrastructure of the antennal circulatory organs in the cockchafer beetle *Melolontha melolontha* L. (Coleoptera, Scarabaeidae). – Zoomorphology **96**: 77–89.
- PASS, G. 1985. Gross and fine structure of the antennal circulatory organ in cockroaches (Blattodea, Insecta). – Journal of Morphology **185**: 255–268.
- PASS, G. 1987. Cercus “heart” in stoneflies: A new type of accessory circulatory organ in insects. – Naturwissenschaften **74**: 440–441.
- PASS, G. 1988. Functional morphology and evolutionary aspects of unusual antennal circulatory organs in *Labidura riparia* Pallas (Labiduridae), *Forficula auricularia* L. and *Chelidurella acanthopygia* Gén  (Forficulidae) (Dermaptera: Insecta). – International Journal of Insect Morphology and Embryology **17**: 103–112.
- PASS, G. 1991. Antennal circulatory organs in Onychophora, Myriapoda and Hexapoda: Functional morphology and evolutionary implications. – Zoomorphology **110**: 145–164.
- PASS, G. 1998. Accessory pulsatile organs. – Pp. 621–640 in: F.W. HARRISON & M. LOCKE (eds.), Microscopic Anatomy of Invertebrates. – Wiley-Liss Inc., New York.
- PASS, G. 2000. Accessory pulsatile organs: Evolutionary innovations in insects. – Annual Review of Entomology **45**: 495–518.
- PASS, G., H. AGRICOLA, H. BIRKENBEIL & H. PENZLIN 1988. Morphology of neurones associated with the antennal heart of *Periplaneta americana* (Blattodea, Insecta). – Cell Tissue Research **253**: 319–326.
- PAWLOWA, M. 1895. Über ampullenartige Blutcirculationsorgane im Kopfe verschiedener Orthopteren. – Zoologischer Anzeiger **18**: 7–13.
- PERNSTICH, A., H. KRENN & G. PASS 2003. Preparation of serial sections of arthropods using 2,2-dimethoxypropane dehydration and epoxy resin embedding under vacuum. – Biotechnic & Histochemistry **78**: 5–9.
- POPOVICI-BAZOSANU, A. 1905. Beiträge zur Kenntnis des Cirkulationssystems der Insekten. – Jenaische Zeitschrift für Naturwissenschaft **33**: 667–696.
- RICHARDS, A.G. 1963. The ventral diaphragm of insects. – Journal of Morphology **113**: 17–47.
- RILLING, G. 1968. *Lithobius forficatus*. – Grosses Zoologisches Praktikum, Heft 13b. 136 pp., 52 pls. Fischer, Stuttgart.
- ROUSSET, A. 1973. Squelette et musculature des regions génitales et postgénitales de la femelle de *Thermobia domestica* (Packard). Comparaison avec la region génitale de *Nicoletia* sp. (Insecta: Apterygota: Lepismatida). – International Journal of Insect Morphology and Embryology **2**: 55–80.
- ROUSSET, A. 1974. Les différenciations postérieures du vaisseau dorsal de *Thermobia domestica* (Packard) (Insecta, Lepismatidae). Anatomie et innervation. – Comptes Rendus de l'Académie des Sciences Paris D **278**: 2449–2452.
- SCHNEIDER, D. & K.E. KAISLING 1959. Der Bau der Antenne des Seidenspinners *Bombyx mori* L. III. Das Bindegewebe und das Blutgefäß. – Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere **77**: 111–132.
- SCHWERMER, W. 1914. Beiträge zur Biologie und Anatomie von *Perla marginata* Scopoli. – Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere **37**: 267–312.
- SELLIN, J., S. ALBRECHT, V. KÖLSCH & A. PAULULAT 2006. Dynamics of heart differentiation, visualized utilizing heart enhancer elements of the *Drosophila melanogaster* bHLH transcription factor Hand. – Gene Expression Patterns **6**: 360–375.
- SELMAN, B.J. 1965. The circulatory system of the alder fly *Sialis lutaria*. – Proceedings of the Zoological Society of London **144**: 487–535.
- SERVATICO, S. 1887. Die Aorta im Brustkasten und im Kopf von *Bombyx mori*. – Zoologischer Anzeiger **10**: 562–563.
- SHANBHAG, S.R., K. SINGH & R.N. SINGH 1992. Ultrastructure of the femoral chordotonal organs and their novel synaptic organization in the legs of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). – International Journal of Insect Morphology and Embryology **21**: 311–322.
- SIEWING, R. 1956. Untersuchungen zur Morphologie der Malacostraca (Crustacea). – Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere **75**: 39–176.
- SNODGRASS, R.E. 1935. Principles of Insect Morphology. – McGraw-Hill, New York.
- STRONG, E.E. & D. LIPSCOMB 1999. Character coding and inapplicable data. – Cladistics **15**: 363–371.
- TERRY, M.D. & M.F. WHITING 2005. Mantophasmatodea and phylogeny of the lower neopterous insects. – Cladistics **21**: 240–257.
- THOMSEN, E. 1938. Über den Kreislauf im Flügel der Musciden mit besonderer Berücksichtigung der akzessorischen pulsierenden Organe. – Zeitschrift für Morphologie und Ökologie der Tiere **34**: 416–438.
- THORNE, B.L. & J.M. CARPENTER 1992. Phylogeny of the Dictyoptera. – Systematic Entomology **17**: 253–268.
- VONDRAN, T. & L.T. WASSERTHAL 1998. The cephalic arterial system in Lepidoptera. – Proceedings of the VIth European Congress of Entomology, Ceske Budejovice: p. 69.
- WASSERTHAL, L.T. 1980. Oscillating haemolymph “circulation” in the butterfly *Papilio machaon* L. revealed by contact thermography and photocell measurements. – Journal of Comparative Physiology **139**: 145–163.
- WASSERTHAL, L.T. 1981. Oscillating haemolymph “circulation” and discontinuous tracheal ventilation in the giant silk moth *Attacus atlas* L. – Journal of Comparative Physiology **145**: 1–15.
- WASSERTHAL, L.T. 1982. Wechselseitige funktionelle und strukturelle Anpassungen von Kreislauf- und Tracheensystem bei adulten Insekten. – Verhandlungen der Deutschen Zoologischen Gesellschaft **75**: 105–116.
- WASSERTHAL, L.T. 1996. Interaction of circulation and tracheal ventilation in holometabolous insects. – Advances in Insect Physiology **26**: 297–351.

- WASSERTHAL, L.T. 1998. The open hemolymph system of Holometabola and its relation to the tracheal space. Pp. 583–620 in: F.W. HARRISON & M. LOCKE (eds.), *Microscopic Anatomy of Invertebrates*. – Wiley-Liss Inc., New York.
- WASSERTHAL, L.T. 1999. Functional morphology of the heart and of a new cephalic pulsatile organ in the blowfly *Calliphora vicina* (Diptera: Calliphoridae) and their roles in hemolymph transport and tracheal ventilation. – *International Journal of Insect Morphology and Embryology* **28**: 111–129.
- WASSERTHAL, L.T. 2003. Circulation and thermoregulation. Pp. 205–228 in: N.P. KRISTENSEN (ed.), *Lepidoptera, Moths and Butterflies, Handbuch der Zoologie*, vol IV, part 36. – De Gruyter, Berlin, New York.
- WETTINGER, O. 1927. Das Circulationssystem der Tipulidenlarven mit besonderer Berücksichtigung von *Tipula selene*. – *Zeitschrift für Wissenschaftliche Zoologie* **129**: 453–482.
- WHEDON, A. 1938. The aortic diverticula of the Odonata. – *Journal of Morphology* **63**: 229–261.
- WHEELER, W.C., M.F. WHITING, Q.D. WHEELER & J.M. CARPENTER 2001. The phylogeny of extant insect orders. – *Cladistics* **17**: 113–169.
- WHITING, M.F., J.C. CARPENTER, Q.D. WHEELER & W.C. WHEELER 1997. The Strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. – *Systematic Biology* **46**: 1–68.
- WIGGLESWORTH, V.B. 1955. *Physiologie der Insekten*. – Birkhäuser Verlag, Basel, Stuttgart.
- WILLE, A. 1958. A comparative study of the dorsal vessels of bees. – *Annals of the Entomological Society of America* **51**: 538–546.
- WIRKNER, C.S. & G. PASS 2002. The circulatory system in Chilopoda: Functional morphology and phylogenetic aspects. – *Acta Zoologica* **83**: 193–202.
- ZAWARZIN, A. 1911. Histologische Studien über Insekten. I. Das Herz der Aeschnalarven. – *Zeitschrift für Wissenschaftliche Zoologie* **97**: 481–510.
- ZIMMERMANN, O. 1884. Über eine eigenthümliche Bildung des Rückengefäßes bei einigen Ephemeridenlarven. – *Zeitschrift für Wissenschaftliche Zoologie* **34**: 404–406.

8. Appendix

The appendix is a compilation of the traits and characters of the circulatory system in hexapods and provides full references of the data base at the species level. The list can give an impression of the usefulness of these organs for phylogenetic studies and reflects our ideas on character construction. The ventral diaphragm and related structures were not considered in this part of the paper, due to the difficulties of comparing the heterogeneous data and our lack of expertise regarding these specific circulatory organs.

8.1. Dorsal vessel and associated structures

Trait 1. Aorta present in: (i) head, prothorax: Orthoptera: see “variable” below; Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951: 516); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 516). **(ii) head, prothorax, mesothorax:** Dermaptera: see “variable” below; Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 516); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 516); Embioptera: *Oligotoma nigra* (NUTTING 1951: 516); Zoraptera: *Zorotypus hubbardi* (NUTTING 1951: 516); Orthoptera: see “variable” below; Isoptera: *Mastotermes darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*, *Nasutitermes costalis* (NUTTING 1951: 516); Hymenoptera: see “variable” below; Lepidoptera: see “variable” below. **(iii) head, prothorax, mesothorax, metathorax:** Protura: *Acerentomon affine* (FRANÇOIS 2003: 263); Diplura: *Campodea augens*, *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999); Ephemeroptera: *Siphylurus lacustris* (DRENKELFORT 1910: 583–584); Odonata: *Aeschna* sp. (ZAWARZIN 1911: 484); Dermaptera: see “variable” below; Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *D. velii eucnemis* (NUTTING 1951: 516); Hymenoptera: see “variable” below; Lepidoptera: see “variable” below. **(iv) head, prothorax, mesothorax, metathorax, abdomen:** Odonata: *Aeschna* sp. (ZAWARZIN 1911: 484); Phthiraptera: *Goniocotes compar*, *Lipeurus baculus*, *Nirmus* sp., *Lipeurus jejunos*, *Gyropus gracilis*, *G. ovalis*, *Menopon pallidum*, *Trichodectes subrostratus* (FULMEK 1917: 10); Hemiptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmostethus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolobrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 377), *Nepa cinerea* (HAMILTON 1931: 1122), *Dysdercus koenigii* (KHANNA 1964: 405), *Rhodnius prolixus* (CHIANG et al. 1990: 10); Megaloptera: *Sialis lutaria* (SELMAN 1965: 506); Hymenoptera: see “variable” below; Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 88); Diptera: *Anopheles quadrimaculatus* (JONES 1954), *Drosophila melanogaster* (DEMEREK 1950: 442, 447), *Calliphora vicina* (WASSERTHAL 1999: 112, 115), *Protophormia terraenovae* (ANGIOY et al. 1999: 23); Siphonaptera: *Ctenocephalides felis* (Tögel & Pass unpubl. data).

Variable. Dermaptera: **(ii)** *Anisolabis maritima*, *Forficula auricularia* (NUTTING 1951: 516). **(iii)** *Hemimerus vosselei* (NUTTING 1951: 516).

Variable. Orthoptera: **(i)** *Ceuthophilus* sp., *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 516). **(ii)** *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelsis* sp., *Capnobotes fuliginosus*, *Pediocetes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve* (NUTTING 1951: 516).

Variable. Hymenoptera: **(ii)** *Leioproctus zonata*, *Hylaeus modestus*, *H. cressoni*, *Colletes punctipennis*, *C. spp. 2–3*, *Ptiloglossa mexicana*, *Augochloropsis brachycephala*, *A. diversipennis*, *A. sparsilis*, *A. cuprea*, *Augochlora pura*, *Augochlora aurata*, *A. striata*, *Agapostemon sericeus*, *A. sp.*, *Ruizantheda divaricatus*, *Halictus hesperus*, *H. ligatus*, *H. parallelus*, *Megalopta genalis*, *Pseudaugochlora graminea*, *Paroxystoglossa jocasta*, *Sphecodes* sp., *Lasioglossum imitatus*, *Dufourea marginata*, *Dieunomia heteropoda*, *Nomia foxii*, *Andrena argemonis*, *A. miserabilis*, *Perdita albipennis*, *Protandrena cockerelli*, *Pseudopanurgus* sp., *Calliopsis andreniformis*, *Oxaea flavescens*, *Heriades carinata*, *H. variolosa*, *Megachile brevis*, *M. sp.*, *Coelioxys octodentata*, *Osmia l. lignaria*, *Anthidium maculosum*, *Trachusa zebatum*, *Paranthidium* sp., *Dianthidium curvatum sayi*, *Trigonopedia oligotricha*, *Exomalopsis solani*, *E. sp.*, *Ancylosceles armata*, *Monoeca mexicana*, *Nomada* sp., *Triepeolus concavus*, *Holcopasites illinoensis*, *Ptilothrix sumichrasti*, *Diadasia diminuta*, *D. enavata*, *Melitoma euglossoides*, *Xenoglossa fulva*, *Tetraloniella spissa*, *Florilegus condignus*, *Thygater analis*, *Svastra obliqua*, *Melissodes coloradensis*, *M. agilis*, *Peponapis* sp., *Anthophora walshii*, *A. spp. 2–3*, *Centris vittata*, *C. lanosa*, *Epicharis elegans*, *Xylocopa fimbriata*, *X. virginica*, *X. brasilianorum*, *Ceratina dupla*, *Trigona angustula*, *T. mombuca aequinotiales*, *T. nigra paupera*, *Scraptothrigona postica*, *Dactylurina staudingeri*, *Meliponula beccarii*, *Cephalotrigona capitata*,

Melipona marginata, *M. schencki picadensis*, *M. scutellaris*, *M. beecheii*, *Lestrimelitta limao*, *Bombus medius*, *B. ephippiatus*, *B. fraternus*, *Apis mellifera*, *Euglossa cupreiventris*, *Eufriesea caerulescens*, *E. mussitans*, *Eulaema meriana*, (WILLE 1958: 539). **(iv)** *Apis mellifera* (FREUDENSTEIN 1928: 409, 426), *Camponotus rufipes* (MARQUES & CAETANO 2001: 553).

Variable. Lepidoptera: **(ii)** *Attacus atlas* (WASSERTHAL 1981: 2), *Bombyx mori* (GEROULD 1938). **(iii)** *Papilio machaon* (WASSERTHAL 1980: 153, fig. 9).

Trait 2. Diameter of dorsal vessel lumen: (i) about the same throughout the whole length: Dermaptera:

Hemimerus vosselei, *Anisolabis maritima*, *Forficula auricularia* (NUTTING 1951); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951); Plecoptera: *Pteronarcys californica* (NUTTING 1951); Embioptera: *Oligotoma nigra* (NUTTING 1951); Zoraptera: *Zorotypus hubbardi* (NUTTING 1951); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *D. velii eucnemis* (NUTTING 1951); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Ceuthophilus* sp., *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelsis* sp., *Capnobotes fuliginosus*, *Pediocetes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Tridactylus apicalis*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonina cubensis* (NUTTING 1951); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsothes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951); Isoptera: *Mastotermes darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*,

Nasutitermes costalis (NUTTING 1951); Diptera: see “variable” below. **(ii) greatest at posterior end:** Phthiraptera: *Goniocotes compar*, *Lipeurus baculus*, *Nirmus* sp., *Lipeurus jejunus*, *Gyropus gracilis*, *G. ovalis*, *Menopon pallidum*, *Trichodectes subrostratus* (FULMEK 1917: 6); Hemiptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmotherus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolabrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 377), *Nepa cinerea* (HAMILTON 1931: 1122), *Dysdercus koenigii* (KHANNA 1964: 405), *Rhodnius prolixus* (CHIANG et al. 1990: 20); Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 129). **(iii) greatest in anterior abdominal region:** Megaloptera: *Sialia lutaria* (SELMAN 1965: 506); Diptera: see “variable” below; Lepidoptera: *Attacus atlas* (WASSERTHAL 1981: 2).

Variable. Diptera: **(i)** *Anopheles quadrimaculatus* (JONES 1954: 77). **(iii)** *Drosophila melanogaster* (DEMEREK 1950: 444–445, fig. 12A), *Calliphora vicina* (WASSERTHAL 1999: 113, 114), *Protophormia terraenovae* (ANGIOY et al. 1999: 17).

Variable. Hymenoptera: **(i)** *Leioproctus zonata*, *Hylaeus modestus*, *H. cressoni*, *Colletes punctipennis*, *C. spp.* 2–3, *Ptiloglossa mexicana*, *Augochloropsis brachycephala*, *A. diversipennis*, *A. sparsilis*, *A. cuprea*, *Augochlora pura*, *Augochlorella aurata*, *A. striata*, *Agapostemon sericeus*, *A. sp.*, *Ruizantheda divaricatus*, *Halictus hesperus*, *H. ligatus*, *H. parallelus*, *Megalopta genalis*, *Pseudaugochlora graminea*, *Paroxystoglossa jocasta*, *Sphecodes* sp., *Lasioglossum imitatus*, *Dufourea marginata*, *Dieunomia heteropoda*, *Nomia foxii*, *Andrena argemonis*, *A. miserabilis*, *Perdita albipennis*, *Protandrena cockerelli*, *Pseudopanurgus* sp., *Calliopsis andreniformis*, *Oxaea flavescens*, *Heriades carinata*, *H. variolosa*, *Megachile brevis*, *M. sp.*, *Coelioxys octodentata*, *Osmia l. lignaria*, *Anthidium maculosum*, *Trachusa zebratum*, *Paranthidium* sp., *Dianthidium curvatum sayi*, *Trigonopedia oligotricha*, *Exomalopsis solani*, *E. sp.*, *Ancylosceles armata*, *Monoeca mexicana*, *Nomada* sp., *Triepeolus concavus*, *Holcopasites illinoiensis*, *Ptilothrix sumichrasti*, *Diadasia diminuta*, *D. enavata*, *Melitoma euglossoides*, *Xenoglossa fulva*, *Tetraloniella spissa*, *Florilegus condignus*, *Thygater analis*, *Svastra obliqua*, *Melissodes coloradensis*, *M. agilis*, *Peponapis* sp., *Anthophora walshii*, *A. spp.* 2–3, *Centris vittata*, *C. lanosa*, *Epicharis elegans*, *Xylocopa fimbriata*, *X. virginica*, *X. brasilianorum*, *Ceratina dupla*, *Bombus medius*, *B. ephippiatus*, *B. fraternus*, *Apis mellifera*. **(ii)** *Trigona angustula*, *T. mombuca aequinotiales*, *T. nigra paupera*, *Scraptostrigona postica*, *Dactylurina staudingeri*, *Meliponula beccarii*, *Cephalotrigona capitata*, *Melipona marginata*, *M. schencki picadensis*, *M. scutellaris*, *M. beecheii*, *Lestrimelitta limao*,

Euglossa cupreiventris, *Eufriesea caerulescens*, *E. mussitans*, *Eulaema meriana* (WILLE 1958: 540).

Note. FREUDENSTEIN (1928: 411), contrary to WILLE (1958), described an enlarged posterior end in *Apis mellifera*.

Trait 3. Heart chambers (segmental enlargements):

(i) absent: Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: fig. 1). **(ii) at anterior region of segment:** Ephemeroptera: *Siphylurus lacustris* (DRENKELFORT 1910: 583) however according to MEYER (1931) there are no chambers; Diptera: see “variable” below. **(iii) at about the middle of segment:** Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 79). **(iv) at posterior end of segment (segmental fold):** Dermaptera: *Hemimerus vosseleri*, *Anisolabis maritima*, *Forficula auricularia* (NUTTING 1951: 518); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 518); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 518); Embioptera: *Oligotoma nigra* (NUTTING 1951: 518); Zoraptera: *Zorotypus hubbardi* (NUTTING 1951: 518); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *Diapheromera velii eucnemis* (NUTTING 1951: 518); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Ceuthophilus* sp., *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelsis* sp., *Capnobotes fuliginosus*, *Pediocetes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Tridactylus apicalis*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 518); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951: 518); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoides*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocer-*

cus punctulatus (NUTTING 1951: 518); Isoptera: *Mastotermes darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*, *Nasutitermes costalis* (NUTTING 1951: 518); Diptera: see “variable” below; Lepidoptera: *Papilio machaon* (WASSERTHAL 1980: fig. 9).

Variable. Diptera: (ii) *Anopheles quadrimaculatus* (JONES 1954: 77). (iv) *Drosophila melanogaster* (DEMEREC 1950), *Calliphora vicina* (WASSERTHAL 1999), *Protophormia terraenovae* (ANGIOY et al. 1999: 17, 19).

Trait 4. Course of the dorsal vessel through thorax:

(i) **central, straight:** Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 119, figs. 1, 2); Hymenoptera: see “variable” below; Diptera: *Drosophila melanogaster* (DEMEREC 1950: 444, fig. 12A), *Calliphora vicina* (WASSERTHAL 1999: fig. 1), *Protophormia terraenovae* (ANGIOY et al. 1999: 23). (ii) **dorsal arch:** Hymenoptera: see “variable” below; Lepidoptera: *Attacus atlas* (WASSERTHAL 1981: 2, fig. 2), *Papilio machaon* (WASSERTHAL 1980: 153, fig. 9).

Variable. Hymenoptera: (i) *Leioproctus zonata*, *Hylaeus modestus*, *H. cressoni*, *Augochlorella aurata*, *A. striata*, *Agapostemon sericeus*, *A. sp.*, *Ruizantheda divaricatus*, *Halictus hesperus*, *H. ligatus*, *H. parallelus*, *Megalopta genalis*, *Pseudaugochlora graminea*, *Paroxystoglossa jocasta*, *Sphecodes sp.*, *Lasioglossum imitatus*, *Dufourea marginata*, *Perdita albipennis*, *Protandrena cockerelli*, *Pseudopanurgus sp.*, *Calliopsis andreniformis*, *Oxaea flavescens*, *Heriades carinata*, *H. variolosa*, *Dianthidium curvatum sayi*, *Osmia l. lignaria*, *Coelioxys octodentata*, *Trigonopedia oligotricha*, *Exomalopsis solani*, *E. sp.*, *Ancylusceles armata*, *Nomada sp.*, *Triepeolus concavus*, *Holcopasites illinoisensis*, *Ceratina dupla*, *Trigona angustula*, *T. mombuca aequinotiales*, *T. nigra paupera*, *Dactylurina staudingeri*, *Scrapotrigona postica*, *Meliponula beccarii*, *Cephalotrigona capitata*, *Lestrimelitta limao* (WILLE 1958: 539). (ii) *Apis mellifera* (FREUDENSTEIN 1928: 431), *Colletes punctipennis*, *C. spp. 2–3*, *Ptiloglossa mexicana*, *Dieunomia heteropoda*, *Nomia foxii*, *Megachile brevis*, *M. sp.*, *Anthidium maculosum*, *Trachusa zebratum*, *Paranthidium sp.*, *Monoeca mexicana*, *Ptilothrix sumichrasti*, *Diadasia diminuta*, *D. enavata*, *Melitoma euglossoides*, *Xenoglossa fulva*, *Florilegus condignus*, *Tetraloniella spissa*, *Thygater analis*, *Svastra obliqua*, *Melissodes coloradensis*, *M. agilis*, *Peponapis sp.*, *Anthophora walshii*, *A. spp. 2–3*, *Centris vittata*, *C. lanosa*, *Epicharis elegans*, *Xylocopa fimbriata*, *X. virginica*, *X. brasilianorum*, *Melipona marginata*, *M. schencki picadensis*, *M. scutellaris*, *M. beecheii*, *Apis mellifera*, *Bombus medius*, *B. ephippiatus*, *B. fraternus*, *Euglossa cupreiventris*, *Eufriesea caerulescens*, *E. mussitans*, *Eulaema meriana* (WILLE 1958: 539). WILLE (1958) described intermediate types in *Augochloropsis brachycephala*, *A. diversipennis*,

A. sparsilis, *A. cuprea*, *Augochlora pura*, *Andrena argemonis* and *A. miserabilis*.

Trait 5. Dorsal vessel with a series of loops in first abdominal segment: (i) present, although number of loops varies: Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 426), *Monoeca mexicana*, *Tetraloniella spissa*, *Thygater analis*, *Svastra obliqua*, *Melissodes coloradensis*, *M. agilis*, *Peponapis sp.*, *Anthophora walshii*, *A. spp. 2–3*, *Centris vittata*, *C. lanosa*, *Epicharis elegans*, *Xylocopa fimbriata*, *X. virginica*, *X. brasilianorum*, *B. ephippiatus*, *Apis mellifera*, *Euglossa cupreiventris*, *Eufriesea caerulescens*, *E. mussitans*, *Eulaema meriana* (WILLE 1958: 540). In the opinion of WILLE (1958), a vessel without loops is the general condition in bees.

Trait 6. Dorsal vessel suspension accomplished by:

(i) **two rows of elastic strands:** Megaloptera: *Sialis lutaria* (SELMAN 1965: 493); Hymenoptera: see “note” below; Coleoptera: *Dytiscus marginalis* (KUHLE 1924). (ii) **four rows:** Hemiptera: *Nepa cinerea* (HAMILTON 1931). (iii) **multiple suspensions:** Hymenoptera: see “note” below. (iv) **dorsal vessel connected directly to tergite:** Sternorrhyncha: *Aleurodes* (WIGGLESWORTH 1955).

Note. Hymenoptera: (i) *Apis mellifera* (FREUDENSTEIN 1928: 411, fig. 3). (iii) *Apis mellifera* (WIGGLESWORTH 1955). The information on *Apis* thus is contradictory.

Trait 7. Alary muscles: (i) well-developed (fan-shaped): Ephemeroptera: *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis sp.*, *Ephemerella ignita*, *Caenis sp.*, *Ephemera vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 10); Odonata: *Aeschna sp.* (ZAWARZIN 1911: 485) (only two pairs in abdominal segments 8 and 9); Dermaptera: *Anisoblabis maritima* (NUTTING 1951: fig. 32); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: fig. 5); Phasmatodea: *Diapheromera covilleae* (NUTTING 1951: fig. 28); Orthoptera: see “variable” below; Mantodea: *Paratenodera sinensis* (NUTTING 1951: fig. 3); Blattaria: *Blaberus trapezoides* (NUTTING 1951: fig. 1); Phthiraptera: *Goniocotes compar*, *Lipeurus baculus*, *Nirmus sp.*, *Lipeurus jejunos*, *Gyropus gracilis*, *G. ovalis*, *Menopon pallidum*, *Trichodectes subrostratus* (FULMEK 1917: 7); Hemiptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmostethus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolabrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 380); *Nepa cinerea* (HAMILTON 1931: 1122), *Dysdercus koenigii* (KHANNA 1964: 407), *Rhodnius prolixus* (CHIANG et al. 1990: 10); Megaloptera: *Sialis lutaria* (SELMAN 1965: 494); Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 125, 134); Hyme-

noptera: *Apis mellifera* (FREUDENSTEIN 1928: 436), *Camponotus rufipes* (MARQUES & CAETANO 2001: 554, not described, but visible in their figs. 1, 2); Diptera: see “variable” below. **(ii) consisting of few fibers (two bundles):** Diptera: see “variable” below. **(iii) reduced, single fibers / discrete, non-anastomosing muscle bundles:** Protura: *Acerentomon affine* (FRANÇOIS 2003: 263); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 534, fig. 34). **(iv) broad multiple origin:** Orthoptera: see “variable” below.

Variable. Orthoptera (figure numbers refer to NUTTING 1951): **(i)** *Acheta assimilis* (fig. 7), *Paroecanthus aztecus* (fig. 9), *Hoplosphyrum boreale* (fig. 11), *Oecanthus nigricornis quadripunctatus* (fig. 12), *Ceuthophilus* sp. (fig. 16), *Grylloblatta campodeiformis* (fig. 14), *Stenopelmatus fuscus* (fig. 18), *Liparoscelsis* sp. (fig. 20), *Eremopedes ephippiatus sonorensis* (fig. 22), *Neoconocephalus ensiger* (fig. 24), *Microcentrum rhombifolium* (fig. 26). **(iv)** *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis*, *Tridactylus apicalis* (fig. 30).

Variable. Diptera: **(i)** *Anopheles quadrimaculatus* (JONES 1954: 81), *Calliphora vicina* (WASSERTHAL 1999: 115). **(ii)** *Drosophila melanogaster* with delicate and inconspicuous muscle fibers (DEMEREK 1950: 448).

Trait 8. Attachment of alary muscles to dorsal vessel:

(i) along ventral midline of dorsal vessel: Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 411, figs. 3, 6). **(ii) along ventral and lateral sides:** Megaloptera: *Sialis lutaria* (SELMAN 1965: 493). **(iii) via filaments (dorsal diaphragm and alary muscles pass under the heart):** Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 83, figs. D, E, F); Diptera: *Protophormia terraenovae* (ANGIOY et al. 1999: 25).

Trait 9. Dorsal diaphragm: (i) present and well-developed:

Protura: *Acerentomon affine* (FRANÇOIS 2003: 263) (only in part of abdomen); Ephemeroptera: *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caenis* sp., *Ephemerella vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 12) (abdominal segments 4–10); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *D. velii eucnemis* (NUTTING 1951: 536–537); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Grylloblatta hexadactyla*, *Ceuthophi-*

lus sp., *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelsis* sp., *Capnobotes fuliginosus*, *Pediodes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Tridactylus apicalis*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951); Blattaria: *Blattella vaga*, *Supella supellectilium*, *Symphloce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 536); Hemiptera: *Nepa cinerea* (HAMILTON 1931); Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 131); Megaloptera: *Sialis lutaria* (SELMAN 1965: 494, 499, fig. 10); Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 436, fig. 17), *Camponotus rufipes* (MARQUES & CAETANO 2001: 552); Diptera: *Anopheles quadrimaculatus* (JONES 1954: 81), *Drosophila melanogaster* (DEMEREK 1950: 448), *Calliphora vicina* (WASSERTHAL 1999: 115), *Protophormia terraenovae* (ANGIOY et al. 1999: 17, 21, 25). **(ii) absent or reduced:** Odonata: *Aeschna* sp. (ZAWARZIN 1911: 485); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951: 529, 536); Isoptera: *Mastoterms darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*, *Nasutitermes costalis* (NUTTING 1951: 536); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 536); Embioptera: *Oligotoma nigra* (NUTTING 1951: 536); Zoraptera: *Zorotypus hubbard* (NUTTING 1951: 536); Hemiptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmotethus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolobrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 391).

Trait 10. Constitution of dorsal diaphragm: (i) single membrane:

Protura: *Acerentomon affine* (FRANÇOIS 2003: 263); Orthoptera: see “variable” below; Blattaria: *Blattella vaga*, *Supella supellectilium*, *Symphloce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycno-*

scelus surinamensis, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951); Megaloptera: *Sialis lutaria* (SELMAN 1965: 494); Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 436–437), *Camponotus rufipes* (MARQUES & CAETANO 2001: 552); Diptera: *Drosophila melanogaster* (DEMEREK 1950: 443). (ii) **double membrane in abdomen**: Dermaptera: *Anisolabis maritima*, *Forficula auricularia*, *Hemimerus vosseleri* (NUTTING 1951: 537). (iii) **double membrane, only in segments bearing excurrent ostia**: Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 521–522); Orthoptera: see “variable” below.

Variable. Orthoptera: (i) *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Ceuthophilus* sp., *Tridactylus apicalis*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 521, figs. 18, 44). (iii) *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediectes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve* (NUTTING 1951: 521–522).

Trait 11. Anterior end of dorsal vessel (neck): (i) enclosing esophagus: Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 432, fig. 13). (ii) **bulb-like sinus or sac:** Diptera: see “variable” below. (iii) **coated with air sacs:** Diptera: see “variable” below.

Variable. Diptera: (ii) *Anopheles quadrimaculatus* (JONES 1954: 78). (iii) *Calliphora vicina* (WASSERTHAL 1999: 117, 127) with valve function.

Trait 12, Character 1. Head vascular system: (0) containing a circumesophageal vessel ring branching off the dorsal vessel posterior of the brain: Collembola: *Onychiurus fimentarius* (DENIS 1928: 121); Diplura: *Campodea augens*, *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999: 73); Archaeognatha: *Dilta* sp. (BITSCH 1963: 583–584, fig. 22); Zygentoma: *Thermobia domestica* (CHAUDONNET 1950: 189,

fig. 29); (1) **containing no circumesophageal vessel ring branching off the dorsal vessel posterior of the brain:** all Pterygota. **Missing data:** Protura: *Acerentomon affine* (FRANÇOIS 2003).

Trait 13, Character 2. Ostia with lips: (0) anterior and posterior lips present (incurrent ostia): Ephemeroptera: *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caenis* sp., *Ephemera vulgata*, *Leptophlebia marginata*, *Habro-leptoides modesta* (MEYER 1931: 5); Odonata: *Aeschna* sp. (ZAWARZIN 1911: 484); Dermaptera: *Hemimerus vosseleri*, *Anisolabis maritima*, *Forficula auricularia* (NUTTING 1951: 519); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 519); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 519); Embioptera: *Oligotoma nigra* (NUTTING 1951: 519); Zoraptera: *Zorotypus hubbardi* (NUTTING 1951: 519); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *Diapheromera velii eucnemis* (NUTTING 1951: 519); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Ceuthophilus* sp., *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediectes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Tridactylus apicalis*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 519); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951: 519); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 519); Isoptera: *Mastotermes darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*, *Nasutitermes costalis* (NUTTING 1951: 519);

Phthiraptera: *Goniocotes compar*, *Lipeurus baculus*, *L. jejunos*, *Nirmus* sp., *Gyropus gracilis*, *G. ovalis*, *Menopon pallidum*, *Trichodectes subrostratus* (FULMEK 1917: 8–9); Heteroptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmostethus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolobrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 377), *Nepa cinerea* (HAMILTON 1931: 1122), *Dysdercus koenigii* (KHANNA 1964: 405), *Rhodnius prolixus* (CHIANG et al. 1990: 10); Coleoptera: *Dytiscus marginalis* (KUHLE 1924: 114), *Oryctes nasicornis* (WASSERTHAL 1982: 107); Megaloptera: *Sialis lutaria* (SELMAN 1965: 492, 506); Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 418–419, fig. 9), *Camponotus rufipes* (MARQUES & CAETANO 2001: 554); Diptera: *Anopheles quadrimaculatus* (JONES 1954: 78, fig. 7), *Drosophila melanogaster* (DEMEREK 1950: 443), *Calliphora vicina* (WASSERTHAL 1982: 107; 1999: 112), *Protophormia terraenovae* (ANGIOY et al. 1999: 16, 25). **(1) posterior lip present only (two-way ostia):** Lepidoptera: *Attacus atlas* (WASSERTHAL 1982: 108), *Bombyx mori* (GEROULD 1929); Trichoptera: *Cyrnus trimaculatus*, *Hydropsyche angustipennis*, *Drusus monticola*, *Mystacides azurea* (Tögel & Pass unpubl. data).

Note. Trichoptera: *Mystacides azurea*: in the posterior-most pair of ostia, two lips are present (Tögel & Pass unpubl. data).

Note. Neuroptera: *Chrysopa vulgaris* (Tögel & Pass unpubl. data); Diptera: *Anopheles quadrimaculatus* (JONES 1954: 78), *Culex* sp. (Tögel & Pass unpubl. data); in these taxa in the posterior-most pair of ostia one lip is present (anterior).

Trait 14. Pocket valves: (i) present: Ephemeroptera: *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caenis* sp., *Ephemerella vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 5–6); Odonata: *Aeschna* sp. (ZAWARZIN 1911: 484).

Trait 15. Lips of opposing ostia: (i) widely separated from each other (lateral position of ostia): Ephemeroptera: *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caenis* sp., *Ephemerella vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 4–5); Dermaptera: *Hemimerus vosseleri*, *Anisolabis maritima*, *Forficula auricularia* (NUTTING 1951: 519); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 519); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 519); Embioptera: *Oligotoma nigra* (NUTTING 1951: 519); Zoraptera: *Zorotypus hubbardi* (NUTTING 1951: 519); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *Diapheromera velii eucnemis*

(NUTTING 1951: 519); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphicausta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplophyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Ceuthophilus* sp., *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediectes americanus*, *Pediectes grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Tridactylus apicalis*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 519); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951: 519); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 519); Isoptera: *Mastotermes darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*, *Nasutitermes costalis* (NUTTING 1951: 519); Phthiraptera: *Goniocotes compar*, *Lipeurus baculus*, *L. jejunos*, *Nirmus* sp., *Gyropus gracilis*, *G. ovalis*, *Menopon pallidum*, *Trichodectes subrostratus* (FULMEK 1917: 8); Hemiptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmostethus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolobrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 377); Neuroptera: *Dilar turcicus*, *Isoscelipteron fulvum*, *Chrysopa vulgaris* (= *Chrysoperla carnea*) (Tögel & Pass unpubl. data); Coleoptera: see “variable” below; Diptera: *Calliphora vicina* (WASSERTHAL 1999: 114, fig. 2), *Tipula* sp., *Ctenophora pectinicornis*, *Culex* sp. (Tögel & Pass unpubl. data); Siphonaptera: *Ctenocephalides felis* (Tögel & Pass unpubl. data); Mecoptera: see “variable” below. **(ii) meet along ventral and dorsal midlines (dorso-ventral position of ostia):** Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 415), *Camponotus rufipes* (MARQUES & CAETANO 2001: 554, fig. 3), *Pris-*

tiphora abietina, *Paravespula germanica* (Tögel & Pass unpubl. data). **(iii) meet along the dorsal mid-line (dorsal position of ostia):** Raphidioptera: *Raphidia* (= *Dichrostigma*) *flavipes*, *Inocellia crassicornis* (Tögel & Pass unpubl. data); Megaloptera: *Sialis lutaria* (SELMAN 1965: 492; Tögel & Pass unpubl. data). Coleoptera: see “variable” below; Trichoptera: *Cyrtus trimaculatus*, *Hydropsyche angustipennis*, *Drusus monticola*, *Mystacides azurea* (Tögel & Pass unpubl. data); Lepidoptera: *Nemophora degeerella*, *Polyommatus icarus* (Tögel & Pass unpubl. data); Mecoptera: see “variable” below.

Variable. Coleoptera: **(i)** *Dytiscus marginalis* (KÜHL 1924: 114, figs. v–y), *Nebria castanea*, *Tenebrio molitor* (Tögel & Pass unpubl. data). **(iii)** *Corymbites cupreus* (Tögel & Pass unpubl. data).

Variable. Mecoptera: **(i)** *Boreus hyemalis* (Tögel & Pass unpubl. data). **(iii)** *Panorpa communis* (Tögel & Pass unpubl. data).

Trait 16. Presence of incurrent ostia in: (i) prothorax, mesothorax, metathorax, abdomen: Orthoptera (this condition presumably belongs to the ground pattern of this order: see “variable” below); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonina cubensis* (NUTTING 1951: 518); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panclhora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 518). **(ii) mesothorax, metathorax, abdomen:** Dermaptera: see “variable” below; Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 518); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 518); Embioptera: *Oligotoma nigra* (NUTTING 1951: 518); Zoraptera: *Zorotypus hubbardi* (NUTTING 1951: 518); Orthoptera: see “variable” below; Isoptera: *Mastotermes darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*, *Nasutitermes costalis* (NUTTING 1951: 518); Lepidoptera: see “variable” below. **(iii) metathorax, abdomen:** Dermaptera: see “variable” below; Hymenoptera: see “variable” below; Lepidoptera: see “variable” below. **(iv) entire abdomen, not thorax:** Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *D. velii eucnemis* (NUTTING 1951: 519); Coleoptera: *Dytiscus marginalis* (KÜHL 1924: 88, 89, figs. 1, 2); Megaloptera: *Sialis lutaria* (SELMAN 1965: 504); Hymenoptera: see “variable” below; Diptera: *Anopheles quadrimaculatus* (JONES 1954: 78), *Drosophila melanogaster* (DEMEREK 1950: 443, fig. 12a), *Calliphora vicina* (WASSERTHAL 1999: 112), *Protophormia ter-*

raenovae (ANGIOY et al. 1999: 17). **(v) only posterior abdominal region:** Ephemeroptera: *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemera ignita*, *Caenis* sp., *Ephemerula vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 5); Odonata: *Aeschna* sp. (ZAWARZIN 1911: 484); Phthiraptera: *Goniocotes compar*, *Lipeurus baculus*, *L. jejunos*, *Nirmus* sp., *Gyropus gracilis*, *G. ovalis*, *Menopon pallidum*, *Trichodectes subrostratus* (FULMEK 1917: 6); Hemiptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmostethus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolabrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 377), *Nepa cinerea* (HAMILTON 1931: 1122), *Dysdercus koenigii* (KHANNA 1964: 405), *Rhodnius prolixus* (CHIANG et al. 1990: 10); Siphonaptera: *Ctenocephalides felis* (Tögel & Pass unpubl. data).

Variable. Dermaptera: **(ii)** *Anisolabis maritima*, *Forficula auricularia* (NUTTING 1951: 518). **(iii)** *Hemimerus vosseleri* (NUTTING 1951: 518–519).

Variable. Orthoptera: **(i)** *Ceuthophilus* sp., *Nomotetix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 518). **(ii)** *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Grylotalpa hexadactyla*, *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediocetes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihasitata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve* (NUTTING 1951: 518).

Variable. Hymenoptera: **(iii)** *Leioproctus zonata*, *Hylaeus modestus*, *H. cressoni*, *Colletes punctipennis*, *C. spp. 2–3*, *Ptiloglossa mexicana*, *Augochloropsis brachycephala*, *A. diversipennis*, *A. sparsilis*, *A. cuprea*, *Augochlora pura*, *Augochlorella aurata*, *A. striata*, *Agapostemon sericeus*, *A. sp.*, *Ruizantheda divaricatus*, *Halictus hesperus*, *H. ligatus*, *H. parallelus*, *Megalopta genalis*, *Pseudaugochlora graminea*, *Paroxystoglossa jocasta*, *Sphcodes* sp., *Lasioglossum imitatus*, *Dufourea marginata*, *Dieunomia heteropoda*, *Nomia foxii*, *Andrena argemonis*, *A. miserabilis*, *Perdita albipennis*, *Protandrena cockerelli*,

Pseudopanurgus sp., *Calliopsis andreniformis*, *Oxaea flavescens*, *Heriades carinata*, *H. variolosa*, *Megachile brevis*, *M. sp.*, *Coelioxys octodentata*, *Osmia l. lignaria*, *Anthidium maculosum*, *Trachusa zebratum*, *Paranthidium* sp., *Dianthidium curvatum sayi*, *Trigonopedia oligotricha*, *Exomalopsis solani*, *E. sp.*, *Ancyllosceles armata*, *Monoeca mexicana*, *Nomada* sp., *Triepeolus concavus*, *Holcopasites illinoiensis*, *Ptilothrix sumichrasti*, *Diadasia diminuta*, *D. enavata*, *Melitoma euglossoides*, *Xenoglossa fulva*, *Tetraloniella spissa*, *Florilegus condignus*, *Thygater analis*, *Svastra obliqua*, *Melissodes coloradensis*, *M. agilis*, *Peponapis* sp., *Anthophora walshii*, *A. spp.* 2–3, *Centris vittata*, *C. lanosa*, *Epicharis elegans*, *Xylocopa fimbriata*, *X. virginica*, *X. brasiliatorum*, *Ceratina dupla*, *Trigona angustula*, *T. mombuca aequinotiales*, *T. nigra paupera*, *T. sp.*, *Scraptostrigona postica*, *Dactylurina staudingeri*, *Meliponula beccarii*, *Cephalotrigona capitata*, *Melipona marginata*, *M. schencki picadensis*, *M. scutellaris*, *M. beecheii*, *Lestrimelitta limae*, *Bombus medius*, *B. ephippiatus*, *B. fraternus*, *Apis mellifera*, *Euglossa cupreiventris*, *Eufriesea caerulescens*, *E. mussitans*, *Eulaema meriana* (WILLE 1958: 539). (iv) *Apis mellifera* (FREUDENSTEIN 1928: 409), *Camponotus rufipes* (MARQUES & CAETANO 2001: 554).

Variable. Lepidoptera: (ii) *Attacus atlas* (WASSERTHAL 1981: 2). (iii) *Papilio machaon* (WASSERTHAL 1980: 153, 158, fig. 9).

Trait 17, Character 3. Dorsal vessel: (0) containing only ostia with lips: all orders except those with state (1). (1) **containing in addition ostia without lips (ex-current ostia):** Dermaptera (this condition presumably belongs to the ground pattern of this order: see “variable” below); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 547–549); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 521, figs. 34, 35, 48); Embioptera: *Oligotoma nigra* (NUTTING 1951: 521, fig. 36); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *Diapheromera velii eucnemis* (NUTTING 1951: 547–549); Orthoptera (this condition presumably belongs to the ground pattern of this order: see “variable” below); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonina cubensis* (NUTTING 1951: 547–549); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 547–549).

Variable. Dermaptera: (0) *Hemimerus vosseleri*, *For-*

ficula auricularia (NUTTING 1951: 547–549). (1) *Anisolabis maritima* (NUTTING 1951: 547–549).

Variable. Orthoptera: (0) *Myrmecophila nebrascensis*, *Ceuthophilus* sp. (NUTTING 1951: 547–549). (1) *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediectes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 547–549).

Trait 18, Character 4. Position and number of ex-current ostia within a segment: (0) ventro-lateral and one pair: Dermaptera: *Anisolabis maritima* (NUTTING 1951: 547–549); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 547–549); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *Diapheromera velii eucnemis* (NUTTING 1951: 547–549); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Gryllotalpa hexadactyla*, *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediectes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 547–549); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria mi-*

nor, *Paramusonia cubensis* (NUTTING 1951: 547–549); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 547–549). **(i) ventro-median and unpaired:** Plecoptera: *Pteronarcys californica* (NUTTING 1951: 521, figs. 34, 35, 48) (ventrally, on the mesothoracic ampulla); Embioptera: *Oligotoma nigra* (NUTTING 1951: 521, fig. 36) (three pairs, from mesothorax to first abdominal segment). **Inapplicable:** all taxa except those with states (0) or (1).

Trait 19. Occurrence of paired excurrent ostia in: (i) mesothorax, metathorax and abdomen: Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 547–549); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Grylotalpa hexadactyla*, *Stenopelmatus fuscus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediectes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femurrubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 547–549); (only in thorax): *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus* (mesothorax, metathorax), *Eugaster spinulosus* (mesothorax) (NUTTING 1951: 547–549); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 547–549). **(ii) metathorax and abdomen:** Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *D. velii eucnemis* (NUTTING 1951: 547–549). **(iii) abdomen:** Dermaptera: *Anisolabis maritima* (NUTTING 1951: 547–549); Mantodea: *Paratenodera sinensis*, *Stag-*

momantis carolina, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951: 547–549).

Trait 20. Number of paired abdominal excurrent ostia: (i) six: Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 547–549) (abdominal segments 1–6). **(ii) five:** Orthoptera (this condition presumably belongs to the ground pattern of this order: see “variable” below). **(iii) four:** Dermaptera: *Anisolabis maritima* (NUTTING 1951: 547–549) (segments 2–5); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951: 547–549) (segments 3–6); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 547–549) (segments 3–6). **(iv) three:** Orthoptera: see “variable” below. **(v) two:** Orthoptera: see “variable” below. **(vi) absent:** Orthoptera: see “variable” below. **Variable.** Orthoptera: **(ii)** *Stenopelmatus fuscus*, *Pterophylla camellifolia*, *Liparoscelis* sp., *Capnobotes fuliginosus*, *Pediectes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femurrubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 547–549). **(iii)** *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Grylotalpa hexadactyla* (NUTTING 1951: 547–549); **(iv)** *Acheta assimilis*, *Grylloides sigillatus*, *Paragryllus martini*, *Amphiacusta* sp., *Paroecanthus aztecus* (NUTTING 1951: 547–549). **(v)** *Nemobius f. fasciatus* (NUTTING 1951: 547–549). **(vi)** *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus* (excurrent ostia in meso and metathorax), *Eugaster spinulosus* (excurrent ostia in mesothorax).

Trait 21. Presence of single median excurrent ostia in: (i) mesothorax, metathorax and abdomen: Embioptera: *Oligotoma nigra* (NUTTING 1951: 521). **(ii) mesothorax:** Plecoptera: *Pteronarcys californica* (NUTTING 1951: 521).

Trait 22. Excurrent ostia open into: (i) unpartitioned abdominal hemocoel (dorsal diaphragm absent): Plecoptera: *Pteronarcys californica* (NUTTING 1951: 521); Embioptera: *Oligotoma nigra* (NUTTING 1951: 521); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonnia cubensis* (NUTTING 1951: 529). **(ii) pericardial sinus (above dorsal diaphragm):** Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *D. velii eucnemis* (NUTTING 1951: 521); Blattaria: *Blattella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 528). **(iii) perivisceral sinus (beneath dorsal diaphragm):** Dermaptera: *Anisolabis maritima* (NUTTING 1951: 521); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 521).

Variable. Orthoptera: **(ii)** *Nemobius f. fasciatus*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Grylotalpa hexadactyla* (NUTTING 1951: 521). **(iii)** *Nomotettix cristatus*, *Taenioptoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 521). **(ii) + (iii)** excurrent ostia which are associated with phagocytic organs open above dorsal diaphragm; excurrent ostia without phagocytic organs open beneath dorsal diaphragm: *Acheta assimilis*, *Grylloides sigillatus*, *Paragrillus martini*, *Amphiacusta* sp., *Pterophylla camellifolia*, *Liparoscelis* sp., *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve* (NUTTING 1951: 521).

Trait 23. Structures associated with excurrent ostia: (i) none: Dermaptera: *Anisolabis maritima* (NUTTING 1951: 521); Plecoptera: *Pteronarcys californica* (NUTTING 1951: 521); Embioptera: *Oligotoma nigra* (NUTTING 1951: 521). **(ii) segmental vessels:** Blattaria: *Blattella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 528); Mantodea (this condition presumably belongs to the ground pattern of this order: see “variable” below).

(iii) two layers of dorsal diaphragm without other structures (i.e., phagocytic organs): Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951: 521); Orthoptera: see “variable” below. **(iv) phagocytic organs without other structures (only in abdomen):** Orthoptera: see “variable” below. **(v) phagocytic organs plus excurrent ostia with double dorsal diaphragm (only in abdomen):** Orthoptera: see “variable” below. **Variable.** Mantodea: **(i)** *Litaneutria minor*, *Paramusonnia cubensis* (NUTTING 1951: 529). **(ii)** *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica* (NUTTING 1951: 528).

Variable. Orthoptera: **(i)** *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*, *O. niveus*, *Eugaster spinulosus*, *Nomotettix cristatus*, *Taenioptoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951: 521, 547–549). **(iii)** *Stenopelmatus fuscus*, *Capnobotes fuliginosus*, *Pediocetes americanus*, *P. grandis*, *P. bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare* (NUTTING 1951: 521, 547–549). **(iv)** *Nemobius f. fasciatus*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Grylotalpa hexadactyla* (NUTTING 1951: 521, 547–549). **(v)** *Acheta assimilis*, *Grylloides sigillatus*, *Paragrillus martini*, *Amphiacusta* sp., *Pterophylla camellifolia*, *Liparoscelis* sp., *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve* (NUTTING 1951: 521, 547–549).

Trait 24, Character 5. Vascular system of anterior abdomen: (0) consisting of the dorsal vessel alone: all orders except those with state (1). **(1) consisting of the dorsal vessel and segmental vessels:** Mantodea (this state presumably belongs to the ground pattern of the order, see “variable” below); Blattaria: *Blattella vaga*, *Supella supellectilium*, *Symploce capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951: 528) (6 pairs: mesothorax, metathorax, abdominal segments 3–6).

Variable. Mantodea: **(0)** *Litaneutria minor*, *Paramusonnia cubensis* (NUTTING 1951: 529) (4 pairs of excurrent ostia occur in abdominal segments 3–6). **(1)** *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*

(NUTTING 1951: 528, fig. 3) (4 pairs: abdominal segments 3–6).

Trait 25. Thoracic intracardiac valve: (i) absent: Coleoptera: *Dytiscus marginalis* (KUHL 1924: 118); Megaloptera: *Sialis lutaria* (SELMAN 1965: 492, 504); Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 412). **(ii) present:** Diplura: *Campodea augens*, *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999: 72); Collembola: *Onychiurus fimentarius* (DENIS 1928: 121); Archaeognatha: “Machiloidea” (BÄR 1912: 43); Zygentoma: *Ctenolepisma campbelli*, *Lepisma saccharinum* (BARNHART 1961: 189); Embioptera: *Oligotoma nigra* (NUTTING 1951: 516, fig. 36, plate 16); Phasmatodea: *Carausius morosus* (OPCZYNSKA-SEMBRATOWA 1936: 414).

Note. NUTTING (1951: 516) could not confirm the presence of such valves in Phasmatodea.

Trait 26. Character 6. Dorsal vessel in abdomen: (0) containing an intracardiac valve: Diplura: *Campodea augens*, *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999: 72); Archaeognatha: *Machilis hrábei* (GEREBEN-KRENN & PASS 2000: 286); Zygentoma: *Lepisma saccharina*, *Thermobia domestica* (GEREBEN-KRENN & PASS 2000: 287), *Thermobia domestica* (ROUSSET 1974: 2450, fig. 1); Ephemeroptera: *Epeorus sylvicola*, *Ephemera danica*, *Cloeon* sp., *Rhithrogena* sp., Heptageniidae sp. (GEREBEN-KRENN & PASS 2000: 288), *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caenis* sp., *Ephemera vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 4), *Cloeon dipterum*, *C. binoculata*, *Palingenia longicaudata*, 2 undetermined species (ZIMMERMANN 1884: 405, larvae), *Ephemera diptera* (CREUTZBURG 1885: 246, larvae), *Cloeon dipterum* (POPOVICI-BAZNOȘANU 1905: 679, larvae), *Siphylurus lacustris* (DRENKELFORT 1910: 583–584). **(1) without intracardiac valve:** all orders except those with state (0).

Trait 27. Spongy cells between two adjacent ostia: (i) present: Diptera: *Tipula* sp., *Ctenophora pectinicornis* (Tögel & Pass unpubl. data), *Chironomus* sp., *Tanyptus* sp. (POPOVICI-BAZNOȘANU 1905), *Calliphora vicina* (WASSERTHAL 1999: 128), *Drosophila melanogaster* (DEMEREK 1950). **(ii) absent:** Diptera: *Culex* sp. (Tögel & Pass unpubl. data); and probably all non-dipteran orders.

Trait 28. Region of dorsal vessel posterior to abdominal intracardiac valve: (i) developed as a caudal chamber: Diplura: *Campodea augens*, *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999: 72–73, fig. 1). **(ii) caudal tube:** *Machilis hrábei* (GEREBEN-KRENN & PASS 2000: 286–287, fig. 1). **(iii) caudal pulsatile**

ampulla: Zygentoma: *Lepisma saccharina*, *Thermobia domestica* (GEREBEN-KRENN & PASS 2000: 287, fig. 1), *Thermobia domestica* (ROUSSET 1974: 2450–2451); Ephemeroptera: *Epeorus sylvicola*, *Ephemera danica*, *Cloeon* sp., *Rhithrogena* sp., Heptageniidae sp. (GEREBEN-KRENN & PASS 2000: 287–288, fig. 1), *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caenis* sp., *Ephemera vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 4), *Cloeon dipterum*, *C. binoculata*, *Palingenia longicaudata*, 2 undetermined species (ZIMMERMANN 1884: 405, larvae), *Ephemera diptera* (CREUTZBURG 1885: 246, larvae), *Cloeon dipterum* (POPOVICI-BAZNOȘANU 1905: 679, larvae), *Siphylurus lacustris* (DRENKELFORT 1910: 583–584).

Trait 29. Posterior end of dorsal vessel: (i) opens into vessels of terminal appendages: Diplura: *Campodea augens*, *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999: 72–73, fig. 1); Archaeognatha: “Machiloidea” (BÄR 1912: 41), “Machilide” (BARTH 1963: 197), *Machilis hrábei* (GEREBEN-KRENN & PASS 2000: 286–287, fig. 1); Zygentoma: *Lepisma saccharina*, *Thermobia domestica* (GEREBEN-KRENN & PASS 2000: 287, fig. 1), *Thermobia domestica* (ROUSSET 1974: 2450, fig. 1); Ephemeroptera: *Epeorus sylvicola*, *Ephemera danica*, *Cloeon* sp., *Rhithrogena* sp., Heptageniidae sp. (GEREBEN-KRENN & PASS 2000: 287–288, fig. 1), *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caenis* sp., *Ephemera vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 4, larvae and adults), *Cloeon dipterum*, *C. binoculata*, *Palingenia longicaudata*, 2 undetermined species (ZIMMERMANN 1884: 405, larvae), *Ephemera diptera* (CREUTZBURG 1885: 246, larvae), *Cloeon dipterum* (POPOVICI-BAZNOȘANU 1905: 679, larvae), *Siphylurus lacustris* (DRENKELFORT 1910: 583–584). **(ii) closed:** Protura: *Acerentomon affine* (FRANÇOIS 2003: 263); Collembola: *Anurida* sp., *Podura* sp., *Isotoma* sp., *Orchesella* sp., *Seira* sp., *Lepidocyrtus* sp., *Actaletes* sp., *Sminthurus* sp., *Neanura* sp., *Tomocerus* sp. (FRISH 1978: 177); Dermaptera: *Hemimerus vosseleri*, *Anisolabis maritima*, *Forficula auricularia* (NUTTING 1951); Grylloblattodea: *Grylloblatta campodeiformis* (NUTTING 1951); Plecoptera: *Pteronarcys californica* (NUTTING 1951), *Perla marginata* (SCHWERMER 1914: 301); Embioptera: *Oligotoma nigra* (NUTTING 1951); Zoraptera: *Zorotypus hubbardi* (NUTTING 1951); Phasmatodea: *Anisomorpha buprestoides*, *Diapheromera covilleae*, *Diapheromera velii eucnemis* (NUTTING 1951); Orthoptera: *Acheta assimilis*, *Grylloides sigillatus*, *Paragrillus martini*, *Amphiacusta* sp., *Nemobius f. fasciatus*, *Myrmecophila nebrascensis*, *Cycloptilum comprehendens fortior*, *Hoplosphyrum boreale*, *Paroecanthus aztecus*, *Anaxipha* sp., *Oecanthus n. nigricornis*, *O. n. quadripunctatus*, *O. californicus*,

O. niveus, *Grylotalpa hexadactyla*, *Ceuthophilus* sp., *Stenopelmatus fuscus*, *Eugaster spinulosus*, *Pterophylla camellifolia*, *Liparoscelsis* sp., *Capnobotes fuliginosus*, *Pediodectes americanus*, *Pediodectes grandis*, *Pediodectes bruneri*, *Eremopedes bilineatus*, *E. ephippiatus sonorensis*, *Atlanticus americanus*, *Neoconocephalus ensiger*, *N. robustus*, *N. retusus*, *Orchelimum erythrocephalum*, *O. vulgare*, *Dichopetala brevihastata*, *Insara e. elegans*, *Arethaea* sp., *Scudderia texensis*, *S. furcata furcifera*, *Amblycorypha oblongifolia carinata*, *Microcentrum rhombifolium*, *M. retinerve*, *Tridactylus apicalis*, *Nomotettix cristatus*, *Taeniopoda eques*, *Romalea microptera*, *Brachystola magna*, *Melanoplus femur-rubrum*, *Schistocerca shoshone*, *Dissosteira carolina*, *Encoptolophus sordidus*, *Trimerotropis maritima*, *T. p. pallidipennis*, *Mermiria maculipennis* (NUTTING 1951); Mantodea: *Paratenodera sinensis*, *Stagmomantis carolina*, *S. californica*, *Litaneutria minor*, *Paramusonia cubensis* (NUTTING 1951); Blattaria: *Blatella vaga*, *Supella supellectilium*, *Symphloe capitata*, *Blatta orientalis*, *Eurycotis floridana*, *E. balteata*, *Periplaneta americana*, *P. australasiae*, *Epilampra burmeisteri*, *Panchlora cubensis*, *Pycnoscelus surinamensis*, *Blaberus craniifera*, *B. trapezoideus*, *Compsodes mexicanus*, *Arenivaga erratica*, *Panesthia javanica*, *Macropanesthia rhinocerus*, *Salganea* sp., *Cryptocercus punctulatus* (NUTTING 1951); Isoptera: *Mastotermes darwiniensis*, *Neotermes castaneus*, *Zootermopsis angusticollis*, *Reticulitermes flavipes*, *Nasutitermes costalis* (NUTTING 1951); Phthiraptera: *Goniocotes compar*, *Lipeurus baculus*, *Nirmus* sp., *Lipeurus jejunos*, *Gyropus gracilis*, *G. ovalis*, *Menopon pallidum*, *Trichodectes subrostratus* (FULMEK 1917: 7); Hemiptera: *Dysdercus fasciatus*, *Phonoctonus nigrofasciatus*, *Triatoma infestans*, *Eurygaster integriceps*, *Heterogaster urticae*, *Enoplops scapha*, *Elasmotherus interstinctus*, *Dolichonabis limbatus*, *Leptopterna dolobrata*, *Velia caprai*, *Gerris lacustris* (HINKS 1966: 378–379, 381), *Rhodnius prolixus* (CHIANG et al. 1990: 11); Neuroptera: *Dilar turcicus*, *Isoscelipteron fulvum*, *Chrysopa vulgaris* (= *Chrysoperla carnea*) (Tögel & Pass unpubl. data); Coleoptera: see “variable” below; Hymenoptera: *Apis mellifera* (FREUDENSTEIN 1928: 409, 413), *Camponotus rufipes* (MARQUES & CAETANO 2001: 552), *Pristiphora abietina*, *Paravespula germanica* (Tögel & Pass unpubl. data); Trichoptera: *Cyrnus trimaculatus*, *Hydropsyche angustipennis*, *Drusus monticola*, *Mystacides azurea* (Tögel & Pass unpubl. data); Lepidoptera: *Nemophora degeerella*, *Polyommatus icarus* (Tögel & Pass unpubl. data), *Attacus atlas* (WASSERTHAL 1982: 108); Megaloptera: *Sialis lutaria* (SELMAN 1965: 493, 505; Tögel & Pass unpubl. data); Diptera: see “variable” below; Siphonaptera: *Ctenocephalides felis* (Tögel & Pass unpubl. data); Mecoptera: *Boreus hyemalis* (Tögel & Pass unpubl. data). (iii) opens into

abdominal hemocoel: Coleoptera: see “variable” below; Diptera: see “variable” below. Raphidioptera: *Raphidia flavipes*, *Inocellia crassicornis* (Tögel & Pass unpubl. data) (single unpaired opening).

Variable. Coleoptera: (ii) *Dytiscus marginalis* (KÜHL 1924: 86), *Nebria castanea*, *Corymbites cupreus* (Tögel & Pass unpubl. data). (iii) *Goliathus goliathus*, *Oryctes nasicornis* (WASSERTHAL 1982: 107) (single unpaired opening).

Variable. Diptera: (ii) *Anopheles quadrimaculatus* (JONES 1954: 78), *Drosophila melanogaster* (DEMEREC 1950: 443), *Culex* sp. (Tögel & Pass unpubl. data). (iii) *Calliphora vicina* (WASSERTHAL 1982: 107) (single pair of openings), *Calliphora vicina* (WASSERTHAL 1999: 112, 115) (two pairs of openings), *Protophormia terraenovae* (ANGIOY et al. 1999: 21, 25) (single unpaired opening: “terminal cone”), *Ceromasia* sp., larvae of *Chironomus* and *Tipula* (SNODGRASS 1935; WIGGLESWORTH 1955), *Tipula* sp., *Ctenophora pectinicornis* (Tögel & Pass unpubl. data) (single unpaired opening with lips: “terminal ostium”).

8.2. Antennal circulatory organs

Trait 30. Antennal vessels: (i) **connected directly to dorsal vessel:** Diplura: *Campodea augens* (PASS 1991: 151), *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999: 73). (ii) **connected to frontal sac:** Zygentoma: *Lepisma saccharina* (Gereben-Krenn & Pass unpubl. data); Odonata, larvae only: *Chalcolestes viridis*, *Aeshna cyanea*, *Libellula depressa* (PASS 1991: 151); Lepidoptera: *Sphinx convolvuli* (BROCHER 1920), *Bombyx mori*, *Syntomis phegea*, *Macroglossum stellatarum* (SELVATICO 1887: 562–563), *Bombyx mori* (SCHNEIDER & KAISLING 1959: 124), Sphingidae sp., Saturniidae sp., Papilionidae sp. (VONDRAN & WASSERTHAL 1998: 69), *Artogeia rapae*, *Vanessa cardui*, *Mamestra brassicae*, *Triodia sylvina* (Pass unpubl. data); Trichoptera: *Philopotamus ludificatus* (Pass unpubl. data). (iii) **separate from dorsal vessel:** Archaeognatha: *Machilis* sp. (BITSCH 1963: 621), *Machilis tyrolensis*, *Trigonophthalmus alternatus* (PASS 1991: 151); Dermaptera: *Forficula auricularia*, *Chelidurella acanthopygia*, *Labidura riparia* (PASS 1991: 154); Grylloblattodea: *Grylloblatta campodeiformis* (PASS 1991: 153); Plecoptera: *Protonemoura* sp. juv., *Isoperla* sp. juv., *Dictyogenus fontium*, *Isogenus nubecula*, *Dinocras cephalotes* juv., *Perla marginata* juv., *P. bipunctata* juv. (PASS 1991: 151); Embioptera: *Haploembia solieri*, *Embia contorta*, *Embia thyrenica* (PASS 1991: 153); Phasmatodea: *Carausius* sp. (PASS 1991: 154); Mantodea: *Mantis religiosa* (PASS 1991: 154), Blattaria: *Blaberus craniifer*, *Periplaneta americana* (PASS 1991: 154; PAWLOWA 1895: 9); Isoptera: *Syntermes molestus* (PASS 1991: 154); Orthoptera: *Grylotalpa grylotalpa*,

Oecanthus pellucens, *Acheta domesticus*, *Tachycines asynamorus*, *Tettigonia viridissima*, *Jimenezia elegans*, *Phaneroptera falcata*, *Platycleis grisea*, *Calliptamus italicus*, *Chorthippus parallelus*, *Chrysochraon dispar*, *Stenobothrus nigromaculatus* (PASS 1991: 154–156), *Locusta migratoria* (BAYER 1968); Hemiptera: *Pyrrhocoris apterus*, *Dolycoris baccharum*, *Stenodema laevigatum*, *Lygus saxatilis*, *Ranatra linearis*, *Naucoris cimicoides* (Pass unpubl. data); Coleoptera: *Cionus scrophulariae* (DÖNGES 1954: 67), *Melolontha melolontha* (PASS 1980: 80), *Ocyopus olens*, *Cantharis fusca*, *Carabus intricatus*, *Abax ovalis*, *Coccinella septempunctata*, *Plagionotus arcuatus* (Pass unpubl. data); Strepsiptera: *Stylops* sp., *Xenos* sp. (KINZELBACH 1966), but no antennal circulatory organ found in *Triozocera mexicana* (Pass unpubl. data); Raphidioptera: *Phaeostigma notata*, *Dichrostigma flavipes* (Pass unpubl. data); Megaloptera: *Sialis lutraria* (SELMAN 1965: 511); Neuroptera: *Libelloides macaronius*, *Chrysopa* sp., *Osmylus fulvicephalus*, *Dilar turicus*, *Micromus* sp. (Pass unpubl. data); Hymenoptera: *Xyela alpigena*, *Cephalcia abietis*, *Urocera augur*, *Neodiprion sertifer*, *Diprion* sp., *Xiphidria* sp., *Allantus* sp., *Pristiophora abietina*, *Tenthredo campestris*, *Trachetus tabidus*, *Janus compressus*, *Hartigia linearis*, *Evania appendigaster*, *Diplolepis rosae*, *Andricus* sp., *Leucospis gigas*, *Amblyteles* sp., *Ophion luteus*, *Scolia hirta*, *Mutilla europaea*, *Dasylabris maura*, *Tiphia femorata*, *Paravespula germanica*, *P. vulgaris*, *Nectarinella championi*, *Lasius niger*, *Camponotus* sp., *Mellinus arvensis*, *Sceliphron* sp., *Ampulex compressa*, *Apis mellifera*, *Bombus hortorum*, *Osmia cornuta*, *Andrena humilis* (MATUS & PASS 1999: 98–102), *Apis mellifera* (FREUDENSTEIN 1928: 454–456); Mecoptera: *Panorpa* sp. (Pass unpubl. data); Diptera: *Dilophus febrilis*, *Nemotelus pantherinus*, *Rhagio strigosa*, *Tabanus* sp., *Bombylius venosus*, *Hemipenthes morio*, *Empis tessellata*, *Dolichopus aeneus*, *Pipunculus* sp., *Eristalis pertinax*, *Micropeza corrigiolata*, *Diasemopsis fasciata*, *Limnia fumigata*, *Carnus hemapterus*, *Melophagus ovinus*, *Calliphora erythrocephala*, *Echinomyia fera* (DUDEL 1977, 1978a,b).

Trait 31. Antennal diaphragms: (i) present: Collembola: *Orchesella cincta*, *Tomocerus longicornis*, *Tetrodontophora bielensis* (PASS 1991); Ephemeroptera: *Ephemera danica* juv. (PASS 1991: 151).

Trait 32, Character 7. Antennal vessel wall: (0) uniform: all species listed in trait 30, except those listed under state (1) in the following. **(1) bipartitioned, proximal portion with additional inner layer of transporting cells:** Mantophasmatodea: *Karoophasma biedouwensis* (Pass unpubl. data); Blattaria: *Periplaneta americana* (PASS 1985), *Blaberus craniifer* (Pass unpubl. data); Mantodea: *Mantis religiosa* (Pass

unpubl. data). **Inapplicable:** Protura lacking antennae, species with antennal diaphragms (trait 31) and taxa without any antennal circulatory organs: Odonata, imagines only: *Chalcolestes viridis*, *Platycnemis pennipes*, *Aeshna cyanea*, *Libellula depressa* (PASS 1991: 151); Phthiraptera: *Pediculus* sp. (Pass unpubl. data); Siphonaptera: *Ctenocephalides canis* (Pass unpubl. data); Strepsiptera: *Stylops* sp. (“blasige Aorta”, no antennal vessel, KINZELBACH 1966: 653), *Triozocera mexicana* (no antennal circulatory organ, Pass unpubl. data). **Missing data:** Zoraptera, Psocoptera, Thysanoptera.

Trait 33, Character 8. Antennal ampullae: (0) not connected by a muscle: Archaeognatha; Zygentoma; all Pterygota except those with state (1), “inapplicable” and “missing data”. **(1) connected by an ampullo-ampullary dilator muscle:** Phasmatodea: *Carausius* sp. (PASS 1991: 154); Mantodea: *Mantis religiosa* (PASS 1991: 154); Blattaria: *Blaberus craniifer*, *Periplaneta americana* (PASS 1991: 154; PAWLOWA 1895: 9); Isoptera: *Syntermes molestus* (PASS 1991: 154); Orthoptera: (this condition presumably belongs to the ground pattern of this order: see “variable” below). **Inapplicable:** Diplura, Protura, Collembola, Ephemeroptera, Odonata, Phthiraptera, Siphonaptera, Strepsiptera. **Missing data:** Zoraptera, Psocoptera, Thysanoptera. **Variable.** Orthoptera: **(0)** *Grylotalpa grylotalpa* (PASS 1991: 154–155) **(1)** *Oecanthus pellucens*, *Acheta domesticus*, *Tachycines asynamorus*, *Tettigonia viridissima*, *Jimenezia elegans*, *Phaneroptera falcata*, *Platycleis grisea*, *Calliptamus italicus*, *Chorthippus parallelus*, *Chrysochraon dispar*, *Stenobothrus nigromaculatus* (PASS 1991: 154–156), *Locusta migratoria* (BAYER 1968).

8.3. Leg circulatory organs

Trait 34, Character 9. Leg hemocoel: (if not otherwise indicated, data from Pernstich & Pass, unpubl. data) **(0) not partitioned:** Diplura: *Campodea augens*, *Metajapyx jonicus*; Protura: *Acerentomon* sp.; Collembola: *Tetrodontophora bielensis*; Archaeognatha: *Machilis hrábei*; Zygentoma: *Lepisma saccharina*. **(1) partitioned by diaphragm composed of connective tissue and associated tracheal tubes:** Ephemeroptera: *Cloeon* sp., *Cloeon dipterum*, *Heptagenia* sp., *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella* sp., *Caenis* sp., *Ephemera vulgata*, *Leptophlebia* sp. (MEYER 1931), *Ameletus inopinatus*, *Ephemera danica*, *Rhithrogena* sp.; Odonata: *Libellula depressa*, *Coenagrion* sp.; Dermaptera: *Forficula auricularia*, *Apterygolia media*; Grylloblattodea: *Grylloblatta campodeiformis*; Plecoptera: *Perla marginata* (SCHWERMER 1914), *P. burmeisteriana*, *Nemoura* sp.; Embioptera: *Haploem-*

bia solieri, *Embia tyrrhenica*, *E. contorta*; Phasmatodea: *Baculum extradentatum*, *Exartosoma tiaratum*; Mantodea: *Mantis religiosa*; Blattaria: *Periplaneta americana* (BROCHER 1922); Isoptera: *Bifiditermes* sp.; Orthoptera: *Gryllotalpa gryllotalpa*, *Acheta domesticus*, *Oecanthus pellucens*, *Tettigonia cantans*, *Ephippiger ephippiger*, *Chorthippus* sp., *Locusta migratoria*; Psocoptera: *Dorypteryx pallida*; Phthiraptera: *Linognathus setosus*, *Haematopinus suis*, *Haemodispus ventricosus*; Thysanoptera: *Gynaikothrips ficorum*, *Aelothrips* sp.; Hemiptera: *Rhodnius prolixus*; Coleoptera: *Cetonia aurata*, *Meloe* sp., *Ocypus olens*, *Nebria castanea*, *Dytiscus* sp.; Raphidioptera: *Subilla physodes*, *Phaeostigma major*, *Puncha ratzeburgi*; Megaloptera: *Corydalis cornutus*, *Chauliodes pecticornis*; Neuroptera: *Sialis lutraria* (SELMAN 1965: 516), *Drepanopteryx phalaenoides*, *Osmylus fulvicephalus*, *Chrysopa pallens*; Hymenoptera: *Apis mellifera*, *Xylocopa violacea*, *Osmia bicolor*, *Vespa* sp., *Tenthredo atra*, *Mutilla europaea*, *Mellinus arvensis*, *Amblyetes* sp., *Rhodites rosae*, *Camponotus* sp., *Formica lemani*; Mecoptera: *Panorpa communis*, *P. alpina*, *Boreus hyemalis*; Siphonaptera: *Ctenocephalides felis*; Strepsiptera: *Triozocera mexicana*; Diptera: *Drosophila melanogaster* (SHANBHAG et al. 1992), *Hippobosca* sp., *Musca domestica*, *Bombylius* sp., *Drosophila melanogaster*, *Tabanus bromius*. **(2) partitioned by diaphragm formed by elastic tracheal sac:** Trichoptera: *Mystacides azurea*, *Drusus monticola*, *Hydropsyche angustipennis*; Lepidoptera: *Deilephila elpenor* (WASERTHAL 1982), *Triodia sylvina*, *Nemophora degeerella*, *Zygaena* sp., *Ochlodes venatus*, *Coenonympha pamphilus*, *Polyommatus icarus*, *Notodonta ziczac*, *Siona lineata*, *Agrius convolvuli*, *Vanessa cardui*.

8.4. Wing circulatory organs

Trait 35. Pulsatile apparatus associated with scutellum: **(i) dorsal vessel modification:** Ephemeroptera: *Cloeon* sp., *Cloeon dipterum*, *Heptagenia sulphurea*, *Ephemera vulgata* (MEYER 1931), *Caenis* sp., *Habroleptoides confusa*, *Ecdyonurus* sp., *Ephemera danica* (KRENN & PASS 1994: 9); Odonata: *Anax junius*, *Tramea* sp., *Libellula* sp., *Sympetrum* sp., *Calopteryx* sp., *Lestes* sp. (WHEDON 1938), *Ischnura elegans*, *Platycnemis pennipes*, *Calopteryx virgo* (KRENN & PASS 1994: 9); Dermaptera: *Labidura riparia*, *Forficula auricularia* (KRENN & PASS 1994: 12); Grylloblattodea: *Grylloblatta campodeiformis* (KRENN & PASS 1994: 12); Plecoptera: *Dictyogenus fontium*, *Leuctra* sp., *Nemoura* sp. (KRENN & PASS 1994: 9); Embioptera: *Oligotoma nigra* (KRENN & PASS 1994: 15); Phasmatodea: *Baculum* sp., *Exartosoma tiaratum* (KRENN & PASS 1994: 13); Mantodea: *Mantis religiosa* (KRENN &

PASS 1994: 12); Blattaria: *Periplaneta americana*, *Ec-tobius sylvestris* (KRENN & PASS 1994: 9–12); Isoptera: *Stenidea* sp.; Orthoptera: *Locusta migratoria*, *Chorthippus parallelus*, *Oedipoda caerulescens*, *Miramella alpina*, *Chrysochraon dispar*, *Tetrix* sp., *Pholidoptera griseoptera*, *Metrioptera roeseli*, *Platycleis grisea*, *Acheta domesticus*, *Phaneroptera falcata*, *Leptophyes punctatissima* (KRENN & PASS 1994: 12); Psocoptera: *Graphopsocus cruciatus* (KRENN & PASS 1994: 15); Coleoptera: (meso- and metathorax:) *Nebria castanea*, *N. jockischii*, (only in metathorax:) *Rhagonycha fulva*, *Ctenicera cuprea*, *Coccinella septempunctata*, *Pityogenus chalcographus* (KRENN & PASS 1994/95: 151). **(ii) pulsatile diaphragm attached to dorsal vessel:** Neuroptera; Trichoptera; Lepidoptera: see “variable” below. **(iii) pulsatile diaphragm separate and unpaired:** Hemiptera: *Alydus calcaratus*, *Pyrrhocoris apterus*, *Miris striata*, *Gerris* sp., *Ranatra linearis*, *Nepa cinerea*, *Psylla* sp., *Cercopis sanguinolenta*, *Rhopalisiphum padi*, *Cicadetta montana* (KRENN & PASS 1994: 15); Megaloptera: *Sialis lutraria* (SELMAN 1965: 518), *Corydalis* sp. (KRENN & PASS 1994/95: 151). **(iv) separate and paired:** Lepidoptera: see “variable” below; Diptera: see “variable” below.

Variable. Neuroptera: **(ii)** *Osmylus fulvicephalus*, *Dilar turicus*, *Hemerobius fenestratus*, *Chrysoperla carnea*, *Libelloides macaronius*. **(iii)** *Mantispa styriaca* (KRENN & PASS 1994/95: 151).

Variable. Lepidoptera: **(ii)** *Micropterix calthella* (mesothorax and metathorax), *Triodia sylvina* (mesothorax, metathorax, muscular cord), *Yponomeuta cagnagella* (mesothorax), *Syntomis phegea* (mesothorax), *Mamestra brassicae* (mesothorax). **(iii)** *Nemophora degeerella* (mesothorax and metathorax), *Yponomeuta cagnagella* (metathorax), *Syntomis phegea* (metathorax), *Mamestra brassicae* (metathorax). **(iv)** *Zygaena filipendula* (mesothorax), *Papilio machaon* (mesothorax), *Heliconius melpomene* (mesothorax), *Polyommatus icarus* (mesothorax) (KRENN & PASS 1994/95: 156).

Variable. Diptera: **(iii)** *Tabanus* sp. (THOMSEN 1938: 420), *Tipula* sp., *Bibio marci*, *Aphidoletes aphidimyza*, *Haematopota pluvialis*. **(iv)** *Musca domestica* (THOMSEN 1938: 420), *Bombylius major*, *Eristalis tenax*, *Epi-syrphus balteatus*, *Drosophila immigrans*, *Ceratitis capitata*, *Musca domestica*, *Calliphora* sp. (KRENN & PASS 1994/95: 159).

Variable. Hymenoptera: **(i)** *Urocerus gigas*, *Pristiphora bietina*, *Macrophya* sp., *Neodiprion sertifer*, *Apantheles* sp. **(iii)** *Ophion luteus*, *Paravespula germanica*, *Ampullex compressa*, *Colletes* sp., *Apis mellifera* (KRENN & PASS 1994/95: 151).

8.5. Circulatory organs of abdominal appendages

Trait 36, Character 10. Cercal vessels: (0) connected to dorsal vessel: Diplura: *Campodea augens*, *Catajapyx aquilonaris* (GEREBEN-KRENN & PASS 1999: 73–74, fig. 1). **(1) separate from dorsal vessel:** Archaeognatha: *Machilis hrábei* (GEREBEN-KRENN & PASS 2000: 286–287, fig. 1); Zygentoma: *Lepisma saccharina*, *Thermobia domestica* (GEREBEN-KRENN & PASS 2000: 287, fig. 1), *Thermobia domestica* (ROUSSET 1974: 2450–2451); Ephemeroptera: *Epeorus sylvicola*, *Ephemera danica*, *Cloeon* sp., *Rhithrogenia* sp., Heptageniidae sp. (GEREBEN-KRENN & PASS 2000: 287–288, fig. 1), *Cloeon dipterum*, *C. similis*, *Heptagenia sulphurea*, *Baetis* sp., *Ephemerella ignita*, *Caelis* sp., *Ephemera vulgata*, *Leptophlebia marginata*, *Habroleptoides modesta* (MEYER 1931: 4, larvae and adults), *Cloeon dipterum*, *C. binoculata*, *Palingenia longicaudata*, 2 undetermined species (ZIMMERMANN 1884: 405, larvae), *Ephemera diptera* (CREUTZBURG 1885: 246, larvae), *Cloeon dipterum* (POPOVICI-BAZNO-SANU 1905: 679, larvae), *Siphylurus lacustris* (DRENKEL-FORT 1910: 583–584); Plecoptera: *Perla marginata*, *Dinocras cephalotes*, *Dictyogenus fontium* (PASS 1987: 440–441). **Inapplicable:** all taxa except those in states (0) and (1). **Not known:** Odonata, Dermaptera.

Trait 37. Terminal filament vessel: (i) present and directly connected to dorsal vessel: Archaeognatha: *Machilis hrábei* (GEREBEN-KRENN & PASS 2000: 286–287, fig. 1), “Machilide” (BARTH 1963), “Machiloidea” (BÄR 1912: 41); Zygentoma: *Lepisma saccharina*, *Thermobia domestica* (GEREBEN-KRENN & PASS 2000: 287, fig. 1; ROUSSET 1974: 2450–2451). **(ii) present with enlarged base and not directly connected but very close to posterior end of dorsal vessel:** Ephemeroptera: *Epeorus sylvicola*, *Ephemera danica*, *Cloeon* sp., *Rhithrogenia* sp., Heptageniidae sp. (GEREBEN-KRENN & PASS 2000: 287–288, fig. 1).

Trait 38, Character 11. Cercal hemocoel: (0) not partitioned: in taxa with a cercal vessel (see trait 36) and Mantophasmatodea: *Karoophasma biedouwensis* (Pass unpubl. data); Embioptera: *Haploembia solieri* (Hartl & Pass unpubl. data); Phasmatodea: *Carausius morosus* (Hartl & Pass unpubl. data); Orthoptera: *Locusta migratoria* (Hartl & Pass unpubl. data); Isoptera: sp.indet. (Hartl & Pass unpubl. data). **(1) partitioned by diaphragm:** Grylloblattodea: *Grylloblatta campodeiformis* (Hartl & Pass unpubl. data); Mantodea: *Mantis religiosa* (Pass unpubl. data); Blattaria: *Blattella germanica* (MURRAY 1967), *Periplaneta americana* (Pass unpubl. data). **Inapplicable:** all taxa except those in states (0) and (1). **Not known:** Odonata, Dermaptera.

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Autor(en)/Author(s): Pass Günther, Merl Monika, Gereben-Krenn Barbara-Amina, Szucsich Nikolaus U., Tögel Markus, Plant John

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