

# Antennal circulatory organs in Onychophora, Myriapoda and Hexapoda: Functional morphology and evolutionary implications

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Received March 27, 1990

**Summary.** A comparative investigation of the antennal circulatory organs in representatives of the Onychophora, all subtaxa of the Myriapoda and numerous taxa of the Hexapoda (comprising a total of 54 species) revealed an unexpected diversity in structure and function.

In the Onychophora, antennal vessels exist which are connected to the enlarged anterior end of the aorta dorsal to the brain.

In the Chilopoda, Diplopoda and Symphyla, antennal vessels exist which originate from the dorsal vessel caudal to the brain. They extend under the optic lobes, lateral to the circumoesophageal connectives, into the antennae.

In the Hexapoda, the investigations include representatives of all higher taxa, apart from the Paraneoptera and the Holometabola. Generally, antennal vessels exist. In the Diplura, they originate from the anterior end of the aorta in front of the brain. In all other insects the antennal vessels are separate from the dorsal vessel. Their proximal ends form ampullary enlargements which are attached to the frontal cuticle near the antenna bases. They communicate via valved ostia with the haemolymph sinus in front of the brain. In the Archaeognatha, Zygentoma, Odonata, certain Plecoptera and the Notoptera, no muscles are connected to these organs. In all other groups the ampullae are pulsatile as a result of associated muscles ("antennal hearts"). These muscles diverge widely in their attachments and act either as compressors (Dermaptera) or dilators of the ampullae (Embioptera, Blattopteroidea, Orthopteroidea, and some Plecoptera).

In the Collembola and Ephemeroptera, special antennal circulatory organs are lacking. In some forms the anatomical arrangement of the inner organs, in conjunction with short diaphragms at the antenna bases, apparently leads to a channelling of haemolymph flow. This condition may be explained by the very short antennae of these insects and is considered as a convergent and apomorphic state in these taxa.

The antennal vessels are supposed to be homologous within the Tracheata and to represent the lateral arteries

of the antenna segment. An origin from the dorsal vessel is considered an ancestral state, which was lost in the stem lineage of the Ectognatha. Specific space constraints within the cephalic capsule are discussed as the possible reason for this loss. The evolution of pulsatile antennal circulatory organs in the Neoptera is the result of the association of muscles with the proximal ampullary ends of the antennal vessels. The attachments and innervation of these muscles indicate a derivation from precerebral pharyngeal dilators.

## A. Introduction

The internal anatomy of arthropods has been worked out in considerable detail in selected species, but relatively few comparative studies of organ systems exist. In particular, the circulatory system of the Tracheata has been neglected. Only a few authors have dealt with the complex vascular system in myriapods (Leiber 1935; Fahlander 1938) and many details remain unclear. In insects, most investigations of the circulatory system concentrate solely on the dorsal vessel ("heart"). Only a few works refer to the accessory pulsatile organs which effect haemolymph circulation in longer body appendages such as the antennae, wings, legs (reviews: Jones 1977; Wasserthal 1982; Miller 1985) and cerci (Pass 1987).

The existence of independent circulatory organs supplying the antennae has been reported from a number of representatives of various high-rank insect taxa (see Jones 1977; Pass 1980; Miller 1985) but in general they have escaped detailed analysis. Only the antennal heart of the cockroach *Periplaneta americana* (Linné, 1785), which was the first such organ to be described more closely (Pawlowa 1895), has become the object of detailed morphological (Pass 1985; Pass et al. 1988a) and physiological studies (Hertel et al. 1985, 1988; Pass et al. 1988b, 1989). The anatomical descriptions of other insect antennal hearts indicate a remarkable diversity in

the functional morphology of these organs (see Pass 1980). This circumstance was the reason to initiate a broad comparative investigation, partly presented in this paper. The aim of this study was, on the one hand to collect and analyse the different types of antennal circulatory organs from a structural and functional point of view, and on the other hand to evaluate their systematic distribution with regard to evolutionary and phylogenetic aspects.

The study in hand includes representatives of the Onychophora, all subtaxa of the Myriapoda and all higher taxa of the Hexapoda apart from the Paraneoptera and the Holometabola. The existing descriptions of the antennal circulatory organs in these taxa are widely scattered in the literature and many of them are merely vague (and sometimes incorrect) marginal notes in anatomical head studies. The primary reason for these shortcomings is the small size of these organs and the difficulty with which useful serial sections of the hard head capsule can be obtained using conventional histological methods. Therefore, nearly all of the previously investigated species were re-examined for the present paper with an improved sectioning technique.

## B. Materials and methods

In the species listed below, serial sections for light microscopical evaluation were made through the head in the antennal heart region. The heads were normally fixed with alcoholic Bouin ("Dubosq-Brasil" mixture), but in some cases simple ethanol-fixed material also gave satisfactory results. The specimens were embedded in epoxy resin (ERL-4206) under vacuum impregnation. The objects were serially sectioned (1 µm) on an ultramicrotome (Reichert OmU3) with glass knives or a semi-diamond knife (Diatome, Switzerland). The sections were stained with a mixture of azure II (1%) and methylene blue (1%) in an aqueous borax solution (1%) at 60° C for about 1 min.

Additionally, some large heads were dissected under the stereomicroscope. Prior fixation in a mixture of indigo carmine (0.1 g) dissolved in saturated aqueous picric acid (30 ml), 40% formaldehyde (10 ml) and glacial acetic acid (1 ml) proved to be ideal.

## List of investigated species

(a = adult, j = juvenile, nd = instar not determined)

Onychophora: *Peripatoides novaezealandiae* (Hutton, 1876), a  
 Chilopoda: *Lithobius* sp., nd; *Scutigera coleoptrata* (Linné, 1758), a; *Scolopendra cingulata* Latreille, 1789, a; *Scolopendra morsitans* Linné, 1758, a; *Geophilus* sp., nd  
 Diplopoda: *Pachyiulini* gen. sp., a; *Polydesmus denticulatus* (C.L. Koch, 1847), a; *Haploglomeris multistriata* (C.L. Koch, 1844), a  
 Symphyla: *Scutigereilla* sp., nd  
 Collembola: *Orchesella cincta* (Linné, 1867), nd; *Tomocerus longicornis* (Müller, 1776), nd; *Tetodontophora bielansensis* (Waga, 1842), a  
 Diplura: *Campodea augens* Silvestri, 1936, a  
 Archaeognatha: *Machilis tirolensis* Verhoeff, 1910, a; *Trigonophthalmus alternatus* (Silvestri, 1904), a  
 Zygentoma: *Lepisma saccharina* Linné, 1758, nd  
 Ephemeroptera: *Ephemerella danica* Müller, 1776, j and a  
 Odonata: *Chalcolestes viridis* (Van der Linden, 1825), j; *Platyneemis pennipes* Pallas, 1771, a; *Aeshna cyanea* Müller, 1764, j; *Libellula depressa* Linné, 1758, j  
 Plecoptera: *Protonemoura* sp., j; *Isoperla* sp., j; *Dictyogenus fontium* Ris, 1896, a; *Isogenus nubecula* Newman, 1833, a; *Dinocras*

*cephalotes* Curtis, 1827, j; *Perla marginata* (Panzer, 1799), j; *Perla bipunctata* Pictet, 1833, j  
 Embioptera: *Haploembia solieri* (Rambur, 1842), j and a; *Embia contorta* Ross, 1966, a; *Embia tyrrhenica* Stefani, 1953, a  
 Neuroptera: *Grylloblatta campodeiformis* Walker, 1914, a  
 Dermaptera: *Forficula auricularia* Linné, 1758, a; *Chelidurella acanthopygia* Génè, 1832, a; *Labidura riparia* Pallas, 1773, a  
 Mantodea: *Mantis religiosa* Linné, 1758, a  
 Blattodea: *Blaberus craniifer* (Burmeister, 1838), a; *Periplaneta americana* (Linné, 1758), j and a  
 Isoptera: *Syntermes molestus* (Burmeister, 1839), soldier  
 Phasmatodea: *Carausius* sp., a  
 Orthoptera: *Gryllotalpa gryllotalpa* Linné, 1758, j and a; *Oecanthus pellucens* Adelung, 1902, a; *Acheta domesticus* Linné, 1758, a; *Tachycines asynamorus* Adelung, 1902, a; *Tettigonia viridissima* Linné, 1758, a; *Jimenezia elegans* I. Bolivar, 1881, a; *Phanoptera falcata* (Poda, 1761), a; *Platycleis grisea* (Fabricius, 1781), a; *Calliptamus italicus* Linné, 1758, a; *Chorthippus parallelus* (Zetterstedt, 1821), a; *Chrysochraon dispar* (Germar, 1835), a; *Gomphocerus sibiricus* (Linné, 1767), a; *Stenobothrus nigromaculatus* (Herrich-Schaeffer, 1840); a

## C. Results

The following subsections present the results in systematic order. They are evaluated together with the data from the literature. This combined treatment was chosen in order to provide the greatest degree of clarity. The discussion section is dedicated to morphological and evolutionary aspects of greater scope. Particular value is attached to the photographic documentation of key microscopic sections. The graphs are highly schematic in order to promote an easy understanding of the various functional principles and to facilitate comparisons.

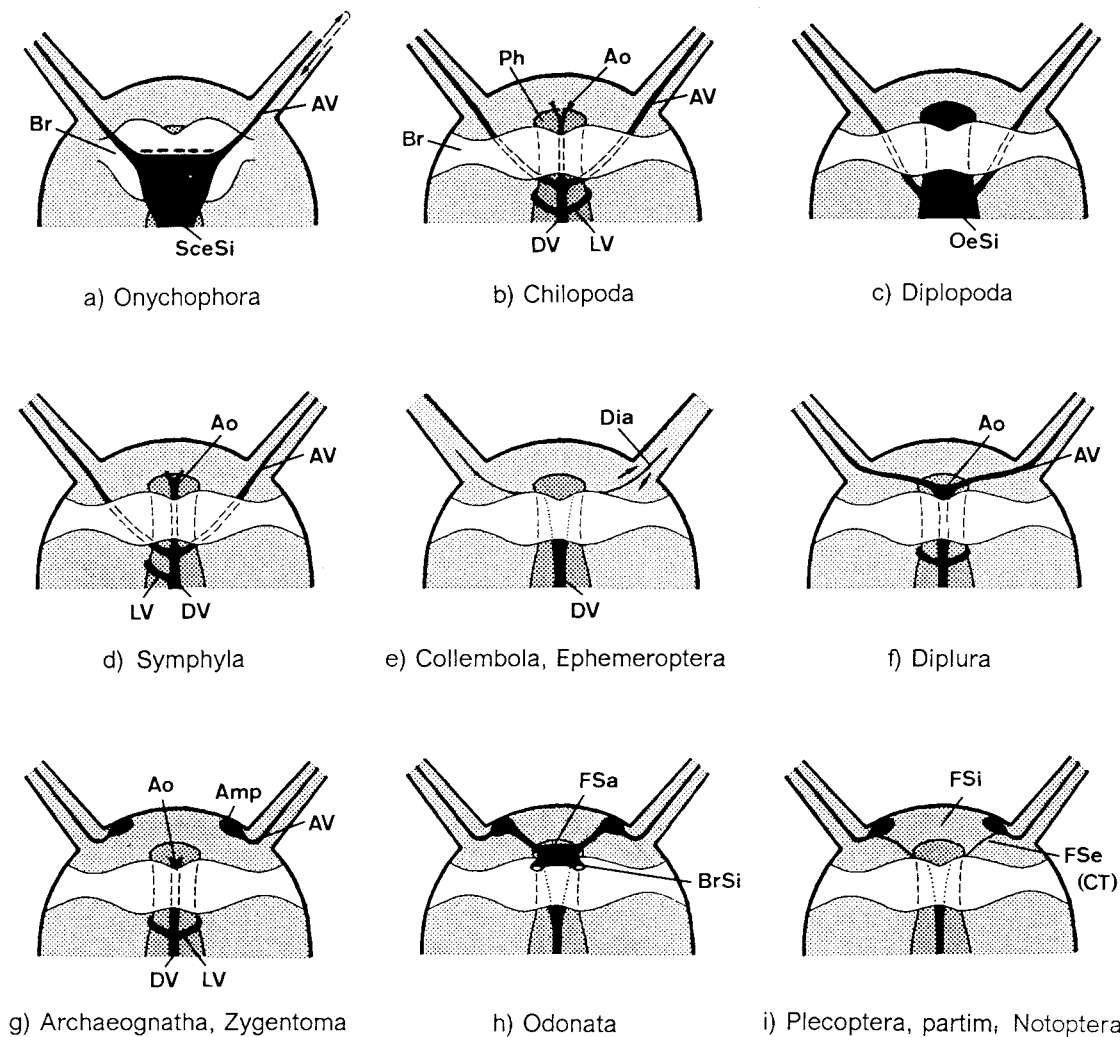
### I. Onychophora (Fig. 1a)

Nothing is known from the literature about antennal circulation in these animals.

In *Peripatoides novaezealandiae*, antennal vessels could be detected extending the length of the antennae. They are connected to the enlarged anterior end of the dorsal vessel. The latter widens distinctly, filling the entire space dorsal to the brain. The ventral part of the aorta wall thereby becomes a horizontal septum delimiting a large supracerebral sinus (Fig. 2a) which opens anteriorly into the general head haemocoel. The antennal vessels arise at the lateral margin of the widened aorta, in a region where the antennal nerve originates (Fig. 2b). Each antennal vessel extends into the antenna dorsally, between the integument and the antennal nerve (Fig. 2c), and opens at the apex. Haemolymph apparently returns to the head via the voluminous antennal haemocoel. The very thin vessel wall contains no obvious muscular elements. However, numerous muscle fibres are loosely arranged around the outside of the vessel (Fig. 2c).

### II. Chilopoda (Fig. 1b)

Most of what is known about the anatomy of the circulatory organs of centipedes can be found in the com-



**Fig. 1 a-i.** Functional types of antennal circulatory organs and their systematic distribution (dorsal view): **a-d, f** antennal vessels connected to dorsal vessel; **e** antennal diaphragms; **g, i** separate antennal vessel with non-pulsatile ampullae, **h** antennal vessel connected to sac-like frontal sinus

parative work of Fahlander (1938), which also contains a detailed and critical survey of the older literature.

In the Lithobiomorpha, the blood vascular system has been best documented in the precise monograph of the anatomy of *Lithobius forficatus* by Rilling (1968). The present reinvestigation of *Lithobius* sp. confirms the above-cited description. In this centipede, the tubular cephalic aorta extends rostrad under the brain, ending in front of the latter. The paired antennal vessels arise laterally from the aorta, caudal to the brain, and run lateroventrally along the antennal nerve into the antennae. The thin vessel wall resembles connective tissue and contains no muscle fibres.

In the Scutigermorpha, essentially the same condition was reported for *Scutigera*, *Thereuopoda* and *Therionema* by Fahlander (1938). The antennal vessels are described as having additional, fine branches extending to the brain. These results were confirmed in the reinvestigation of *Scutigera coleoptrata*.

In the Scolopendromorpha, special pulsatile organs for antennal circulation were reported for *Scolopendra*

*morsitans* by Rajulu (1967). He described two small ampullae, anterior to the brain, from which antennal vessels arise. The ampullae are connected by thin vessels to the anterior end of the aorta. Furthermore, muscle fibres attached to both the ampulla wall and the anterior surface of the brain, considered to be dilators of the ampullae, were described. A thorough reinvestigation of *Scolopendra morsitans* and *S. cingulata*, however, failed to support Rajulu's conclusion. What he noticed is obviously the anterior end of the aorta, which is not involved in antennal circulation. Anterior to the brain the aorta does, in fact, split into two vessels which extend to the antenna bases, but they terminate there. However, as in the other centipedes, vessels arising from the aorta caudal to the brain do enter the antenna (Fig. 3), which was also reported earlier by Dubosq (1898) and Fahlander (1938).

In the Geophilomorpha, antennal circulation has not yet been investigated. The situation found in the present investigation in *Geophilus* entirely parallels that in other centipede groups: antennal vessels connected to the tubular aorta, caudal to the brain.

### III. Diplopoda (Fig. 1c)

The vascular system of diplopods is not as well known as that of chilopods. The only study of circulatory organs in the head (Leiber 1935) does not mention antennal circulation.

In the present paper, representatives of several major groups (Glomerida, Polydesmida, Julida) were investigated. In all cases a comparable situation was found. The dorsal vessel ends in the head in a sinus covering the dorsal side of the oesophagus or even surrounding the latter, as was also seen by Leiber. Antennal vessels arise from this sinus caudal to the brain and extend laterally around the circumoesophageal connectives into the antennae (Fig. 4a–d). The sinus delimiting membrane resembles connective tissue, like the antennal vessels. Sporadically, small short vessels branch from the latter.

### IV. Symphyla (Fig. 1d)

The existence of antennal vessels connected to the cephalic aorta, noted by Tiegs (1940) could be confirmed in the present paper.

In *Scutigere* sp. small antennal vessels arise from the aorta caudal to the brain (Fig. 5a). They run latero-ventrally along the antennal nerves (Fig. 5b) into the antennae. The tubular aorta extends under the brain and opens in front of the latter. This situation strongly resembles that described for centipedes.

### V. Collembola (Fig. 1e)

No evidence exists in the literature for antennal circulation in these insects.

The present study also failed to reveal the existence of antennal vessels or special pulsatile organs. A certain degree of circulation, however, results from the anatomical arrangement of the inner organs, which defines a distinct haemolymph path. In the proximal annule of their antennae, the antennal nerve is partly attached to the integument by thin bands of connective tissue. In this way a kind of diaphragm is formed which divides the antennal haemocoel. The medial sinus communicates with the haemocoel in front of the brain, where haemolymph from the aorta enters. Clearly, haemolymph flows along this path to the antennae and probably returns to the head in the lateral sinus. This separation by the diaphragm, however, is confined to the antenna base. Distally there is no haemocoel separating structure (Fig. 6).

### VI. Diplura (Fig. 1f)

Marten (1939) gives a short note on antennal circulation in these insects. In living *Campodea* he observed distinct haemolymph streams in front of the head leading to

the antennae, which he described as flowing within arterial vessels.

The existence of antennal vessels is confirmed in the present investigation of *Campodea augens*. They are connected to the anterior end of the aorta. The latter extends forward to the front of the brain where it ends with a slight enlargement enclosing the posterior precerebral pharynx dilators. The antennal vessels arise laterally and accompany the antennal nerve up to the tip of the appendage (Fig. 7).

### VII. Archaeognatha and Zygentoma (Fig. 1g)

Antennal circulatory organs have been described for some Machilidae (Bitsch 1963) as well as for *Thermobia* (Chaudonneret 1950). These descriptions are in agreement with the results presented here.

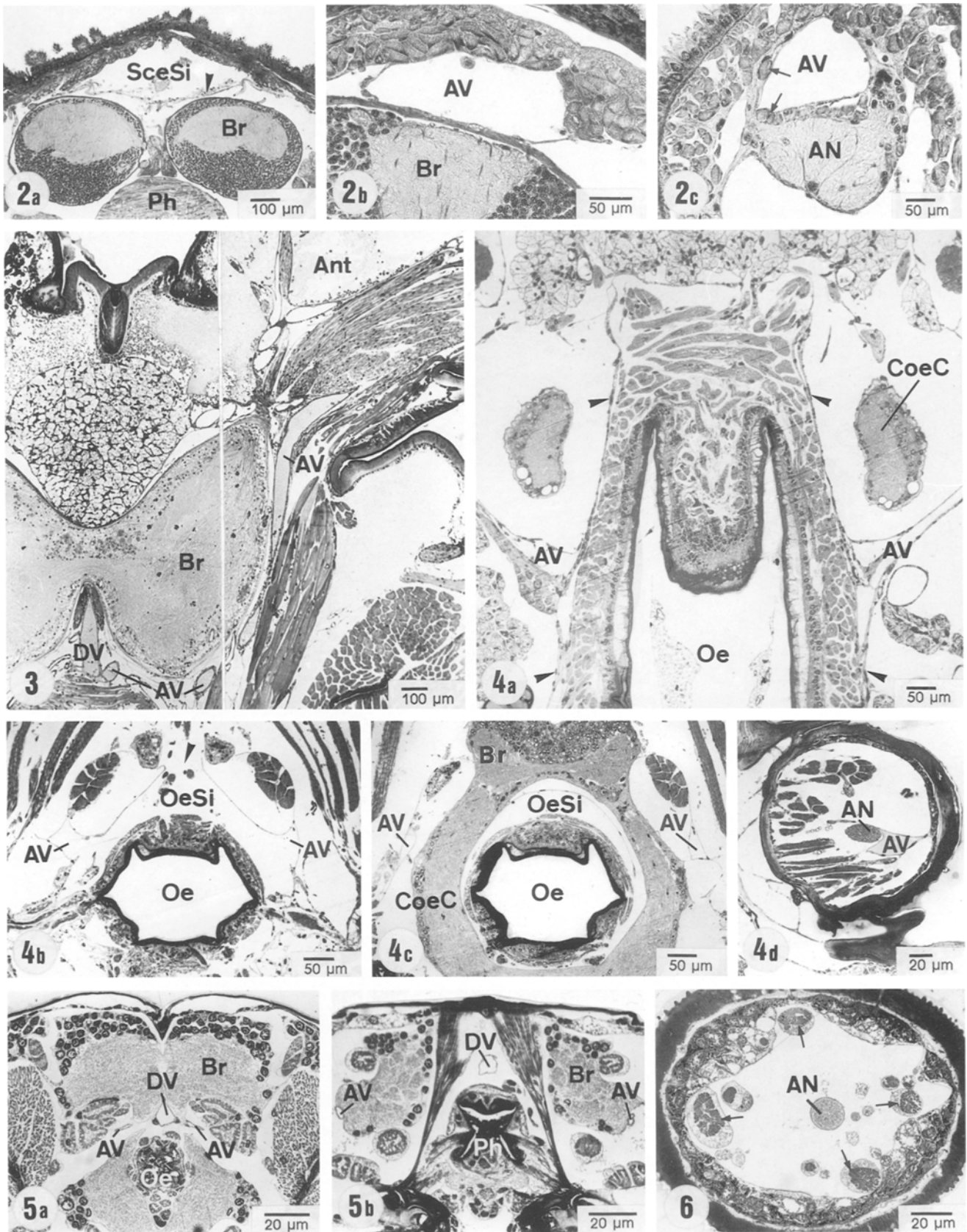
The antennal vessels of these animals are not connected to the aorta. The latter extends to the anterior margin of the brain where it opens into a narrow frontal sinus. The separate antennal vessels bear, at their proximal ends, ampulla-like enlargements (Fig. 8a). No muscle was found to be associated with the ampullae, indicating that they are not pulsatile. They are located anteroventrally in a niche formed by the antennal nerve and communicate via valved ostia with the haemolymph stream coming from the aorta into the frontal sinus (Fig. 8b). This narrow sinus is delimited for the most part by the anterior face of the brain which closely adjoins the frontal integument and completely fills the anteriormost section of the cephalic capsule. The ventral border is formed by the pharynx. Dilatory movements of the latter must compress this sinus thereby further increasing the pressure of the haemolymph stream entering the ampullae. From the antenna the haemolymph returns to the head into a sinus extending caudolateral to the brain. The afferent and efferent antennal haemolymph streams, therefore, are separated by anatomical structures.

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**Figs. 2–6.** Antennal circulatory organs in Onychophora, Chilopoda, Diplopoda, Symphyla and Collembola

**Fig. 2a–c.** *Peripatoides novaeseelandiae* (cross-sections): **a** Head. Enlarged anterior end of aorta forms supracerebral sinus delimited by septum (arrow). **b** Left half of head anterior to **a**. Antennal vessel arises dorsally between brain and musculature of body wall. Nerve fibre area within brain represents antennal nerve root. **c** Antenna. Antennal vessel dorsally between antennal nerve and integument. Note cross-sectioned muscle fibres scattered around vessel (arrows)

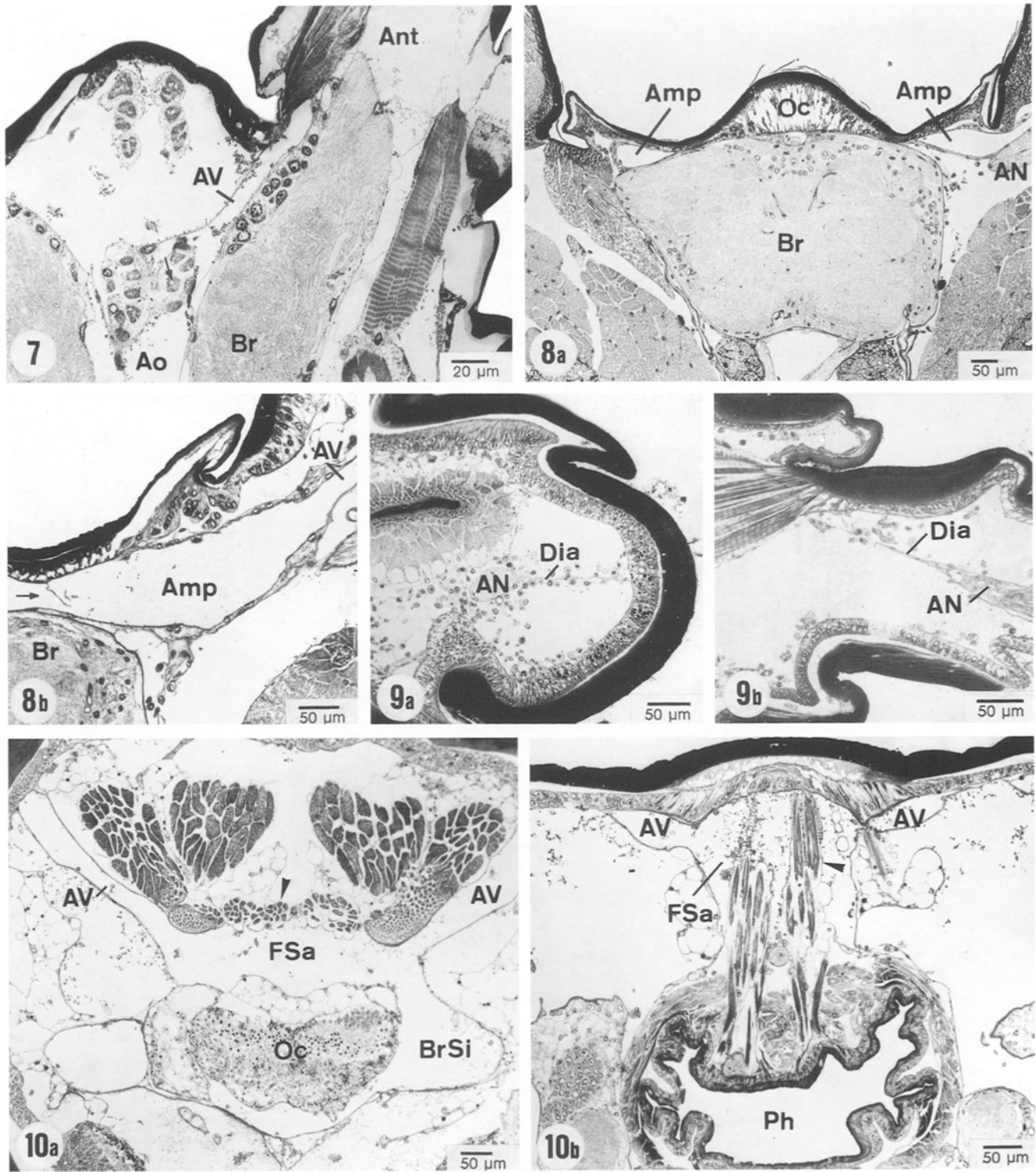
**Fig. 3.** *Scolopendra cingulata*, right half of head (composite picture of two horizontal sections from different levels). Caudal to brain, right antennal vessel originates from dorsal vessel and extends laterally along brain to antenna

**Fig. 4a–d.** *Polydesmus denticulatus*: **a** Head (horizontal section). Antennal vessels originate from oesophageal sinus, delimited by thin connective tissue sheath (arrows). **b** Head posterior to brain (cross-section). Antennal vessels arise from oesophageal sinus; latter with dorsal opening (arrow). **c** Head anterior to **b**. Antennal vessels extend lateral to brain. **d** Antenna. Vessel attached to antennal nerve



**Fig. 5a, b.** *Scutigrella* sp., head (cross-sections): **a** Just behind brain, antennal vessels originate from dorsal vessel. **b** Anterior to **a**. Dorsal vessel extends forward under brain; antennal vessels attached lateroventral to deutocerebral lobes

**Fig. 6.** *Tetodontophora bielensis*, middle region of antenna (cross-section). Antennal haemocoel contains no circulatory organ. *Arrows* indicate antennal muscles



**Figs. 7–10.** Antennal circulatory organs in Diplura, Archaeognatha, Ephemeroptera and Odonata

**Fig. 7.** *Campodea augens*, right half of head (horizontal section). Antennal vessel originate laterally from anterior end of aorta. *Arrow* indicates precerebral pharynx dilators within aorta

**Fig. 8a, b.** *Machilis tirolensis*, head (horizontal sections): **a** Ampullae between frontal cuticle and brain. **b** Right antenna base showing ampulla with ostial valve. *Arrow* indicates direction of probable haemolymph stream from narrow frontal sinus

**Fig. 9a, b.** *Ephemerella vulgata*, antenna base: **a** Cross-section with antennal diaphragm between epidermis and antennal nerve. **b** Sagittal section. Diaphragm extends obliquely in first antennal segment, forming valve

**Fig. 10a, b.** *Chalcolestes viridis*, head of larva: **a** Horizontal section. Antennal vessels originate from sac-like frontal sinus; latter delimited anteriorly by row of pharynx dilators (*arrow*; same muscles longitudinally sectioned in **b**). Lateral branch of sinus extends to dorsal side of brain, centrally ocellus. **b** Cross-section. Sac-like frontal sinus dorsal to pharynx with pharynx dilators located centrally (*arrow*). Antennal vessels arising dorsolaterally from frontal sinus

### VIII. Ephemeroptera (Fig. 1e)

A thorough study of the circulatory system of mayflies can be found in Meyer (1931). In numerous in vivo observations of larvae (*Cloeon dipterum*, *Heptagenia sulphurea* and *Caenis* sp.) he also followed the flow of haemolymph within the antennae. According to these investigations the haemolymph stream from the aorta is divided in the frontal sinus and continues to the antenna bases. A portion enters each antenna medially. In the basal antennal segment the flow changes direction and returns to the head along the lateral side of the antenna. The existence of a pumping apparatus, as postulated earlier by Vayssière (1882) according to in vivo observations of haemolymph flow in the antennae, could not be confirmed by Meyer (1931) on the basis of serial sections.

In the present study the antennal circulation in *Ephemera danica* was investigated. As in most other mayflies the antennae of juvenile and imaginal instars differ considerably in length: mature larva 6.2 mm, imago 1.6 mm. No special pulsatile antennal circulatory organs could be found in either larvae or imagines. The arrangement of the inner organs in conjunction with membranous diaphragms, however, channels the haemolymph into the antennae in a fashion similar to that seen in the Collembola. These diaphragms extend horizontally between the lateral integument of the antennae and the antennal nerve (Fig. 9a). Sagittal sections show that the proximal ends of these structures are attached laterally to the cuticle of the dorsal half of the antenna (Fig. 9b). This valve-like structure indicates that haemolymph must flow distally in the ventral sinus and return dorsally. The diaphragms extend only the length of the first antennal segment. Distally, no evidence of a haemolymph channelling structure could be found. In the imagines the diaphragms are less conspicuous. A similar configuration could also well explain the haemolymph flow observed by Meyer (1931) in the antennae of other mayfly species.

### IX. Odonata (Fig. 1h)

The only reference to antennal circulation in dragonflies was by Brocher (1917). He observed haemolymph movements in the heads of live Zygoptera larvae. In the antennae he found two counter-currents, the medial one flowing distally and the lateral one back into the cephalic capsule. He did not explain, however, the structural basis for the separation of the two currents.

In the investigated larvae a unique functional type of circulatory organ was discovered: antennal vessels continuous with a voluminous, sac-like sinus in front of the brain (Fig. 10a, b). This sinus, in turn, communicates with the aorta via the tubular space formed by the oesophagus and the brain. The sinus also gives off branches to the optic lobes. The membranous sinus wall contains no muscle fibres. Its frontal face is more or less closed by a series of pharynx dilators (Fig. 10a). One can reasonably assume that contraction of these muscles leads to an elevation of the pharynx roof, there-

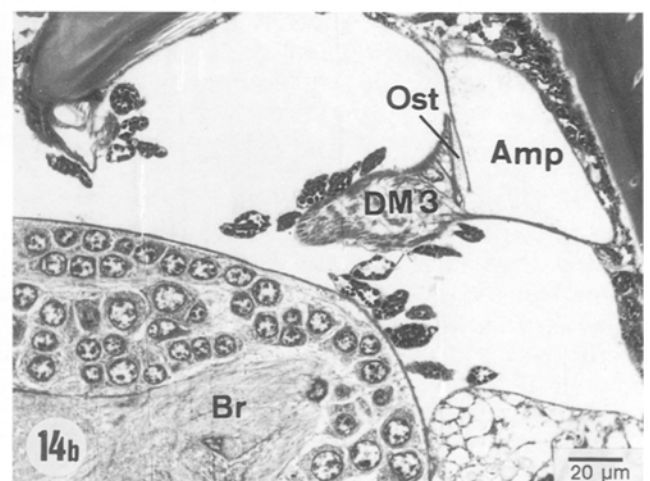
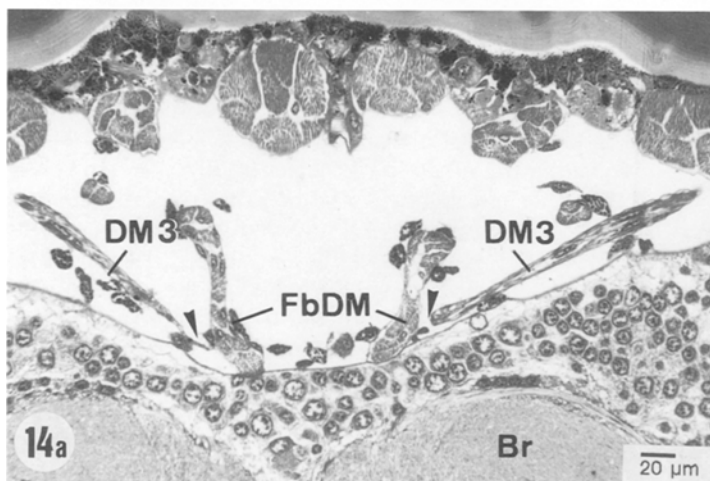
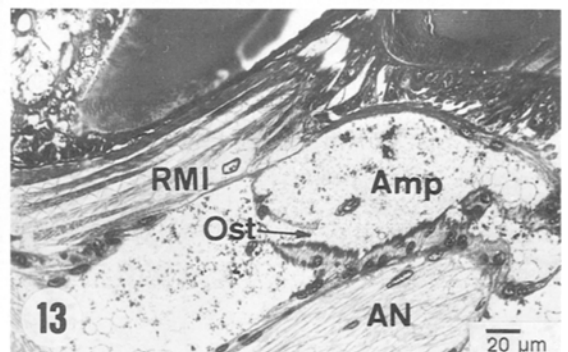
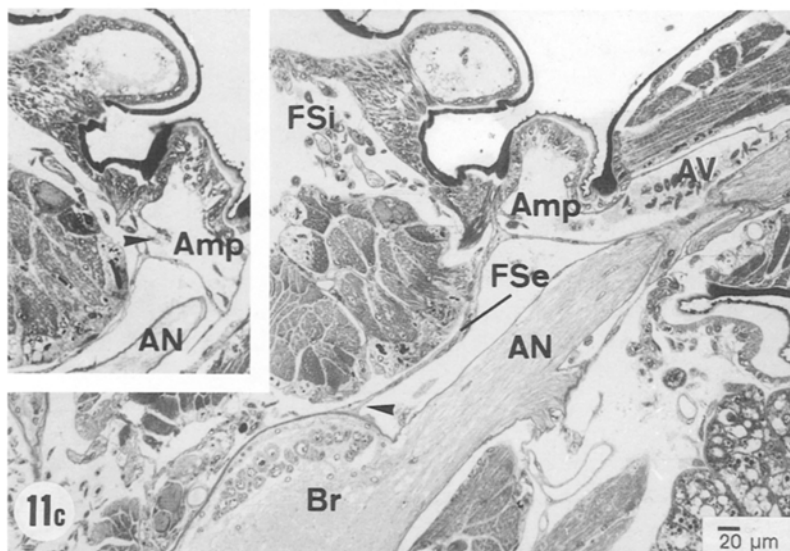
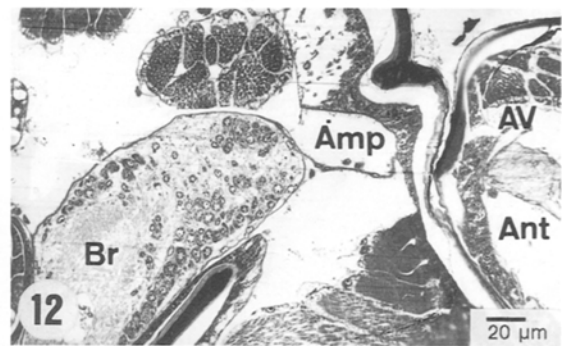
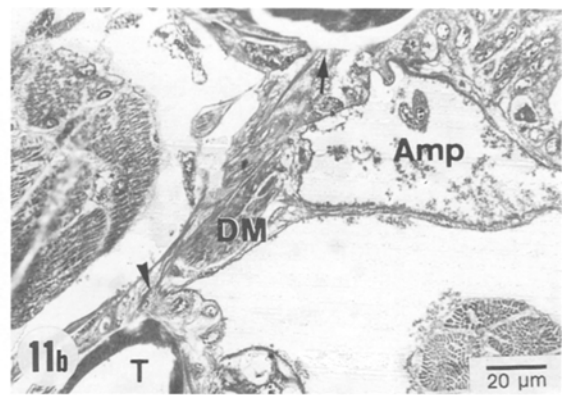
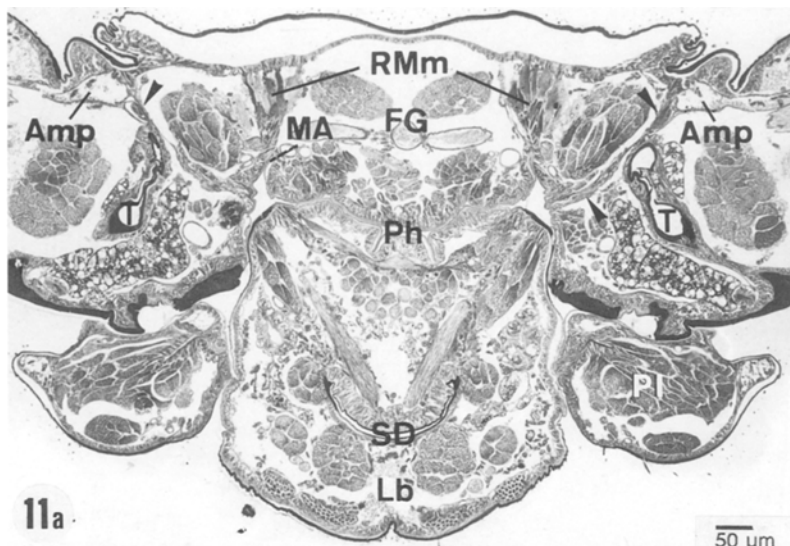
by compressing the frontal sinus (Fig. 10b). This must increase the pressure on the haemolymph originating from the dorsal vessel. Haemolymph is obviously thereby pressed into the antennal vessels. Medial to the antenna bases the vessels widen forming ampullary enlargements which are attached to the frontal cuticle. The diameter of the outgoing vessels into the antennae itself measures only a third of the latter. In the dragonfly imagines, which have very short, bristle-like antennae, no special circulatory organ could be found.

### X. Plecoptera (Figs. 1i, 15a)

Schwermer (1914), describing antennal circulatory organs in *Perla marginata*, found vessels arising from ampullae located at each antenna base. A small bundle of muscle fibres was noted as being attached to both the ampulla and the pharynx, and was considered to be a dilator of the ampullae. The existence of a muscle layer in the ampulla wall was assumed and it was concluded that this would be responsible for the compression of the ampulla. Moulins (1968) described ampullae and antennal vessels in *Nemoura cinerea* but did not mention associated muscles.

The present study is based on a number of stonefly species, for the most part larvae; some imagines are included. Antennal vessels were found in all cases. At their proximal end they bear ampulla-like enlargements which are attached to the cuticle near the anteriomedial margin of the antenna bases. No muscle fibres could be discovered in their walls. With regard to the attachments of the muscles associated with the ampullae in the Plecoptera, functionally important differences were found between the investigated species. It was not possible to positively identify their point of origin in each case. In *Protonemoura* and *Dinocras* no muscle was connected to the ampullae (Figs. 12, 13; functional scheme Fig. 1i). A thin pharyngeal dilator muscle (lateral retractor of the mouth-angle) originates at the cuticle very close to the attachment of the ampullae, but obviously is not involved in the function of the latter (Fig. 13). However, in the other investigated plecopterans (*Isoperla*, *Dictyogenus*, *Isogenus* and *Perla*), apparently only some fibres of the homologous muscle are attached to the frontal cuticle, whereas others are attached to the ampulla wall (Fig. 11 a, b; functional scheme Fig. 15a). We must assume that the latter act as ampulla dilators. The muscle fibres are attached very closely together giving the appearance of a single muscle at first glance. This muscle generally inserts laterally at the pharynx, but in *Isoperla* some fibres are also attached to the anterior tentorial arm (Fig. 11 a, b).

Of particular interest are the large, laterally situated, vertical septa, found in all investigated Plecoptera. They probably consist of connective tissue and extend from the lateral wall of the ampullae to the front of the brain, fusing there with the neural lamella (Fig. 11 c; functional schemes Figs. 1i, 15a). These septa separate a frontal sinus from the central head haemocoel. The haemolymph entering this frontal sinus from the aorta must



**Figs. 11–14.** Antennal circulatory organs of Plecoptera and Ephemeroptera

**Fig. 11a–c.** *Isoperla* sp., head: **a** Cross-section showing ampullae medial to antenna bases. Note muscles extending between ampullae and pharynx (arrows). **b** Magnified detail from right half of **a** to show muscle attachments in detail: some fibres attach to ampulla wall, others to frontal cuticle (tailed arrow); attachment on the other end to tentorium (arrow), some fibres extend to pharynx. **c** Horizontal section. Frontal sinus septum extends from ampulla

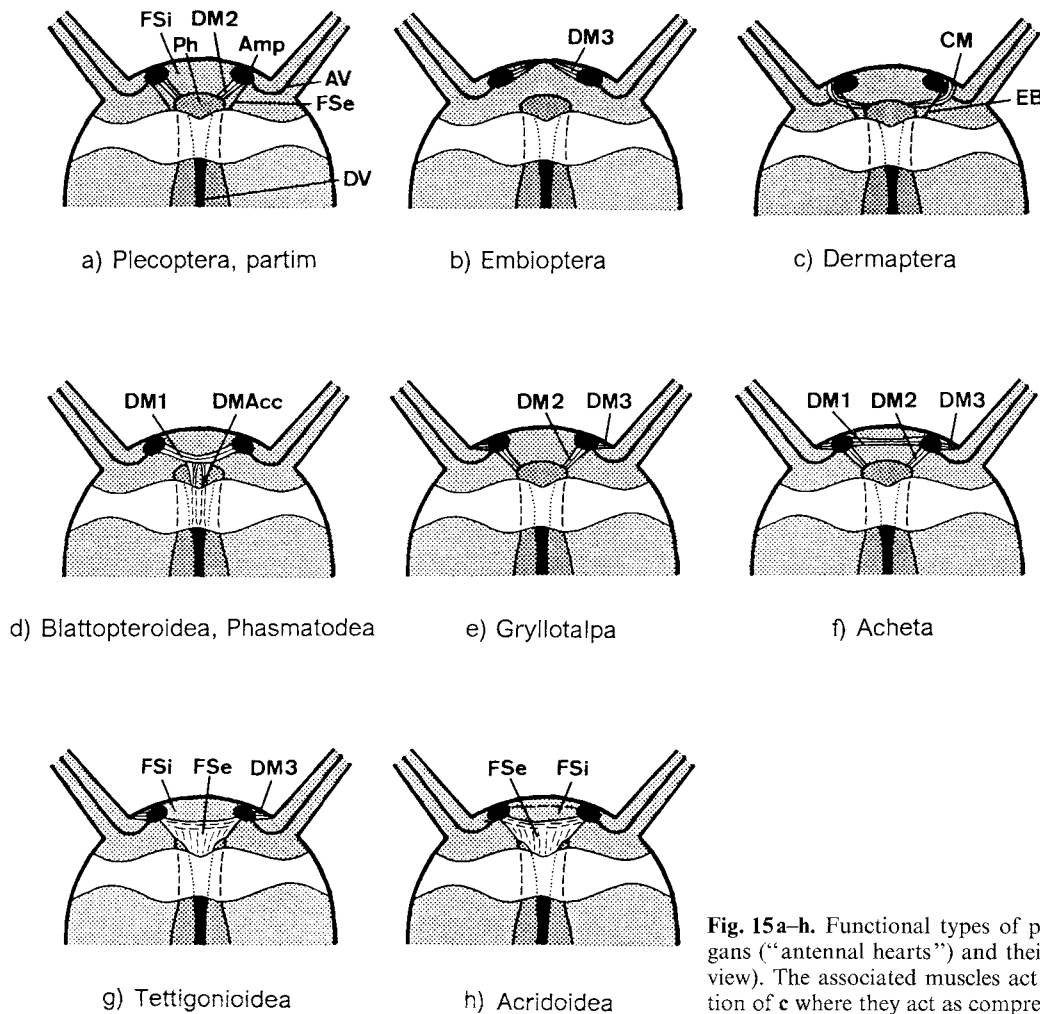
to anterior face of brain fusing with neural lamella (arrow). *Inset* Ampulla at deeper level with valved ostium (arrow)

**Fig. 12.** *Protonemoura* sp. Head, cross-section. Right ampulla without associated muscle

**Fig. 13.** *Dinocras cephalotes*. Head, horizontal section. Ampulla with valved ostium. Note lateral retractor muscle of mouth-angle attached to cuticle next to ampulla

**Fig. 14a, b.** *Embia contorta*: **a** Horizontal section directly beneath cuticle. Dilator muscles of ampullae originate in front of brain close to fronto-buccal pharynx dilator muscles (arrows). **b** Right ampulla in detail with valved ostium and attached dilator muscle





**Fig. 15a-h.** Functional types of pulsatile antennal circulatory organs ("antennal hearts") and their systematic distribution (dorsal view). The associated muscles act as ampulla dilators with exception of **c** where they act as compressors

leave it in a caudal direction, mainly ventrolateral to the pharynx. Another pathway is via the antennae. Haemolymph enters the ampullae through a slit-shaped ostium and, after passing through the antennal vessel, returns in the antennal haemocoel to the head caudal to the aforementioned septum. The afferent and efferent antennal haemolymph streams are therefore separate. Anatomical considerations allow the conclusion that this flow is amplified by pharynx dilations, as they must increase the pressure in the frontal sinus. Thus, antennal circulation in species lacking pulsatility of their ampullae by dilator muscles is also conceivable.

#### XI. Embioptera (Fig. 15b)

The short description of Rähle (1970), the only author to note the existence of special antennal circulatory organs in this group, is of special interest. In *Embia ramburi*, he found antennal vessels with ampullae near the antenna bases. These ampullae were described as being connected to the aorta by small vessels. Associated muscles were lacking.

Reinvestigations of two *Embia* species and *Haploembia solieri*, however, gave a very different result. Al-

though the existence of antennal vessels and ampullae was confirmed, a connection to the aorta could not be established. The supposed connecting vessels are clearly muscles (Fig. 14a, b). They are very thin and consist of only a few fibres, so that in certain sections the connective sheath may resemble a thin vessel. Rähle was probably not completely sure of his observation, as he pointed out that these vessels always had a collapsed appearance. The attachments of these muscles are at the ampulla wall (Fig. 14b) and the frontal cuticle, caudal to the posterior fronto-buccal muscles (Fig. 14a). They no doubt act as dilators of the ampullae.

#### XII. Notoptera (Fig. 1i)

Nothing is known so far about antennal circulation in these insects.

In *Grylloblatta campodeiformis*, antennal vessels with ampullae near the antenna bases could be found. Small tissue bands extend between the ampullae and the anterior of the brain. They consist of cells with long-ovoid nuclei and a fibrous like appearing cytoplasm. These bands are believed to be connective tissue. From the position and attachments one can compare this band

with the frontal septum of the Plecoptera or a similar structure in the Dermaptera. However, while these are wide, membranous structures it is a relatively small and compact tissue strand in *Grylloblatta*. It probably serves only as a suspending structure for the ampullae within the head capsule. There is no muscle associated with the ampullae of grylloblattids, indicating that they are not pulsatile.

### XIII. Dermaptera (Fig. 15c)

Moulins (1969) discovered the antennal hearts in these insects but provided only a cursory description. Their very unusual functional morphology was described in detail in a separate paper (Pass 1988). The anatomy of this organ is identical in all species examined. As in most other insects, ampullae are connected to antennal vessels. The unique feature is the function of the muscle associated with each ampulla: it compresses the latter upon contraction. The attachments of this muscle are at the frontal cuticle, lateral to the ampulla, and at the mouth-angle of the pharynx. Diastole of the ampulla is obviously effected by the elasticity of the ampulla wall and by a thin band of connective tissue running from the lateral wall of the ampulla to the anterior face of the brain, where it fuses with the neural lamella. This band resembles in structure and attachments the frontal septum described in the Plecoptera.

### XIV. Mantodea, Blattodea and Isoptera (Fig. 15d)

These three taxa, which are generally considered as a monophyletic entity (Blattopteroidea sensu Hennig 1969), can be dealt with collectively here, as form and function of their antennal hearts are virtually identical. While the structure of these circulatory organs has been studied in detail in cockroaches (Pawlowa 1895; Pass 1985; Pass et al. 1988a), their existence in the other two groups was not yet known.

The present paper documents the organs of *Mantis religiosa* (Fig. 16a, b). The two ampullae are attached to the frontal cuticle medial to the antenna bases. They are interconnected by a prominent ampullo-ampullary muscle, acting as a dilator of the ampullae (Fig. 16a). Two delicate muscle strands are attached to the middle of the transverse muscle. They extend under the brain backwards to the dorsal wall of the aorta (Fig. 16 b); they act as accessory ampulla dilators. The ampulla wall resembles that of *Periplaneta* and contains no muscle fibres.

### XV. Phasmatodea (Fig. 15d)

According to the description of Scholl (1969) the two ampullae in *Carausius morosus* are interconnected by a prominent ampullo-ampullary dilator muscle (unfortunately termed "*musculus connectivus antennae*" despite the correct description of its attachments to both ampul-

lae). He further described intersecting muscle fibres which are attached to the middle of the dilator muscle and run posteriorly below the brain to the dorsal side of the aorta.

The present study fully confirms the above description. Both the structure and function of this organ corresponds to that in cockroaches.

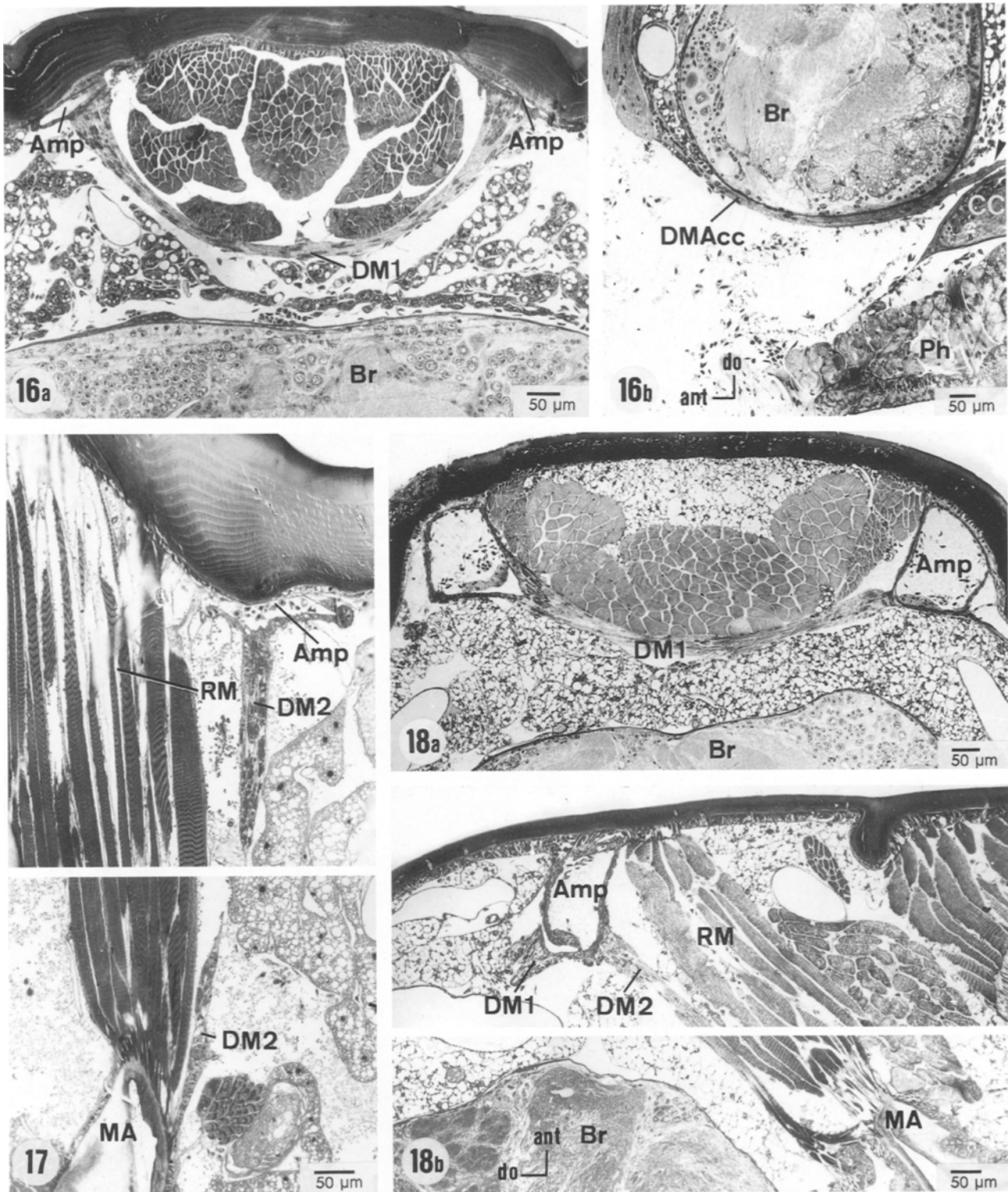
### XVI. Orthoptera (Fig. 15e-h)

The only orthopteran known so far to have an antennal heart is *Locusta migratoria* (Bayer 1968).

In the present study such organs could be demonstrated in all investigated species although in different configurations. Especially remarkable is their condition in the Grylloidea. *Gryllotalpa* has relatively small ampullae to which thin muscles are attached (Fig. 17; functional scheme Fig. 15e). For the most part they insert at the mouth-angle of the pharynx next to the major retractor of the latter. In addition, some muscle fibres extend from the ampullae lateral to the adjacent cuticle. Both muscles work as ampulla dilators. In *Acheta*, beside such ampullo-pharyngeal and ampullo-frontal muscles a prominent ampullo-ampullary muscle is also present (Fig. 18a, b; functional scheme Fig. 15f). In *Oecanthus* the antenna bases lie close to the midline; all types of ampullary muscles are present as in *Acheta*. However, there are very few ampullo-pharyngeal muscle fibres, whereas both the ampullo-ampullary and the ampullo-frontal muscles are well developed (Fig. 19a, b).

In the Tettigonioidea the space between the frontal cuticle and the brain is very largely filled with fat tissue and large tracheal sacs which delimit, together with thin connective tissue membranes, distinct haemolymph channels. Directly beneath the cuticle there is a relatively small frontal sinus receiving haemolymph from the aorta. The delimiting septum encloses the two ampullae and extends laterad from the latter to the cuticle (Figs. 20, 21). Between the ampullae the septum is coated by a layer of ampullo-ampullary fibres which differs in thickness between individual species. A few muscle fibres attached to this septum extend caudally; their second attachment could not be followed with certainty (Fig. 20; functional scheme Fig. 15g). Other muscle fibres are attached to both the ventrolateral wall of the ampullae and the lateral pharynx. In addition bundles of muscle fibres extend from the ampullae dorsad to the frontal cuticle. The mechanism itself is not easy to interpret. Assuming simultaneous activity of all these muscles a contraction must lead not only to a dilation of the ampullae but also to an expansion of this sinus. Upon their relaxation the sinus wall must return to the original state, which results in its compression, thereby probably forcing haemolymph into the ampullae.

The condition described in detail for the antennal heart in *Locusta migratoria* (Bayer 1968) was found to be valid in essence for all Acridoidea investigated in the present paper (functional scheme Fig. 15h). It resembles in many respects that described for the Tettigonioidea. The aorta enters a large frontal sinus formed by the

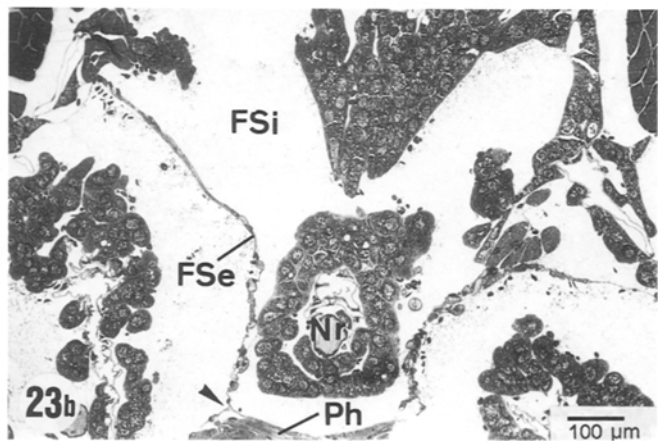
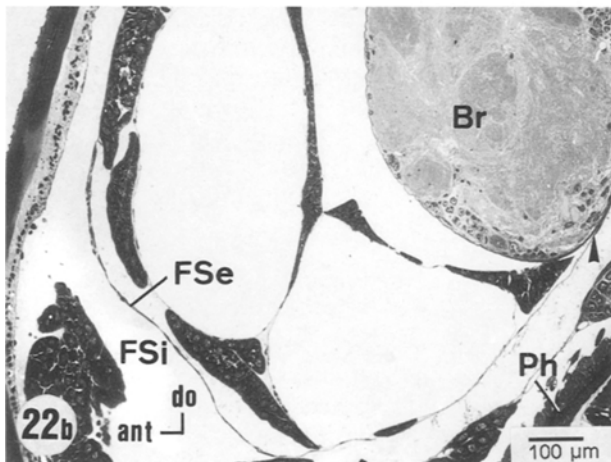
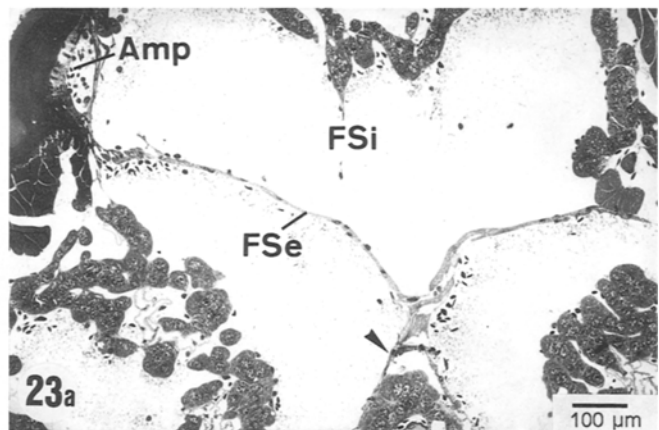
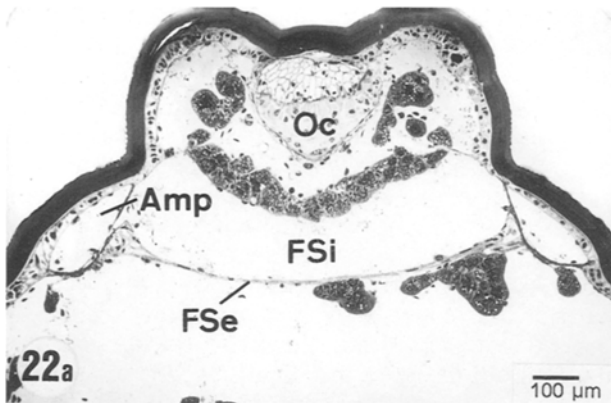
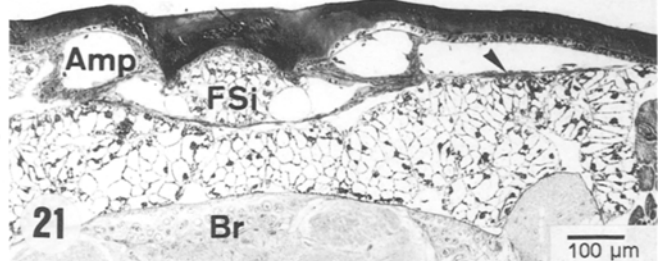
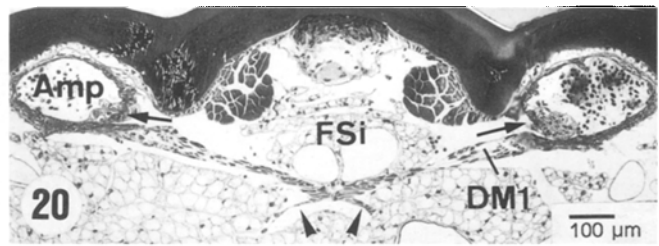
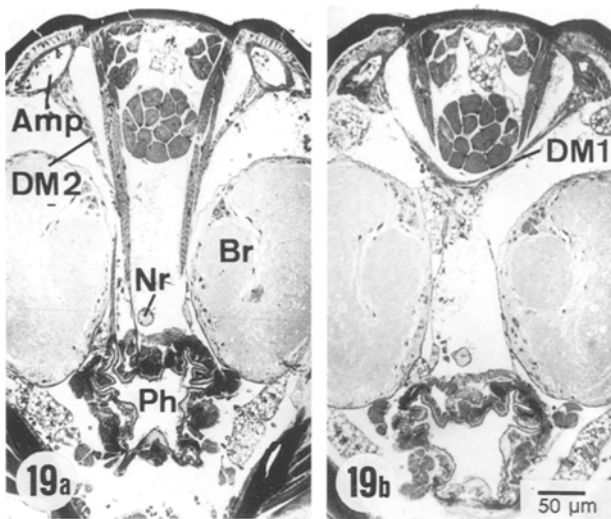


**Figs. 16–18.** Antennal circulatory organs in Mantodea and Orthoptera

**Fig. 16a, b.** *Mantis religiosa*, head: **a** Cross-section. Ampullae attached to frontal cuticle and interconnected by ampullo-ampullary dilator muscle. **b** Sagittal section. Accessory dilator muscle extends closely under brain to anterior end of aorta (arrow)

**Fig. 17.** *Gryllotalpa gryllotalpa*, detail of right half of head (composite picture of two cross-sections from different levels). Small right ampulla with ampullo-pharyngeal muscle inserting at mouth-angle of pharynx. Medial to latter, prominent retractor muscle of mouth-angle

**Fig. 18a, b.** *Acheta domestica*, head: **a** Cross-section. Ampullae interconnected by ampullo-ampullary dilator muscle. **b** Sagittal view (composite picture of two sections from different levels). In addition to ampullo-ampullary muscle ampullo-pharyngeal dilator inserting at mouth-angle of pharynx



**Figs. 19–23.** Antennal circulatory organs in Orthoptera

**Fig. 19a, b.** *Oecanthus pellucens*, head (cross-sections): **a** Ampullae with ampullo-pharyngeal dilator muscles **b** Posterior to **a**. In addition to ampullo-pharyngeal muscle, ampullo-ampullary dilator **Fig. 20.** *Jimenezia elegans*, head (cross-section). Thin ampullo-ampullary muscle between ampullae encloses frontal sinus; additional small muscle bundles extend backward (arrows). Note position of ostia of ampullae (tailed arrows)

**Fig. 21.** *Tachycineta asynamoros*, head (cross-section). Frontal sinus enclosing ampullae; septum extends laterad from ampulla to cuticle (arrow)

**Fig. 22a, b.** *Chorthippus parallelus*, head: **a** Horizontal section. Frontal sinus delimited by septum with few ampullo-ampullary muscle fibres. **b** Sagittal section. Frontal sinus septum extends backwards to brain fusing with neural lamella (arrow)

**Fig. 23a, b.** *Calliptamus italicus*, head (horizontal sections): **a** at higher level than **b**. Thin muscular frontal septum delimits funnel-like frontal sinus enclosing ampullae. **b** Attachment of lateral part of frontal septum at pharynx (arrow)

**Table 1.** Morphometric data on antenna and antennal circulatory organ in some Ensifera species

	Antenna length (mm)	Ampulla diameter ( $\mu\text{m}$ )	Ampulla wall thickness ( $\mu\text{m}$ )
<i>Gryllotalpa gryllotalpa</i>	17	120	8
<i>Oecanthus pellucens</i>	35	100	12
<i>Acheta domesticus</i>	36	160	10
<i>Platycleis grisea</i>	65	160	14
<i>Phaneroptera falcata</i>	70	160	10
<i>Tachycines asynamorus</i>	97	150	11
<i>Tettigonia viridissima</i>	108	220	16
<i>Jimenezia elegans</i>	190	250	21

projecting medial part of the frons (Figs. 22a, 23a). It contains tracheae and fat tissue which form, together with connective tissue membranes, distinct sinuses and channels. In *Locusta* Bayer described these structures in detail and termed them "Frontalsack". However, these formations do not have such a closed sac-like appearance in most species. The membranes are partly coated by layers of muscle fibres. Thicker bundles exist, spanning both between the ampullae (Fig. 22a) and between ampullae and pharynx (Fig. 23b). Additional fibres extend under the brain and seem to be attached to its neural lamella (Fig. 22b), others probably to the anterior end of the aorta. In contrast to the Tettigonioidae no ampullo-frontal muscles could be demonstrated.

Due to the wide range of antennal lengths in the Orthoptera there is the possibility of testing for a possible correlation between antenna configuration and circulatory organ structure. Morphometric data were gathered for a number of species of the Ensifera including antenna length, ampulla diameter and ampulla wall thickness (Table 1). The three cited parameters are reasonably correlated; the most conspicuous difference is the ampulla wall thickness. The antennal vessels extend throughout the antennae. The wall thickness in the proximal region is in most cases remarkably thicker than distally. Its inner diameter remains rather constant, e.g. in *Jimenezia* with an extreme antenna length of 190 mm (body length 32 mm!) it measures ca. 20  $\mu\text{m}$  the whole antenna length.

## D. Discussion

### I. Comparative morphological aspects

The following is an attempt to order the diversity of the antennal circulatory organs according to criteria of their functional morphology.

#### 1. Antennal vessels connected to dorsal vessel

In the Onychophora, Myriapoda and Diplura, the antennal vessels are connected to the dorsal vessel, albeit with certain differences in their point of origin. The wall of

the antennal vessels in all these taxa is generally very thin and no muscle fibres could be detected by light microscopy. Ultrastructural investigations of other fine blood vessels in a few myriapods revealed solitary muscle fibres which, however, do not seem to have significant contraction power; they are very thin and contain only a few irregularly arranged myofilaments (Seifert and Rosenberg 1973, 1978). The loose network of the muscle fibres around the outside of the antennal vessels in the Onychophora no doubt permits a certain degree of contractibility. However, the main driving force for haemolymph flow in the antennal vessels of these animals probably stems from the pumping activity of the dorsal vessel.

#### 2. Antennal vessel connected to frontal sinus

Apart from the Diplura, the antennal vessels in insects are always separate from the aorta. The proximal ends of the vessels communicate with the haemolymph sinus in front of the brain. In the Archaeognatha, Zygentoma, certain Plecoptera and the Notoptera, no muscle could be found associated with the ampulla-like basal enlargements of the antennal vessels. Antennal circulation can be explained here only by the specific anatomical arrangement of the internal organs in the head which channels the afferent and efferent haemolymph streams. The frontal sinus is separated from the general haemocoel and directs the haemolymph flow from the aorta to the ampullae. The function of the ampullae is obviously only to funnel the haemolymph into the antennal vessels; their ostia valves hinder backflow. Dilatory movements of the pharynx probably amplify flow pressure through the antennae. The sac-like frontal sinus in the Odonata probably functions in a comparable way. While its wall lacks contractile elements, it may still function as a pump: pharynx dilations must compress the sac and force haemolymph into the antennal vessels.

#### 3. Pulsatile organs ("antennal hearts")

Most of the insects investigated possess antennal vessels with proximal ampullae and associated muscles. These ampullae are pulsatile and act as pumps.

The configuration and histology of the various ampullae are very similar. Each has a slit-shaped ostium formed by the overlapping walls of the ampullae which is closed during systole. In the first description of this organ, the ampulla wall was considered to contain muscle fibres, no doubt due to its pulsatile character (Pawlowa 1895). This interpretation was subsequently repeated in the descriptions of other antennal hearts (*Perla*: Schwermer 1914; *Periplaneta*: Arnold 1960; *Rhodnius*: Pinet 1964; *Sialis*: Selman 1965). However, the minuteness of these structures precludes a definite determination by light microscopy. Ultrastructural investigations in *Periplaneta americana* revealed that the ampulla wall contains no muscular elements (Pass 1985). They possess thick external laminae consisting of a fine network of

filaments having the appearance and staining properties of elastic fibres. They obviously lend a certain degree of elasticity to the ampulla wall, the basis of which acts antagonistically to the associated muscles.

It should be noted that the ampullae may be neurohaemal organs in addition to their function as circulatory pumps. In *Periplaneta americana*, numerous terminals of neurosecretory cells have been found in the ampullae walls (Beattie 1976; Pass et al. 1988a). Their secretions are apparently pumped into the antennae and may play a role in the antennal sensory system (Pass et al. 1988b). The existence of such neurohaemal structures in the ampullae of other insects must be verified by further ultrastructural research. Earlier descriptions of ampulla innervation in *Thermobia* (Bitsch 1963) and *Machilis* (Chaudonneret 1950) may, in fact, refer to such neurohaemal structures.

The various antennal hearts differ in the attachments and functions of the associated muscles. From a functional point of view one can distinguish between ampulla compressors and ampulla dilators. In the insects investigated here, compressor muscles were found only in the Dermaptera. They attach to the frontal cuticle and the pharynx. All others possess only dilator muscles. At one end they attach to the ampulla wall itself; the attachment site of the other end varies: ampullo-pharyngeal, ampullo-frontal and ampullo-ampullary dilator muscles can be distinguished. In some cases, small muscles extend from the ampullo-ampullary muscle under the brain to the end of the aorta (accessory dilator muscle of the Blattopteroidea and Phasmatodea). A special condition can be seen in certain Orthoptera, where the frontal septum is coated with thin muscle layers, which probably causes not only simultaneous dilation of the lumina of the ampullae, but also an expansion of the frontal sinus.

In all insects the antennal vessels extend the length of the antennae and open at the tip. Muscle fibres could not be demonstrated for the vessel wall. In *Periplaneta*, small additional distal pores have been described (Pawlowa 1895; Kapitskii 1984); their existence, however, could not be confirmed (Pass 1985). The antennal vessels may also show regional differentiation. Their proximal portion can be enlarged in diameter (Dermaptera) or curled, forming a kind of glomerule (Blattodea). Ultrastructural investigations of *Periplaneta americana* revealed a remarkable difference in the wall of the two vessel regions: the distal portion consists of a very thin epithelium without a conspicuous structure, while the wall of the proximal portion consists of a transport epithelium (Pass 1985). The cells of the latter are probably involved in iono- or osmoregulation of the haemolymph pumped into the antennae.

#### 4. No special organs, eventually antennal diaphragms

In virtually all forms with longer antennae distinct circulatory organs are present. Ephemeroptera larvae are an exception which may prove the rule as their antennae reach up to 6.2 mm, yet lack accessory circulatory pumps. In insects with very short antennae a circulatory

motor is obviously not a physiological requirement and diffusion alone can probably effect haemolymph exchange. Additionally, the arrangement of the inner organs in the head capsule can result in a channelling of the haemolymph flow. This may be supported by small diaphragms of connective tissue dividing the haemocoel at the base of each antenna into an afferent and an efferent sinus. Such is the situation in the Collembola, but also in the imagines of the Ephemeroptera and Odonata, which both have very short, bristle-like antennae.

## II. Evolutionary and phylogenetic aspects

### 1. Onychophora

The similarity of the dorsal hearts in both the Onychophora and the Euarthropoda is said to be synapomorphic and one of the characters which establish their phylogenetic relationship (Boudreaux 1979; Weygoldt 1986). Only the dorsal heart has previously been described in onychophorans; the existence of antennal vessels remained undetected. The connection of the latter to the dorsal vessel resembles, from a functional point of view, the condition in the Myriapoda and the Diplura. However, the extension of the widely enlarged anterior end of the aorta dorsal to the brain, and the origin of the antennal vessels above the root of the antennal nerve, distinguishes this condition from that found in any of the Antennata. Furthermore, the association of muscle fibres with the vessel wall is a feature unique to these animals. A homology with the antennal vessels of the Euarthropoda seems therefore rather questionable, although not inconceivable.

### 2. Myriapoda

Whether the various myriapod subtaxa represent a mono- or a polyphylum is a point of controversy just as are their relationships to insects (Tiegs and Manton 1958; Dohle 1980, 1988). Considering the present state of the arguments, I agree with Dohle (1988) that these questions should be left open for the time being. Despite these discussions a complex vascular system is generally considered a plesiomorphic state for the Tracheata (Boudreaux 1979; Dohle 1985). This interpretation is based on the concept that the common ancestor of the arthropods derives from an annelid-like ancestor which had a segmented body with septal partitions and a closed vascular system which enabled bulk fluid transport along its length. The evolution of the mixocoel in arthropods makes such a vascular system unnecessary and would coincide with its regression (see Ruppert and Carle 1983; for a different view see Clarke 1979).

Apart from the Pauropoda, which lack any circulatory organ at all (Tiegs 1947), all myriapod groups have a relatively complex vascular system. One characteristic trait is the existence of lateral arteries originating from the dorsal vessel. This metameric element is found in

a different configuration in the Chilopoda, Diplopoda and Symphyla (Leiber 1935; Fahlander 1938; Tiegs 1940). With regard to the antennal vessels it can be supposed that they represent the lateral arteries of the antenna segment. Their points of origin caudal to the brain may be explained as a result of the ontogenetic development of the antenna segment. It is namely primarily postoral or paraoral in origin; the typical adult preoral condition is reached later in ontogeny (see Siewing 1963b).

The configuration of the anterior aorta varies distinctly from group to group. While in the Chilopoda and the Symphyla it extends as a tube under the brain, in Diplopoda it forms an oesophageal sinus. The latter appears rather to be derived, while a tubular cephalic aorta probably represents an ancestral state.

Remarkably, a similar situation with regard to antennal circulation is also found in some of the Crustacea. Only for the Malacostraca have special organs for the antennae been reported. There are antennal vessels in almost all subtaxa, which originate as lateral arteries from the aorta caudal to the brain (reviews: McLaughlin 1983; Schram 1986). The interpretation of this apparent similarity depends primarily on where one stands regarding the mono- or polyphyly of arthropods (Anderson 1973; Manton 1977; Weygoldt 1986; Briggs and Fortey 1989). However, if the arthropods are a monophylum and the Malacostraca a group in the Crustacea with an ancestral condition of the circulatory system (Siewing 1956; Schram 1986), then it seems reasonable that their antennal arteries are homologous to those of the myriapod subtaxa and represent the plesiomorphic condition of this character within the Mandibulata. Therefore, the specific anatomy of the antennal circulatory organs in the various subtaxa of the Myriapoda cannot contribute towards the argument concerning their mono- or polyphyletic status.

### 3. Entognatha and Ectognatha, part: non-Neoptera

Nearly all insects possess antennal vessels which are structurally very similar to those in other arthropods. It is suggested that they be considered primary circulatory organs. The lack of vessels in the Collembola, Ephemeroptera and the imagines of the Odonata seem to be derived states which may be explained by the fact that the short antennae in these insects makes such organs unnecessary.

Only in the Diplura are the antennal vessels directly connected to the dorsal vessel; in all others insects they are separate. In contrast to the situation in the myriapod subtaxa and the Malacostraca, the point of origin of the dorsal vessel in the Diplura differs in being not behind but in front of the brain. When one considers the distinct constructional changes that have occurred within the head capsule at the phylogenetic beginning of insects, a shift of the point of origin of the antennal vessels or even a disconnection from the dorsal vessel due to several developmental and spatial constraints is imaginable. On the one hand there is the development

and enlargement of the brain which would narrow the antennal vessel path. On the other hand there is the evolution of head endoskeletons which coincides with considerable changes in the muscle arrangement (see Snodgrass 1960; Matsuda 1965; Denis and Bitsch 1973; Weidner 1982). Furthermore, the distribution of the two different antenna types within the Tracheata should be mentioned in this context. The segmented or muscled antenna is supposed to be the more ancestral type and is present in all myriapod subtaxa, the Collembola and the Diplura. The annulated or non-muscled type is restricted to the Ectognatha and is one of the most important constitutive characters of this monophyletic group (Imms 1939; Remington 1955; Kristensen 1981). Remarkably, only in the latter do antennal vessels exist which are separate from the dorsal vessel.

In the Archaeognatha and the Zygentoma the anatomy of the antennal vessels and the ampullary proximal ends is nearly identical. This also holds true for other peculiarities of the circulatory organs in the head. Both groups possess a pair of lateral vessels originating from the dorsal vessel behind the brain, surrounding the gut and joining to form a short suboesophageal vessel (Chaudonneret 1950; Bitsch 1963); such a vessel arch has not been found in the head of any other insect.

Within the Pterygota the antennal diaphragms in the Ephemeroptera are unique and may therefore be considered a derived and autapomorphic character. The antennal vessels in the Odonata, which only could be demonstrated in juvenile instars, can be interpreted as plesiomorphic; the frontal sac to which they are connected, however, represents an autapomorphic character.

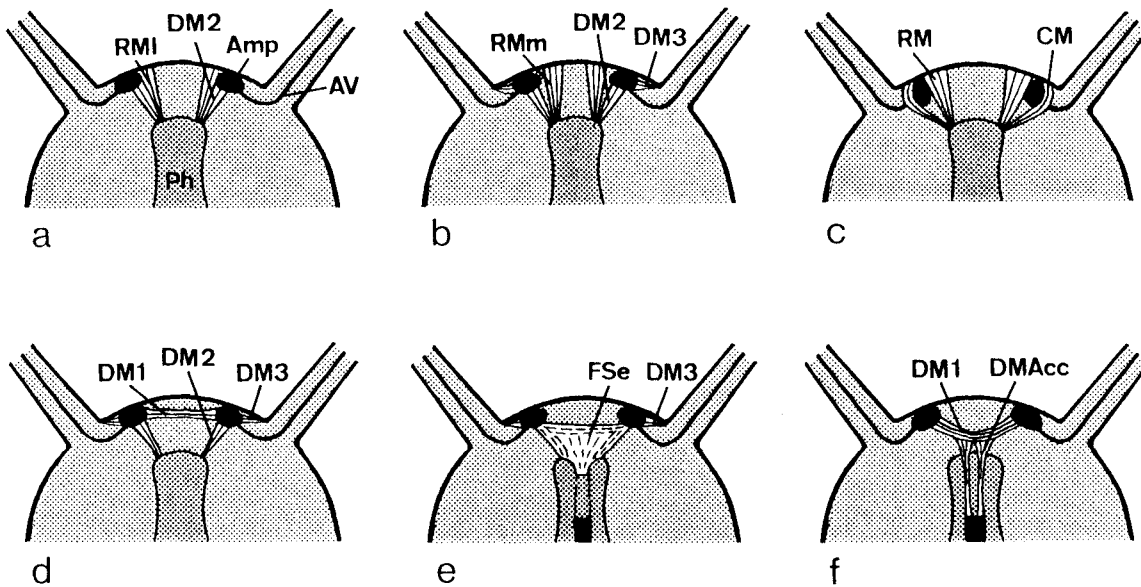
### 4. Neoptera, part: non-Holometabola

Apart from the Notoptera and certain Plecoptera, pulsatile circulatory organs for the antennae are present in all of the investigated Neoptera. While only moderate differences were found in the arrangement and function of the ampullae and antennal vessels, the associated muscles vary greatly in their attachment sites. Furthermore, the distinct arrangement of elastic connective tissue structures which act as antagonists to these muscles is important for the functional differences in this organ.

*a) Muscle attachments and innervation.* The comparative investigation of position and innervation of some ampullary muscles makes a homologization possible despite different attachments. Furthermore, a close relationship between these muscles and the precerebral fronto-pharyngeal dilator muscles becomes apparent.

The derivation of the ampulla muscle from a pharyngeal dilator muscle is best illustrated in the Plecoptera. The thin lateral retractor of the mouth-angle is spatially closely related to, but functionally not associated with, the ampulla in some genera (*Protonemoura* and *Dinoceras*). In other cases (*Isoperla*, *Dictyogenus*, *Isogenus* and *Perla*) certain fibres of this muscle attach to the ampulla wall and act as ampulla dilators (Fig. 24a).

A comparable situation can be found in the Grylloidea. In *Gryllotalpa*, some of the muscle fibres attached



**Fig. 24a-f.** Hypothetical relationships of ampulla muscles. **a-c** Possible derivation of ampulla muscles from pharynx dilator (retractor muscle of mouth-angle) by splitting of some fibres and change of attachments: **a** Plecoptera and **b** *Grylotalpa*: ampullo-pharyngeal and ampullo-frontal dilator muscle. **c** Dermaptera: fronto-pharyngeal compressor muscle. **d-f** Possible derivations of ampullo-ampullary and ampullo-pharyngeal muscles: **d** *Acheta*: all mus-

cles as prominent bands, probable ancestral state; **e** Tettigonoidea: muscular frontal sinus septum contains ampullo-ampullary as well as ampullo-pharyngeal fibres, probable derived state; **f** Blattopteroidea, Phasmatodea: prominent ampullo-ampullary dilator and pair of accessory dilator muscles; the latter probably derived from ampullo-pharyngeal muscles

to the ampulla wall originate near by at the frontal cuticle, while others extend to the pharynx and insert there at the mouth-angle. Next to the ampullo-pharyngeal dilator, the much stronger retractor of the mouth-angle has virtually the same point of insertion, but an origin at the frontal cuticle, close to the attachment of the ampulla (Fig. 24b). This muscle is present in all insects with typical chewing-biting mouthparts. Its contraction widens the pharynx and simultaneously pulls the hypopharynx forwards and upwards. This forces the food from the cibarial chamber into the mouth (see Denis and Bitsch 1973). The close spatial relationship between the retractor of the mouth-angle and the antennal heart in *Grylotalpa* makes a splitting of some of its muscle fibres and their lateral displacement and attachment to the ampulla wall conceivable, resulting in both the ampullo-pharyngeal as well as the ampullo-frontal dilators.

The muscle associated with the ampulla in the Dermaptera also shows distinct affinities to the retractor of the mouth-angle. The attachments of the ampulla compressor muscle are the same as those of the latter, i.e. the frontal cuticle and the mouth-angle at the pharynx. Only its origin at the cuticle is laterally displaced (Fig. 24c).

Certain insects, e.g. *Acheta* not only have ampullo-frontal and ampullo-pharyngeal muscles but also prominent ampullo-ampullary muscles (Fig. 24d). This suggests an independent derivation of the latter muscle. Ampullo-frontal, ampullo-pharyngeal and ampullo-ampullary elements also occur in the thin layers of muscle fibres at the frontal septum in the Tettigonoidea, which could be derived from solid muscle bands as in *Acheta* (Fig. 24e). A derivation from ampullo-pharyngeal dila-

tor muscles is also suggested for the accessory dilator muscles in the Blattopteroidea and Phasmatodea, despite their unusual attachment sites on both the transverse muscle and the anterior end of the aorta.

The innervation of the muscles associated with the ampullae has been studied in the earwigs (Pass 1988) and in greater detail in the cockroach *Periplaneta americana* using the cobalt filling technique (Pass et al. 1988a). The results in both cases support the postulated relationship of antennal heart muscles and precerebral fronto-pharyngeal muscles. The innervation of all these muscles stems from the stomatogastric nervous system and the tritocerebrum (Denis and Bitsch 1973; Penzlin 1985); some nerves also contain fibres from neurones of the suboesophageal ganglion (Gundel and Penzlin 1978; Pass et al. 1988a).

**b) Membranous structures.** In the Plecoptera and the Dermaptera, we find similar membranous structures in a virtually identical situation, but with a different function. While in the Plecoptera the frontal septa are haemocoel-separating structures, in the Dermaptera these are primarily elastic structures antagonistic to the ampulla compressors. The question of homology of these structures arises, yet evidence is scarce and any interpretation remains very speculative.

**c) Possible constraints.** Changes in organ structure are generally due to changes in functional requirements. In the organ under consideration this might have been the result of a different structure of the antennae and/or changes in pharynx configuration.



With respect to the antennae, one could expect a correlation between circulatory organ configuration and antenna length and volume. The morphometric investigation of various Ensifera with a wide spectrum of antenna length revealed some differences. The clearest relation is that of the thickness of the ampulla wall versus the antenna length. For example, *Jimenezia* has an antenna ten times longer than *Grylotalpa* and an ampulla wall three times thicker. As the elasticity of the ampulla is probably responsible for its systolic compression, it is reasonable to assume that the strength of the elastic power is increased with a thicker wall. However, it must be mentioned that it is not possible to deduce from the structure alone the effectiveness of different types of circulatory organ. This is especially true for the antennal heart musculature. Only in *Grylotalpa* does the existence of only a few and very thin ampulla dilator muscles clearly reflect a relation with its short antennae. In summary, the relatively minor differences in antennal heart configuration between forms with different antenna length may be explained as a result of the special physical laws involved in microcirculation within extremely narrow tubes (see Kaley and Altura 1977; Fung 1984); further experimentation is required here.

With regard to the pharynx, the investigated insects exhibit no major variations. All species are characterized by typical chewing-biting mouthparts and by similar foregut structures. It might be mentioned here that, in contrast to ampullo-pharyngeal muscles, the development of ampullo-ampullary and ampullo-frontal dilator muscles results in antennal heart pulsations independent of pharynx movements.

*d) Phylogenetic considerations.* The relationships between the higher subtaxa of the Neoptera have not yet been definitely clarified (see Hennig 1969; Kristensen 1975, 1981). When considering the antennal hearts one must be aware that we are dealing with relatively simply built organs and the possibility of homologies must be taken into account. Such may be the case in the evolution of pulsatile organs in the Plecoptera.

Within the Orthopteromorpha, the Notoptera are the only representatives which have no muscle associated with the ampullae suggesting a plesiomorphic condition for this organ, as has also been concluded for their dorsal vessel (Nutting 1951). The antennal hearts of the Dermaptera are clearly autapomorphic. Beyond these groups the Orthopteromorpha contain, according to Hennig (1969), two subunits, the Orthopteroidea and the Blattopteroidea. The monophyly of the latter is evident (Marks and Lawson 1962; Kristensen 1981), which is supported by the identical anatomy of their antennal hearts. Antennal circulatory organ structure in the Orthopteroidea presents a varied picture. This heterogeneity reflects that found in other characters which resulted in different conclusions regarding their being a monophylum or a polyphylum (Hennig 1969; Kristensen 1975, 1981; Baccetti 1987). Of particular interest is the condition in the Grylloidea. If one bears in mind the above-discussed recruitment of fronto-pharyngeal muscles for antennal heart function, then the solid dilator muscles in

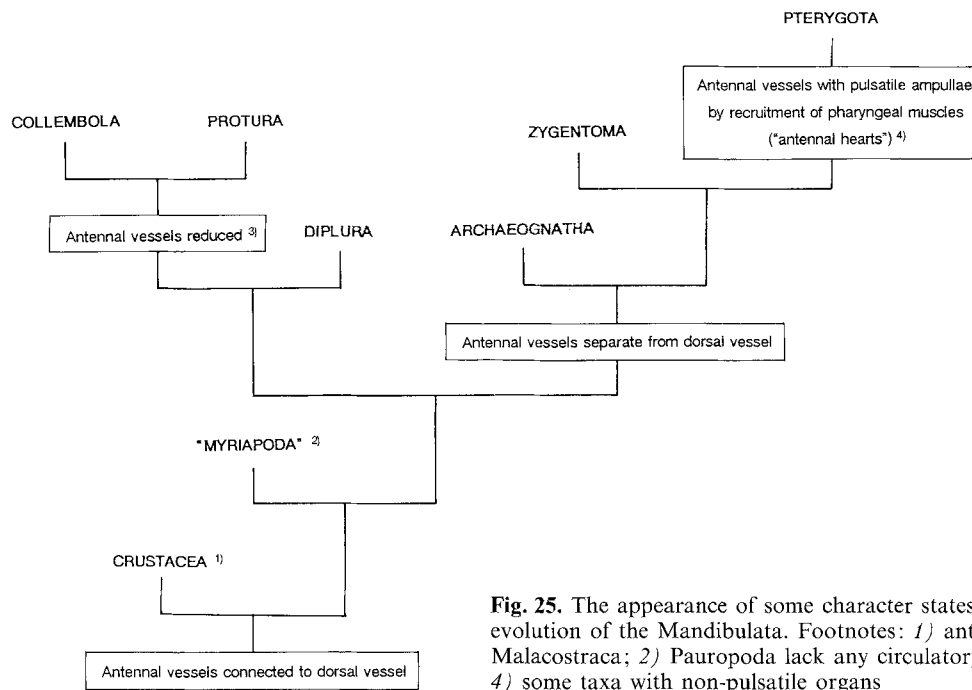
the Grylloidea suggest an ancestral state, compared to the more advanced muscular frontal sac of the Tettigonoidea and Acridoidea. Within the Grylloidea, *Grylotalpa* is an ancestral form in many respects (Hennig 1969), which seems also to be reflected by the structure of its antennal heart. It is the sole representative with only ampullo-pharyngeal and ampullo-frontal muscles. All of the other investigated Orthopteroidea also have ampullo-ampullary muscles as do the Blattopteroidea and Phasmatodea. This would imply that an ampullo-ampullary muscle has evolved independently which is also indicated by analysis of the evolution of the antennal circulatory organs according to the principle of parsimony using the Wagner network method (Pass, in preparation).

The striking similarity in the relatively complex anatomy of the antennal hearts between the Blattopteroidea and the Phasmatodea suggests homology. This is remarkable as the phylogenetic relationships of the latter group are an especially controversial topic (see Kristensen 1975). Detailed studies of the innervation of their antennal hearts with determination of neurone types and location, as has been done for *Periplaneta* (Pass et al. 1988a), may help to evaluate whether these organs are actually homologous.

### III. Conclusions

The exchange of haemolymph within the antennae of arthropods is generally realized by vessels transporting in a distal direction; backflow to the head occurs in the haemocoel of these appendages ensuring circulation in the true sense of the word. Vessels are lacking only in the Pauropoda, Collembola and Ephemeroptera. These groups are characterized either by minute body size or at least by very short antennae. For this reason, and due to the phylogenetic positions of these taxa, it is suggested that they represent convergent and derived states.

The antennae of the Tracheata are considered extremities of the homologous metamer (see Weber 1952; Weygoldt 1986; Dohle 1988). Assuming a monophyly of arthropods, the first antennae of the Crustacea are concluded to be homologous (see Siewing 1963b; Schram 1986). Blood vessels represent a constitutive element of these appendages and there is no valid argument against their being homologous within the Mandibulata. If the view is correct that arthropod hearts were originally comprised of a pair of lateral vessels per segment (Tjønneland et al. 1987; Siewing 1963a), then one can recognize the antennal vessels as the lateral arteries of the antenna segment. An origin from the dorsal vessel is then concluded to be the plesiomorphic condition (Fig. 25). Obviously, in the stem lineage of the Ectognatha this connection has been lost. This coincides with the evolution of the annulated antenna type and with fundamental constructional changes within the head capsule. The latter resulted in space constraints which may have been responsible for this loss. The next step was the evolution of pulsatile antennal circulatory organs by the association of muscles with the enlarged



**Fig. 25.** The appearance of some character states of antennal circulatory organs during evolution of the Mandibulata. Footnotes: 1) antennal vessels present only in Malacostraca; 2) Pauropoda lack any circulatory organ; 3) Protura lack antennae; 4) some taxa with non-pulsatile organs

ampullary base of the antennal vessels in the Neoptera. Despite different configurations and attachments, there are good indications that all these muscles derive from precerebral pharynx dilators.

Summing up the results from a general point of view, one can state that the simple and clearly arranged anatomy of antennal circulatory organs makes them vivid models for evolutionary consideration. They give us a good idea of how an organ can evolve, with all stages of transition being functional and not requiring the invention of bizarre intermediate steps.

*RMm* medial retractor of mouth-angle  
*SD* salivary duct  
*T* tentorium  
*ScSi* supracerebral sinus

**Acknowledgements.** Supported by P 5790 of the Austrian Science Foundation. I thank Dr. A. Hantschk, B. Köhler, Dr. H. Krenn and Dr. F. Ladich for their careful technical assistance. Thanks also to Prof. M. Mizzaro and H. Grillitsch for help with the illustrations and to B. Lorenz and Dr. M. Stachowitsch for patient help with the translation. Furthermore I am obliged to several colleagues for species determination and specimens.

## Abbreviations

<i>Amp</i>	ampulla	<i>DMAcc</i>	accessory dilator muscle of ampulla
<i>Ant</i>	antenna	<i>DV</i>	dorsal vessel
<i>ant</i>	anterior	<i>EB</i>	elastic band
<i>AN</i>	antennal nerve	<i>FbDM</i>	fronto-buccal pharynx dilator muscle
<i>Ao</i>	aorta	<i>FG</i>	frontal ganglion
<i>AV</i>	antennal vessel	<i>FSa</i>	frontal sac
<i>Br</i>	brain	<i>FSe</i>	frontal septum
<i>BrSi</i>	brain sinus	<i>FSi</i>	frontal sinus
<i>CC</i>	corpora cardiaca	<i>Lb</i>	labium
<i>CoeC</i>	circumoesophageal connectives	<i>LV</i>	lateral vessel of aorta
<i>CM</i>	compressor muscle of ampulla	<i>MA</i>	mouth-angle
<i>CT</i>	connective tissue	<i>Nr</i>	nervus recurrens
<i>Dia</i>	diaphragm	<i>Oc</i>	ocellus
<i>do</i>	dorsal	<i>Oe</i>	oesophagus
<i>DM</i>	dilator muscle of ampulla	<i>OeSi</i>	oesophageal sinus
<i>DM1</i>	ampullo-ampullary dilator muscle	<i>Ost</i>	ostium
<i>DM2</i>	ampullo-pharyngeal dilator muscle	<i>Ph</i>	pharynx
<i>DM3</i>	ampullo-frontal dilator muscle	<i>Pl</i>	labial palpus
		<i>RM</i>	retractor muscle of mouth-angle
		<i>RMl</i>	lateral retractor of mouth-angle

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