

ACCESSORY PULSATILE ORGANS: Evolutionary Innovations in Insects

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■ **Abstract** In addition to the dorsal vessel (“heart”), insects have accessory pulsatile organs (“auxiliary hearts”) that supply body appendages with hemolymph. They are indispensable in the open circulatory system for hemolymph exchange in antennae, long mouthparts, legs, wings, and abdominal appendages. This review deals with the great diversity in the functional morphology and the evolution of these accessory pulsatile organs. In primitive insects, hemolymph is supplied to antennae and cerci by arteries connected to the dorsal vessel. In higher insects, however, these arteries were decoupled and associated with autonomous pumps that entered their body plan as evolutionary innovations. To ensure hemolymph supply to legs, wings, and some other appendages, completely new accessory pulsatile organs evolved. The muscular components of these pulsatile organs and their elastic antagonists were recruited from various organ systems and assembled to new functional units. In general, it seems that the evolution of accessory pulsatile organs has been determined by developmental and spatial constraints imposed by other organ systems rather than by changes in circulatory demands.

INTRODUCTION

In the open circulatory system of insects, the pumping organs of the central body cavity cannot circulate hemolymph in long body appendages. Diffusion must also be ruled out as a feasible exchange mechanism because low velocity restricts it to cellular dimensions. Therefore, auxiliary circulatory structures are indispensable for hemolymph circulation. In some noninsect arthropods and primitive insects (hexapods¹), appendages are supplied by arteries originating from major vessels (52, 58). In most modern insects, however, this task is accomplished by means of so-called accessory pulsatile organs (39, 68).

¹Modern taxonomic nomenclature utilizes “Hexapoda” for “Insecta s.l.” (47). Various conceptions prevail concerning the term “Insecta s. str.”(21). For the sake of simplicity, “insects” is used synonymously for “hexapods” in this review.

As a rule, these auxiliary hearts are separate from the dorsal vessel and function autonomously. An insect can possess a considerable number, so we may think of insects as the animals richest in hearts (Figure 1). Most accessory pulsatile organs are evolutionary innovations that emerged in primitive pterygotes and have since become integral elements of their body plan. Auxiliary hearts have long failed to receive due recognition, and even their great diversity has only recently been uncovered (45, 46, 67, 68). This review examines (a) the functional morphology

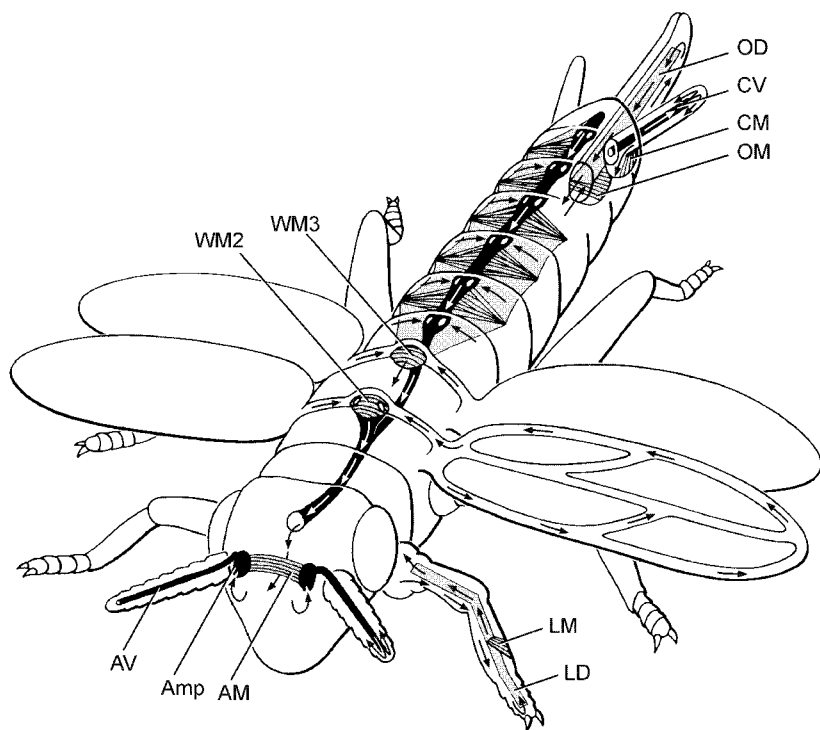


Figure 1 Diagram of an idealized insect with the maximum possible set of circulatory organs. Vessels are in *solid black*, diaphragms and pumping muscles are in *gray*; *arrows* indicate hemolymph flow directions. Central body cavity: dorsal vessel composed of anterior aorta and posterior heart region (with paired ostia, dorsal diaphragm, and alary muscles); ventral diaphragm concealed. Antennae: ampullae (*Amp*) with ostia connected to antennal vessels (*AV*); pumping muscle (*AM*) associated with ampullae. Legs: diaphragm (*LD*) pulsatile owing to associated pumping muscle (*LM*). Wings: dorsal vessel muscle plate with ostia pair in mesothorax (*WM2*); separate pumping muscle in metathorax (*WM3*). Cerci: cercal vessel (*CV*) with basal suction pump (*CM*). Ovipositor: each valvula with nonpulsatile diaphragm (*OD*) and basal forcing pump (*OM*). Among insect species, the functional morphology of the accessory pulsatile organ in a given body appendage may be heterogeneous.

and physiology, (b) the phylogenetic pathways, and (c) the evolutionary innovations in insect circulatory organs.

STRUCTURE AND FUNCTION OF CIRCULATORY ORGANS

Methodological intricacies related to small body size and open circulatory systems contribute to the gaps in the understanding of hemolymph circulation and routing through an insect's body. From a hemodynamic point of view, it is crucial to know that hemolymph is not exclusively transported by pumps. Shifting of hemolymph bulk by certain muscle contractions and volume changes of the abdomen may also play an essential role (85, 86, 91, 95–99). Moreover, the tracheal system of some endopterygotes has turned out to be a powerful antagonist to the action of the circulatory organs (97–101).

Central Body Cavity

Although the accessory pulsatile organs of various insect body appendages constitute nearly autonomous systems, they may also be linked to the circulatory organs of the central body cavity. Because the structure and function of dorsal vessels have been treated in several other reviews (39, 57, 107), a detailed analysis is not required here. The basic type of dorsal vessel is a rather uniform muscular tube bearing valved ostia in most thoracic and abdominal segments (45). In many species, the dorsal vessel is partitioned into a posterior pumping region, the heart, and an anterior poorly contractile region, the aorta. The two regions differ not only in the strength of the muscular wall but also in the presence of ostia, dorsal diaphragm, and alary muscles (35, 46). An accessory pulsatile organ associated with the aorta was recently discovered in the head of the blow fly (102).

The dorsal vessel can be linked to other vessels that may then be regarded as arteries. Some of these serve hemolymph circulation in long body appendages (antennae, cerci, and terminal filament). Other vessels distributing hemolymph from the dorsal vessel without detour to certain regions of the central body cavity are the segmental vessels in the thorax and the abdomen of cockroaches, mantids, and orthopterans (51, 57, 62) and the circumesophageal vessel ring in the head of apterygotes² (8, 24).

The view generally held presumes that the dorsal vessel collects hemolymph in the abdomen via incurrent ostia and transports it toward the head by peristaltic contractions. The flow mode, however, may be substantially different. All apterygotes and the mayflies feature a bidirectional flow in their dorsal vessel: Hemo-

²Despite their status as paraphyletic taxa, the terms “apterygotes” and “exopterygotes” are retained for clarity in this review.

lymph is propelled toward the front except in the most posterior vessel portion, where it exclusively flows toward the rear; intracardiac valves shunt these flow directions (24, 54). Where this bidirectional flow mode applies, the dorsal vessel is posteriorly open and communicates with vessels supplying the caudal appendages. Heartbeat reversal, with its periodic change of pumping directions, is another flow mode common among endopterygotes in particular (25, 39). This mode is associated either with a posteriorly open dorsal vessel, the presence of excurrent ostia, or even two-way ostia allowing selective shunting (95, 100, 101).

Diaphragms of connective tissue and/or muscle channel the various hemolymph flows in the central body cavity and can also actively aid hemolymph circulation via undulating movements. In particular, a ventral diaphragm is widespread and can be variously developed (76).

Antennae

The functional morphology of antennal circulatory organs has been quite thoroughly investigated in many insects (6, 13, 16–18, 50a, 63, 64, 66–68, 81). This investigation yielded results on the stupendous diversity of these accessory pulsatile organs (for details on functional types and distribution among insect orders, see Figures 2 and 3). Insects usually possess vessels in their antennae, except for a few species whose short antennae lack circulatory organs altogether or have tiny diaphragms. The vessels serve the efferent hemolymph supply; the afferent current into the head capsule leads through the antennal hemocoel. Hemolymph enters the antennal vessels in different ways in the various insect taxa (67, 68). They may be directly linked with the dorsal vessel (Figure 2a), but in most insects they are separate and have ampullary enlargements with valved ostia at their bases. Ampullae are paired or unpaired; in a few species, they constitute large frontal sacs. Rarely, the ampullae just funnel hemolymph into the antennal vessels without acting as pumps (Figure 2b) or are indirectly compressed via dilation of the pharynx. As a rule, however, the ampullae are autonomous pulsatile circulatory organs and can be called antenna-hearts because they are independent from the dorsal vessel.

Muscles associated with the ampullae vary considerably in anatomy and function. In the majority of species, the muscles dilate the ampullae (Figures 2c, d, e); in only a few do the muscles compress them (Figure 2f; 63, 66). Elastic properties of the ampulla wall or of suspending structures antagonize the action of these muscles. They may attach to a number of structures: compressor muscles to the frontal cuticle or to the pharynx; dilator muscles always have one attachment site at the ampulla wall and the other at the pharynx (Figure 2d), the frontal cuticle, or the anterior end of the aorta (Figure 2e). Another type of dilator muscle spans the two ampullae and causes their simultaneous dilation upon contraction (Figure 2d and e; 64).

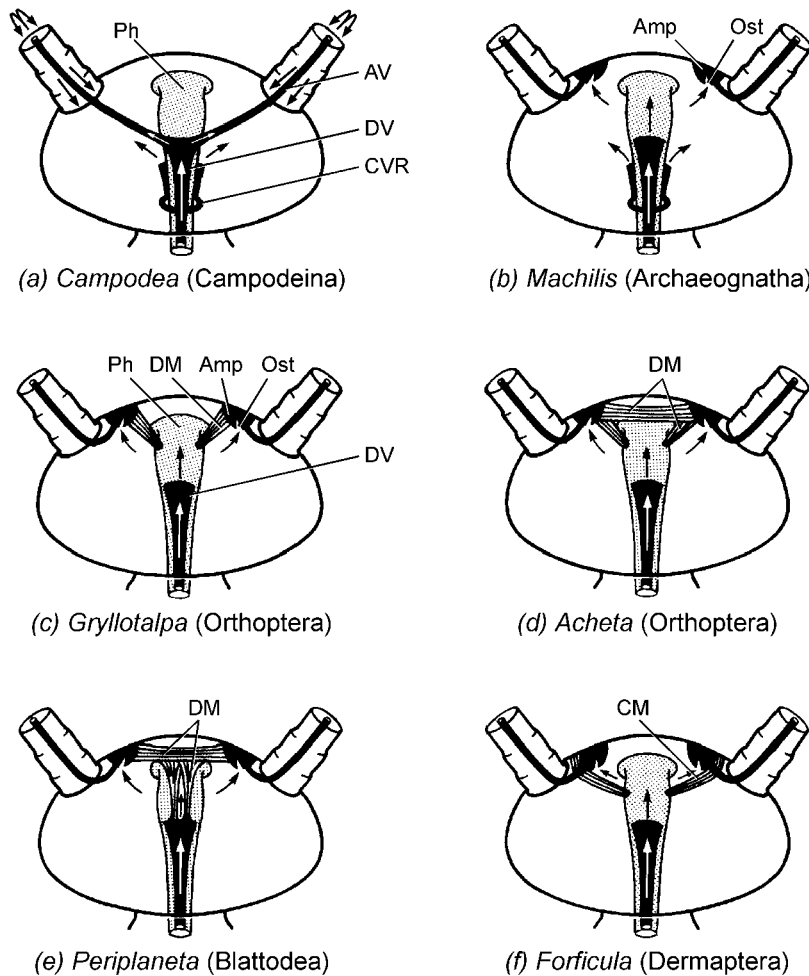


Figure 2 Antennal circulatory organs. Head diagram in dorsal view in different species. Vessels and their derivative structures in *solid black*; foregut is *stippled*; *arrows* indicate hemolymph flow. In nonpulsatile organs, antennal vessels are either (a) connected to the dorsal vessel or (b) separate from the dorsal vessel having basal nonpulsatile ampullae with ostia (Ost) communicating with the frontal sinus. In pulsatile organs, the basic layout is uniform except for the attachment sites and functions of the associated pumping muscles: (c) ampullo-pharyngeal dilator, (d) ampullo-pharyngeal and ampullo-ampullary dilators, (e) ampullo-ampullary dilator and accessory dilators attached to anterior end of aorta, (f) fronto-pharyngeal compressor. In (a) and (b), also note the circumesophageal vessel ring with ventral trumpet-shaped opening. Abbreviations: ampulla (Amp), antennal vessel (AV), compressor muscle (CM), circumesophageal vessel ring (CVR), dilator muscle (DM), dorsal vessel (DV), ostium (Ost), pharynx (Ph).

	Non-pulsatile organs			Pulsatile organs					
	1	2	3	ampulla compressor		ampulla dilator			
				4	5	6	7	8	9
Apterygotes									
COLLEMBOLA	-	-	-	-	-	-	-	-	-
PROTURA	-	-	-	-	-	-	-	-	-
CAMPODEINA	■	□	□	□	□	□	□	□	□
JAPYGINA	■	□	□	□	□	□	□	□	□
ARCHAEOGNATHA	□	■	□	□	□	□	□	□	□
ZYGENTOMA	□	■	□	□	□	□	□	□	□
Exopterygotes									
EPHEMEROPTERA	-	-	-	-	-	-	-	-	-
ODONATA	□	□	■	□	□	□	□	□	□
PLECOPTERA	□	■	□	□	□	■	□	□	□
BLATTODEA	□	□	□	□	□	□	■	■	□
ISOPTERA	□	□	□	□	□	□	■	■	□
MANTODEA	□	□	□	□	□	□	■	■	□
GRYLLOBLATTODEA	□	■	□	□	□	□	□	□	□
DERMAPTERA	□	□	□	■	□	□	□	□	□
ORTHOPTERA	□	□	□	□	□	■	■	■	□
PHASMATODEA	□	□	□	□	□	□	■	■	□
EMBIOPTERA	□	□	□	□	□	□	□	□	■
ZORAPTERA	?	?	?	?	?	?	?	?	?
PSOCOPTERA	?	?	?	?	?	?	?	?	?
PHTHIRAPTERA	-	-	-	-	-	-	-	-	-
HEMIPTERA	□	□	□	□	■	□	□	□	□
THYSANOPTERA	?	?	?	?	?	?	?	?	?
Endopterygotes									
STREPSIPTERA	?	?	?	?	?	?	?	?	?
COLEOPTERA	□	□	□	□	■	□	□	□	□
MEGALOPTERA	□	□	□	□	□	□	□	■	□
RAPHIDIOPTERA	?	?	?	?	?	?	?	?	?
NEUROPTERA	□	□	□	□	□	■	□	□	□
MECOPTERA	□	□	□	□	□	■	□	□	□
SIPHONAPTERA	-	-	-	-	-	-	-	-	-
DIPTERA	□	□	□	□	□	□	■	■	□
TRICHOPTERA	□	□	■	□	□	□	□	□	□
LEPIDOPTERA	□	□	■	□	□	□	□	□	□
HYMENOPTERA	□	□	■	□	□	□	□	□	□

Figure 3 Functional types of antennal circulatory organs and their occurrence in insect orders. Numbers 1–9 indicate different organ designs. Nonpulsatile organs: 1 antennal vessels connected to dorsal vessel; 2 antennal vessel with non-pulsatile ampulla; 3 ampullae or frontal sacs indirectly compressed by pharynx movements. Pulsatile organs with associated 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; - no organ, ? not investigated. Data compiled from references 13, 16–18, 66–68, 81.

Mouthparts

Hemolymph pumping organs have hitherto been found linked only to the lepidopteran proboscis and are involved in its hydraulic extension (4, 42). They are located near the proboscis base and consist of compressible cuticular tubes with associated muscles. Contraction presses the tubes together whereby hemolymph is forced into the proboscis. Elongate mouthparts of other insects presumably also contain special circulatory organs for hemolymph exchange. In some maxillary and labial palps, diaphragms partition the hemocoel into two sinuses, in which countercurrent hemolymph streams can be observed (G Pass, unpublished data); propagation of these streams remains unclear.

Legs

Pulsatile organs in legs are known only in Orthoptera and Hemiptera (39, 68). In these insects a delicate nonmuscular diaphragm takes over the channeling function for each extremity. It longitudinally spans the entire leg and ends just short of the tip. The leg hemocoel is thereby partitioned into two sinuses with countercurrent flows. The efferent flow in one sinus doubles back at the tip where it becomes the afferent flow returning to the thorax in the other sinus.

The pulsatile apparatuses are dissimilar in the two taxa. In the trochanter of the locust middle leg, two small muscles attach to the diaphragm, raising it upon contraction (38); muscle relaxation is followed by flattening of the diaphragm, which forces hemolymph towards the thorax. In Hemiptera, the pumping muscle is associated with the longitudinal diaphragm in the tibia (14, 26, 41; Figure 4*a, b*). Its contraction narrows one sinus and propels hemolymph towards the thorax channeled by a valve flap. Consequently, hemolymph is sucked out of the thorax into the other now dilated sinus. Attachment sites of the leg-heart muscle vary among Hemiptera (cf. Figure 4*a, b*).

Leg diaphragms without associated pumping muscles are reported from a number of other insects (68, 83); how the observed countercurrent flows are generated is not yet fully understood.

In the legs of adult Lepidoptera, an entirely different scheme regulates hemolymph circulation: A large tracheal sac replaces the diaphragm as a partitioner of the leg hemocoel. Mutual dependent fluctuations in the tracheal volume and the thoracic hemolymph bulk caused by heartbeat reversal are considered the impetus for hemolymph exchange (100, 101). The distension of the tracheal sac may be more pronounced in one sinus than in the other, resulting in a forced hemolymph propulsion through the countercurrent sinuses.

Wings

Insect wing veins contain living cells that rely on hemolymph supply. Hemolymph flow generally follows a basic circulation pattern: Anterior veins carry efferent flows and posterior veins afferent ones (1). Pulsatile organs in the thorax power

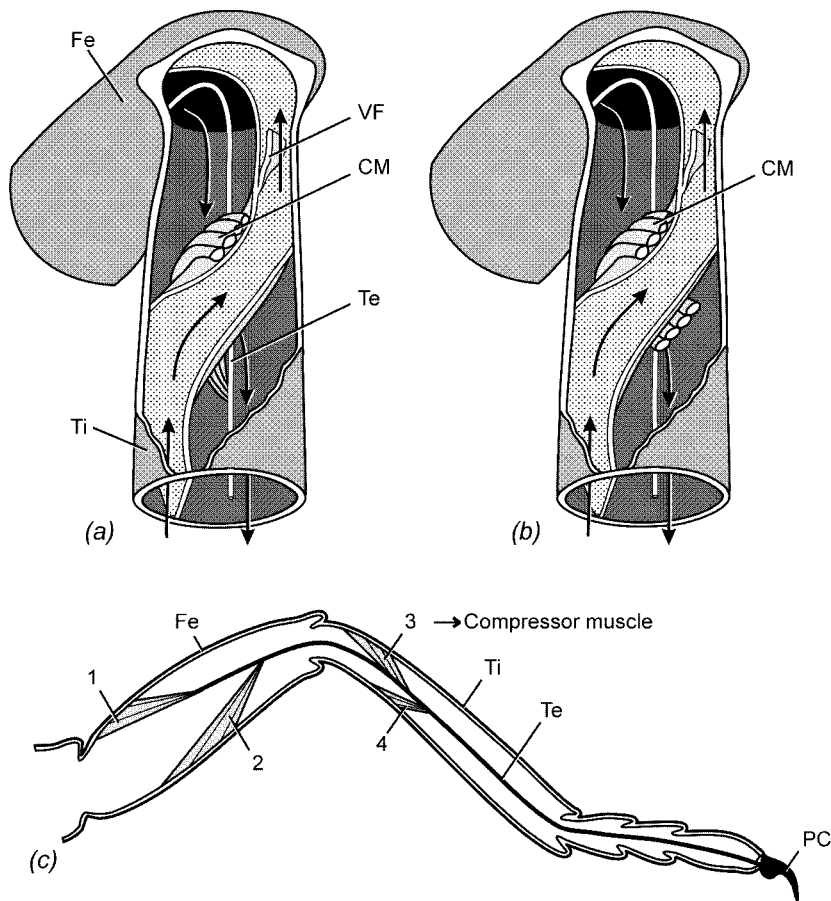


Figure 4 Leg circulatory organs. (a, b) Diagrams of the joint region between femur and tibia in two different hemipteran species. Proximal part of tibia opened to show leg-heart region, *arrows* indicate hemolymph flow direction. Longitudinal diaphragm (*stippled*) twisted within the leg hemocoel separate efferent from afferent sinus; valve flap in efferent sinus precludes backflow. The pumping muscle may attach to different locations: (a) to the tibia cuticle and tendon of the pretarsal claw flexor as in most Hemiptera; (b) the leg-heart muscle has both attachment sites at the tibia cuticle as in Belostomatidae, Nepidae, and Reduviidae partim. (c) The pretarsal claw flexor consists of four separate muscle portions (indicated by numbers) inserting at the long tendon, which runs through the entire leg. In Hemiptera, one tibial portion of the pretarsal claw flexor (labeled 3) was obviously recruited for the leg-heart function. Abbreviations: compressor muscle (*CM*), femur (*Fe*), pretarsal claw (*PC*), tendon of pretarsal claw flexor (*Te*), tibia (*Ti*), valve flap (*VF*).

this circulation (for details on functional types and distribution among insect orders, see Figures 5 and 6). They are located in the winged segments directly beneath the scutellum, which forms the pumping case, and communicate with the posterior wing veins via cuticular tubes. Although these cuticular components are rather invariable in their design, the anatomy of the pulsatile apparatus is not. However, it always functions by the same principle, sucking hemolymph out of the posterior veins. In many species, the pulsatile structures are modifications of the dorsal vessel (6, 11, 43, 45, 46, 104; Figures 5*a, b, c*). They represent simple enlargements or diverticles whose dorsal wall musculature is reinforced and attached to the basal ridge of the scutellum. When relaxed, they occupy part of the small sinus beneath (Figure 5*a*). Contractions flatten the dorsal portion of the pulsatile structure, thereby widening that sinus. This action results in hemolymph suction out of the wing veins (Figure 5*b*). Elastic suspending strands antagonize the muscle contraction and redilate this portion of the dorsal vessel, compressing the small sinus beneath the scutellum. Consequently, hemolymph streams into the lumen of the dorsal vessel via ostia; concurrently, a valve prevents backflow into the wing veins. In other species, the pumping apparatus is made up of a muscular plate called the pulsatile diaphragm (10, 44–46). It may be attached to or be entirely separate from the dorsal vessel (Figures 5*d* and *e*, respectively). In the latter case, hemolymph is being carried through a valved opening directly into the thoracic hemocoel instead of into the dorsal vessel lumen. Typically, one pulsatile diaphragm exists per winged segment, although paired pulsatile diaphragms, one at each wing base, may also occur (46, 92).

In some Coleoptera and Lepidoptera, the so-called tidal flow is still another mode of hemolymph exchange in the wings (95, 98–101). Hemolymph flow into and out of all wing veins occurs simultaneously. The flows are correlated with periodic heartbeat reversal, intermittent pulse activity of the wing-hearts, slow volume changes of the abdomen and the consequential fluctuations of the wing trachea volume. The withdrawal of hemolymph from the wing veins by the concerted action of the pumping organs effects widening of these elastic wing tracheae; upon their relaxation, hemolymph is again sucked back into the wing veins.

Abdominal Appendages

Information is scarce on circulation in the various abdominal body appendages. Vessels communicating with the dorsal vessel supply the long cerci and the terminal filament of apterygotes and mayflies (5, 24, 79; Figure 7*a*). This condition goes along with a bidirectional hemolymph flow within the dorsal vessel. Ephemeroptera have a caudal pulsatile ampulla with a conspicuous muscular wall (54). This structure is linked to the posterior end of the dorsal vessel but contracts with different beat frequencies. The activity of the ampulla contributes significantly to hemolymph propulsion through the abdominal appendages. In Plecoptera, the cercal vessels are separate from the dorsal vessel, which is posteriorly closed. Here, specific pulsatile organs in the anal lobes assume hemolymph circulation

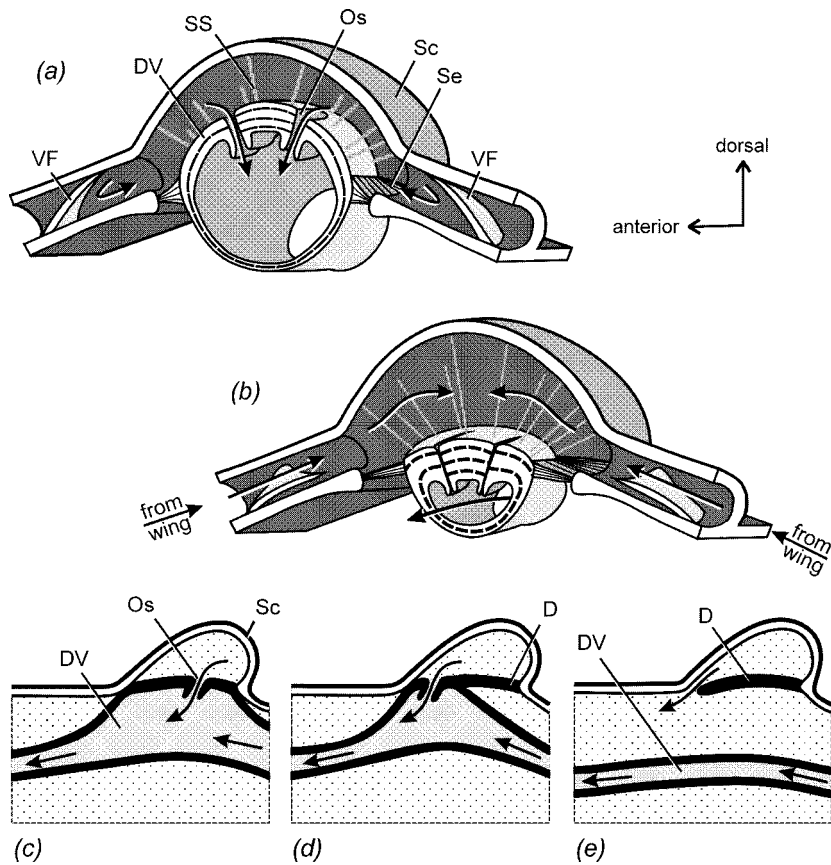


Figure 5 Wing circulatory organs. (a, b) Dorsal vessel modification in two distinct phases of action. Diagrams show dorsal portion of a winged thoracic segment in cross section. Scutellum and supplying tubes cut open to show pulsatile apparatus and hemolymph flow directions (arrows). The pulsatile apparatus consists of an enlarged vessel portion with strengthened dorsal wall bearing a pair of ostia; it is attached to cuticular structures by a connective tissue septum and numerous elastic suspending strands. See text for functional explanation. (c, d, e) Organization levels in different taxa. Midline views of thorax regions. The basic type is dorsal vessel modification (c) where hemolymph from wing veins is propelled into dorsal vessel lumen via ostia; in the attached pulsatile diaphragm (d), hemolymph is propelled by action of a muscular plate linked to the dorsal vessel; in the separate pulsatile diaphragm (e), no link to the dorsal vessel exists and hemolymph is forced directly into the thoracic cavity. Abbreviations: dorsal vessel (DV), ostium (Os), pulsatile diaphragm (D), scutellum (Sc), suspending septum (Se), suspending strands (SS), valve flap (VF).

	Dorsal vessel modifications	Pulsatile diaphragms		
		attached unpaired	separate unpaired	separate paired
Exopterygotes				
EPHEMEROPTERA	■	□	□	□
ODONATA	■	□	□	□
PLECOPTERA	■	□	□	□
BLATTODEA	■	□	□	□
ISOPTERA	■	□	□	□
MANTODEA	■	□	□	□
GRYLLOBLATTODEA	-	-	-	-
DERMAPTERA	■	□	□	□
ORTHOPTERA	■	□	□	□
PHASMATODEA	■	□	□	□
EMBIOPTERA	■	□	□	□
ZORAPTERA	?	?	?	?
PSOCOPTERA	■	□	□	□
PTHIRAPTERA	-	-	-	-
HEMIPTERA	□	□	■	□
THYSANOPTERA	□	□	□	□
Endopterygotes				
STREPSIPTERA	?	?	?	?
COLEOPTERA	■	□	□	□
MEGALOPTERA	□	□	■	□
RAPHIDOPTERA	□	□	■	□
NEUROPTERA	□	■	■	□
MECOPTERA	□	□	■	□
SIPHONAPTERA	-	-	-	-
DIPTERA	□	□	■	■
TRICHOPTERA	□	■	■	□
LEPIDOPTERA	□	■	■	■
HYMENOPTERA	■	□	■	□

Figure 6 Functional types of wing circulatory organs and their occurrence in insect orders. ■ trait present; □ trait absent; - wingless no organ; ? not investigated. (Data compiled from 45, 46.)

in the cerci (65, Figure 7b). Cercal vessels have been found in no other insects investigated so far. Instead, the hemocoel is partitioned by a diaphragm channeling countercurrent flows, whose source of propulsion is unknown (60).

In many insects, the ovipositors can be of considerable length. Very recently, autonomous pulsatile organs have been discovered in the cricket ovipositor (G Pass, BA Gereben-Krenn, R Hustert, unpublished data). The hemocoels of the

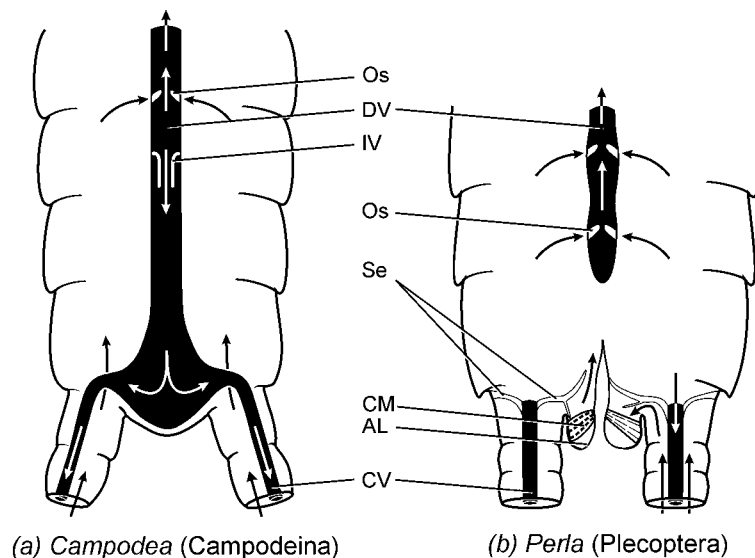


Figure 7 Cercal circulatory organs. Diagram of posterior abdominal segments with cerci. Vessels in *solid black*; *arrows* indicate hemolymph flow directions. (a) Intracardiac valve enforces posteriorly directed hemolymph flow within dorsal vessel continuing into cercal vessels. (b) Dorsal vessel separate from cercal vessels; cercus hemocoel isolated by septum from central body cavity. Pulsatile organ in the anal lobes depicted during different phases of action: left anal lobe indented by contraction of pumping muscle thereby forcing hemolymph through valve opening into body cavity; in right anal lobe, relaxation of muscle allows lobe cuticle to return to original shape drawing hemolymph from cercus into anal lobe and from body cavity into cercal vessel. Abbreviations: anal lobe (*AL*), cercal vessel (*CV*), compressor muscle (*CM*), dorsal vessel (*DV*), intracardiac valve (*IV*), ostium (*Os*), septum (*Se*).

ovipositor valvulae are all partitioned by delicate diaphragms. Countercurrent streams in the two sinuses are generated by the action of a pumping muscle at the base of each valvula.

Cardiac Activity and Physiology

Heart physiology is rather well known in the dorsal vessel (39, 56, 57, 107), yet investigation on accessory pulsatile organs is often limited to the registration of pumping activity. As a rule, the auxiliary hearts pulse independently, and their beat frequencies are not synchronized. The rates may be considerably faster (26) or slower (31) than those of the dorsal vessel. Where there is a series of pulsatile organs, such as the six leg-hearts, the beat frequencies are about the same, although they are not exactly in phase (26). Some accessory pulsatile organs work continuously (31, 44) and others discontinuously, with rests of up to a few minutes

(26). Lepidopteran wing-hearts are known to beat intermittently in coordination with the periodic beat reversal in the dorsal vessel (95, 100); during adult eclosion and wing expansion, however, the dorsal vessel pumps only toward the head and the wing-hearts work continuously.

A myogenic pacemaker is inherent in the dorsal vessels of all investigated insects (39, 57). Beat frequencies may be neuronally or hormonally modulated (55, 56). All this also holds true for the investigated accessory pulsatile organs. The cockroach *Periplaneta americana* has been the favorite vehicle for the bulk of studies on auxiliary hearts. Research covers a wide range of topics spanning functional morphology (64), neuroanatomy (7, 69), neurochemistry (70, 72, 106), pharmacology and electrophysiology (31–34, 77). This interest makes the cockroach antenna-heart the best understood of any insect accessory pulsatile organ. Its myogenic rhythm (31, 77) is modulated by neurons located in the subesophageal ganglion (69). Neuroactive substances involved in regulation include octopamine as an inhibitor and some neuropeptides, especially proctolin, as powerful excitors (31–34). Further electrophysiological investigation is as yet restricted to the locust leg-heart; here, the myogenic rhythm is normally controlled by neurons located in the mesothoracic ganglion and occurs synchronously with abdominal ventilatory movements (38).

PHYLOGENETIC PATHWAYS OF CIRCULATORY ORGANS

The newly discovered striking similarities in the developmental genetics of insect and vertebrate hearts point to the very ancient roots of circulatory organs (9, 27). Their common ancestor obviously already had a circulatory system with a contractile dorsal vessel (15). Hence, the notion of the arthropod circulatory organ as a newly emerged functional system (12) becomes implausible. The general tenet holds that the open circulatory system in arthropods is derived from the closed vascular system of annelidlike ancestors (87). Despite doubts about a close relationship between these two taxa (19), the traces of metamery in the vascular system of many primitive arthropods imply a derivation from an ancestor with a segmented body cavity (80). When the metameric organization of the body cavity disappeared in arthropod evolution, a complex vascular system became dispensable. Simple circulatory designs, such as those in insects, must then be derived designs.

In trying to unearth the circulatory design of the common ancestor of insects, the enigmatic and controversial arthropod relationships prove a major obstacle (21, 90, 105). The traditional notion of tight links between insects and myriapods (50, 103) contrasts with the new idea that certain crustaceans are the sister group of insects (3, 22, 75). Remarkably, primitive taxa of both groups possess complex vascular systems whose major components are well-developed dorsal and ventral

longitudinal vessels (52, 58, 84). Their body appendages are supplied by arteries originating from these vessels. Accessory pumping structures have also been described: Rather well known are the frontal hearts in Malacostraca (36, 88, 89), which are widenings of the aorta associated with rhythmically contracting esophageal muscles. Separate and autonomous pulsatile organs are absent in nonhexapod arthropods.

Apterygotes

A recurrent trait in apterygotes is small body size, a feature also postulated for their common ancestor, which may have been a reason for reductions of the original arthropod vascular system. Dorsal vessels have nevertheless prevailed in all apterygotes. They appear as uniform, unchambered tubes with segmental ostia. The dorsal diaphragm and alary muscles are poorly developed, and a ventral diaphragm is generally absent. A peculiarity of the dorsal vessel in apterygotes is its inherent bidirectional flow (24). The functional significance of the posteriorly directed flow lies in the supply of the abdominal appendages whose vessels may be linked in different ways with the dorsal vessel.

In apterygotes, there are distinct differences in the hemolymph supply of the antennae. In diplurans, supply is achieved via arteries linked with the anterior end of the dorsal vessel (67). Typically in insects, however, the antennal vessels are separate from the dorsal vessel and have ampullae at their bases. Outgroup comparison suggests that the situation in diplurans is the plesiomorphic character state in insects, whereas the presence of separate antennal vessels is a synapomorphy of Ectognatha.

A circulatory structure unique to apterygotes is the circumesophageal vessel ring in their head (Figures 2*a*, *b*); its absence is a synapomorphy of Pterygota. Remarkably, a similar structure called the mandibular arch exists in the head of some chilopods (20); homology of these ring vessels is currently intangible.

Exopterygotes

Distinct accessory pulsatile organs first appeared in Pterygota. In most exopterygotes, autonomous pulsatile organs serve to supply the antennae. Ampulla muscles may attach at very different anatomical structures and may also vary in their modes of function (Figure 3; 67, 68). The fact that evolutionary changes in muscle attachment sites cannot be clearly recognized suggests a multiple and independent development of the pulsatile circulatory organs serving antennae.

In pterygotes, the need to supply hemolymph to wings is a new objective, and additional circulatory organs have evolved to meet this demand. The scutellum as a pumping case, with its supplying tubes, is derived from parts of the tergal cuticle. These cuticular structures are uniform in their basic design among all winged insects and can be considered a synapomorphy of Pterygota (45). In almost all orders of exopterygotes, the pulsatile structures of the wing circulatory

organs are dorsal vessel modifications and can be considered the plesiomorphic type (cf. Figure 6). Hemiptera are the only exopterygotes to have pulsatile diaphragms separate from the dorsal vessel. This type of wing circulatory organ is normally associated only with endopterygotes and is presumably the result of parallel evolution.

Because data on leg circulatory organs are scarce, conclusions regarding phylogenetic pathways of these organs are not yet possible, except for the respective pulsatile apparatuses of Orthoptera and Hemiptera, which have undoubtedly evolved independently from each other.

Hemolymph supply to abdominal appendages is accomplished in different ways among exopterygotes. Vessels exist only in Ephemeroptera and Plecoptera and diaphragms elsewhere. The caudal pulsatile ampulla of mayflies is probably an autapomorphy; remarkably, these insects are the only pterygotes that share with apterygotes the bidirectional flow design in the dorsal vessel. A clear autapomorphy of stoneflies, on the other hand, is their pulsatile pump in the anal lobes serving cercal circulation.

Endopterygotes

The trend of differentiating the dorsal vessel into a cephalo-thoracic aorta and an abdominal heart is most pronounced in endopterygotes. Within the thorax, the aorta may bend in one or two long loops or follow a straight central course (35, 46). Heartbeat reversal in several endopterygote orders is reflected in various anatomical modifications of the rear end of the dorsal vessel (25, 101).

The great variety of antennal circulatory organ types does not allow for a reconstruction of major evolutionary pathways (Figure 3; 68). The plesiomorphic condition in Endopterygota also remains unresolved at this time. Potential candidates, given their basic design, could be the ampullae of Hymenoptera, which are compressed via the pharynx (50a).

Regarding circulation in wings, dorsal vessel modifications can be found in only two orders (Coleoptera and Hymenoptera; Figure 6). Because the primitive taxa in both orders share these modifications with exopterygotes, these modifications may therefore be regarded as the plesiomorphic condition of wing circulatory organs in endopterygotes (46). Elsewhere, pulsatile diaphragms are either attached to or separate from the dorsal vessel. Transformation lines in some groups suggest that the character state polarity leads from an attached to a separate mode. The distribution of separate pulsatile diaphragms along a cladogram of Endopterygota clearly shows that they must have evolved multiple times, notwithstanding their nearly identical designs (Figure 6). Paired pulsatile diaphragms are unique to endopterygotes (46).

Hemolymph exchange in wing veins and legs supported by volume changes of elastic tracheae or air sacs has so far been substantiated in only Coleoptera and Lepidoptera (98, 100, 101) and is likely to be a derived condition.

EVOLUTIONARY INNOVATIONS IN CIRCULATORY ORGANS

Accessory pulsatile organs are genuine body plan innovations of insects. In the course of their formation, existing organs have been subjected to modifications and other sets of structures have been assembled to build new functional units. Discussion of evolutionary innovation usually focuses on diversification and adaptive radiation (37, 61, 93). However, the internal workings of morphological innovations, such as the questions of from where organ components are recruited and how organ reassembly is triggered, have received less attention (59, 74). The striking diversity of these innovations in accessory pulsatile organs is another aspect that calls for an explanation. In fact, it seems implausible that the pulsatile organs should have such different designs, in one given appendage, when they all serve the same function.

The next sections attempt to give some framework for the emergence and morphological radiation of accessory pulsatile organs. Circulatory organs seem to be choice material for this kind of study given their relatively simple design and the fact that modifications are rather obvious. Starting from the hemodynamic basics, change in functional demands and spatial constraints imposed by other organ systems are discussed as possible forces for the evolution of accessory pulsatile organs.

Hemodynamic Principles

To make hemolymph circulation in body appendages possible, a structure is required separating efferent from afferent flows. This may be a vessel, a diaphragm, or even a tracheal sac. Some smaller appendages such as mouthparts, tracheal gills, and styli demonstrate that accessory pumps are not strictly needed, although countercurrent hemolymph flows occur. Conceivably, different hemolymph flow velocities at the efferent and afferent sinus bases may effectuate slight differences between the hydraulic pressure there; in turn, this condition may enforce a bulk propulsion through the two sinuses. However, almost all body appendages of greater length evolved specific pulsatile organs that enable hemolymph circulation independent from that in the central body cavity.

Still, hemodynamics in insects is an uncharted field. Because hemolymph is a suspension of hemocytes in plasma liquid, its currents in narrow appendages are subjected to a different set of variables than in the wide sinuses of the central body cavity (23, 48, 82). Viscosity of hemolymph within tubes of diameters from hemocyte cell size up to about 500 μm must be substantially lower than its bulk viscosity due to the Fahraeus-Lindquist effect (73).

The hydraulic pressure needed to force hemolymph through long body appendages may be considerable, but it is not accessible to experimental measurement or to calculation owing to a multitude of unmeasurable parameters. Remarkably, some insects manage to move body appendages by creating highly localized fluc-

tuations in hydraulic pressures by means of accessory pulsatile organ action. Examples include the uncoiling of the lepidopteran proboscis (4, 42) and the spreading of the lamellate antennae of scarabaeid beetles (63).

Circulation in appendages is rather slow. For example the hemolymph in the antennae of *Periplaneta americana* requires 10 minutes to exchange (70). In pierid butterfly wings, major veins take 10 to 20 minutes to be dyed in vital staining experiments, whereas the entire veinal system may take up to one hour (99).

Functional Demands

Bearing in mind the huge variation in the dimensions of certain insect body appendages, it would be plausible to assume that alterations in appendage size and volume have been an essential factor in accessory pulsatile organ evolution. Antennae provide good examples of this issue. In an investigation of several orthopterans with drastically different antenna lengths, positive correlations were found between antenna length and strength of the antenna-heart. Its design, however, was basically the same in all (67). This result may be an indication against variation in appendage size as a decisive reason for morphological radiation of accessory pulsatile organs.

Deletion or acquisition of functions is thought to be another impetus for the emergence of evolutionary innovations. The shift of oxygen transport from the circulatory to the tracheal system is widely believed to have effected the profound reductions in the insect vessel system compared with that of their arthropod ancestors (53, 71, 87). In some endopterygotes, however, the circulatory and tracheal systems have again evolved close functional ties (100, 101). These mutual interactions between circulation and tracheal ventilation constitute a highly efficient mechanism for both oxygen supply and hemolymph exchange. They go along with heartbeat reversal and are also the basis for hemolymph exchange via trachea volume fluctuations in body appendages. This new functional link is prone to replace accessory pulsatile organs in legs and wings of some endopterygotes (46, 101).

Thermoregulation as an additional functional innovation has become another chore of the circulatory system in "hot-blooded" insects (28–30). Long aorta loops in the thorax are morphological adaptations enhancing heat absorption by the passing hemolymph. The accessory pulsatile organs, however, are not known to play a significant part in thermoregulation (40, 94). Preliminary investigations reveal that the hemolymph volume in the appendages would be too small and its flow too slow to be relevant for heat dissipation; this condition at least holds true for larger insects.

Hormone distribution certainly requires a high-performance circulatory system. Beyond the mere pumping function, accessory pulsatile organs can also be the sites of hormone release. For example, the antenna-heart of the cockroach *Periplaneta americana* acts as a neurohemal organ (7, 69). Hormones released there are pumped into the antennae and the complex antennal sensory system is

their probable target site. Neurochemical studies have uncovered high concentrations of octopamine in the neurohemal areas of the cockroach antenna-heart (70); octopamine released there might well modulate antennal receptor sensitivity. Such a neurohemal function could be quite widespread in accessory pulsatile organs because many insect appendages bear numerous sensilla.

Principles of Organ Design

Evolutionary changes in circulatory organs may have their roots in modifications of their functional demands as well as in constraints appearing in the course of reconstruction in other organ systems. Generally, a hierarchy seems to exist determining whether a certain structure or organ can be easily subjected to alteration or whether it is invariably fixed in the body plan of the respective organism (59, 74). The degree of evolutionary plasticity of a structure may be related to its functional burden (78). In insects, alterations in other organ systems can obviously impose a number of reconstructions on circulatory organs. In several cases, the resulting spatial constraints may have decoupled the task of hemolymph supply from the dorsal vessel. Decoupling of previously linked structures or functions is seen to be one of the most common ways to induce evolutionary innovations (2, 59). In this manner, body appendage supply became independent from the dorsal vessel, and accessory pulsatile organs eventually appeared. In wing circulatory organs, for example, reconstructions of the flight apparatus may have triggered the individualization of wing-hearts from the dorsal vessel (46). Thus the appearance of accessory pulsatile organs during insect evolution may be interpreted as a result of alteration in other organ systems.

Conceivably, building blocks for new organs are recruited from various systems and assembled in new ways. Construction of a pump requires muscles as well as elastic antagonists such as connective tissue structures or flexible cuticle. Comparative investigation of the attachment sites, innervation, and ultrastructure of accessory pulsatile organ muscles has revealed their heterogeneous provenance (Table 1). Circulatory muscles may have been recruited by splitting some fibers off a muscle and shifting their attachment sites, or by displacement of a muscle portion. The former mode has probably been realized in some antenna-hearts (67),

Table 1 Survey of the accessory pulsatile organ components and their supposed provenance

Appendage	Pulsatile organ		Hemolymph flow conduit
	Contractile component	Elastic antagonist	
Antenna	Pharynx dilator	Connective tissue	Vessel
Mouthpart	Skeletal muscle	Flexible cuticle	Diaphragm
Leg	Skeletal muscle	Connective tissue	Diaphragm
Wing	Myocardium	Connective tissue	Cuticular tube
Cercus	Rectum dilator	Flexible cuticle	Vessel
Ovipositor	Genital chamber muscle	Flexible cuticle	Diaphragm

whereas the recruitment of an entire muscle portion is evident in leg-hearts (26, 29; Figure 4c). The wing-hearts, on the other hand, are supposed to be individualized portions of the myocardium (46), a conclusion that is supported by developmental genetics (49). Obviously, any muscle system is liable to become a component of a circulatory pump given that its location is close to the reconstruction site. Further developmental studies on this subject would certainly be rewarding. Because myogenic autonomy is inherent to all known accessory pulsatile organs, the recruited heart muscles must have attained pacemaker rhythmicity. Analogously, nervous control of the newly assembled hearts must have evolved toward a modulation of the autonomous rhythmic muscle contraction.

CONCLUSION

Because of the limited number and clear arrangement of the involved components, accessory pulsatile organs graphically illustrate the ways in which new organs enter and prevail in the insect bodyplan. Several building blocks originating from various organ systems have been reassembled to form new functional units with their own new physiological properties. These new entities cannot be homologized with any predecessor organ and are therefore evolutionary innovations (59). The functional design of an accessory pulsatile organ can be realized in very different ways in a body appendage, depending on the respective anatomical situation and the available building blocks. Even more astonishing is the diversity of the pulsatile organs of a given appendage in different species. The huge gaps in the understanding of microcirculation notwithstanding, changes in circulatory demands do not seem to be the decisive evolutionary forces for accessory pulsatile organ modification. Instead, developmental and spatial constraints resulting from reconstructions in other organ systems may be responsible for both the appearance of the new pulsatile organs and their subsequent morphological radiation. Accessory pulsatile organs therefore well illustrate the principle that changes in single organ systems can be fully grasped only if examined along with the evolution of the entire organism.

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LITERATURE CITED

1. Arnold JW. 1964. Blood circulation in insect wings. *Mem. Entomol. Soc. Can.* 38:5–60
2. Arnold SJ, Alberch P, Csány V, Dawkins RC, Emerson SB, et al. 1989. Group report: How do complex organisms evolve? In *Complex Organismal Functions: Integration and Evolution in Vertebrates*, ed. DB Wake, G Roth, pp. 403–33. New York: Wiley
3. Averof M, Akam M. 1995. Insect crustacean relationships—insights from comparative developmental and molecular studies. *Philos. Trans. R. Soc. London Ser. B* 347:293–303
4. Bänziger H. 1971. Extension and coiling of the lepidopterous proboscis—a new interpretation of the blood-pressure theory. *Mitt. Schweiz. Entomol. Ges.* 43:225–39
5. Barth R. 1963. Über das Zirkulationssystem einer Machilide (Thysanura). *Mem. Inst. Oswaldo Cruz* 61:371–439
6. Bayer R. 1968. Untersuchungen am Kreislaufsystem der Wanderheuschrecke (*Locusta migratoria migratorioides* R. et F., Orthopteroidea). *Z. Vergl. Physiol.* 58:76–155
7. Beattie TM. 1976. Autolysis in axon terminals of a new neurohaemal organ in the cockroach *Periplaneta americana*. *Tissue Cell* 8:305–10
8. Bitsch J. 1963. Morphologie céphalique des Machilides (Insecta, Thysanura). *Ann. Sci. Nat. Zool. Paris Sér.* #12, 5:501–706
9. Bodmer R. 1993. The gene tinman is required for specification of the heart and visceral muscles in *Drosophila*. *Development* 118:719–29
10. Brocher F. 1919. Les organes pulsatiles méso- et métatergaux des Lépidoptères. *Arch. Zool. Exp. Gén.* 60:1–45
11. Bruserud A. 1985. The ultrastructure of the larval heart and aortic diverticula in *Coenagrion hastulatum* Charpentier (Odonata, Zygoptera). *Zool. Anz.* 214: 25–32
12. Clarke UK. 1979. Visceral anatomy and arthropod phylogeny. In *Arthropod Phylogeny*, ed. AP Gupta, pp. 467–549. New York: Van Nostrand. 762 pp.
13. Clements AN. 1956. The antennal pulsatile organs of mosquitoes and other Diptera. *Q. J. Microsc. Sci.* 97:429–35
14. Debaisieux P. 1936. Organes pulsatiles des tibias de Notonectes. *Ann. Soc. Sci. Bruxelles Ser. B* 56:77–87
15. De Robertis EM, Sasai Y. 1996. A common plan for dorsoventral patterning in Bilateria. *Nature* 380:37–40
16. Dudel H. 1977. Vergleichende funktions-anatomische Untersuchungen über die Antennen der Dipteren. I. Bibiomorpha, Homoeodactyla, Asilomorpha. *Zool. Jahrb. Abt. Anat. Ontog. Tiere* 98:203–308
17. Dudel H. 1978. Vergleichende funktions-anatomische Untersuchungen über die Antennen der Dipteren. II. Cyclorrhapha (Aschiza and Schizophora-Acalypratae). *Zool. Jahrb. Abt. Anat. Ontog. Tiere* 99:224–98
18. Dudel H. 1978. Vergleichende funktions-anatomische Untersuchungen über die Antennen der Dipteren. III. Calypratae (I.O.Cyclorrhapha). *Zool. Jahrb. Abt. Anat. Ontog. Tiere* 99:301–70
19. Eernisse DJ. 1998. Arthropod and annelid relationships re-examined. In *Arthropod Relationships*, ed. RA Fortey, RH Thomas, pp. 43–56. London: Chapman & Hall. 383 pp.

20. Fahlander K. 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoden. *Zool. Beitr. Uppsala* 17:1–148
21. Fortey RA, Thomas RH, eds. 1998. *Arthropod Relationships*. London: Chapman & Hall. 383 pp.
22. Friedrich M, Tautz D. 1995. Ribosomal DNA-phylogeny of the major arthropod classes and the evolution of myriapods. *Nature* 376:165–67
23. Fung YC. 1984. *Biodynamics: Circulation*. Berlin/Heidelberg/New York: Springer-Verlag. 404 pp.
24. Gereben-Krenn BA, Pass G. 1999. Circulatory organs in Diplura: the basic design in Hexapoda? *Int. J. Insect Morphol. Embryol.* 28:71–79
25. Gerould JH. 1933. Orders of insects with heartbeat reversal. *Biol. Bull.* 64:424–31
26. Hantschk A. 1991. Functional morphology of accessory circulatory organs in the legs of Hemiptera. *Int. J. Insect Morphol. Embryol.* 20:259–73
27. Harvey RP. 1996. NK-2 homeobox genes and heart development. *Dev. Biol.* 178:203–16
28. Heinrich B. 1971. Temperature regulation of the sphinx moth *Manduca sexta*. II. Regulation of heat loss by control of blood circulation. *J. Exp. Biol.* 54:153–66
29. Heinrich B. 1976. Heat exchange in relation to blood flow between thorax and abdomen. *J. Exp. Biol.* 64:561–85
30. Heinrich B. 1993. *The Hot-Blooded Insects, Strategies and Mechanisms of Thermoregulation*. Cambridge, MA: Harvard Univ. Press. 601 pp.
31. Hertel W, Pass G, Penzlin H. 1985. Electrophysiological investigation of the antennal heart of *Periplaneta americana* and its reactions to proctolin. *J. Insect Physiol.* 31:563–72
32. Hertel W, Pass G, Penzlin H. 1988. The effects of the neuropeptide proctolin and of octopamine on the antennal heart of *Periplaneta americana*. *Symp. Biol. Hung.* 36:351–62
33. Hertel W, Penzlin H. 1992. Function and modulation of the antennal heart of *Periplaneta americana*. *Acta Biol. Hung.* 43:113–25
34. Hertel W, Rapus J, Richter M, Eckert M, Vettermann S, Penzlin H. 1997. The proctolinergic control of the antenna-heart in *Periplaneta americana* (L.). *Zoology* 100:70–79
35. Hessel JH. 1969. The comparative morphology of the dorsal vessel and accessory structures of the Lepidoptera and its phylogenetic implications. *Ann. Entomol. Soc. Am.* 62:353–70
36. Huber B. 1992. Frontal heart and arterial system in the head of Isopoda. *Crustaceana* 63:57–69
37. Hunter JP. 1998. Key innovations and the ecology of macroevolution. *TREE* 13:31–36
38. Hustert R. 1999. Locust middle legs are supplied with an accessory pump. *Int. J. Insect Morphol. Embryol.* 28:91–96
39. Jones JC. 1977. *The Circulatory System of Insects*. Springfield, IL: Thomas. 255 pp.
40. Kammer AE, Bracchi J. 1973. Role of the wings in the absorption of radiant energy by a butterfly. *Comp. Biochem. Physiol.* 45:1057–63
41. Kaufman WR, Davey KG. 1971. The pulsatile organ in the tibia of *Triatoma phyllosoma pallidipennis*. *Can. Entomol.* 103:487–96
42. Krenn HW. 1990. Functional morphology and movements of the proboscis of Lepidoptera (Insecta). *Zoomorphology* 110:105–14
43. Krenn HW. 1993. Postembryonic development of accessory wing circulatory organs in *Locusta migratoria* (Orthoptera: Acrididae). *Zool. Anz.* 230:227–36
44. Krenn HW, Pass G. 1993. Wing-hearts in Mecoptera (Insecta). *Int. J. Insect Morphol. Embryol.* 22:63–76
45. Krenn HW, Pass G. 1994. Morphological

- diversity and phylogenetic analysis of wing circulatory organs in insects. Part I: Non-Holometabola. *Zoology* 98:7–22
46. Krenn HW, Pass G. 1995. Morphological diversity and phylogenetic analysis of wing circulatory organs in insects. Part II: Holometabola. *Zoology* 98:147–64
 47. Kristensen NP. 1991. Phylogeny of extant hexapods. In *The Insects of Australia*, ed. Commonw. Sci. Ind. Res. Organ. (CISRO), pp. 125–40, Carlton, Victoria: Melbourne Univ. Press. 2nd ed.
 48. LaBarbera M. 1990. Principles of design of fluid transport systems in zoology. *Science* 249:992–1000
 49. Lawrence PA. 1982. Cell lineage of the thoracic muscles of *Drosophila*. *Cell* 29:493–503
 50. Manton SA. 1977. *The Arthropoda: Habits, Functional Morphology and Evolution*. Oxford: Clarendon Press. 527 pp.
 - 50a. Matus S, Pass G. 1999. Antennal circulatory organ of *Apis Mellifera* L. (Hymenoptera: Apidae) and other Hymenoptera: functional morphology and phylogenetic aspects. *Int. J. Insect Morphol. Embryol.* 28:97–109
 51. McIndoo NE. 1939. Segmental blood vessels of the American cockroach (*Periplaneta americana* L.). *J. Morphol.* 65:323–51
 52. McLaughlin PA. 1983. Internal anatomy. In *The Biology of Crustacea*, ed. LH Mantel, 5:1–53. New York: Academic. 479 pp.
 53. McMahon BR, Burnett LE. 1990. The crustacean open circulatory system: a reexamination. *Physiol. Zool.* 63:35–71
 54. Meyer E. 1931. Über den Blutkreislauf der Ephemeren. *Z. Morphol. Oekol. Tiere* 22:1–51
 55. Miller TA. 1979. Nervous versus neurohormonal control of insect heartbeat. *Am. Zool.* 19:77–86
 56. Miller TA. 1985. Heart and diaphragms. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, ed. GA Kerkut, LI Gilbert, 11:119–29. Oxford: Pergamon. 575 pp.
 57. Miller TA. 1985. Structure and physiology of the circulatory system. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, ed. GA Kerkut, LI Gilbert, 3:289–353. Oxford: Pergamon. 625 pp.
 58. Minelli A. 1993. Chilopoda. In *Microscopic Anatomy of Invertebrates*, ed. FW Harrison, ME Rice, 12:57–114. New York: Wiley. 484 pp.
 59. Müller GB, Wagner GP. 1991. Novelty in evolution: restructuring the concept. *Annu. Rev. Ecol. Syst.* 22:229–56
 60. Murray JA. 1967. Morphology of the cercus in *Blattella germanica* (Blattaria: Pseudomopinae). *Ann. Entomol. Soc. Am.* 60:10–16
 61. Nitecki MW, ed. 1990. *Evolutionary Innovations*. Chicago: Univ. Chicago Press. 304 pp.
 62. Nutting WL. 1951. A comparative anatomical study of the heart and accessory structures of the orthopteroid insects. *J. Morphol.* 89:501–97
 63. 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
 64. Pass G. 1985. Gross and fine structure of the antennal circulatory organ in cockroaches (Blattodea, Insecta). *J. Morphol.* 185:255–68
 65. Pass G. 1987. “Cercus heart” in stoneflies—a new type of accessory circulatory organ in insects. *Naturwissenschaften* 74:440–41
 66. 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). *Int. J. Insect Morphol. Embryol.* 17:103–12
 67. Pass G. 1991. Antennal circulatory

- organs in Onychophora, Myriapoda and Hexapoda: functional morphology and evolutionary implications. *Zoomorphology* 110:145–64
68. Pass G. 1998. Accessory pulsatile organs. In *Microscopic Anatomy of Invertebrates*, ed. F Harrison, M Locke, 11B:621–40. New York: Wiley. 296 pp.
69. Pass G, Agricola H, Birkenbeil H, Penzlin H. 1988. Morphology of neurones associated with the antennal heart of *Periplaneta americana* (Blattodea, Insecta). *Cell Tissue Res.* 253:319–26
70. Pass G, Sperk G, Agricola H, Baumann E, Penzlin H. 1988. Octopamine in a neurohaemal area within the antennal heart of the American cockroach. *J. Exp. Biol.* 135:495–98
71. Paul RJ, Bihlmayer S, Colmorgen M, Zahler S. 1994. The open circulatory system of spiders (*Eurypelma californicum*, *Pholcus phalangioides*): a survey of functional morphology and physiology. *Physiol. Zool.* 67:1360–82
72. Predel R, Agricola H, Linde D, Wollweber L, Veenstra A, Penzlin H. 1994. The insect neuropeptide corazonin: physiological and immunocytochemical studies in Blattariae. *Zoology* 98:35–49
73. Pries AR, Neuhaus D, Gaegtens P. 1992. Blood viscosity in tube flow: dependence on diameter and hematocrit. *Am. J. Physiol.* 263:1770–78
74. Raff RA. 1996. *The Shape of Life: Genes, Development and the Evolution of Animal Form*. Chicago: Univ. Chicago Press. 520 pp.
75. Regier JC, Shultz JW. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. *Mol. Biol. Evol.* 14:902–13
76. Richards AG. 1963. The ventral diaphragm of insects. *J. Morphol.* 113:17–47
77. Richter M, Hertel W. 1997. Contributions to physiology of the antenna-heart in *Periplaneta americana* (L.) (Blattodea: Blattidae). *J. Insect Physiol.* 43:1015–21
78. Riedl R. 1978. *Order in Living Organisms: A Systems Analysis of Evolution*. Chichester: Wiley. 313 pp.
79. Rousset A. 1974. Les différenciations postérieures du vaisseau dorsal de *Thermobia domestica* (Packard) (Insecta, Lepismatida). *Anatomie et innervation. C. R. Acad. Sci. Paris D* 278:2449–52
80. Ruppert EE, Carle KJ. 1983. Morphology of metazoan circulatory systems. *Zoomorphology* 103:193–208
81. Schneider D, Kaissling KE. 1959. Der Bau der Antenne des Seidenspinners *Bombyx mori* L. III. Das Bindegewebe und das Blutgefäß. *Zool. Jahrb. Abt. Anat. Ontog. Tiere* 77:111–32
82. Secomb TW. 1995. Mechanics of blood flow in the microcirculation. In *Biological Fluid Dynamics*, ed. CP Ellington, TJ Pedley, pp. 305–21. Cambridge: Co. Biol. 363 pp.
83. Selman BJ. 1965. The circulatory system of the alder fly *Sialis lutaria*. *Proc. Zool. Soc. London* 144:487–535
84. Siewing R. 1956. Untersuchungen zur Morphologie der Malacostraca (Crustacea). *Zool. Jahrb. Abt. Anat. Ontog. Tiere* 75:39–176
85. Sláma K. 1976. Insect haemolymph pressure and its determination. *Acta Entomol. Bohemoslov.* 74:362–74
86. Sláma K, Baudry-Partiaogolou N, Provansal-Baudez A. 1979. Control of extracardiac haemolymph pressure pulses in *Tenebrio molitor*. *J. Insect Physiol.* 25:825–31
87. Snodgrass RE. 1938. Evolution of the Annelida, Onychophora and Arthropoda. *Smithson. Misc. Collect.* 97:1–159
88. Steinacker A. 1978. The anatomy of the decapod auxiliary heart. *Biol. Bull. Woods Hole* 154:497–507
89. Steinacker A. 1979. Neural and neurosecretory control of the decapod crustacean auxiliary heart. *Am. Zool.* 19:67–75
90. Stys P, Zrzavý J. 1994. Phylogeny and

- classification of extant Arthropoda: review of hypotheses and nomenclature. *Eur. J. Entomol.* 91:257–75
91. Tartes U, Kuusik A. 1994. Periodic muscular activity and its possible functions in pupae of *Tenebrio molitor*. *Physiol. Entomol.* 19:216–22
92. Thomsen E. 1938. Über den Kreislauf im Flügel der Musciden, mit besonderer Berücksichtigung der akzessorischen pulsierenden Organe. *Z. Morphol. Oekol. Tiere* 34:416–38
93. Thomson KS. 1992. Macroevolution: the morphological problem. *Am. Zool.* 32:106–112
94. Wasserthal LT. 1975. The role of butterfly wings in regulation of body temperature. *J. Insect Physiol.* 21:1921–30
95. Wasserthal LT. 1976. Heartbeat reversal and its coordination with accessory pulsatile organs and abdominal movements in Lepidoptera. *Experientia* 32:577–78
96. Wasserthal LT. 1980. Oscillating haemolymph “circulation” in the butterfly *Papilio machaon* L. revealed by contact thermography and photocell measurements. *J. Comp. Physiol.* 139:145–63
97. Wasserthal LT. 1981. Oscillating haemolymph “circulation” and discontinuous tracheal ventilation in the giant silk moth *Attacus atlas* L. *J. Comp. Physiol.* 145:1–15
98. Wasserthal LT. 1982. Antagonism between haemolymph transport and tracheal ventilation in an insect wing (*Attacus atlas* L.): a disproof of the generalized model of insect wing circulation. *J. Comp. Physiol.* 147:27–40
99. Wasserthal LT. 1983. Haemolymph flows in the wings of pierid butterflies visualized by vital staining (Insecta, Lepidoptera). *Zoomorphology* 103:177–92
100. Wasserthal LT. 1996. Interaction of circulation and tracheal ventilation in holometabolous insects. *Adv. Insect Physiol.* 26:297–351
101. Wasserthal LT. 1998. The open haemolymph system of Holometabola and its relation to the tracheal space. In *Microscopic Anatomy of Invertebrates*, ed. F Harrison, M Locke, 11B:583–620. New York: Wiley. 296 pp.
102. Wasserthal LT. 1999. Functional morphology of the heart and of a new cephalic pulsatile organ in the blowfly *Calliphora vicina* (Diptera: Calliphoridae) and their role in hemolymph transport and tracheal ventilation. *Int. J. Insect Morphol. Embryol.* 28:111–29
103. Weygoldt P. 1979. Arthropod interrelationships—the phylogenetic-systematic approach. *Z. Zool. Syst. Evolutionsforsch.* 24:19–35
104. Whedon A. 1938. The aortic diverticula of the Odonata. *J. Morphol.* 63:229–61
105. Wheeler WC, Cartwright P, Hayashi CY. 1993. Arthropod phylogeny: a combined approach. *Cladistics* 9:1–39
106. Woodhead AP, Stoltzman CA, Stay B. 1992. Allatostatins in the nerves of the antennal pulsatile organ muscle of the cockroach *Diploptera punctata*. *Arch. Insect Biochem. Physiol.* 20:253–63
107. Woodring JP. 1985. Circulatory systems. In *Fundamentals of Insect Physiology*, ed. MS Blum, pp. 5–183. New York: Wiley. 598 pp.