Gross and Fine Structure of the Antennal Circulatory Organ in Cockroaches (Blattodea, Insecta)

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ABSTRACT The antennal circulatory organ of *Periplaneta americana* and *Blaberus craniifer* was investigated by light and electron microscopy. This organ consists of two pulsatile ampullae located near the antennal base which are interconnect by a large transverse muscle and associated blood vessels which run into the antennae. Diastole is caused simultaneously in both ampullae by the transverse muscle. Systole is produced passively by the elasticity of the wall of the ampullae and minute accessory tendons. Both elastic structures contain fine unbanded extracellular filaments.

The antennal vessels possess two distinct regions: a proximal convoluted region lying within the hemocoeol of the head and a narrower distal region running through the antenna and opening near the antennal apex. The length of the proximal portion increases markedly during ontogeny in correlation with the growing antenna. Its wall consists of a high-prismatic epithelium ensheathed by a thick layer of collagen fibrils. The structure of the wall cells is comparable to that found in some salt transporting epithelia: it shows a polar organization with basal infoldings, a large number of mitochondria, and typical arrangement of the junctions or mitochondrialarificial junctional complexes. The possible physiological function of this epithelium in ionic or osmoregulation of the hemolymph entering the antenna is discussed. The wall of the distal vessel region consists of a flat single-layered epithelium and seems to be specialized only for delivery of hemolymph to antennae. The structure and function of the antennal heart in cockroaches is compared to that found in other insects.

Independent pulsatile circulatory organs for the antennae are known to occur in several orders of insects, but have usually been described only cursorily (reviews: Hoffmann, '76; Jones, '77). The first detailed description of such an antennal heart was published by Pawlowa (1895) in studying cockroaches and grasshoppers. Her schematic drawing of this circulatory organ in *Periplaneta* has been adopted by nearly all textbooks in entomology. These observations were confirmed in general with only a few additional notes by Brocher ('22), Kloska ('24) and Arnold ('60); some brief ultrastructural remarks were reported by Beattie ('72; '76). Using both light and electron microscopy, the present study refines and in some aspects corrects the currently accepted description of the morphology of the pulsatile antennal heart in the cockroach.

MATERIAL AND METHODS

**Animals**

Early instars and imagines of both sexes of *Periplaneta americana* Linnaeus bred in the laboratory of the institute were used in this study. For comparison some specimens of *Blaberus craniifer* Burmeister were also investigated.

**Light microscopic techniques**

For dissection the heads were injected with a mixture of indigocarmin (0.1 g) diluted in saturated aqueous picric acid (30 ml), 40% formol (10 ml) and glacial acetic acid (1 ml). For histological investigations the organs were fixed in Dubosq-Brasil (Romeis, '68) and embedded in the epoxy resin ERL-4206. Semithin sections (1 μm) were stained with 0.1% toluidine blue in 1% borax solution. Paraffin
sections were used for staining of elastic connective tissue (azan, orcein, resorcin-fuchsin, PAS: Romeis, '68). For proof of chitin whole mounts of ampullae were examined with the chitosan test after a modified moderate maceration (Richards, '51). Possible pinocytotic activity of some cells was investigated in adult cockroaches by injection of 0.1 ml of a 1% trypan blue solution in saline into the abdominal hemocoel. The animals were killed after different intervals (1, 6, 12, and 24 hours) and the coloration of the dissected tissue examined.

Transmission electron microscopy

The organs were fixed several times with the classical fixative mixtures (cf. Glauert, '75). However, best results were obtained with low osmium pre-fixation (Eisenman and Alpert, '82) or a mixture of equal volumes of 2.5% glutaraldehyde and 1% osmium tetroxide, in a 0.1 M sodium cacodylate buffer (pH 7.4, 4°C, 1 hour). The tissues were stained en block in a 1% aqueous solution of uranyl acetate, subsequently dehydrated with ethanol and embedded in ERL-4206. Ultrathin sections were stained with 5% uranyl acetate and 0.5% lead citrate and examined in a Zeiss EM-9S2.

Scanning electron microscopy

Fixation was the same as for transmission electron microscopy. The preparations were briefly sonicated, dehydrated with acetone, and critical point dried. After coating with gold they were examined in a Cambridge Mk2a scanning electron microscope.

RESULTS

General morphology

In cockroaches the aorta ends in the head directly at the back of the brain where it forms a funnel-like enlargement (Fig. 1). This partly fibrous formation is connected laterally with the oesophagus and dorsally with the connective tissue sheath of the brain, largely enclosing the retrocerebral gland complex. Blood, passing through the dorsal vessel, flows between oesophagus and brain into a frontal sinus from which several blood streams radiate into different portions of the head.

The antennal circulatory organ lies within the frontal sinus and its lateral branches, and it is functionally almost independent of the dorsal vessel. Situated medially to each antennal base, the antennal heart consists of pulsatile ampullae that are associated with blood vessels running into these appendages. The two ampullae are interconnected by a large transverse muscle (Figs. 2 and 4). In addition, two very delicate fan-shaped muscles, originating from the enlarged end of the aorta, extend beneath the brain up to the large transverse muscle and insert on its medial ventral surface (Figs. 3, 4 and 5).

Two regions can be distinguished in the antennal vessel: a relatively thick proximal portion which lies coiled near the antennal base in the hemocoel of the head, and a much narrower distal part which extends through the antenna all the way to the antennal apex where the vessel opens. The blood streams back to the head capsule in the more voluminous antennal hemocoel. Reaching a sinus below the deutocerebrum, the blood flows to the occipital parts of the head and then finally back to the dorsal thorax through the neck of the animal.

Abbreviations

Amp, Ampulla
AN, Antennal nerve
Ao, Aorta
AS, Antennal sclerite
AV, Antennal vessel
BL, Basal lamina
Br, Brain
Ca, Corpora allata
Cc, Corpora cardiaca
CE, Compound eye
Co, Collagen
Cut, Cuticle
D, Desmosome
Damp, Dilatator muscle of ampulla
Damp a, Accessory dilatator muscle of ampulla
EAn, Enlarged anterior end of aorta
EL, External lamina
ET, Elastic tendon
F, Fibrocyte
Fd, Hemidesmosome
Hem, Hemocyte
Hypo, Hypodermis
L, Lumen of vessel
Lamp, Lumen of ampulla
M, Mitochondrion
N, Nucleus
Nr, Nervus recurrent
Oc, Ocellus
Oes, Oesophagus
Ost, Ostium
OstV, Ostial valve
RGI, Retrocerebral glands
SJ, Scalariform junction
Tr, Trachea
W, Wall of ampulla
**Structure and functional mechanism of ampullae**

The two ampullae are lenticular vesicles (diameter in imagines about 450–500 μm) attached directly to the integument of each antennal base medially, just beneath the ocellus. Their position is marked externally by small cupola-like elevations on the frontal surface. In *Periplaneta* the cuticle in this area is somewhat transparent enabling clear observation of pulsation activities of the ampullae in living animals under the dissecting microscope.

Structure and histology of the ampullae have only been briefly described and in some respects misinterpreted by earlier investigators. The outer wall of the ampulla is formed to a large extent by the hypodermis of the head capsule; the inner wall is between 9–20 μm thick and consists of a loosely arranged epithelium covered with thick extracellular laminae on both sides (Figs. 6 and 7). Medially the two vesicles are linked by the large transverse muscle which inserts on their walls. The contraction of this muscle enlarges the lumina of both ampullae simultaneously by stretching their inner wall slightly upward in an oblique, medial direction (Fig. 8a). From a functional point of view this muscle must be referred to as dilator of the ampullae. The delicate muscle strands between the large transverse muscle and the enlarged anterior end of the aorta can be designated as accessory dilators.

These smaller muscles have no strong contractile power but their function is to keep the transverse muscle in an arched position in tension, as can be concluded from observing the pumping of the intact antennal heart in an opened head. If the accessory dilator muscles are cut, the large muscle extends straight between both ampullae and still contracts. In diastole blood enters each vesicle through a single vertical slit-shaped ostium located just beneath the insertion of the dilator muscle (Figs. 6 b, 9, and 12). The lowered pressure at that moment is obviously responsible for the temporary constriction of the base of the vessel hindering backflow of blood from the antennal vessel into the lumen of the ampulla; this is easily
Figs 2-5. Sections through the head of Periplaneta. 2, Cross section at the level of the ampullae and the transverse dilator muscle. ×60. 3, Parasagittal section showing the position of the dilator muscles of the ampullae. ×100. 4 and 5, Ventral views of the antennal heart (oesophagus removed). ×70.
Fig. 6. Sections through the ampulla of the antennal heart of Periplaneta: a and b, Cross sections (levels indicated by broken lines in c); c, sagittal section. ×150.

Fig. 7. Cross section through the inner wall of ampulla with the inserting dilatator muscle. ×3,700. Inset: filamentous external lamina. ×42,000.
observed in isolated preparations of the working antennal heart.

The antagonistic force to the dilator muscle causing ampullar systole lies in the elasticity of the wall of the ampullae themselves and in small accessory tendons connecting the ampullae with the integument near the antennal sclerite (Figs. 6 b and 9). During relaxation of the dilator muscle, the vesicles are thereby flattened and blood is pressed into the antennal vessel. Elasticity of the ampullar wall is based on the thick external laminae covering the epithelium on both sides. In the electron microscope they appear as a dense meshwork of very thin, unbanded filaments (Fig. 7). The small tendon consists entirely of such filaments. Under the light microscope, whole mounts of the ampulla show the filaments to be organized in cylindrical bundles (Fig. 12). The external laminae of the ampulla stain somewhat like elastic connective tissues in vertebrates: blue with azan and purple with resorcin-fuchsin. However, the staining was not very intense with orcein, even using different modifications. No positive staining reaction could be observed with the PAS-reaction or with the chitosan test.

During systole, bloodflow out of the ampullar lumen is prevented by closure of the ostial valve (Figs. 6 and 8 b). It consists of a very thin (1.5 \( \mu \)m) tissue-fold which extends transversely from the bottom to about the middle of the ampullar lumen. This value is not covered by filamentous laminae as is the epithelial wall of the ampulla.

The antennal vessel

a. Proximal region

The proximal part of the antennal vessel lying in the hemocoel of the head is coiled in close loops forming a kind of glomerulus near the base of the antenna (Figs. 9 and 10). In adult males of Periplaneta this region is about 2.5–3.0 mm long with an external vessel diameter of about 70 \( \mu \)m and a lumen diameter of 40 \( \mu \)m; just before entering the antenna the vessel narrows considerably. In early instars the proximal vessel is only slightly thinner (e.g., when body length is 8 mm, external vessel diameter is about 50 \( \mu \)m) but much shorter (about one tenth of its length in the adult), and practically without loops (Fig. 11). As the insects grow older and show increased length and volume of the antenna, the proximal portion of the antennal vessel becomes markedly longer and more convoluted. Maximum size is reached in adult males which possess the longest antennae, surpassing even their own body length.

The proximal region of the antennal vessel differs from the distal one not only in dimensions and general morphology, but also in its histological structure. The distal wall consists of two different layers: an inner epithelium of high-prismatic cells overlain by a thick layer of extracellular collagen fibrils interspersed with some fibrocytes (Fig. 13). The cells show a distinctly polar organization: basally (adlumenally) there are various infoldings of the plasma membrane, a very large number of mitochondria mainly in a middle region, and apically, the nuclei. The
basal infoldings (Fig. 14) are irregular and of varying depth (sometimes up to a third of the cell height) and are interdigitated with the lateral membranes of adjacent cells. The apical (abluminal) cell membrane shows no special surface differentiations.

In the basal region junctions between the membranes are formed by numerous maculae adhaerentes. Apically the lateral membranes are connected all around by a tortuous zonula septata (Figs. 13 and 19). Characteristically in these wall cells there are long

Figs. 9–12. Views of the right antennal base showing one antennal circulatory organ of Periplaneta. 9, Scheme. 10, Adult male. 11, Early instar (body length about 8 mm). 12, Whole mount, phase contrast. Figs. 10–12: ×45.
scalariform junctions, occurring basally, which are formed either homocellularly by interdigitations of adjacent cells or autocellu-
larly by infoldings of the membranes of one cell (Figs. 15–18). Along their course the scalariform junctions are sometimes provided with desmosomes (Fig. 17) and interrupted by gap junctions (Fig. 18), by nonjunctional regions or by dilatations of the intercellular space (Fig. 15). Two juxtaposed mitochondria are frequently associated with the mem-
branes, forming mitochondrial-scalariform junction complexes (Figs. 14, 15, and 18).

The cytoplasm of the cells contains a striking number of microtubules that are found in parallel bundles in the basal region (Fig. 15). Furthermore, in the perinuclear cyto-
plasm, annulate lamellae are sometimes observed (Fig. 20). Despite the numerous mitochondria, other organelles which are generally characteristic of actively synthetic cells, such as endoplasmic reticulum and dictyosomes, are not remarkably abundant. Indica-
tions of augmented endo- or exocytotic activity could not be seen either. This is also confirmed by trypan blue injections; the dye was not visible in the cells even after circu-
lating for 24 hours in the blood.

The vessel is lined by an extraordinarily thick basal lamina (up to 0.5 μm) which is anchored to the plasma membrane by hemi-
desmosomes (Fig. 16). Within the amorphous matrix of that lamina some collagen fibrils and thin unbanded filaments can be found. The outer collagenous sheath of the proximal segment measures about a third of the wall thickness. The fibrils are in bundles and nearly all of them are longitudinally ori-
ented (Fig. 13). Between fibrils some tracheal and tracheoles can be found. Externally, the vessel is covered with a relatively thin amorphous extracellular coat (0.05–0.1 μm thick) which lacks fibrils.

Nerve fibers could not be detected in connection with the antennal vessel.

b. Distal region

Beyond the scape, the vessel, passing through the center of the antenna, runs mediolateral up to the tip attached to the hypo-
dermis (Figs. 22 and 24). Entering the anten-
a the lumen of the vessel narrows mark-
edly, but once within the antenna, the diameter remains almost constant (about 25 μm). The wall of the vessel consists of a single flattened epithelial layer; the collagenous sheath of the proximal part is reduced and ends in the basal antennal segments. The wall itself becomes gradually thinner up to the tip (from 8.2 μm to 0.2 μm, Fig. 24). The cells contain numerous microtubules but lack both polar organization and the numerous mitochondria which are characteristic of the inner epithelium of the proximal vessel re-
gion. The cells are interconnected by irregu-
lar folds of their lateral membranes that regularly possess septate desmosomes. The wall of the distal vessel region is covered externally with laminae as is the proximal part; the thin unbanded filaments of the inner lamina, however, are concentrated in longitudinal bundles.

The vessel opens in the terminal segment of the flagellum through a laterally positioned pore (Fig. 21). In addition to this opening, Pawlowa (1895) described numerous small circular pores in the vessel wall through which she observed the passage of hemocytes. However, I could not confirm the existence of such openings, neither from ob-
servations of the blood stream in intact anten-
nae nor from evaluation of serial sections of the outermost antennal segments. In contrast to Pawlowa’s observations that hemocytes seldom pass through the terminal pore, I observed an intense efflux of them.

Occasionally cockroaches lose some distal segments of their antennae. Investigations of the tips of such antennae showed that the blood vessel does not become enclosed in the blood clot closing the wound; the blood still streams from a terminal pore.
Figs. 21-24. The distal region of the antennal vessel of Periplaneta. 21, Sagittal section through the antennal apex. 22, Cross section through the basal flagellar segment. 23, Cross section through the outermost distal flagellar segment. Figs. 18-20: ×250. 24, Cross section through the antennal vessel in the outermost flagellum segment. ×5,700.
DISCUSSION

A lack of detail in most descriptions of the functional morphology and histology of antennal hearts in insects makes broad comparisons difficult. However, from the few thorough investigations, it is obvious that there exist some distinct functional types of this organ within the pterygotes. The differences especially concern the working mechanism of the ampullae (Pass, '80). In cockroaches two pulsating ampullae exist which are functionally connected by a transverse muscle. Its contraction causes diastolic expansion of both vesicles simultaneously, and hemolymph can enter through the valved ostium.

Different views exist about the mechanism of the systolic compression of the ampullae by which the hemolymph is expelled into the antennal vessel. Pawlowa (1895) conjectured that the elasticity or contractility of the ampullae was based on their wall cells, and considered them muscle fibers. Arnold (‘60) assumed that contractility of the ampullae required muscular power as well, and he described a thin sheath of muscle fibers overlying the wall epithelium; such fibers were described as spreading from the dilator muscle and inserting in the cuticle around the circumference of the vesicles. However, even by careful ultrastructural investigation, muscle fibers which might function as constrictors of the ampullae could not be found. Rather it is obviously the elasticity of filamentous structures which cause systolic compression of the vesicles, as also assumed by Beattie (‘72). They form thick extracellular laminae on both sides of the epithelial wall of the ampullae as well as minute tendons connecting the outer wall of the vesicles with the cuticle of the head capsule. Morphologically comparable unbanded filaments within contractile structures, said to be elastic, are known from some connective tissues in insects (reviews: François, ’76; Ashhurst, ’82). They have been found in arthropods in the extracellular sheath covering the dorsal vessel (Bacetti and Bigliardi, ’69; Seifert and Rosenberg, ’78), in acellular strings attaching the dorsal vessel to nearby tissues (Locke and Huie, ’72, ’75), and in mesenteric connective tissue (François, ’78). The chemical nature of these elastic structures has not yet been identified. Their digestion by pancreatic elastase (Bacetti and Bigliardi, ’69) should be interpreted with caution because of the regular contamination of such biochemical preparations with other enzymes (cf. Ashhurst, ’82). As the protein elastin has not yet been determined unambiguously by chemical methods in any invertebrate species, and because the structure of elastic tissue in insects differs markedly from that in vertebrates (cf. Knese, ’79), it seems unlikely that both have the same chemical composition (cf. Ashhurst, ’82; Sage and Gray, ’79). Nevertheless, the staining properties of the elastic structures of the antennal ampullae in cockroaches resemble somewhat those of vertebrate elastic connective tissue. No histochemical indications of polysaccharides, chitin, or related substances could be detected in the elastic structures of the antennal hearts. In any case, it is very unusual that the active, blood-propelling force of a circulatory pump is based on elastic structures and not on muscle.

From descriptions of antennal hearts of other insect species, one can infer that functionally similar types of organs exist in other pterygotes (Locusta: Bayer, ’68; Carausius: Scholl, ’69; Sialis: Selman, ’65; Hemipenthes: Dudel, ’77). In Diptera the anatomical situation is somewhat varied. In some cases the dilator muscle of the ampullae does not interconnect the two vesicles, but originates from the aorta wall or the tentorium (Clements, ’56; Dudel, ’77, ’78a, b). The functional morphology of these organs in the coleopteran Melolontha is completely different: systole of the ampulla is caused by a compressor muscle, whereas an elastic band dilates the lumen of the vesicle after relaxation of the muscle (Pass, ’80). Additional functional types of the antennal organs were described in Rhodnius (Pinet, ’64) and in Apis (Freudenstein, ’28). However, both descriptions require additional investigation with the electron microscope to confirm the reported views.

The antennal vessel in cockroaches is unique among investigated insects in possessing a convoluted proximal region lying in the hemocoel of the head capsule. This proximal region invites special attention both because of its extraordinary length, which increases as the antenna grows, and because of the histological structure of its wall. Based upon cytomorphology and organelle arrangement, the inner epithelium seems to have a special physiological function beyond that of a blood vessel. The distinct polarity in the structural organization of these cells is simi-
lar to various transporting epithelia, as was noted by Beattie ('72, '76). The shared characteristics are the highly infolded basal plasma membrane, the great number of mitochondria, and the intercellular junctions (cf. Berridge and Oschman, '72; Cioffi, '84; Hakim and Baldwin, '84). The basal infoldings increase the cell surface for substance exchange and may also provide enclosed spaces for formation of ion gradients. The various kinds of junctions and their positions strongly resemble the situation found in transporting epithelia. Four types of junctions occur in these cells: pleated septate junctions, desmosomes and hemidesmosomes, gap junctions, and scalariform junctions. In addition to an adhesive function that maintains tissue integrity, one can assume an electrical or chemical coupling of the epithelial cells by the gap junctions. The zonula septata may also play a role as a partial permeability barrier for paracellular flow (cf. Lane and Skaer, '80; Lane, '82). Scalariform junctions have been found only in transporting epithelia of arthropods and related phyla. These junctions are thought to keep the intercellular cleft open in regions where rapid ion pumping and transport is required. Mitochondrial-scalariform junctional complexes seem to be limited to epithelia specialized for the active transport of fluid and solutes against a concentration gradient. The essential function of these complexes is assumed to involve the efflux of some ions into the narrow extracellular channels between cells, thus creating the driving force for a transepithelial fluid flow (Noirot-Timothée and Noirot, '80). However, proximal vessel wall cells would be rather unusual for transporting epithelia by lacking microvilli at the apical membrane and by having majority of the mitochondria in the middle region of the cells.

Secretory activity of the proximal vessel tissue is suggested by the stacks of annulate lamellae which are generally characteristic of cells specialized for protein synthesis (cf. Altmann, '73). However, except for the mitochondria, other organelles normally involved in secretory processes are not extraordinarily developed nor were any striking endo- or exocytoytic activities observed. The large number of microtubules in these cells possibly serve only a cytoskeletal function as indicated by their parallel arrangement.

A structural relationship of these cells can be found with the tissues of organs concerned with excretory and osmoregulatory functions. Nephridial organs generally consist of various regions on which a distinct tissue structure is associated with reabsorptive or secretory function. The ultrastructural organization of the epithelial wall of the antennal vessel definitely resembles tissues for which reabsorptive activities have been established, especially of ions and water. In addition, a secretory function has also been assumed for such cells in some cases (cf. Berridge and Oschman, '72; Kümmel, '77; Cioffi, '84). However, unlike the epithelia of kidney or nephridial tubules (e.g., the distal region of the vertebrate nephron or the crustacean antennal gland) structural polarity in the antennal vessel suggests transport mainly in the opposite direction.

From a functional point of view it may be argued that the wall tissue of the proximal antennal vessel region changes or controls in some way the chemical composition of the hemolymph entering the antennae. These head appendages with their numerous mechano- and chemosensory organs (Schaller, '78) are extremely important in the behavioral ecology of cockroaches (Roth and Willis, '52; Barth, '70; Rust et al., '76; Bell and Kramer, '79). The task of the vessel wall tissue may be of special significance for this antennal sensory complex, since the antennae otherwise contain only hypodermis and tracheae. Perhaps the cells are involved in the regulation of the homeostatic environment necessary for the functioning of nerve cells (cf. Treherne, '74; Treherne and Schofield, '81), which is of special importance in view of the large fluctuations that may occur in the chemical composition of the hemolymph plasma in insects (Pichon, '70; Florkin and Jeuniaux, '74).

Because of its anatomical position and structural similarities, a phylogenetic relationship of the proximal portion of the antennal vessel to the segmental organs of other arthropods is conceivable. Such organs are found in the anterior tagma of chelicerates, crustaceans, and lower tracheates and are often regarded as derivatives of metanephridia (cf. Seifert, '79). For the antennal segment such organs are known from crustaceans (reviews: Riegel and Cook, '75; Mantel and Farmer, '83). In the Tracheata, segmental tubules are known to be derived only from other segments of the head.
Distally, the antennal wall tissue is not characterized by any special organization and generally resembles that found in the antennal vessel of Melolontha (Pass, '80). The function of the distal vessel wall seems, therefore, to only provide a path for the entering hemolymph, thereby permitting circulation and rapid blood exchange within the antenna.

The extraordinarily thick basal lamina lining the vessel may perhaps be understood in connection with the strength of the wall and hemodynamic aspects. Besides its protective function it may minimize the frictional forces set up at the wall by the flowing hemolymph (cf. Luft, '76). Because of its fibrillar composition it may be termed a reticul lamina (cf. Francois, '76). Similar thick extracellular laminae are found in circulatory organs of insects (Baccetti and Bigiardi, '69; Locke and Huie, '72; Seifert and Rosenberg, '78). In addition, the proximal vessel segment is mechanically strengthened to resist distension by its thick outer collagenous sheath. Arnold ('60) mistook the collagenous layer for muscle. In the present study no muscle fibers could be found in the antennal vessel throughout its whole length. Therefore, it does not function peristaltically as does the muscular dorsal vessel. The circulatory pressure within the antennae is provided only by the pumping movements of the ampullae. Blast pressure phenomena, known for the elastic vertebrate aorta and arteries, probably play some role in blood transport within the antennae, since the stream is more or less continous distally.

The vessel extends out to the outermost flagellar segment and opens there by a single terminal pore. Additional circular perforations in the vessel in some distal segments through which an extrusion of hemocytes occur, as described by Pawlowa (1895), could not be confirmed. Perhaps Pawlowa made her observations on antennae which had been injured and showed abnormal circulation. Arnold ('60) described in mature embryos of Blaberus a tubular vessel extending from the ampulla only as far as the antennal pedicel; there the blood empties into the antennal hemocoeol which is divided by a median septum into an ascending and a descending stream.

The physiology of the antennal heart of Periplaneta has been investigated recently (Hertel et al., in press). Based upon this electrophysiological study, this accessory circulatory organ has to be classified as a myogenic motor. Since the dilatator muscles are innervated, a neuronal modulation of rhythmicity can be assumed.

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