The Antennal Pulsating Organs of Mosquitoes and other Diptera

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SUMMARY

The antennal pulsating organ of mosquitoes consists of two vesicles, each sending a blood-vessel to the antenna of its side and each connected to the aorta by a muscle. Contraction of the muscle causes blood to enter the vesicle through a valve and relaxation allows an elastic contraction of the vesicle so that the blood is discharged through the blood-vessel to the antenna. The organ appears to be myogenic.

Antennal pulsating organs occur in most families of the Diptera Nematocera but not all, and a similar organ is present in Drosophila.

INTRODUCTION

The heads of certain Diptera contain a small organ which has long been familiar to the morphologists who have studied these insects but which has generally received only brief mention incidental to other observations. Superficially the organ has the appearance of a pair of vesicles lying under somewhat modified areas of cuticle, each vesicle sending a prominent nerve to the brain. Dufour (1851) described the organ in Tipula oleracea and suggested that it represented vestigial ocelli. A similar nature has been ascribed to the organ in Chironomus (Miall and Hammond, 1900), Culex and Anopheles (Thomson, 1905), and Phlebotomus (Christopher, Shortt, and Barraud, 1926). Jobling (1928), studying Culicoides, considered the organ to be functional ocelli. Recently it has been described at some length in Aedes aegypti and has been called a sense organ, possibly sensitive to changes in atmospheric pressure (Day, 1955).

The ocellar nature of the organ was questioned by Clements (1953), who showed that the structures which had been called nerves were muscles running to the aorta between the lobes of the brain. In fact, clues to its real function were provided by Eggers (1924) and Risler (1953, 1955), who described blood-vessels entering the antennae of mosquitoes, although they did not describe their origin from the organ in question here. Miller (1950) briefly mentioned a single vesicle in the head of Drosophila from which two muscles ran to join the aorta at the back of the head. He suggested that this organ resembled the antennal pulsating organs of other insects but was unable to show how it could function as such. In the pages which follow, a description is given of the structure of the organ in mosquitoes, with an account of its probable method of functioning. These views were briefly expressed by Clements (1956).

METHODS

The use of a polarizing microscope was indispensable for studying the distribution of muscle fibres in the organ and for this purpose unstained sections

were used. In addition, sections were stained with Masson's trichrome stain after fixation in alcoholic Bouin, or with Samuel's silver stain after fixation in the recommended modification of Bouin's solution (Samuel, 1953).

**Structure and Function in *Culex pipiens* L.**

The structure of the organ can be seen best in sagittal section. It consists of two vesicles lying medially, just below the compound eyes, each giving off a vessel to the antenna of its side and each connected by a muscle to the aorta (figs. 1, 2). As Thomson (1905) has shown, the organ first appears during the pupal stage. It is not present immediately after the pupal moult but appears during the following 24 hours.

The organ shows externally as a pair of depressions, each about the width of an ommatidial facet, situated just under the compound eyes, one on each side of the midline. In section, the cuticle of the depression is seen to be flat, of normal thickness and bearing minute hairs. The epidermis underlying the cuticle forms the distal end of the vesicle and this small group of cells has the nature of columnar epithelium. The cells are very large with their nuclei disposed towards the free border. The walls of the vesicle arise from the edges of the group of columnar cells. The walls are clearly cellular near the cuticle but posteriorly form a flattened, nucleated layer. An opening into the vesicle is always present posteriorly, the dorsal wall extending into the sac and apparently forming a valve which would close the opening under certain circumstances (figs. 1, 2).

Ventrally, the sac gives rise to a vessel which runs into the antenna of the same side. This vessel has been called a trachea (Clements, 1953; Day, 1955),

![Diagram of antennal pulsating organ](image-url)
but it is more likely to be the blood-vessel described as entering the antenna by Eggers (1924). The wall of the vessel is thick and nucleated and it does not show the taenidia of tracheae of the same size. Occasionally, sections show branches from the trachea to the antenna which rise vertically to pass close to the vesicle but do not penetrate it.

Behind the vesicle is a spherical mass consisting of a very large number of nuclei narrowly separated by cytoplasm, apparently without cell boundaries. These are called receptor cells by Day (1955), but they bear no resemblance to typical sense cells and apparently are not innervated. From this syncytial body fine filaments run to the vesicle and to the integument, probably serving to hold the vesicle in position during contraction of the muscle. Possibly the syncytial body has the nature of connective tissue.

The aorta of mosquitoes is said by Jones (1954) to end as an inverted trough between the supraoesophageal ganglion and the pharynx, but in longitudinal sections it can be seen to extend as a tube over the pharynx for some distance in front of the brain. Between the syncytial body and the aorta run a number of distinctly striated muscle fibres formed into a rather loose bundle without a sheath. The fibres appear to splay out over the syncytial body and they are possibly attached to the vesicle. Some of the fibres are attached to the aorta in front of the brain; others, as can be seen with polarized light, run under the brain to be attached to the aorta much farther back. It is these two muscle bundles which have been called nerves by previous authors. The muscles show strong birefringence with polarized light. The vesicle, antennal vessel, and aorta are weakly birefringent; no muscle fibres can be seen in them, so they may consist of an elastic connective tissue.

Despite examination of a large number of specimens, including silver-stained material, no nervous connexions to the pulsating organ have been found. Jones (1954) concluded that the mosquito heart was myogenic, after failing
to find any direct innervation and after applying certain physiological tests. It appears that the pulsating organ is also myogenic.

Contraction of the muscles of the pulsating organ will extend the vesicles and will also, as occasional sections show, enlarge the lumen of the aorta in front of and below the brain. It may be presumed that blood will enter the expanding vesicles through the valves and that relaxation of the muscles will allow an elastic contraction of the vesicles causing a flow of blood through the antennal vessels, the valves being closed, and also forward from the aorta. Without experimental evidence it is impossible to say what part the pulsating organ plays in the movements of the antennal flagella, but if the pulsating organ is not under nervous control it cannot effectively control flagellar movement.

**Other Diptera**

An antennal pulsating organ is present in several families of the Diptera Nematocera. In the Culicidae it has been found in the genera *Anopheles*, *Culex*, *Theobaldia*, *Aedes*, and *Chaoborus*. It has been recorded in Tipulidae (Dufour, 1851), Chironomidae (Miall and Hammond, 1900), Ceratopogonidae (Jobling, 1928), Psychodidae (Christophers, 1926), and Rhyphidae, Cecidomyiidae, Mycetophilidae, and Sciaridae (Day, 1955). A study of the organ throughout the order, now being undertaken by the present author, has shown the organ to be present also in the Ptychopteridae (*Ptychoptera contaminata* (L.)), Trichoceridae (*Trichocera saltator* (Harris)), Scatopsidae (*Scatopse transversalis* Loew) and Blepharoceridae (*Liponeura* sp.). The organ is not to be found in either sex in *Thaumalea testacea* Ruthe (Thaumaleidae), *Simulium ornatum* Mg. (*Simuliidae*), or *Dilophus febrilis* (L.) (*Bibionidae*).

The structure of the organ is broadly similar in mosquitoes and the other families of the Diptera Nematocera, but minor differences are to be found. For example, the cuticle over the organ is often raised slightly rather than depressed, and in *Chironomus* the pulsating organ lies within the frontal tubercles. The epidermis is rarely hypertrophied, although this condition occurs in *Trichocera saltator* as in mosquitoes. As Day (1955) has pointed out, the presence of the antennal pulsating organ together with ocelli in certain families shows that these two organs are quite distinct.

Day was unable to find the organ in *Neoexaireta spinigera* Wied. (Stratiomyiidae) or *Musca domestica* L., and considered that it was probably entirely absent from the Diptera Brachycera. However, Miller's account of an antennal pulsating organ in *Drosophila melanogaster* Mg. has been confirmed by examining *D. funebris* (Fab.), where it consists of a single vesicle, below the ptalinum, from which two muscles arise directly without a distinct syncytial organ and run to the aorta. Antennal vessels pass from each side of the vesicle to the antennae.

Examination of *Panorpa germanica* L. (Mecoptera) has revealed an antennal pulsating organ strikingly similar to that found in Diptera. Accessory hearts supplying the antennae have been described in Orthoptera, Dictyoptera, and
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Hymenoptera (Wigglesworth, 1950) and it seems likely that they will be found in most insects.

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