Blood Circulation in Insect Wings

by

JOHN W. ARNOLD
Entomology Research Institute
Research Branch, Canada Department of Agriculture
Ottawa, Ontario.

Memoirs
of the
Entomological Society of Canada

No. 38, 1964

CONTENTS

PAGE

Introduction 5

Historical Review 6

Methods 7

Observations and Discussion 10

Features of wing circulation in insect orders 10

Ephemeroptera 10

Odonata 11

The orthopteroid complex 13

Cursoria 13

Orthoptera 15

Plecoptera 17

Hemiptera 18

Heteroptera 19

Homoptera 20

Neuroptera 22

Hymenoptera 23

Coleoptera 25

Mecoptera 27

Trichoptera 28

Lepidoptera 30

Diptera 32

Discussion and Conclusions 35

Acknowledgments 41

Appendix (list of insects) 42

References 46

Illustrations 48

Blood Circulation in Insect Wings

By JOHN W. ARNOLD

Entomology Research Institute
Research Branch, Canada Department of Agriculture
Ottawa, Ontario.

INTRODUCTION

It has long been known that blood circulates in the wings of insects. Apparently the phenomenon was reported first by Baker (1744) who observed it in the wings of a grasshopper. Since then it has been reported for numerous species in several orders and there is now little doubt that it occurs to some degree in all winged insects. It is true for definitive wings as well as for developing ones, and for modified wings such as tegmina, elytra, hemelytra, and halteres as well as for those that are specialized for flight.

The route and mechanism of blood circulation in the wings are understood in broad outline and are fundamentally alike in all species and in all forms of wings. In general, blood from the lateral intermuscular spaces of the thorax enters a wing at the humeral angle, flows distally to the wing apex through the large anterior veins and moves en route through cross veins toward the posterior margin. It returns to the body via posterior veins and empties into the pericardial sinus or the dorsal vessel by way of the axillary cord which extends from the anal angle of the wing to the scutellar region of the thorax. It is believed that the blood is propelled along this route by a combination of forces which include the aspirating action of subscutellar pulsatile organs, the pressure of blood flowing posteriorly from the head past the wing bases, the influence of respiratory and other movements, and in some insects the action of pulsatile structures within the wing itself. Nevertheless, the circulatory routes in the wings are as different in detail as the wing venation, and the forces involved in wing circulation differ in their relative importance in conjunction with structural features of the wings and of the insect.

Despite their inert appearance, the wings of insects are living evaginations of the meso- and metathoracic body wall. In this sense, and quite literally during wing development, the dorsal and ventral walls are structural duplicates of the body wall and contain between them blood, tracheae, and nerves. The definitive wings of the adult insect are of course modified by union of the two walls over much of their area so that the original condition is retained only along the veins. The latter are essentially remnants of the body haemocoel. Even here the inner layers of the original body wall, the epidermis and basement membrane, are sometimes much reduced or absent and the cuticle is thickened. The permanently appressed areas between the veins, i.e., areas of the wing membrane, appear to be entirely cuticular. However, tracheae and nerves pass through some of them and it seems likely that the union of the two walls is not always complete and may permit a slow percolation of haemolymph. Wings become dry and brittle in areas where blood circulation has ceased, and it seems evident that some exchange of materials is necessary in the wing membrane to maintain the resilience of the wing. In the main, however, tracheae and nerves lie within the wing veins and it is here also that an active circulation of blood occurs.

In view of the unique development of insect wings for flight and their modifications for functions other than flight, for example to protect, camouflage, and display, the necessity for nourishing them with a continuous supply of blood seems obvious. This requirement is also evident from a consideration of the

known and suspected physiological roles of the wings. In some insects the wings are, for example, sites of metabolic activity. This involves particularly the formation of pigments which, as in the case of the pteridines in developing wings of Lepidoptera, have fundamental roles in body metabolism. They also support numbers of sensillae which are concentrated mainly along the veins; the nerves which serve them lie within the veins. In some insects the wings are known to absorb radiant energy from the environment and transfer it to the body, presumably via the blood. In this way the internal temperature is raised in preparation for flight. A period of wing movement may precede flight for the same reason. It is logical to assume that the reverse is also true and that heat developed internally from the action of flight muscles can be dissipated by blood flowing from the thorax through the wings. This possibility is unproven and apparently was not entirely explored by Church (1960) in his excellent study of heat loss in insects. In the same way it is conceivable that waste metabolites from flight muscle action are removed rapidly from the thorax by blood flowing into the wings and may be removed from the blood in wing sinuses and deposited there in some form. Again, and contrary to some evidence, it may be suggested that the wings in some insects have at least a small respiratory function. Some contain an extensive tracheal system with loops of tracheoles suspended in the blood, particularly in sinuses near the wing bases. Finally, the existence of blood sinuses in the wings of many insects and the concentration within them of haemocytes and pigments emphasizes the suggestion of metabolic activity there and implies a role as a storage vehicle for haemocytes and as a site for their differentiation or destruction.

Flight is such a highly developed attribute of insects and is achieved in such a unique manner that each facet of its mechanism warrants study. The present work is a study of blood circulation within the wings. It attempts to compile existing information on the subject, presents circulation maps for the wings in representative species in the major insect orders, and as far as possible within the context demonstrates the mechanisms involved in wing circulation.

Historical Review

Despite the obvious need for blood to circulate in the wings as in the other appendages, and the existence of numerous publications on the subject, the fact of blood circulation in the wings is still not generally appreciated. References to the dry and lifeless nature of the insect wing can be found in recent publications and this impression is not an uncommon one. There has been a long history of doubt concerning not only circulation in the wings but of blood circulation in any form in insects. This doubt seems to have stemmed in the past from a failure to conceive of the idea of an open circulatory system and a reluctance to accept it when presented. Some of the great anatomists of the 18th and 19th centuries searched for veins and arteries in insects. Their failure to find them convinced many scholars of that era that the blood did not circulate and that the dorsal vessel, which was recognized by some as a pumping organ, had other roles. Almost one hundred years after Baker's (1744) observations on circulation in the wings were published and his further notes (1755) on pulsation of the dorsal vessel and leg hearts were recorded, James Rennie (1832), professor at King's College, London, stated "there is not, and cannot be, any real or direct circulation of blood in insects". In stating this he was knowingly refuting the several publications of Carus (1827, 1828, 1831), one of which (1831) includes the still acceptable "Carus rule" concerning the route of circulation in the insect wing. Strangely enough, Rennie's statement was not entirely unrealistic, for William Orr (1833) in reviewing Rennie's book and in quoting the statement, commented

that until lately blood circulation in insects had been considered very doubtful. In the same year Bowerbank (1833) published some general observations on blood circulation in insects including a note that he had observed blood flowing in the wing veins of *Phlogophora meticulosa.* Later (1836) he published a detailed account of circulation in the wings of *Chrysopa perla* and there is little doubt that his observations were considered by active entomologists of the day to be new discoveries. This opinion was also expressed by Tyrrel (1835) in his account of circulation in insects.

In the decade around 1830 the concept of a true blood circulation in insects was gaining general acceptance. The literature contains a variety of observations by authors such as Behn (1835), Bowerbank (1833, 1836), Burmeister (1832), Carus (1827, 1828, 1831), Duvernoy (1839), Newport (1837), Treviranus (1831), Tyrrel (1835), and Wagner (1832). Among these reports are several that record observations of circulation in the wings. Bowerbank noted it in the two insects mentioned previously. Carus detected it in the elytra, in the hind wings, or both, of a number of insects including *Semblis viridis, Eristalis apiformis, Lampyris noctiluca, Lycus sanguineus, Melolontha Frichii, Dermestes lardarius, Chrysomela menthae,* and some unnamed ephemerids and beetles. He also reported that a Professor Gruithuisen of Munich had previously (1812) observed wing circulation in *Gryllus viridissimus* and other insects. Charbrier, according to Kirby and Spence (1826), thought that insects were able to propel a fluid into and withdraw it from their wing nervures as the wings became elevated or depressed. Duvernoy merely reported that blood enters the wing veins. Ehrenberg and Hemprich, according to Verloren (1847), observed circulation in the wings of a *Mantis.* Göring and Pritchard (Verloren 1847) reported it for the elytra of *Dytiscus* and in the wings of *Semblis bilineata* and *Perla viridis.* Tyrrel saw it in species of *Hemerobius, Panorpa, Phryganea, Ephemera,* and in *Musca domesticus.* It is surprising then to find that Dufour (1841) vigorously challenged the whole concept of blood circulation in insects and supported his view by reference to the works of Cuvier, Malpighi, Swammerdam and some of the other great anatomists. In turn, Dufour's stand was assailed by Verloren (1847) who refuted the claim of support from those savants, tabled 90 species of insects and the regions within them in which blood circulation had been observed by 17 different authors, and presented a lucid account of the open system of blood circulation. Verloren's paper provides much information on the whole subject as it was understood at that time and a wealth of early references.

Although Verloren's outburst must have convinced most scholars of the efficacy of open blood circulation in insects, it apparently escaped the notice of some subsequent workers. There was still some tendency to believe in the existence of blood vessels and to try to relate blood circulation and respiration. Thus Agassiz (1851), Bassi (1851), and Blanchard (1851) became involved in exploring the possibility that certain tracheae served as blood conduits. On the other hand authors such as Moseley (1871), and Nicolet (1847) reported their observations on circulation in the wings as though the idea was not uncommon. During the last half of the 19th century interest in the subject seemed to lapse, except intermittently, and was revived early in the present century by workers such as Pawlowa and Brocher who were concerned with the mechanism of circulation. The work of authors in this recent period will be discussed in the text in conjunction with specific insect groups.

Methods

The wings of most insects are clear enough that blood circulation may be seen with the compound microscope at magnifications sufficient to reveal the

haemocytes. Sometimes the general course of blood circulation can be determined without resorting to special techniques. However, relatively few of them are clear enough for detailed observation under high magnification without some manipulation. Generally the vein walls are thick, sculptured, pigmented, or clothed in a variety of bristles or scales. In the case of modified wings such as elytra they are often heavily sclerotized and sculptured and frequently too contoured and inflexible for easy examination. Where the normal haemocyte complement in the blood is low, as in many species of Diptera for example, the complete course of flow can be determined only through long observation. The same is true for insects in which the lumens of the wing veins are narrow or the wing base is so constructed that entrance of haemocytes is limited. This is common in the hind wings of Coleoptera and Hemiptera. Positioning the wings in an unnatural fashion, or merely confining the insect for observation, in some cases causes erratic or reduced wing circulation. Nevertheless, careful examination of a number of individuals of each species will reveal routes of circulation that are acceptable as normal for the resting insect.

The methods used to observe circulation directly were relatively simple and similar to those described previously (Arnold 1959). For general scrutiny the insect was usually inverted on a glass slide and the wings were spread at a natural angle that did not interfere with normal circulation. Glass coverslips of suitable size were applied to the wings and a drop of water, to which a trace of detergent had been added, was led beneath. The wings were thus sandwiched in water between glass, and the insect's body was unrestrained and free from contact with the water. The water tension alone was sufficient to hold most insects in the inverted position and there was no evidence that circulation was affected adversely. Some of the large and active species required additional means of restraint. This was accomplished usually by stretching elastics across the body to hold the insect without undue pressure. The layer of water wetted the wing surfaces and greatly increased the clarity. Immersion oil was equally effective but tended to creep onto the insect's body. It was used to advantage only with Lepidoptera where the water mounts were unsatisfactory. Correct positioning of the insect was important and usually required the use of carbon dioxide as an anaesthetic. This frequently caused a temporary cessation of heartbeat and of circulation in the wings followed immediately on recovery by abnormally high rates of flow and erratic circulation including reversal in direction. Although this reaction was often troublesome it did nevertheless demonstrate forces involved in circulation by temporarily eliminating all or some of them and revealing them as they became reestablished in sequence and in an exaggerated condition. It also made it necessary to delay observations of the normal circulatory route until a steady pattern of flow returned. The method of Yeager and Hendrickson (1933) for examining circulation with light reflected from a white surface placed beneath the wing was found to be awkward with many species and was seldom employed.

To observe the action of the heart and pulsatile organs in relation to circulation in the wings, the insect had to be held in an upright position with the wings spread. This was accomplished by using a glass apparatus designed to accommodate the insects in this position. Standard microscope slides were fixed with transparent glue to the surface of a large glass slide in the form of an insect spreading board. The standard slides formed the supports for the wings and were separated by a space just large enough to contain the insect's body. A number of these were prepared in a variety of sizes to conform to the width and depth of the body for various species. The insects were handled as described above with the wings again held in position mainly by coverslips and water.

When necessary, the insect was further restrained by small blocks inserted before and behind it in the channel that contained the body.

Observations were made with a Leitz Ortholux microscope equipped with an Ultropak incident light illuminator. Both transmitted and reflected light were used, the choice depending entirely on the effectiveness of the illumination for the particular insect under observation. The Ultropak was employed mainly because the lenses with the aperture most commonly employed had a long working distance and were suitable for observing large insects and those with thick or contoured wings. Coloured filters were used as required to aid in detecting the moving haemocytes which in some insects are quite hyaline. It was also found useful to vary the position of the substage condenser and its magnifying lens for the same reason. In general, phase contrast was not useful because of the short working distance that its lenses allow and the confusing visual effects created by sculptured wing surfaces.

In an effort to determine the causes of circulation in the wings and of its variability within individual insects and between species, counts were made of various movements and pulsations that might be involved. These were visual counts, using a mechanical counter and timer, and included the heart-beat at different regions of the body, contractions of accessory pulsatile structures, waves of peristalsis in the thorax and abdomen, respiratory movements, and pulsations of the blood when evident at different regions in the wings. For the same reason and also to determine whether certain veins regulated the direction of blood flow within the wings, individual veins were severed in some species and the resultant course recorded. The veins were severed with a micro-scalpel with the wing held only at the apex.

For the most part the insects used were newly obtained in the field by sweeping with a net or by collection at lights. They were examined as soon as possible after collection. Where an appreciable delay in examination was unavoidable, the insects were held in screen cages in the presence of water. Whenever possible several specimens of each species were collected and examined to appreciate variations in the circulatory route, obtain an average of pulse rates, and to provide specimens for identification and the preparation of permanent wing mounts. Some were also used for dissection and for sectioning by standard histological methods. Generally the age of the insects was unknown, but those that showed signs of senescence were not used in the main studies. A few species were reared in the laboratory or obtained at the time of adult emergence and served to determine the effects of age on circulation. A number of insect orders are of course not considered in the present work. Some of them may be of special interest and it is hoped that future studies will include them.

The permanent whole mounts of wings were used to prepare the illustrations of wing venation by direct projection-tracing with a photographic enlarger. The illustrations incorporate details which are only recognizable in the living wings, such as the position of sinuses, from sketches made at the time of observation.

The vein nomenclature and general wing terminology used here is mainly that of Comstock (1918). His treatise seems to be the most extensive and generally accepted one on the subject of venation. Some use is also made of terms from Snodgrass (1935) and reference is made to taxonomic studies for particular insect groups. Ross' (1956) taxonomic grouping of insects at the order level is adhered to. The terms "afferent" and "efferent" concerning the direction of blood flow are used here as they are by Clare and Tauber (1940) to conform with their meaning in vertebrate studies: "afferent" refers to flow toward the distal part of the appendage; "efferent" refers to flow from the appendage toward the body.

Observations and Discussion

Although certain features of wing circulation vary considerably among the insects, and are reported hereafter for several orders, a basic route of circulation tends to be stable throughout the class and the mechanism of circulation is usually the same. At the risk of being repetitious, it seems useful to summarize the common or generalized features of circulation before describing characteristics peculiar to the phenomenon in different groups of insects. In this way some clarity may be contributed to the text.

In general, the anterior basic wing veins, costa, subcosta, radius, and media are afferent channels for the blood, and the posterior basic wing veins, the cubito-anal group, are efferent. Cross-veins anterior to the radius usually carry blood toward the costal margin and the others carry it posteriorly. In other words, blood flows from the insect body toward the wing apex through longitudinal veins in the anterior portion of the wings, moves posteriorly through cross-veins, and returns to the body through longitudinal veins in the posterior region of the wings; it re-enters the body via the axillary cord. This route will be referred to in the text as the basic pattern or basic route of circulation. Some of the blood that enters the wings avoids this route by flowing immediately to the axillary cord through the wing base or in cross-veins just beyond the base.

Also in general, two forces cooperate to cause the circulation of blood in the wings. A propulsive force, created mainly by the heart, pushes blood into the anterior portion of the wings through an opening near the humeral angle, and an aspiratory force draws blood out of the wings through the axillary cord. The aspiratory force is attributable mainly to accessory pulsatile organs that lie beneath the scutellum in the thorax. The two forces are not well coordinated, however, and the system is influenced continuously and may be intermittently dominated by pressure changes within the body; as parts of the haemocoel, the wing veins are subject to whatever fluctuations in pressure occur in the body as a result of respiratory or other movements.

Features of Wing Circulation in Insect Orders

Order: Ephemeroptera

The mayflies have long been favourite insects for the demonstration of blood circulation because of the transparency of their cuticle. Much of the published work deals entirely with the larvae, and the few papers that do include observations on the adults refer to wing circulation only in a general way. Such is the case, for example, in the previously mentioned early papers of Carus and of Tyrrel. Similarly, Drenkelfort (1910) noted circulating blood in cubital veins and suggested that meso- and metathoracic heart diverticula were somehow involved in wing circulation. Other authors referred to special features of ephemerid wing circulation without describing the system as a whole.

Materials

Species from several genera were examined but detailed studies of wing circulation were limited to *Hexagenia rigida* McD. and of an unidentified species of *Stenonema*. Consistent with the slight differences in venation, the circulatory route and features of circulation were basically alike in the fore and hind wings of individuals and in the various species examined. Circulation was always more vigorous in the fore than in the hind wings.

Observations and Discussion

The irregularity of circulation was a feature in the wings of all individuals of the species examined. It received comment from other authors as well.

Bervoets (1913) observed the passage of blood cells in the subcosta and radius and mentioned the intermittent refluxing of the blood there and the pulsations caused by heart systole. He suggested that blood circulated through the wings but that much of it returned to the body by the same route it entered. Meyer (1931) commented similarly but he also described the aspiration of blood from the wings by thoracic pulsatile organs to complete a regular circuit.

The irregularity of circulation occurred as an intermittent gushing of blood into and out of the wings and periodically as a complete and steady reversal of the normal direction of flow. It was true for adults of different age, for anaesthetized and for untreated individuals, for restrained and for unrestrained ones, and for those with the wings spread or with the wings held vertically in the normal resting position. There is little doubt that it is a normal occurrence which reflects unusual structural features at the junction of the wing base with the thorax, the pliable nature of the body wall, or perhaps a lack of efficiency on the part of the thoracic pulsatile organs. One might suspect that the development of wing tracheae from a single trunk in Ephemeroptera (Chapman 1918; Whitten 1962) rather than from two trunks as in other insects is somehow involved. Also in these primitive insects the wings are not flexed at rest but are held vertically above the body. The articular areas, especially the axillary sclerites are less well-defined than in wing-folding insects and less obstructive to blood movement. The wing bases are relatively open sinuses which connect broadly to the thorax (Fig. 3) and are especially subject to pressure changes within the body.

Despite the variability of wing circulation a basic circulatory route does occur (Figs. 1, 2 and 3). It is the course frequently followed by the blood when respiratory movements and heart activity are slow and steady. The costa, subcosta and radius are the principal afferent veins. The extensive sinuses at the wing bases and the prominent radio-medial cross-vein influence the flow in the media which tends to be efferent along with the cubital and anal veins. Some alternation in the direction of flow occurs in successive distal branches of the afferent veins but is not a dependable feature.

Order: Odonata

Although blood circulation in the developing wings of naiads of Odonata has been reported by a number of authors, scarcely any reference is made to circulation in the wings of adults. Carus (1831) noted circulation in the wings of newly-emerged adults of *Libellula depressa* and Bervoets (1913) reported that blood flowed from the cut extremities of the wings of a dragonfly. Otherwise, even among authors who worked almost exclusively with Odonata, the opinion was held that the adult wings were devoid of blood. Tillyard (1917) mentioned the remnant of blood sinus around the wing tracheae but did not suggest an active circulation of blood therein. Indeed the thought was discouraged by a subsequent statement that the tracheae withdrew from the wing and shrivelled up at metamorphosis. More recently Whedon (1938) described the meso- and metathoracic aortic diverticula in nymphs and adults of aeschnids and libellulids. He described their function of aspirating blood from the nymphal wings and from the basal sinuses of the adult wings but he considered that the adult wing distal to its thoracic junction was bloodless.

The impression of a bloodless condition in odonatan wings is not entirely surprising. Although the wings are transparent the veins are thick-walled and frequently pigmented. The lumens of the veins are narrow and to some extent limit the passage of the haemocytes, which is usually the most obvious visual evidence of circulation. Nevertheless a comparatively strong and regular circulation occurs throughout the wings and follows a relatively constant route. It

is quite different from the situation in Ephemeroptera, despite the primitive position of the group, and reflects the great differences in the structure of the thorax and wing bases as well as of the wings themselves.

Materials

A number of species were examined from five genera, mainly from *Cordulia* in the Anisoptera and from *Lestes* in the Zygoptera (see Appendix). There were no major differences in wing circulation among the species or between the fore and hind wings of individuals.

Observations and Discussion

The wings of Odonata, like those of the Ephemeroptera, are not flexed at rest but the wing bases are dissimilar in the two groups. The significant differences in blood circulation include the presence in Odonata of one true axillary sclerite (Snodgrass 1935) and of a thin cuticular wall which partially separates the afferent and efferent portions of the bases (Fig. 9). These structures limit the posterior flow of blood through the bases and direct it mainly outwards into the veins. They undoubtedly contribute to the strong and comparatively steady circulation in the wings. Some blood moves posteriorly in the wing bases but mainly in close proximity to the thoracic wall and in the adjacent cross-veins which form a structural part of the bases.

Comstock (1918) pointed out the uniqueness of odonatan wing venation and particularly of what he termed the invasion of the area of the radial sector by one or more branches of the media. Whether or not his interpretation of the vein homologies is correct, the venation in this area is unique and one might expect to find commensurate changes in the circulatory route. This however is not the case and the route of circulation (Figs. 4 and 5) is not significantly different from the basic route in most insects. It seems clear that the position of the veins and not their origin is the governing principle in establishing the circulatory route. Unusual conditions occur mainly at the nodus, the arculus, and the stigma.

The nodus, which is essentially a prominent cross-vein situated midway along the wing and joining the afferent veins, is peculiar to the odonatan wing and is significant in blood circulation. It diverts a portion of the blood from the afferent into the efferent streams and thereby provides a short route for the blood through the wings. In the antenodal region the route is typical and blood flows afferently in the costa, subcosta, and in the combined radius-media. Postnodally the route is also typical but it is accomplished via veins that occupy unusual positions according to Comstock's view. There the costa continues to support an afferent current which hesitates only slightly as it crosses the nodus. The subcosta terminates at the nodus. Blood that issues from it into the nodus separates into two streams (Fig. 7), one deflecting anteriorly to join the postnodal current in the costa and the other posteriorly to join the stream in radius-one. Radius-one reportedly occupies the position usually held by the subcosta in this region and assumes its function of carrying blood afferently. Similarly, media-one in its new position tends to accept the normal role of radius-one and is usually efferent. The short radius-media probably carries the greatest volume of blood afferently but part of it is deflected almost immediately into the arculus and the remainder continues in the radius to the nodus. Here its stream again divides, part of it crossing the nodus and proceeding afferently in radius-one, and the remainder moving posteriorly in the subnodus to join the efferent stream in media-one.

Structurally the arculus appears to be a cross-vein that extends from the radius to the cubitus near the wing base; the media appears to extend from it. The arculus is a constant feature in the odonatan wing, it occurs also in some other

groups and is significant in wing circulation wherever it occurs. In addition to diverting blood from the radius or radius-media (Fig. 8) it accepts efferent streams from the medial veins and from the radial sector. The radial sector here is a functional part of the medial system and is efferent. The arculus empties into the cubito-anal veins which unite in the axillary cord and like the nodus, provides a short route through which the blood may return quickly to the body and avoid the distal veins. The nodus and arculus together, because of their position and configuration, may be responsible for the noticeable reduction in the strength of the blood current in the wing extremities and for the tendency for those areas to become dry and to fragment in the late stages of adult life.

The pterostigma (Fig. 6) which joins the costa and radius-one near the wing apex is a constant feature in most species of Odonata and occurs in certain other orders. It is a box-like sinus which accepts blood from the surrounding veins but does not significantly alter the course of circulation. Its structure and possible origin and significance have already been discussed (Arnold 1963).

The Orthopteroid Complex

The taxonomic composition of the Orthopteroid complex is highly controversial and little help in resolving the arguments is gained from a consideration of blood circulation within the group. Although basic similarities exist in wing structure and in circulation in the wings in each of the component orders, there are also unique features in some of them and a general diversity in details of circulation, especially in the fore-wings. The main similarities do not usually extend above the suborder level and some distinctions occur at lower levels. As a result, the complex cannot be discussed readily as a unit.

By chance, the portions of the complex reported upon here, Cursoria (Blattaria and Mantodea) and Orthoptera (Saltatoria), have the fore-wings modified as tegmina. The orders Isoptera, Dermaptera, and Embioptera, along with the suborders Phasmida and Grylloblattodea usually included in the complex, were not studied. In some of them the fore-wings are not tegmina and should prove interesting from a comparative viewpoint.

Order: Cursoria

Suborder: *Blattaria*

Circulation in the wings has been studied more extensively in orthopteroids than in any other group of insects, and species from the suborder Blattaria have served for the bulk of experimental work in this field. The blattids are especially suitable for several reasons. Their wings are flat, not usually obscured by pigment or structural features, and support a strong current of blood which is clearly visible under the microscope by reason of its large complement of haemocytes. The insects are relatively easy to handle and generally do not respond unfavourably to manipulation. These features are much less true of the other orthopteroids, but many species within the complex provide excellent demonstrations of circulation.

Moseley (1871) was the first author to seriously study the wing circulation in a cockroach. His observations were confined to *Blatta orientalis* and mainly to the hind wings but he presented a reasonably clear account of the circulatory route with few references to conditions that might now be considered abnormal; e.g. reversal of direction of flow, and fluctuation in the wing base.

The principal investigations of wing circulation in blattids have come from the associated authors Yeager, Hendrickson, Tauber, and Clare. Yeager and Hendrickson (1933) in presenting a method for the study of wing circulation in

Periplaneta americana Linn. commented on the circulatory route and the efferent streams through meso- and metatergal pulsatile organs into the heart. They also included in their observations *P. orientalis* L., *B. fulginosa*, and *Blattella germanica* (L.). Later (1934) they gave a detailed account of circulation in the wings of *P. americana*. Clare and Tauber (1940) described circulation in *B. germanica*, studied the effect of cutting certain of the blood channels on the circulatory route (Tauber and Clare 1942), and examined circulation in the articular membrane (Clare and Tauber 1942). Some of their findings warrant special comment below in connection with similar studies on another species.

Materials

The giant cockroach *Blaberus giganteus* (L.) was used almost exclusively. *P. americana* and *B. germanica* were examined only briefly to ensure that the circulatory route conformed generally to the accepted pattern.

Observations and Discussion

The circulatory route for *B. giganteus* was described and illustrated previously (Arnold 1959). It conforms generally to the route described for *P. americana* and *B. germanica* by the previously mentioned authors. Structural differences in the tegmina of various species are the main cause of variation in details of circulation. In *B. giganteus* for example the proximal area of the tegmen anterior to the subcosta is essentially a sinus where the vein walls are represented only by pillars of cuticle and unlike those of other blattids. There the blood moves freely outwards for a short distance before it becomes confined to the veins. In the same insect the cubitus arises close to the base of the media and on occasion is afferent. According to Comstock the costa is not a readily definable vein in blattids. However a prominent blood channel always occurs in the position normally occupied by that vein and represents it functionally at least. Unlike the condition in *P. americana* (Yeager and Hendrickson 1934), the costal streams in tegmina and hind wings of *B. giganteus* flowed around the wing apex. There is however a tendency for circulation to become retarded at the apex and for the wing tip to desiccate and fragment in old age. The ambient extension of the costa continues along the posterior margin of the tegmina, but in the hind wing does not occur beyond the median fold. Consequently the posterior margin of the hind wing desiccates and fragments early in adult life.

A portion of the blood that enters the wing bases in *B. giganteus* re-enters the body without penetrating the veins. This is unlike the situation reported for *B. germanica* where the articular membrane in the tegmen was completely fused in the jugal area and prevented blood from re-entering the body except via the veins (Clare and Tauber 1942). The same authors found that folds in the hind wings retarded circulation and that flow was increased when the wings were extended in the position of flight. This is not true in *B. giganteus* where a taenidia-like structure characterizes the vein walls at the main wing folds and prevents their collapse when folded.

Suborder: Mantodea

Although circulation in the wings of the mantids is strong and easily visible there seems to be only a single brief reference to its observation in the literature. Verloren (1847) cites the authors Ehrenberg and Hemprich as having observed blood circulating in the wings of a mantid.

Materials

Only three specimens of *Mantis religiosa* Linnaeus were examined in the present study. However, in each individual the circulation was strong, the route was clear, and the features of circulation were alike.

Observations and Discussion

Circulation is more vigorous in the fore than in the hind wings but the route is similar in each except for differences imposed by structure. The route (Figs. 10 and 12) is generally similar to that in the blattids but is less controlled and less confined to the veins. In these respects it is more closely akin to circulation in wings of some of the saltatorial orthopterans. Afferent flow occurs in the costa, subcosta, radius, and the proximal part of the media. The cubitus is normally efferent and contributes blood to a large basal cross-vein from the media (Figs. 11 and 13). Although the afferent veins support vigorous currents many of them are not completely closed and there is a continual leakage of blood from them into the surrounding areas. Consequently much of the remigium of the tegmen and a less extensive area in the anterior part of the hind wing are, in effect, sinuses. They contain layers and clumps of tissue, apparently composed largely of haemocytes intermingled with deposits of pigment. The areas are obviously sites of metabolic activity and warrant further study. Efferent flow is confined in closed veins. In the tegmina an ambient extension of the costa carries blood efferently from the apex along the posterior margin of the wing and donates blood en route to the efferent veins and proximally to the jugal veins. A similar vein occurs in the hind wing but, as in all orthopteroids, it extends from the apex only for a short distance beyond the vannal fold. The hind wing is highly pleated in the vannal area but there is no evidence of interruption to blood flow when it is in the folded condition. The illustration (Fig. 12) serves as well for the other orthopteroids.

Although the mantid wings are flexed at rest and contain the normal complement of articular sclerites, the bases are nevertheless flexible and contain sinuses which are relatively open to the body cavity (Figs. 11 and 13). In this respect they resemble the simpler wing bases of the ephemerids. Part of the blood that enters the bases passes directly through the sinuses and re-enters the body. Heart pulsations are frequently evident in the bases and in the proximal part of the remigium. There is also some tendency for the blood to gush and to flow in the reverse direction in response to struggling and exaggerated respiratory movements.

Order: Orthoptera

Suborder: Saltatoria

The suborder Saltatoria includes several families in which there is a great diversity in the form and venation of the tegmina, both within and between families, and what seems to be a corresponding diversity in the circulatory routes. This diversity however is only in minor features, and the basic scheme of venation or of circulation is unaltered. Comstock considered that there were no distinguishing characters separating the wings of saltatorial Orthoptera and the Blattaria, and his view is supported in general by the present studies of circulation. In both groups and also in the Mantodea, which Comstock did not study, the afferent and efferent routes are very similar. Also in each a transverse proximal vein plays a prominent role in circulation by diverting blood from the bases of the afferent costo-radial veins to the axillary cord and receiving blood from the efferent cubito-anal veins. The media, because of its position, may be either afferent or efferent in each group of insects depending on the blood pressure.

It tends to be afferent when the pressure is high and efferent when low. Blood circulation in the hind wings is almost identical in all of these insects.

The literature contains very few references to circulation in the wings of the Saltatoria. Aside from the early ones of Baker (1744) and Gruithuisen (Carus 1831) previously referred to, only Brocher (1916) has contributed and then only briefly. He merely noted that thoracic pulsatile organs similar to those of *Dytiscus marginalis* occur in crickets.

Family: Locustidae
Materials

Circulation was studied in wings of a number of specimens of the following locustids: *Melanoplus femur-rubrum* (DeGeer) *Encoptolophus sordidus* (Burm.), and *Chorthippus curtipennis* (Harris). It was examined briefly in a number of other species (see Appendix) to determine the consistency of the route within the family. There was close similarity in the routes and of the features of circulation in all of them.

Observations and Discussion

The tegmina of locustids (Fig. 14) feature numerous intercalary veins which seem to complicate the circulatory route. However the intercalary veins merely add to the number of channels through which blood flows in the same general direction as in the principal veins between which they are located. The basic route remains the same, with the costa, subcosta and radius as the main afferent channels and with the cubito-anal group as efferent veins. The direction of blood flow in the media is variable depending upon pressure. The costa is not identifiable as a vein in the usual sense but exists as a channel that is apparently formed by the union of the distal ends of veins from the subcosta. The ambient extension of the costa along the posterior margin of the tegmen is well defined. Perhaps because of the large number of intercalary veins in the tegmen circulation near the wing apex is less forceful than elsewhere and the veins there tend to become occluded with haemocytes early in adult life. Consequently the apex becomes dry and brittle. There are frequent examples of this in the wings of many insects, principally at the apex and along the posterior margin. They demonstrate clearly that the formed cuticle is not simply an inert substance but is rather a metabolizing system.

Circulation in the hind wings is almost identical to that in other orthopteroids and as illustrated for Mantodea. Veins near the apex are incompletely closed and result in the formation of a stigma-like sinus. The ambient extension of the costa extends only as far as the vannal fold. Again, folding of the hind wings does not retard circulation in them, but characteristically the flow there is slower, steadier, and less obvious than in the tegmina. It also seems less affected by exaggerated respiratory or other movements.

Family: Tettigoniidae
Materials

Circulation was studied in wings of *Scudderia furcata* Brunn., *S. pistillata* Brunn., and *Conocephalus fasciatus* (DeGeer). There were no major differences between them.

Observations and Discussion

As in the Locustidae, the tegmina of tettigoniids feature large numbers of intercalary veins (Fig. 15) and the circulatory route in the two groups is very

similar. Unlike the former, however, circulation here is relatively strong throughout the tegmina, apparently as a result of assistance from respiratory movements of the thorax which seem to be especially prominent. A pulse that averaged about 30 beats per minute and was attributable only to respiratory movements was usually evident in the afferent veins. Pulsations in the efferent veins averaged about 78 beats per minute and were directly attributable to the mesothoracic pulsatile organs. There appeared to be no relationship between the afferent and efferent pulse and the efferent one remained fairly constant despite variations in the other. The veins anterior to the large subcosta are mainly open. The main blood current and most of the haemocytes remain within them but there is a continual leakage into the surrounding broad sinus. The costa, like that of the locustids, occurs as a union of tips of veins from the subcosta. Its ambient extension forms a prominent conduit along the posterior margin to the jugal area.

The circulatory route in the hind wings is basically similar to that in the other orthopteroids. Again open veins create a stigma-like sinus near the apex. The ambient extension of the costa is somewhat shorter than in the preceding families and reaches only a short distance beyond the apex. The current is slower and more constant in the hind wings than in the tegmina and much less affected by respiratory movements.

Family: *Gryllidae*

Materials

The studies were restricted mainly to species of *Oecanthus*, primarily because of their availability and ease of handling. A number of other crickets were examined but their short, contoured tegmina were not well suited for microscopic examination and the insects did not accept confinement. Despite their unusual structural features, the wings showed no peculiar conditions of circulation.

Observations and Discussion

Although the tegmina in species of *Oecanthus* appear to differ widely from those of other orthopteroids, the system of venation in Comstock's view is basically the same. Circulation is not altered from the normal pattern (Fig. 16), but it is simpler than in the preceding families because of the comparative scarcity of intercalary veins. As in the tettigoniids, afferent flow in the tegmina is strongly influenced by respiratory movements. An afferent pulse of about 25 beats per minute was usually evident in veins near the base of the remigium and coincided with thoracic movements. An efferent pulse in the axillary cord and in flexible portions of the anal veins averaged about 112 beats per minute and was attributable to thoracic pulsatile organs. Unlike the tettigoniids however most of the veins are closed, and leakage into sinuses is restricted to small areas near the apex in both the tegmina and hind wings. Circulation in the hind wings is identical to that in the other orthopteroids.

Order: Plecoptera

Few insects provide a better demonstration of circulation in the wings than do the stoneflies, but strangely enough there are scarcely any references to them in the literature in this regard. Their mention in the early works of Carus and of Goring and Pritchard, already referred to, seem to stand alone. The order is a primitive one allied to the orthopteroids (Ross 1956) and this is evident in features of circulation which in many respects resemble those of the family Gryllidae.

Materials

Only two species from the order were studied extensively here, a small unidentified species of *Perla,* and a large one, *Acroneuria arenosa* Pictet. The route and features of circulation were similar in the two species despite the great difference in size and it seems likely that they fairly represent the order. *A. arenosa* served for most of the detailed observations and can be highly recommended as an experimental animal for studies of this kind. Wing circulation is vigorous, the vein walls are clear, the blood contains a high complement of large haemocytes, and the insect is relatively easy to handle under the microscope.

Observations and Discussion

Wing venation in Plecoptera approximates that of the hypothetical primitive wing, and the circulatory routes (Figs. 17 and 18) conform closely to the basic pattern. The costa, subcosta, and radius are the main afferent veins in both wings. The media is usually afferent only in the proximal region but may be largely afferent when the blood pressure is especially high. A prominent basal transverse vein (Fig. 19) allows blood to proceed directly from the humeral angle to the axillary exit without entering the veins and receives blood from efferent veins, including the media. Blood may also move through the sinuses of the wing bases and avoid the veins. Here it is directly subject to pressures from the body and fluctuates in response to thoracic movements. Excessive movements are also expressed in the flow in the veins, and may cause a complete or partial reversal of the direction of flow.

In both wings a relatively extensive stigma-like sinus occurs in the region where the costa and subcosta join. These areas, as in orthopteroids, result from leakage of blood from open veins. The ambient extension of the costa is an important efferent channel in both wings. In the hind wings it continues around the circumference of the large vannal area to the axillary cord and is therefore a much more extensive and important channel than it is in orthopteroids.

Perhaps the most unusual feature of wing circulation in Plecoptera is the apparent lack of independent pulsatile organs beneath the scutellum. They were not detected by direct observation or by dissection. Direct observation showed that blood from the wing flowed through the axillary cord and entered the thorax beneath the scutellum. There it was joined by blood from lateral spaces of the thorax and entered the heart directly through ostia. Evidently circulation through the wings is effected by the action of the heart and with assistance from respiratory movements. The heart in these insects is unusually strong and its action is characterized by violent peristaltic contractions. Its pulse is evident in the proximal regions of the remigium and in flexible portions of the anal veins. Histological studies may reveal the organs, or some reduced representative of them, joining the axillary cords to the heart. However it seems reasonable that the system can function without them where the aspirative force of the heart is strong and operates close to the exit from the axillary cords. A slow circulation of blood occurs in the wings of many other insects during periods when their accessory pulsatile organs are not functioning.

Order: Hemiptera

The order Hemiptera includes many diverse insects which are grouped into the two suborders Heteroptera and Homoptera partly on the basis of wing structure. The structural differences in the wings also impose some circulatory distinctions between the two groups even though the main features are alike.

Circulation in the wings of Hemiptera has been scarcely mentioned in the literature, and not without reason. In many species the circulation is slow, and

in most of them it is difficult to detect because of the nature of the wings and of the blood. This is particularly true of Heteroptera but applies to some extent also in Homoptera. In the former, the dense pigment and heavy cuticle in the corium of the hemelytra obscures direct observation, while in the distal membrane circulation is very limited. In the hind wings the lumens of the veins are narrow and restrict the entrance of haemocytes which are the principal indicators of circulation. The complement of haemocytes in the blood is also relatively low in Hemiptera and often the main evidence of circulation is obtained from observing the flow of particulate matter rather than cells in the haemolymph. Only two references of significance were located: Bervoets (1913) stated that blood occurred in the hemelytra of *Notonecta*, *Corixa*, and *Nepa*, but did not mention a circulatory route; similarly Patch (1909) failed to observe circulation in Homoptera but recognized that blood occurred in the costal vein as far as the stigma. Nevertheless, circulation occurs in all members of the order and is quite efficient in some.

Suborder: Heteroptera

Materials

Circulation was examined in the wings of one or more species (see Appendix) in the families Belostomatidae, Corixidae, Miridae, Nabidae, and Phymatidae. In these widely different insects the course followed by the blood in the wings was similar except for minor variations resulting from differences in venation. Likewise, features of circulation such as the rate of flow, the extent of sinuses, and the rate of afferent and efferent pulsations showed common characteristics but varied somewhat between species.

Observations and Discussion

The conditions of circulation in the wings of species from the family Miridae are fairly representative of the suborder and are the ones discussed particularly here. The circulatory route in wings of *Adelphocoris lineolatus* (Reuter) is illustrated (Figs. 20 and 21). Unlike the conditions in the insect orders already discussed, the structure and venation of the fore and hind wings are quite different and the circulation likewise is dissimilar.

The whole corium of the hemelytra is a thin sinus through which blood trickles slowly. The main current is confined within the open veins which continually leak blood into the surrounding areas. Sinuses that are relatively free from obstructions and support a full current of blood occur at the base of the hemelytra and in the region where the embolium and cuneus join. Blood flows afferently in all of the veins of the corium to its junction with the distal membrane. A channel at this junction carries the blood posteriorly to the termination of the anal furrow where the course becomes directly efferent. This is the only point of afferent-efferent change and is a unique feature of the hemipteran wing. Efferent flow from this point occurs mainly in the large vein that extends along the posterior margin of the clavus. This vein seems to be considered a united postcubitus and first anal (Davis 1961). Some efferent flow occurs also in the smaller cubitus and there is generally a slow trickling of blood throughout the clavus which contains, like the corium, a thin sinus. The membrane of the hemelytra is poorly served by the blood and its margin tends to become dry and brittle. The flow there is restricted to two venal loops, presumably extensions of the media and cubitus, but some leakage of blood occurs into the closely adjacent areas.

Although some of the blood that enters the humeral sinus of the hemelytra finds its way through the basal sinuses and avoids the veins, most of it follows a

complete course through the wings. There is little evidence of an afferent pulse in the corium, except during periods of struggling, and the blood moves outward from the body in a slow, steady fashion. Efferent flow however, being restricted largely to one vein, moves rapidly and is strongly aspirated by the thoracic pulsatile organs. Their action appears to be assisted by tissue located in the common junction of veins at the distal end of the anal furrow. Although the tissue is reminiscent of the tibial pulsatile organs common to insects in this order, its mechanism is less clear and it acts always in rhythm with the thoracic pulsatile organs. Its movement diminishes with age and it is seldom evident in old adults, even where circulation is still vigorous. Its characteristics suggest that it is a flexible area of the vein wall that responds vigorously to the action of the thoracic pulsatile organs and affords some advantage in aspirating blood from the corium. A histological investigation of the area seems warranted.

The hind wings are entirely membranous and the venation is much reduced from the hypothetical primitive condition and from the system in the hemelytra. The volume of blood circulation in them is also reduced and the route is much simplified. Part of the blood that enters the wing bases by-passes the veins via the broad basal transverse vein (Fig. 21) and re-enters the body. Within the wing, afferent flow is entirely confined to the large vein at the costal margin. This vein, the homology of which seems to be obscure or controversial, forms a loop with one that is generally accepted as the composite medio-cubital and carries the blood efferently to the basal transverse vein. Thus the blood flows through a simple circular path in the wing without the deviations through branches and cross-veins that characterize the wings of the insects already discussed. Veins that radiate from this loop are "blind", i.e. not otherwise connected, and are not involved in the circuit even though they contain blood. Haemocytes may be seen to flow into them periodically and to remain for a time and be drawn out again during a period of accelerated flow in the main circuit. Although it might be considered that reduction of circulation to this extent would expose the wing to desiccation, they nevertheless remain flexible during most of the adult life. Possibly leakage of haemolymph occurs from the veins and much of the wing area is actually served by blood. Perhaps the fluid traverses the relatively wide areas of membrane in a circular route and utilizes the "blind" veins to rejoin the regular circuit. Few haemocytes enter the hind wings but there is a slow and steady circulation of haemolymph without prominent pulsations.

The preceding discussion, as mentioned, pertains especially to members of the family Miridae but is generally true for the whole suborder Heteroptera. In some other families however the venation is more extensive in both pairs of wings and warrants some mention. The circulatory system in the wings of two other families is therefore illustrated, Phymatidae (Fig. 24) where venation is only slightly more elaborate, and Belostomatidae (Figs. 22 and 23) where numerous accessory veins occur. In each of them the course of circulation is similar but the blood is more closely confined to definite channels.

Suborder: Homoptera

Materials

Circulation was examined in the wings of species from the families Cicadellidae, Cicadidae, Membracidae and Aphididae (see Appendix). It was similar in the first three families, which are allied also by a number of other features, but quite different in the last one.

Observations and Discussion

In the family Cicadellidae the structure of the fore wings and their venation is highly varied. They range from a Heteroptera-like condition, subcoriaceous and with simple venation (Fig. 27), through those where the venation is increased (Fig. 25) to some that are strangely modified, delicate, and Lepidoptera-like (Fig. 28) with numerous accessory veins. Although the details of circulation are appropriately varied the basic scheme remains the same in all of them. Afferent flow is confined to the area anterior to the anal furrow and efferent flow occurs posterior to it. As in the Heteroptera, most of the blood that enters the wings passes through a common channel at the distal end of the anal furrow at the start of its efferent course. Also, whereas the afferent flow is usually slow and steady, efferent flow is characterized by a strong and rapid pulse directly attributable to the action of the thoracic pulsatile organs. The pulsations here are more obvious than in Heteroptera and are evident not only in the rapid movement of the haemocytes but also as strong contractions of the entire vein walls at the flexible distal end of the anal furrow, in flexible parts of the efferent veins, and in the axillary cords. Although these separate pulsating areas suggest the presence of independent pulsatile tissues within the wing, they act in rhythm with the thoracic organs and reflect their activity. In species where the venation is simple (Fig. 27) most of the veins are open and blood moves slowly through the entire wing while the main flow remains in the veins. In species where the venation is more complex (Fig. 25) there is a tendency for the sinuses to be reduced in area and restricted mainly to the costal and anal regions. Where accessory veins are very numerous (Fig. 28) the sinuses are insignificant or entirely absent. Thus by one means or another, through leakage from open veins or by the presence of numerous veins, blood permeates the fore wings.

In the other two families of the so-called "needle-horned series" of Homoptera examined here, circulation in the fore wings was quite similar to the above but the blood was more confined. In Cicadidae (Fig. 29) the blood flows in thick-walled veins except in two sinuses, one between the open costa and the combined subcosta-radius, and the other located around the arculus. The arculus is a prominent feature in all members of the series and provides a short course for the blood to flow from the proximal regions of afferent veins to the anal angle while receiving blood from the distal regions of the wing through efferent veins. A short course is also provided by the transverse basal vein (Fig. 31). Also in Cicadidae, the common vein at the distal end of the anal furrow (Fig. 30) is typical of the structure in the other families but somewhat more rigid; pulsations of the thoracic organs are evident there but less obvious than in families with more flexible wings. In members of the family Membracidae (Fig. 32) no sinus occurs at the costal margin, but open veins are present elsewhere in the wing and blood leaks from them into small surrounding areas.

In the same series of insects the structure and venation of the hind wings is quite different from that of the fore wings and blood circulation likewise is different. The hind wings are fully veined and the branches are joined terminally by the ambient costa or its equivalent. This vein undulates parallel to the outer margin of the wing and approaches the edge along the inner margin. Comstock considered it to be a characteristic of the wings of most membracids and cicadas and termed it the "marginal vein". Apparently he was unaware that a similar vein unites the tips of the longitudinal veins in many other insects but is usually less obvious and located at the edge of both the outer and inner margins. It is always an important vein for blood circulation and there seems little reason to distinguish it particularly in this group of insects. From discussions with a num-

ber of taxonomists it is clear that the vein is generally recognized only as the costa, and it is termed here the "ambient costa" to indicate its continuation around the circumference of the wing. The circulatory route in the hind wing of a cicadellid (Fig. 26) is fairly representative for the entire group. Circulation is comparatively slow and steady and the blood contains relatively few haemocytes. Most of the haemocytes appear to be excluded at the entrance to the wing base, and the few that enter pass through the veins singly and sluggishly. A portion of the blood that enters the wing base always avoids the circuit through the veins by flowing directly to the anal angle via an open transverse basal vein.

In the family Aphididae the venation is highly modified (Patch 1909). In the fore wings only two principal veins extend outward from the base and unite at a pterostigma. In the hind wings the pterostigma is absent, but two similar veins unite at the wing apex. In both the fore and hind wings these veins (Fig. 33) form a complete loop, reminiscent of the condition in the hind wings of Heteroptera; branches from the loop, except those near the apex, are not connected terminally. It might therefore be expected that blood would flow afferently in the anterior vein and return via the posterior one, thus completing a circuit; this happens only irregularly. Generally the wing circulation is weak and intermittent, without regular pulsations. Often the blood moves afferently in both of the main veins, stops for an interval and returns in the same way. Its movement seems to depend almost entirely on changes in pressure within the body haemocoel, apparently with little if any assistance from thoracic pulsatile organs. The apparent absence of pulsatile organs and the lack of separation between the bases of the two main veins likely account for the irregularity in the volume and the course of circulation. Few haemocytes enter the veins and then only singly. In the fore wings they seldom travel beyond the pterostigma. Circulation in that structure has already been described (Arnold 1963).

Order: Neuroptera

The wings of Neuroptera usually have numerous accessory veins and the radial sector is often pectinately branched. As a result, the venation in most species is extensive and unusual but is basically similar to the hypothetical primitive condition.

The literature contains no recent references to circulation in wings of Neuroptera. Among early accounts however are the noteworthy ones of Tyrrel (1835) and Bowerbank (1836). The former mentions briefly the movement of globules in the wing veins of some species of *Hemerobius*. The latter provides a detailed description of circulation in the wings of *Chrysopa perla*. It contributed much to the general acceptance of the reality of blood circulation by entomologists of that time.

Materials

Circulation was studied in one or more species from the families Chrysopidae, Hemerobiidae, Mantispidae and Myrmelionidae (see Appendix). Circulation was moderately vigorous in each of them and the circulatory route was generally similar. Species of *Chrysopa* served for most of the detailed observations.

Observations and Discussion

A general description of circulation in any one of the insects examined would serve for all of them and for either the fore or hind wings which are almost identical. The route adheres closely to the basic pattern of circulation in the wings despite the characteristically large numbers of accessory veins. They merely increase the number of channels through which the blood flows in the

same general direction as in the main longitudinal veins from which they are derived. This is evident from a comparison of the route in *Myrmeleon* sp. (Fig. 34) where accessory and cross-veins are very numerous as compared with the number in *Chrysopa* sp. (Fig. 35). The venation seems particularly well suited to carry blood throughout the wings. For example the pectinately branched radial sector gives a more positive direction to the blood currents than the more familiar dichotomous arrangement in other insects; the gradate veins which are especially prominent in *Hemerobius* sp. provide clear channels for efferent flow in the distal regions of the wings; the numerous accessory marginal veins in conjunction with the ambient costa ensure complete circulation around the periphery and there is seldom any evidence of wing deterioration even in old adults. Variations in details of venation account for differences in the circulatory routes between species, but these are seldom great. Variations in venation near the wing base, which were stressed in Comstock's interpretations of vein homologies in different families, are mechanically similar at least and provide a recurrent course for the blood from afferent to efferent veins. An obvious feature of wing circulation that is not present in all members of the order is the stigma-like sinus illustrated for the wing of *Mantispa brunnea* Say (Fig. 36) and discussed previously (Arnold 1963).

Although the current in the veins is moderately strong in all of the species examined, a noticeably large portion of the blood passes directly through the basal sinuses and the recurrent configuration of basal veins (Fig. 37) and re-enters the body. Fluctuations in haemocoelic pressure within the body are reflected in the wings by changes in the strength of the current and in the direction of flow. Reversal of flow is not uncommon during periods when the insect struggles or when respiratory movements are exaggerated. Obviously these occurrences influence circulation in the wings, but the flow is usually regular and maintained through the efficient action of the thoracic pulsatile organs. Their pulsations are evident in identical contractions of flexible portions of the axillary cords, of proximal regions of the anal veins, and in movements of loose tissues in the basal sinuses. Relatively few haemocytes enter the wing veins. Most of them are almost as wide as the lumen of the veins and are forced to move singly through them.

Order: Hymenoptera

In the Hymenoptera wing, venation is much reduced and altered from the hypothetical primitive condition and there is no firm agreement on the homologies. Comstock noted that wing venation precedes tracheation in these insects and that the courses of tracheae could not be depended upon for determining vein homologies. Undoubtedly this is true also for other groups of insects where discrepancies between wing venation and wing tracheation are less obvious. It points to a limitation of the system of homologizing veins broadly on the basis of tracheation but does not discredit its general usefulness. Comstock's concept of the venation in the forewings of Hymenoptera was derived mainly from studying similar developments in the Diptera where the various modifications could be followed more clearly. In the hind wings of Hymenoptera venation is so reduced that he was unable to determine homologies except by interpretation from the work of MacGillivray (1906) with the suborder Chalastogastra where venation is the most generalized. Nevertheless, the venation in most Hymenoptera is basically alike and so also is the route of blood circulation.

It is not surprising that the literature contains few references to wing circulation in Hymenoptera; the walls of the veins are thick and often pigmented, and the haemocytes are not easily detected in the swift current as they are relatively

few in number and mostly hyaline. The earliest reference is that of Moseley (1871) where mention is made of three pulsating dilated areas in vessels of the hind wings of some small, unidentified Hymenoptera. Janet (1906) described thoracic pulsatile organs in the ant *Lasius niger* but apparently did not fully understand their role in wing circulation. Similarly, Brocher (1920b) demonstrated rudimentary pulsatile organs in the mesothorax of *Vespa crabro* and suggested their presence also in the metathorax. He was well aware of their role from his earlier discoveries of similar structures in other insects. Their rudimentary aspect in *V. crabro* led him to suggest that their original function of aspirating blood from the wings had been assumed largely by abdominal respiratory movements and that the pulsatile organs open into the body cavity and not into the heart. Freudenstein (1928) also made mention of pulsatile organs in the thorax of *Apis mellifera* and suggested their involvement in wing circulation. Wille (1958) however in his comparative studies on the hearts of bees made no mention of accessory structures in the thorax.

Materials

Observations were limited to the suborder Apocrita and included species from eight families (see Appendix). The honey bee, *Apis mellifera* L., and several species of Ichneumonidae served for most of the detailed studies and much of the discussion will pertain directly to them. In all of the families however the route and features of circulation were remarkably similar, except in highly specialized forms, and require little separate comment.

Observations and Discussion

In the Hymenoptera the lumens of the veins are remarkably free of obstructions. The tracheae and nerves, where they occur, are mainly small and simple and the surfaces of the vein walls are free of cells and membranes. Blood circulation is generally swift. Bullae occur where the veins cross furrows; they are clear and corrugated and permit circulation to continue unobstructed when the wing is folded. The current that passes directly through the wing bases (Fig. 40) is generally insignificant. The veins in the hind wings are structurally similar to those in the fore wings but appreciably smaller in diameter. In them the circulation of haemocytes is restricted by the narrow lumen and the few that enter the veins move through singly. The pterostigma of the fore wings is unlike the similarly termed structure in the wings of Odonata and some other insects (Arnold 1963); it is simply an enlarged junction of several veins. Nerves and tracheae branch out within it (Fig. 41) but it is otherwise unobstructed. Blood passes through it without hesitation.

In the fore wings of species in most families of Hymenoptera, four longitudinal veins extend outward from the wing base. An afferent outflow of blood occurs in each of the three anterior ones, and efferent flow is limited to the single posterior one. The crossover from the afferent veins to the efferent one is accomplished through one or at most two veins which have the function of cross-veins with regard to blood circulation but are apparently considered to be branches of the media and cubitus. The first and second afferent veins pour blood into the pterostigma where streams are directed onwards into the veins that emerge distally from it. In one of the largest families, Ichneumonidae, the first and second afferent veins are joined longitudinally as a wide costal channel (Fig. 38). The two veins retain their separate identities superficially but the wall between them is incomplete and blood passes freely from one to the other. In most other families, e.g. Apidae, (Fig. 39), the two veins are clearly separate. In either case a portion of the blood in the second afferent vein is directed posteriorly

to the third afferent vein as illustrated. In the former case it is directed there through a vein which branches from the entrance to the stigma. In the latter it flows through a comparable vein which leaves the second afferent before it reaches the stigma. This stream merges with the one in the third afferent vein and crosses to the single efferent vein through the more proximal of the two "cross-veins". The more distal cross-vein, where it occurs, receives blood mainly from the vein complex which lies distal to the stigma. Circulation in that complex is circuitous and somewhat variable in different families, in conjunction with variations in the configurations of the veins and the size and form of the wing cells. The vein at the costal margin seldom extends beyond the apex, and the outer margin of the wing is consequently devoid of blood. It tends to become dry and brittle and is seldom entire in the late stages of adult life. In some families, e.g. Formicidae, the distal vein complex is reduced (Fig. 42) and the distal cross-vein to the efferent channel is absent. The condition is more striking in species of Chrysididae (Fig. 44) where the distal complex is absent. This pattern of venation and of circulation which features a single efferent channel and only one or at most two routes of access to it is reminiscent of the Hemipteran wing despite the wide differences that otherwise separate the two orders.

Some of the principles governing circulation in the wings were revealed when individual veins were blocked. Where blood is carried from the afferent veins to the efferent vein through two channels, destruction of either one of them causes the blood to flow entirely through the other but does not alter the main course of flow in other areas of the wing. Destruction of both of them or of the efferent vein itself reduces wing circulation to a comparatively passive and unregulated mechanism which functions only intermittently and not very effectively. Under these circumstances the third afferent vein may intermittently accept the efferent role. It performs this function more effectively in families such as Vespidae where the third afferent vein emerges separately from the wing base than in those such as Apidae and Formicidae where it branches from the base of the second afferent vein. Destruction of the third afferent vein without injuring the others does not alter the course of circulation.

Throughout the order there is considerable variation in the venation and route of circulation in the hind wings. In many families the hind wings are simplified versions of the fore wings and the circulatory routes are comparable. Simplification is mainly in the distal area, but the first afferent vein may also be reduced and cease to carry blood. The simple route of circulation is illustrated for Ichneumonidae (Fig. 38) and for Formicidae (Fig. 42). Circulation is never strong in the hind wings and in some Hymenoptera, e.g., Chrysididae, the venation is so reduced that a complete circuit of blood cannot occur. In such cases blood occurs in two simple and unconnected veins and presumably moves inwards and outwards only in response to pressure changes in the body. Also in Chrysididae, the venation of the fore wings is much reduced and the circulatory route (Fig. 44) is similar to that in the hind wings of the families already illustrated.

In the family Chalcididae the venation is very much reduced in both fore and hind wings and here again a complete circuit of blood cannot occur. The single vein in each wing (Fig. 43) contains blood which apparently enters and leaves periodically as a result of pressure changes in the body and is unassisted by accessory pulsatile organs.

Order: Coleoptera

The extreme modifications in form and structure of the wings of Coleoptera impose some unusual circulatory problems. However the problems are much

the same throughout the order and there is remarkable constancy in the circulatory route and features of circulation among the different families.

Despite the rather obvious difficulties in observing blood circulation in coleopteran wings a number of authors have reported upon it. They are mainly among the early workers referred to previously and their observations were not extensive. Neither were the more recent observations of Bervoets (1913) on *Dytiscus* and *Meloë* and of Lehr (1914) on *Dytiscus marginalis*. Undoubtedly the most extensive work in Coleoptera was that of Brocher (1916). It was concerned mainly with the anatomy and function of the accessory pulsatile organs, but included a number of pertinent observations on circulation within the wings of *D. marginalis* and *D. punctulatus*. Particularly, Brocher's observations led him to believe that circulation in the hind wings occurred only on certain occasions, as during flight, despite the presence of pulsatile organs. Later (Brocher 1929) he carried out similar studies with *Coccinella conglobata* and *Galeruca crataegi* and decided that the pulsatile organs were mainly responsible for wing circulation but were assisted by respiratory movements. Similar studies by Kuhl (1924) with *D. marginalis* confirmed the anatomy of the pulsatile organs and their connections but gave no indication of the importance of the organs in circulation.

Materials

Circulation was studied in the wings of members of nine families of Coleoptera (see Appendix) where the wings were much different in size and form. Circulation was of course much different in the fore and hind wings but was otherwise similar throughout the group. These insects are among the most trying for observations of this kind. They are generally less sensitive to carbon dioxide than other insects and are consequently more difficult to handle. Many of them are hard to confine because of the shape of the body and elytra, and most of them resist confinement vigorously. Their resistance inevitably causes irregular circulation and the blood gushes into and out of the wings in response to pressure changes in the body haemocoel. Nevertheless, on occasion the blood can be seen to follow a complete circuit in the wings and in a steady fashion. On such occasions the regular pulsations in the axillary cords provide convincing evidence of the role of the accessory pulsatile organs in normal wing circulation.

Observations and Discussion

Essentially the elytra are sinuses (Fig. 45) through which the veins are open, longitudinal channels, extending from base to apex with few and incomplete branches. The veins are unobstructed and blood moves through them more swiftly than in the surrounding areas. This is especially true of the costal or marginal vein which conducts blood around the circumference from the humeral angle to the axillary cord and accepts blood en route from the afferent portion of the wing; it also contributes blood to the efferent portion of the wing. There is no clear distinction between afferent and efferent areas but the blood moves in a circular path outward in the anterior half of the elytron and back toward the base in the posterior half. At the wing base (Fig. 48) this path is accomplished relatively swiftly via a basal transverse channel. The areas around the veins receive blood from them but its flow is impeded by indentations and by pillars of cuticle that join the dorsal and ventral surfaces and are more or less concentrated in different regions in different species. These areas tend to become repositories for haemocytes which settle from the slow current and create further obstructions to flow. In general the lack of closed veins does not interfere with the main course of circulation but it undoubtedly dissipates the force of the current. During periods of rest the only evident pulsations are in the axillary cord and

these reflect the action of the pulsatile organs in the thorax. The normal changes in the substance of the elytra during early adult life are undoubtedly provided for by the ample blood supply.

In the hind wings the venation is also highly modified and primarily, it would seem, to permit the transverse folding which is characteristic of the wings in this order. Despite specific differences in the plan of folding, the basic system of veins is relatively constant in form, if not in extent, and the blood circulates through a relatively simple route (Figs. 46 and 47). During periods of rest the current in the veins is slow and steady and pulsations are evident only in the axillary cord. Haemocytes are relatively scarce in the veins and the route is often obscure. Periodically the blood gushes through the veins in conjunction with obvious respiratory movements or struggling. Then the route is clear and sinus areas become apparent around the distal junction of veins proximal to the main transverse fold. At the same time the route through the basal transverse channels (Fig. 49) is also clear. These observations support Brocher's aforementioned suggestion that respiratory movements are important for wing circulation in these insects, but suggest that the less vigorous circulation is regulated by the thoracic pulsatile organs.

Considering the degree of flexibility required for the wings to fold beneath the elytra it seems almost essential that haemolymph should circulate outside the veined area. No direct evidence of this was obtained during the usual periods of observation or from dye injections, and the indirect evidence is not strong. Nevertheless, in newly emerged adults the position of the definitive veins is occupied by wide channels which are open to the unveined areas of the wing. Blood moves through the channels swiftly in the normal circuit and also escapes into the unveined areas which at that time are thin sinuses. The entire wing is filled with circulating blood and this condition may persist for some hours after wing extension and folding. This is the case at least in *Coccinella transversoguttata quinquenotata* Kby., where these observations were made. The two wing surfaces gradually become appressed and the apparent extent of circulation is reduced to the lumen of the veins and to a few small sinuses. Probably the apposition of the two surfaces is incomplete and spaces remain and support a slow percolation of haemolymph.

Order: Mecoptera

In Mecoptera the two pairs of wings are similar in size, form, and venation. The arrangement of the veins closely approximates the hypothetical primitive condition and the route of circulation conforms to the basic pattern.

Only two references to circulation in this order were located in the literature and these were very brief. Tyrrel (1835) included *Panorpa* among the insects in which he observed wing circulation, and Brocher (1916) mentioned that the same genus had accessory pulsatile organs similar to those which he described for *Dytiscus*.

Materials

Observations were limited to only a few individuals of *Panorpa* sp. and in these the circulatory routes were distinct and alike. Presumably it is similar in other members of the order.

Observations and Discussion

For several reasons species of *Panorpa* are better subjects for demonstrating a simple, basic system of circulation in the wings than many of the more primitive insects: there is an even distribution of blood and a comparatively clear separation

between afferent and efferent portions of the system (Fig. 50): the ambient extension of the costa joins the ends of the longitudinal veins so that an uninterrupted marginal circuit is provided from the humeral sinus to the axillary cord; open veins are a feature of the wings around the distal junction of the costa and subcosta where a stigma-like sinus is formed. The mechanism involved in circulation in the wings is also comparatively clear: the thoracic pulsatile organs are more clearly visible than in most other insects and can be seen to aspirate blood from the wing with sufficient force to cause movements of the axillary cord and of flexible areas at the basal junction of the anal veins; at the same time blood in the thorax can be seen flowing past the wing bases uninfluenced by the action of the pulsatile organs. Along with these features, the insects are relatively placid, the few pigmented areas in the wings do not obscure the veins, and circulation is moderately strong and clearly visible due to its high complement of haemocytes.

As in almost all other insects, a portion of the blood that enters the wing base avoids the circuit through the veins and passes directly to the axillary cord. In *Panorpa* this route is via a basal medio-cubital channel (Fig. 51) which joins directly with the flexible union of the cubitus and the anal veins at the axillary cord. A more distal medio-cubital cross-vein also directs blood from the afferent stream in the proximal part of the media to the efferent one in the cubitus. When the current in this cross-vein is swift, the distal portion of the media is efferent and contributes blood to the same stream.

The activity of the thoracic pulsatile organs and its effect on the efferent current in the wing veins is comparatively clear in these insects. The flexible areas in the axillary cord and in the basal junction of the cubitus and anal veins pulsate in rhythm with the organs and the action is expressed in the pulsing movement of the blood in the neighboring veins. There is considerable fluctuation in the activity of the organs and the rate of pulsation may vary from approximately 65 to 100 beats per minute. It is usually more rapid than the beat of the heart in the same region. The rate is the same in the two wings of each pair but is usually slightly different between the two pairs. There is little doubt that the nervous control for the pulsatile organs is distinct from that for the heart, and that there is no regulatory mechanism operating to maintain equivalent action in the two.

Order: Trichoptera

Blood circulation is seldom strong in the wings of Trichoptera but the current is comparatively steady and the route distinct and constant. The fore and hind wings are somewhat different in the species studied here, mainly in the greater extent of the anal area in the hind wings. The only reference to wing circulation in these insects is a brief one by Tyrrel (1835) where *Phryganea* is included among the insects in which he observed the phenomenon.

Materials

Observations were made on species from the families Hydropsychidae, Limnophilidae, and Phryganeidae (see Appendix). The observations included some on the effects of blocking certain veins to determine the resultant routes and thereby the mechanical principles involved in the pattern of flow. The paucity of tracheae in the veins of Trichoptera make them especially suitable for studies of this nature.

Observations and Discussion

Although the wing venation in Trichoptera is basically similar to the hypothetical primitive system and not unlike the system in Mecoptera, it is sufficiently

different to cause significant changes in the route of blood circulation, particularly in the fore wings. The changes involve mainly the distal branches of the radius and media where a series of cross-veins, close to the final bifurcations, form an interrupted channel across the wing proximal to the outer margin (Figs. 53 and 54). This channel, despite its lack of continuity, carries a stronger current than the more distal ambient costa and attracts blood from the latter through all, or almost all, of the terminal longitudinal veins. In the fore wings this route crosses to the posterior edge of the wing and finally contributes blood to the cubitus and the distal portions of the anal veins via a short channel reminiscent of the common afferent-efferent cross-vein in the fore wing of Hemiptera. In the hind wings it terminates at a branch of the media and is not closely associated with the afferent-efferent cross-veins. In both wings the ambient costa provides a direct marginal route for the blood from the humeral angle to the axillary cord; from it the anal veins of the hind wings receive all of their blood supply. Among the species examined, only *Limnophilus rhombicus* (L.) had a stigma-like sinus from open veins around the costa-subcosta junction, but it probably occurs in other species. In all cases a constant stream of blood passes directly from the humeral sinus to the axillary cord via the arculus-like transverse basal channel (Fig. 52) without entering the veins. A portion of the blood in the media is also directed almost immediately into the efferent stream of the cubitus via the proximally situated medio-cubital cross-vein. Infrequently in most individuals there occur periods of fluctuating blood pressure in the wings and reversal of the normal direction of flow in association with struggling movements of the insect.

The comparatively weak, steady current of blood in the wings is concomitant with rapid, shallow pulsations of the thoracic pulsatile organs and this relationship seems to be somewhat characteristic of the order. The organs were only vaguely visible in a few of the insects examined but their pulsations were usually evident in the axillary cords. In the majority of specimens the rate of pulsation was greater than the heart beat at the same region and often it was approximately double the heart rate. In *Pycnosyche* sp. for example, the relationship of heartbeat to pulsatile organ activity for five individuals averaged 51 to 98 beats per minute respectively. In *Limnephilus* sp. it was 41 to 82. In *Macronema zebratum* however the relationship was reversed (63 to 33) even though circulation in the wings was no less efficient than in the others.

The experimental blockage of individual veins caused only local changes in the circulatory route and these changes were predictable from principles of haemodynamics. For example, blockage of any of the unbranched veins such as the costa, subcosta, or radius-one caused the stoppage of flow only within themselves because the remainder of the system is a complete circuit without them (see Fig. 53). Blockage of the main stem of a branching vein, such as the radial sector or the media, resulted in cessation of flow within the vein and removed the original afferent force from its branches. The branches then accommodated a reduced current of blood from other sources and in directions that continued to complete the circuit without the stem vein. Thus in the case of the blockage of the radial sector, the anterior branch of its bifurcation (radius-two plus three) received blood from veins anterior to it (e.g. radius-one or radius-two or both) and became efferent. The blood flowed slowly toward the point of blockage. At the bifurcation it necessarily reversed direction and flowed afferently in the posterior branch (radius-four plus five) as it had done originally. The whole sector continued to receive blood at a reduced rate with only slight modification of the circulatory route.

Order: Lepidoptera

Wing venation in the Lepidoptera corresponds closely to Comstock's hypothetical primitive type. The main divergence from it in certain families is in the reduction of the media and its branches. The route of circulation conforms generally to the basic pattern for such a system of veins and with appropriate changes where such divergences occur. However, the amount of blood in the wings and the force of the current are markedly less than in most other insect orders. This is due to the large wing tracheae which almost fill the lumens of the main veins and occupy a considerable portion of many of their branches (Fig. 59). In some veins the blood channel is little more than a thin space around the tracheae and is scarcely wide enough for haemocytes to pass singly. The haemocytes also have difficulty in entering the wings, because of the large tracheal trunks in the bases, and comparatively few occur in the veins at a given time. In many cases their scarcity and the obstructions to their movement make it difficult to detect circulation in the wings even when the surface scales have been removed or cleared. Nevertheless, circulation is moderately strong in young adults of some species and follows a complete circuit. It becomes noticeably reduced with age, and this undoubtedly accounts for the progressive fraying of the distal margins of the wings and the eventual cessation of wing circulation when cross channels are broken.

Early workers apparently failed to see circulation in wings of Lepidoptera although some suggested that it must occur. Recent authors have mentioned it sparingly. Bervoets (1913) noted blood in the hind wings of a pierid. Brocher (1916, 1919) demonstrated the function of the thoracic pulsatile organs, mainly in *Sphinx convolvuli,* without commenting particularly on circulation within the wings themselves. His work was recognized by Portier (1932) who suggested, with some experimental evidence, that wing circulation assisted respiration during flight. This suggestion has not been confirmed by recent studies. Zeller (1938) described circulation in the pupal wings of *Anagasta* (*Ephestia*) *kuhniella* Zell. but observed that circulation in the adult wings was slight even in young individuals. He felt that the thoracic pulsatile organs drew blood only from the wing bases and his observations were supported by those of Stehr (1947) with the same insect. In the present studies *A. kuhniella* was not included among the pyralids examined but it seems unlikely that it would differ significantly from others. In the ones examined, wing circulation was perhaps weaker and less obvious than in species from other families but it was nevertheless complete and generally typical of the order.

Materials

Observations were confined to members of the suborders Frenatae and Rhopalocera but there is little reason to suspect major differences among the Jugatae which were neglected here. Species from five families were represented (see Appendix), and special attention was given to those from Geometridae and Noctuidae, where circulation was most vigorous.

Observations and Discussion

The circulatory route in a geometrid (Figs. 55 and 56) is basically representative of the Lepidoptera. There, as in the species examined from other families, the main stem of the media is absent and there is no blood channel in its position. Presumably, in species where the media persists it will carry an afferent current as it does, basically, in other insects with similar venation. In the absence of the media the afferent and efferent veins in different species are more or less widely separated by the cell R + M. The main afferent flow occurs in the veins anterior

to the cell and efferent currents characterize those posterior to it; there is, of course, some efferent movement of blood in certain distal branches of the afferent system near the apex and some afferent flow in one or more of the veins leading from the end of the cell to the outer margin. In the fore wings the change-over from the afferent to the efferent veins is accomplished through two channels: one is the cross-vein or series of short veins which join the radius and cubitus at the end of the cell R + M and unites the bases of the medial branches; the other is the ambient costa which carries blood marginally to the axillary cord. In the hind wings, as described below, the change-over may or may not occur in the same way according to the family.

A peculiar feature of circulation in the fore wings of geometrids is the movement of blood in opposite directions on the two sides of a trachea suspended centrally in the lumen of certain veins (Fig. 58). It was not observed in members of other families but it may not be uncommon; similar double circulation occurs in short portions of some veins in the tegmina of cockroaches. In the geometrids it occurs principally in the distal branches of the radius and media. Blood flows afferently in the anterior half of the veins to their termination in the ambient costa at the outer margin of the wings. Midway along the veins however part of the blood passes around the trachea and flows efferently behind it to join the current in the aforementioned radio-cubital channel. The reversal occurs at about the same region of the veins whether the trachea continues in its suspended position or becomes adherent to the vein wall. Apparently the blood flows through openings in the membrane that suspends the trachea and divides the veins longitudinally. The change in the direction of flow behind the tracheae demonstrates a haemodynamic principle and reflects the difference in the size of the two afferent-efferent cross channels and the force of the currents within them. The radio-cubital channel is the larger, is closer to the wing base, and carries the stronger current. It therefore attracts more blood from the distal regions than the ambient costa which, because of its small size, cannot accept the normal outflow from the afferent veins. In so doing it allows circulation to continue in the main area of the wings in old adults where the outer margins, including the ambient costa, are broken.

The venation in the hind wings is quite different from that of the fore wings, in Comstock's view, but distinctions between them in the route of circulation are not great. The main stem of the media was absent from the hind wing of all of the species examined here, and, as in the fore wings, the main afferent veins were separated from the main efferent ones by a long discal cell. In some families, as in Geometridae (Fig. 56), the cell is terminated by a discal cross-vein extending from the radius to the cubitus or their corelatives and the afferent-efferent exchange of blood is then the same as in the fore wings. In others however, as in Olethreutidae (Fig. 60), the cross-vein is absent and the only course of exchange is via the ambient costa in the outer margin. Consequently, complete circulation in the wings is limited and depends upon the persistence of this single vein. This limitation is presumably responsible for modifications in the route of circulation in the region anterior to the discal cell where blood flows afferently only in the vein at the costal margin and in the main trunk of the other compound vein. The anterior branches of the latter carry blood to it from the costal vein in an efferent direction. The names of these veins seem to be controversial, partly because the costa is considered to be reduced or absent. The present studies show that it is present as a blood channel, but not heavily sclerotized.

There is some direct flow of blood through the wing bases (Fig. 57) but, as in the veins, its movement is hindered by the large tracheae. The suggestion by

aforementioned authors that this is the main passageway for the blood is untenable. Pulsations are rarely observed in the wings or their bases despite the presence of active thoracic pulsatile organs. Their action was faintly visible in some species, particularly of geometrids and pterophorids, and coincided with shallow pulsations of the axillary cords. The rate of pulsation was variable but usually greater than that of the heart.

Order: Diptera

In the generalized members of the Diptera the wing venation is said to be only slightly modified from the hypothetical primitive type. However the route of circulation is quite different from the basic pattern. At the same time the route is simple, direct, and easily observed, and the current is usually vigorous. In the specialized members of the order, the venation is variously reduced and the route of circulation conforms to it while maintaining the basic circuit of the generalized members; it is more difficult to observe, partly because the current is not usually strong, and partly because the haemocytes are hyaline and comparatively few in number.

A number of authors have published accounts of wing circulation in the order, mainly of species that may be considered specialized. Tyrrel (1835) commented briefly on blood circulation in the wings of *Musca domestica.* Bervoets (1913) recognized the presence of blood in the wings of the "bluebottle" fly and noted that less blood flowed from cuts made at the wing tip than from those made at the base. Brocher (1916) noted the pulsatile organs in tipulids and remarked on their similarity to those of *Dytiscus.* Comprehensive studies of wing circulation were later carried out by three authors. Hase (1927) described circulation in the wings of *Hippobosca equina* L. and noted variations in the rate of pulsation of "wing hearts". Thomsen (1938) worked similarly with *Musca domestica* L. and reported subscutellar pulsatile organs and four separate pulsatile organs within the wings. Perttunen (1955) studied circulation in the wings of *Drosophila funebris* and *D. melanogaster* and counted five accessory pulsatile organs within the wings.

Materials

Wing circulation was studied in members of each of the suborders Nematocera, Brachycera, and Cyclorrhapha. Representatives from 17 families were included: six families were among the Nematocera, six also from the Brachycera, and five from the Cyclorrhapha (see Appendix). Experimental studies to determine circulatory paths following the blockage of certain veins were carried out mainly with species from Tipulidae.

Observations and Discussion

There are significant differences at the family level in the route of blood circulation in the wings of the Diptera. These differences are mainly attributable to the presence or absence in combination of two features of the venation, the ambient or marginal extension of the costa, and the arculus or a functionally equivalent sinus in its position; although the arculus is generally recognized only in the family Tipulidae, the term is used here in its broadest sense, as by Comstock, to indicate a cross-vein (or blood channel) extending from radius to cubitus near the wing base. Less significant differences also occur concomitantly with minor variations in the venation and in the structure of the bases of the wings, and there are some rather exceptional variations in families such as Simuliidae where venation is highly modified.

There are three main routes of circulation in the different families of Diptera, each basically similar but with certain distinctive features. For comparison, the families may be separated into two groups, those in which the ambient costa extends around the entire margin of the wing, and those in which it terminates a short distance beyond the apex. Among the families examined here, the first group included Tipulidae, Asilidae, and Tabanidae, in each of which the wings also feature a prominent arculus. The second group may be subdivided into families in which the arculus or an equivalent sinus is prominent, and those in which it is insignificant or absent. It was prominent in the families Syrphidae, Sciomyzidae, Stratiomyiidae, and Simuliidae, among those examined, and absent in the remainder. The three categories have little or no taxonomic significance, except perhaps the third one which characterizes the Cyclorrhapha.

The ambient costa, in its position around the entire wing margin and as the terminus of the afferent and efferent longitudinal veins, provides for the circulation of blood throughout the wing. This is true of the vein in whatever insect it occurs, but among the Diptera it is especially effective and important as a channel for afferent-efferent exchange. This is partly because it is comparatively large and partly, or perhaps mainly, because of its association with a prominent arculus. The arculus carries a strong current of blood posteriorly near the wing base and the current in adjoining veins is directed toward it. This is a unique occurrence in a system of veins that approximates the hypothetical primitive condition. It is exemplified in the wings of Tipulidae.

In the Tipulidae (Figs. 61 and 70) a broad arculus crosses the wing near the base and joins the intervening veins from the radius to the cubitus. It occurred as a blood channel in each of the species examined, but was not always as heavily sclerotized as the other veins. This would account for the fact that it is not recognized in all members of the family and is used as a taxonomic character. Afferent flow occurs in the costa and subcosta to the wing apex and in the radius and media only as far as the arculus. Beyond the arculus and posterior to the subcosta all of the veins are efferent. They carry blood from the distal regions to the arculus which acts as a common channel directing blood into the axillary cord. Only the ambient costa by-passes the arculus completely and joins the axillary cord more or less separately. The current in the arculus is strong and combines the force of the afferent streams from the bases of radius and media with the aspirating force of the thoracic pulsatile organs. The latter is the more significant; this is evident from pulsations of flexible portions of the arculus wall and of contained tracheae and associated tissues in synchrony with movements of similar areas and structures in the wing base, of the axillary cords, and of the pulsatile organs themselves. The average rate of pulsation for ten individuals was 116 per minute and exceeded the heart-beat, which was 83 per minute, at the same region. Both were variable, however, and periodically the rate of the pulsatile organs was less than that of the heart or exceeded it greatly. There was no evidence to indicate that separate pulsing areas and tissues, that occur particularly in the wing bases and arculus of several species, were independent pulsatile structures. Their activity was usually attributable to pulsations of the thoracic organs or the heart and they appeared to be flexible areas of the vein walls or portions of connective strands that attached tracheae or nerves to the walls. This is contrary to the findings of aforementioned authors with species other than the ones studied here.

In Tipulids, as mentioned previously, the efferent flow of blood from the outer margin of the wings to the arculus and thence to the axillary cord is effected mainly by the aspirative force of the strong current in the arculus. This

current was studied experimentally by blocking separately, and in combination, the veins that enter the arculus and by blocking the arculus separately at its entrance and exit. Blockage of one or more of the efferent veins stopped the flow only in the affected vein and resulted in local re-routeing of the streams through distal cross-veins without changing the main course of circulation. Blocking the afferent veins to the arculus, particularly the radius, resulted in an appreciable decrease in the force of circulation in the wing without altering the main course. Blocking the entrance to the arculus also failed to change the main course of circulation, except that the radius became afferent for its whole length. Finally, blocking the arculus at its exit into the first anal vein caused a temporary complete stoppage of wing circulation followed by a slow return with the current much reduced in strength and with the course somewhat altered and variable. The entire wing continued to be served by blood which now flowed from the outer margin to the axillary cord via the anal veins and ambient costa. Blood also continued to flow from the outer margin to the arculus, but slowly and only in the anterior veins, radius and media; it moved slowly away from the arculus in the posterior veins. Obviously the afferent veins that enter the arculus contribute significantly to the current there but the main force is derived from the thoracic pulsatile organs. When this force is eliminated from the arculus the efferent movement of blood to that vein is reduced to a passive condition and the main course of flow is peripheral.

Although in Diptera the arculus and the ambient costa are associated with relatively vigorous circulation throughout the wing, they are not as closely interrelated functionally in all forms as they are in the tipulids. In the Asilidae, for example (Fig. 62), the arculus accepts only part of the blood from the radius and the main current continues afferently to the outer wing margin. The afferent-efferent exchange is then obtained through three channels, the arculus, the radio-medial cross-vein, and the ambient costa. Efferent flow in the cubito-anal veins converges to the common union at the base of the arculus and thence to the axillary cord. The main force is still derived from the thoracic pulsatile organs but it acts less through the arculus and more directly in the cubito-anal veins. The same course is followed in Tabanidae (Fig. 63) but there the current is somewhat dissipated in sinuses around open veins at the stigma area and at the arculus.

In the absence of the ambient costa the outer and inner margins of the wings are not served by the blood, the longitudinal veins are not all joined terminally, and the afferent-efferent exchange of blood in the distal regions occurs entirely through cross-veins or by unions of the longitudinal veins in other ways. Some changes in the route of circulation are necessarily involved and the area of the wings included in the direct route of circulation is reduced by different amounts in various families. There is also usually a reduction in the relative vigor of wing circulation, not necessarily attributable to the absence of the ambient costa. In its absence however circulation is generally more effective where an arculus is prominent than where it is small or absent. In the former case, for example in members of the family Syrphidae (Fig. 64), the route of circulation is only slightly modified from that in tipulids. The basic distinction between the two is in the extent of confluence of the radius and arculus. Whereas in tipulids all of the blood from the radius enters the arculus, in Syrphidae only part of it does and the remainder continues to flow afferently. The unique "'spurious vein" of the syrphids is also afferent. Although the ambient costa is lacking, the longitudinal veins approach the outer and inner margins at several points and most of the wing is included in the direct route of circulation. This is not the case in members of other families such as Sciomyzidae (Fig. 66) where the confluence of

anal veins is removed from the margins. It is still less so in Mycetophilidae (Fig. 67) and in Simuliidae (Fig. 68) where the outer region is more or less devoid of circulating blood. In Mycetophilidae, blood occupies the cubito-anal veins but they are not a part of the direct circuit. Blood enters and leaves them intermittently in conjunction with gushing of blood in the wings. In Simuliidae, circulation is limited to the anterior margin and the wing base; the basic mechanism is unchanged but radius-one and the radial sector serve as efferent channels for blood from the costa near the wing apex.

In Diptera where both the arculus and ambient costa are absent, as in the family Dolichopodidae (Fig. 65), most of the blood that enters the wing follows a complete course through the veins. The only short course available to it proximally from the afferent to the efferent sectors is through the small radio-medial cross-vein. Alternation of the direction of flow is common in successive veins, apparently to compensate for the few available channels, and the anal area is poorly served. Circulation tends to be less vigorous than in wings where the arculus is prominent but it is nevertheless comparatively steady.

In all Diptera some of the blood that enters the wings follows a rather tortuous course through the wing base to the axillary cord without entering the veins. In those without an alula (Fig. 70) the basal stream joins directly at the anal angle with blood flowing from the vein complex and the current is relatively swift. It is less swift but the route is similar in forms such as tabanids (Fig. 71) where the anal veins are not prominent and are removed from the inner margin at the anal angle. Where alulae are well developed, as in muscids (Fig. 72), the route is similar again but less direct; part of the blood is directed through the margins of the alulae before entering the axillary cord.

The halteres also support a circulation of blood (Fig. 69) but the flow is generally slow and irregular. The route followed is basically the same as in the normal wing. Blood enters the anterior channel, circles through the knobbed extremity, and returns to the body through a posterior channel that terminates in the facsimile of the axillary cord. The irregularity of the pulse suggests that the flow is not controlled by pulsatile organs, but responds to heart activity and respiratory and other movements.

Discussion and Conclusions

Blood circulation in one form or another was a constant feature in the wings of all the insects examined during the course of this study. Approximately 100 species from fourteen orders were included, and they represent a fair sampling from the class, with the wings widely varied in size, form, and venation. They add to the already large number and variety of species in which wing circulation has been reported, and confirm the opinion that circulation occurs in the wings of all pterygotes, however modified these appendages may be.

In a very general sense, the route of blood circulation in insect wings is described in Carus' (1831) rule which states that blood flows from the insect body through the anterior margin of the wings and returns to the body in the posterior margin. For most insects, the route may be described more precisely than this, as in the preamble to the preceding section, but it is difficult to conceive of comprehensive rules or laws of circulation that would apply to all species. Probably the closest facsimile to these would be a synopsis of circulation that gives the normal direction of blood flow in the basic wing veins and their main branches along with notations on the most frequent deviations.

The following synopsis of wing circulation applies most readily to wings that approximate Comstock's (1918) interpretation of the hypothetical primitive

condition, but may be interpreted also for those where the number of veins is increased or moderately reduced; extreme reduction in venation may completely alter the basic course of circulation in the wings. Specialization of the wings by addition of veins increases the number of accessory or intercalary veins, not the number of basic veins, and merely provides more channels through which blood is carried in the same direction as it is in the basic veins from which they branch or between which they are inserted. Similarly, a moderate reduction in venation implies that neighboring veins within one of the basic groups have coalesced, or at least that one or more members of a group are absent. In either case, the original direction of blood flow is maintained in the remaining veins of the group. Comstock's system of wing venation is based on the premise that the main wing tracheae are constant in number and that the principal veins form along the courses of tracheae. It has been shown by several authors, and recently by Whitten (1962), that certain aspects of this premise are questionable and certain of its corollaries, particularly with regard to tracheal homologies at broad taxonomic levels and to tracheal fusion and migration, are untenable. The present study demonstrates further that some principal veins occur in the adult wing where apparently no tracheae existed during wing development. In some instances these veins are not evident in dead specimens and were considered by Comstock to have fused with neighboring veins; his interpretations of the structural composition of some veins was consequently mistaken. Regardless of the significance of these findings in phylogenetic and other studies however, they do not seriously affect vein terminology, and the present synopsis uses Comstock's system.

Costa: this vein, or the channel or sinus that occupies its position along the costal margin of the wing, is invariably afferent during normal circulation and usually supports a strong current of blood, at least in the proximal region. Despite its prominence as a blood channel it is not always evident in dead wings and was overlooked by Comstock in some insects. In many insects it extends around the entire margin of the wing, receives blood from the other afferent veins, contributes blood to terminal efferent veins, and is a direct conduit for blood around the circumference of the wing to the anal region. Comstock considered this to be a thickening of the wing margin and termed it the *ambient vein;* here it is termed the *ambient costa.*

Subcosta: the subcosta is normally afferent throughout its length. Frequently it supports a stronger flow of blood than the costa and contributes some of it to the latter via cross-veins or sinuses. The current in the *humeral cross-vein*, which commonly joins the bases of the costa and subcosta, may be in either direction depending on its position in different species and on the relative force of the current in the two main veins.

Radius: the main trunk of the radius is normally afferent and usually carries the major outflow of blood from the body. The direction of flow in its branches is less definite, but it too is basically afferent. There is a tendency, however, for successive branches of the radius to carry blood in opposite directions. Ideally this creates an extensive alternating movement of blood in the distal part of the wing. In species where this does occur, *radius-one* is efferent; it accepts blood from the costa or its equivalent and directs it inward toward the radial sector; some of it becomes diverted posteriorly through the *radial cross-vein* and the remainder continues inward and becomes reversed in direction as it joins with the strong afferent current in the radial sector. The *radial sector* is afferent and so are both branches from its initial bifurcation. However its terminal branches, *radius-two, -three, -four,* and *-five* tend to be consecutively efferent and afferent, as mentioned above. This tendency is seldom dependable over a period of time

and the blood may flow in either direction intermittently while following a course that is mainly toward the posterior. This direction is obtained by means of the *sectoral* and the *radio-medial cross-veins* or their equivalents and by the ambient costa. In some insects, and especially during periods when the blood pressure is high, all of these branches are afferent.

Media: fundamentally the media is an afferent vein and the blood course in it and its branches is similar to that in the radius. However, the current in it is seldom as strong as that in the radius and the direction of flow is consequently more variable. In insects where the base of the media is more closely associated with the cubitus than with the radius, or where the basal *medio-cubital cross-vein* is prominent, the course is mainly efferent, especially when the blood pressure is low.

Cubitus: the cubitus and its branches are typically efferent; generally they accept blood from the ambient costa or from cross-veins from the radio-medial system, or both, and contribute it directly into anal veins or into the wing base at the anal angle. Occasionally the course of flow is variable.

Anal: the anal veins are invariably efferent; they accept blood from the ambient costa, where it exists, and from cubital cross-veins and carry it directly into the basal region of the axillary cord.

Not all of the blood that enters the wings continues through the veins. Part of it may immediately flow posteriorly through the wing base or through channels just beyond the base and reenter the body directly. The proportion which thus by-passes the main area of the wings is probably small in most insects but it is variable and seems to be governed partly by structural features such as the size and position of the axillary sclerites, the completeness of membranes in the wing bases, the nature of the wing veins, and partly by the blood pressure. Axillary sclerites and membranes in the wing bases tend to obstruct the current. On the other hand, where the lumen of a vein is narrow and the walls inflexible the blood tends to follow the easier course through the base or near it. Similarly, this course tends to be followed when the blood pressure is low.

The above synopsis of the circulatory route refers briefly to a common feature of wing circulation, the variability in the course of flow that results from fluctuations in blood pressure. Periodically in any insect, circulation in the wings may falter, reverse its direction of flow completely or in part, or stop entirely for short intervals. These periods of change tend to increase in frequency and duration with age, but they are normal occurrences at any age. They are unquestionably expressions of the unconfined nature of the circulatory system as a whole, and of inefficiency on the part of the mechanism for wing circulation.

The open circulatory system in insects permits the occurrence of shifts in pressure within areas of the haemocoel as a result of muscular contractions. This is a useful feature and serves a variety of functions, but it also interferes with the normal course of circulation in the wings; the wing veins are extensions of the haemocoel and the blood there is subject to pressure changes in the body. When these changes are marked, they dominate the regular forces involved in wing circulation. In some insects, for example, blood may be forced back and forth through the wings in rhythm with pressure changes accompanying exaggerated respiratory movements, even though the heart and accessory pulsatile organs are apparently functioning in normal fashion. Similarly, contraction of the abdomen in certain insects may cause a steady reversal of the normal direction of blood flow in the wings. Such extreme cases are more common among insects where the wings approximate the hypothetical primitive condition than among special-

ized forms, but they are not confined to them. Undoubtedly the rate and direction of blood flow varies in the wings during periods of activity such as flight when pressure changes in the thorax are probably extreme and rapid. The decline in circulation in the wings with age reflects the general retardation of circulation and, in wings with extensive venation, of occlusion of increasing numbers of veins by haemocytes.

The degree of constancy of circulation in the wings varies in different taxonomic groups. In some orders, such as Ephemeroptera, fluctuations are almost continual, whereas in others, such as Hymenoptera, they are comparatively rare. Similarly, the strength or rate of wing circulation is broadly characteristic of taxonomic groups. In Plecoptera and Hymenoptera, for example, the flow is vigorous and seldom falters, whereas in certain members of Trichoptera and Lepidoptera it is comparatively slow and feeble. These distinctions are easily recognized but difficult to interpret precisely. Undoubtedly the constancy and vigour of circulation in the wings are related to features of general morphology and particularly to the structure of the thorax and the wing bases. Certainly they are also related to the nature, extent, and complexity of the blood channels in the wings as well as to the efficiency of the circulatory system as a whole. A simple analogy would suggest that a more efficient pumping mechanism is required to provide equal circulation in a wing with extensive venation or one with large sinuses than in one where the venation is in the form of a simple circuit. It does not necessarily follow, however, that circulation is vigorous in wings where the venation is simple. Other factors, as mentioned above, complicate the situation. For example, where the entrance to the wings at the humeral angle is narrow or largely occupied by tracheae the flow of blood may be limited, regardless of the simplicity of venation. The same may be true where the veins are narrow or their lumens obstructed. In any case, the circulation may be slight during periods of rest and swift during periods of activity when the blood pressure is high, depending upon the efficiency of the heart and the accessory pulsatile organs.

There is some evidence of a relationship between wing circulation and flight, but it is only partly convincing. In Ephemeroptera and Odonata, for example, flight is more efficient in Odonata where circulation also is more controlled. Similarly, in many Hymenoptera and Diptera where flight is rapid and can be sustained for long periods blood circulation in the wings is noticeably more efficient than in some Cursoria or Orthoptera where flight is feeble. Other examples of a direct relationship may be selected, but it seems much more likely that structural differences, rather than circulatory ones, are primarily involved, along with such factors as the ratio of body weight to wing area or to volume of flight muscles, and with physiological distinctions. Moreover, if certain related insects are compared, such as tipulids and syrphids, circulation seems equally strong in the wings of each but flight efficiency is quite different; in this case the syrphids are much the stronger fliers. Further speculation might suggest that the volume or weight of blood in the wings in relation to wing area is an inverse function of flight efficiency. This too is not very convincing. It is true that tegmina, hemelytra, and elytra, which are not effective in flight, contain more blood than flight wings in the same insects that bear them, and also that the wings of many feeble fliers, such as plecopterans and neuropterans, are extensively veined and must contain relatively large quantities of blood per unit area. On the other hand, the flight wings of flightless cursorians apparently contain no more blood than those of some arboreal orthopterans which are capable of sustained flight, and the strongly flying syrphids have relatively more blood in the

wings than the weaker simuliids. Obviously, these relationships are difficult to equate, but it seems unlikely that circulation in the wings is directly significant in the mechanics of flight. Indirectly, however, it is undoubtedly important in maintaining the structural integrity of the wing and in nourishing sensory structures that are directly or indirectly involved in orientation and stabilization of flight.

The mechanism for circulating blood in the wings is complex, and a complete explanation of it awaits further study. It is basically the same in all insects but varies in detail and is influenced by different factors in the various groups. In general, the main forces involved come from the heart, which indirectly propels blood into the anterior portion of the wings, and the thoracic accessory pulsatile organs which draw blood from the posterior portion and return it to the body. These two forces working together maintain the circular route of flow which is generally characteristic of the wings in all orders. There is no doubt that the blood enters the wings under pressure, for pulsations of the heart are often apparent in the afferent veins, and changes in pressure within the body affect the flow in the wings. The pulsations from the heart are not normally discernible at the apex of the wing, and apparently the original propulsive force is dissipated in the afferent system of veins. The force required to move the blood through the efferent system of veins and thus complete the circuit is the one, already mentioned, provided by the accessory pulsatile organs acting through the axillary cord. It is reportedly supplemented in some insects by pulsatile tissues within the wings, but this was not confirmed in this study. Some of the force may also develop from the heart which is connected with the pulsatile organs and acts in a similar fashion; it normally aspirates blood from the pericardial sinus in many insects, and in the same way may draw blood from the pulsatile organs. In some insects it is difficult to distinguish the action of heart and pulsatile organs because of the close degree of their association and the synchronization of their pulsations. In a few, distinctive pulsatile organs are not evident but seem to be represented by lateral extensions of the heart. Generally, however, the beat of the heart and of the pulsatile organs are not synchronous, and it is the beat of the organs that is expressed in the flexible portions of the axillary cord and anal veins. Occasionally, pulses that are attributable only to respiratory movements register also in these flexible areas and suggest that normal, rhythmical, respiratory movements also assist in drawing blood from the wings. On the other hand, the rhythmical contractions of connective tissue which cause the constant undulation of viscera and contribute to the movement of blood in the body cavity evidently do not affect wing circulation; at least no comparable pulse is evident in the wings. The effectiveness of the whole mechanism depends on the efficiency of the organs involved and on structural features of the thorax, wing bases and veins. In insects where the wings are highly modified the mechanism may be rudimentary or absent and circulation in the wings is reduced to a relatively passive condition; blood gushes into and out of the wings intermittently in response to changes in pressure in the body haemocoel and may or may not follow a circular path.

There is a general tendency for blood circulation to be less extensive and slower in the hind wings than in the fore wings, especially where there is an appreciable discrepancy in the size or nature of the two pairs. Circulation in the hind wings tends also to be less affected by changes in pressure within the body haemocoel. Presumably these distinctions are due to structural differences, including the smaller size of pulsatile organs of the metathorax. There may be some slight advantage to this tendency in keeping the weight of blood in the wings low while a constant supply is assured to maintain flexibility and sensitivity.

Differences in the circulatory route in the wings of various taxonomic groups are due mainly to the influence of distinctive features of wing structure and venation on the manner in which the blood can be accommodated. Features which alter the route significantly are usual at the order level of the taxonomic system, occur commonly at the family level, and may be evident at the generic level in some families. Specific differences are usually insignificant. Whatever these features may be, whether they are extensive structural characteristics of the entire wing as in tegmina or elytra, less obvious structural details of the wing bases, peculiarities in size or configuration of the veins, etc., they can modify the circulatory route only within the framework of haemodynamic principles which govern the flow. Undoubtedly, the movement of blood in the wings is governed by those physical laws which apply to the flow of liquids in any system of connected cylindrical tubes and is comparable, with certain reservations, to flow in the mammalian vascular system. It is complicated by the aforementioned and other peculiar structural features and by a number of unestimated and variable factors such as the combined volume output of the heart and accessory pulsatile organs, blood viscosity, blood volume, elasticity of the wing veins, leakage from the veins, and resistance to flow. It is also complicated by the physical separation between the two pumping mechanisms involved, the heart and the pulsatile organs, and the fact that their action may not be synchronous and result in some damming back of the blood in parts of the system; the same result may develop from shifts in pressure within the body haemocoel. It is in this aspect, the damming back of blood, probably more than in the others that the system in insects differs from the mammalian; in the latter, both sides of the heart eject the same quantity of blood in a given time and the problem is avoided.

In spite of these complicating factors, certain recognized haemodynamic principles are seen to operate in the wings, at least during periods when the circulation is stable. Probably the most obvious principle involved, and perhaps the most important, is the inverse relationship between lateral pressure and velocity of outflow. It accounts for the movement of blood toward veins wherein the flow is swiftest, and accordingly for its direction into main channels which lead most directly from the entrance to the exit from the wing. It is evident, for example, in the movement of blood toward the arculus in certain dipterans, in the flow through cross-veins between parallel, longitudinal veins of different size, e.g. from subcosta to costa or radius, and in the flow of blood in opposite directions in the two branches at a bifurcation where one branch is larger than the other; the latter is exemplified by the efferent current in radius-one toward the afferent stream in the radial sector. The same principle probably accounts for the greater precision and constancy of circulation in wings where the venation is reduced than in those where it is similar to or more extensive than the hypothetical primitive condition. Where the venation is reduced, as in the Hymenoptera, the pressure gradient in the relatively direct circuit from entrance to exit is great and the current is swift; blood in the distal portion of the vein complex is caused to flow toward the exit in a precise route also. Where the venation is extensive, as in Orthoptera, the route from entrance to exit is indirect and pressure is dissipated en route; pressure gradients are comparatively slight, the currents are relatively slow, and the direction of flow may be somewhat imprecise and variable.

Undoubtedly, a number of other haemodynamic principles are involved in wing circulation but their effect is entirely speculative. Some are mentioned here to show possible causes for variability in the course and velocity of flow and to suggest areas for further study. The principle that resistance to flow varies

directly with the length of a cylinder is likely involved in the reduction of circulation that is commonly found near the wing apex. This effect probably also involves another principle, the inverse proportionality of velocity of flow to sectional area of a cylinder; presumably this operates as a result of the change in the diameter of veins as they proceed distally. Again, cross-veins introduce another principle of flow and another factor in directing wing circulation; longitudinal veins are divided into areas of relatively high pressure proximal to a cross-vein and low pressure distal to it, thereby complicating the route where venation is extensive, and again tending to keep circulation most vigorous near the wing base. These principles, and probably others, are involved in a complex interrelationship that directs blood through a surprisingly constant course in the wings. The degree of their involvement and a full understanding of the mechanism of wing circulation will come from measurements of pressure at various points in the system of veins.

The subject of the development of wing venation and of the homologies of veins continues to be controversial, and a knowledge of circulatory routes in the wings does not contribute convincingly to its solution. Obviously, the routes of circulation conform to the peculiarities of venation, not the reverse, and they can scarcely serve as criteria for establishing vein homologies. Nevertheless, they merit consideration, particularly in a role of demonstrating the existence of some veins which are not evident in the wings of dead specimens, and from which a concept of venation and vein homologies has been derived. Very often, for example, the costa has been considered absent where a clear blood channel exists in the normal position of that vein. Similarly, blood channels show the position of veins in the hemelytra of Heteroptera, and demonstrate the existence of an arculus in certain Diptera, where they are not detectable in dead specimens. These and certain other discrepancies that are mentioned in the text do not alter the basic concept of wing venation, but they may contribute to a correct interpretation of the composition of the vein complex in a number of insects. Present concepts of wing venation rest on either structural bases, derived from comparisons of modern with fossil insects, or on tracheal pathways in developing wings. Some of the main contributors include Tillyard (1917), Comstock (1918), Lameere (1922), Needham (1935), Forbes (1943), and Edmunds and Traver (1954). Few have mentioned the blood and nerve supply to the wings as potential adjuncts to the other criteria for determining vein homologies. Forbes (1943) mentioned the nerve supply but felt that knowledge of it was insufficient for interpretation. This is probably justified, but at the same time, the criteria already used are not entirely sound; there is still much to be learned of wing structure, and there is increasing evidence (Whitten 1962) that tracheal pathways are not as reliable as previously considered. This is not meant to imply that the criteria which have been used in the past are invalid or that present concepts of wing venation and vein homologies are unsound. It merely suggests that other criteria may be usefully included in future studies and in re-examinations of the subject.

Acknowledgments

I am indebted to officers of the Insect Systematics Section of the Entomology Research Institute, Ottawa, for identifying specimens and for contributing useful advice on aspects of the study that relate to taxonomy. Acknowledgment is also due to G. B. Wiggins, Royal Ontario Museum, Toronto, for determinations of Trichoptera, and to W. E. Ricker, Fisheries Research Board of Canada, Nanaimo, B. C. for determinations of Plecoptera. I wish also to thank J. A. Downes for critical comments which added materially to the manuscript.

APPENDIX

List of identified insects used in the present study of wing circulation.

Order: Ephemeroptera
- Family: Hexageniidae
  - *Hexagenia rigida* McD.
  - *Stenonema* sp.

Order: Odonata
- Family: Agrionidae
  - *Enallagma ebrium* (Hagen)
  - *Ischnura verticalis* (Say)
  - *Lestes unquiculatus* Hagen
- Family: Libellulidae
  - *Cordulia* sp.
  - *Sympetrum* sp.

Order: Cursoria
- Family: Blattidae
  - *Blaberus giganteus* (L.)
  - *Blattella germanica* (L.)
  - *Periplaneta americana* (L.)
- Family: Mantidae
  - *Mantis religiosa* Linnaeus

Order: Orthoptera
- Family: Gryllidae
  - *Oecanthus* sp.
- Family: Locustidae
  - *Melanoplus femur-rubrum* (DeGeer)
  - *Melanoplus bivittatus* (Say)
  - *Chorthippus curtipennis* (Harris)
  - *Chortophaga viridifasciata* (DeGeer)
  - *Dissosteira carolina* (Linnaeus)
  - *Encoptolophus sordidus* (Burm.)
- Family: Tettigoniidae
  - *Conocephalus fasciatus* (DeGeer)
  - *Scudderia furcata* Brunn.
  - *Scudderia pistillata* Brunn.

Order: Plecoptera
- Family: Pteronarcidae
  - *Acroneuria arenosa* Pictet
- Family: Perlidae
  - *Perla* sp.

Order: Hemiptera (Heteroptera)
- Family: Belostomatidae
  - *Belostoma fluminea* (Say)
- Family: Corixidae
  - *Corixa* sp.
- Family: Miridae
  - *Adelphocoris rapidus* (Say)
  - *Adelphocoris lineolatus* (Reuter)
  - *Liocoris* sp.

Family: Nabidae
Nabis ferus (Linnaeus)
Family: Phymatidae
Phymata fasciata (Gray)

Order: Hemiptera (Homoptera)
Family: Aphididae
Aphis viburniphila Patch
Family: Cicadellidae
Draeculacephala producta (Wlk.)
Graphocephala coccinea (Forst.)
Gyponana sp.
Idiocerus sp.
Ormenis pruinosa Stal.
Philaenus spumarius (L.)
Family: Cicadidae
Okanagana sp.
Family: Membracidae
Acutalis tartarea (Say)
Campylenchia latipes (Say)
Gargara genistae Am. & Serv.
Stictocephala faurina (Harr.)

Order: Neuroptera
Family: Chrysopidae
Chrysopa sp.
Family: Hemerobiidae
Hemerobius sp.
Family: Mantispidae
Mantispa brunnea Say
Family: Myrmeleonidae
Myrmeleon sp.

Order: Hymenoptera
Family: Apidae
Apis mellifera Linnaeus
Colletes sp.
Family: Bombidae
Psithyrus sp.
Family: Chalcididae
Pachyneuron sp.
Family: Chrysididae
Elampus sp.
Family: Formicidae
Formica sp.
Lasius sp.
Myrmica sp.
Family: Ichneumonidae
Enicospilus sp.
Mimesa sp.
Pimplopterus sp.
Temelucha sp.

Family: Sphecidae
Ammophila sp.
Family: Vespidae
Polistes sp.

Order: Coleoptera
Family: Cantharidae
Cantharis scitulus Say
Family: Cerambycidae
Physocnemum brevilineum Say
Family: Chrysomelidae
Diabrotica duodecimpunctata F.
Oedionychis vians Ill.
Family: Cicindelidae
Cicindela punctulata punctulata Oliv.
Family: Coccinellidae
Coccinella transversoguttata quinquenotata Kby.
Family: Hydrophilidae
Tropisternus sp.
Family: Lampyridae
Ellychnia sp.
Family: Staphylinidae
Gyrohypnus sp.
Quedius sp.

Order: Mecoptera
Family: Panorpidae
Panorpa sp.

Order: Trichoptera
Family: Hydropsychidae
Macronema zebratum Hagen
Family: Limnephilidae
Anabolia bimaculata Walk.
Limnephilus rhombicus (L.)
Limnephilus submonilifer Walk.
Pycnopsyche sp.
Family: Phryganeidae
Phryganea cinerea Walk.

Order: Lepidoptera
Family: Geometridae
Deuteronomos magnarius Gn.
Prochoerodes transversata Dru.
Family: Noctuidae
Oligia mactata Gn.
Family: Olethreutidae
Eucosma sp.
Family: Pyralididae
Crambus trisectus Wlk.

Order: Diptera
- Family: Bibionidae
  - *Bibio* sp.
- Family: Mycetophilidae
  - *Epicypta* sp.
- Family: Psychodidae
  - *Psychoda* sp.
- Family: Simuliidae
  - *Simulium* sp.
- Family. Tipulidae
  - *Limonia cinctipes* (Say)
  - *Limonia parietina* (O.S.)
  - *Ormosia* sp.
  - *Tipula* sp.
- Family: Asilidae
  - *Asilus paropus* Walk.
- Family: Dolichopodidae
  - *Hydrophorus* sp.
- Family: Stratiomyiidae
  - *Sargus decorus* Say
- Family: Tabanidae
  - *Tabanus lineola scutellaris* Wlk.
- Family: Heleomyzidae
  - *Allophylla laevis* Lw.
- Family: Muscidae
  - *Coenosia tigrina* (Fab.)
  - *Musca domestica* L.
- Family: Sciomyzidae
  - *Hedroneura rufa* (Panz.)
- Family: Sphaeroceridae
  - *Leptocera* sp.
- Family: Syrphidae
  - *Eristalis arbustorum* (L.)
  - *Sphaerophoria robusta* Cn.

References

Agassiz, L. 1851. Note sur la circulation des fluides chez les insectes. *Ann. Sci. nat.* 15: 358-362.

Arnold, J. W. 1959. Observations on living hemocytes in wing veins of the cockroach *Blaberus giganteus* (L.) (Orthoptera: Blattidae). *Ann. ent. Soc. Amer.* 52: 229-236.

Arnold, J. W. 1963. A note on the pterostigma in insects. *Canad. Ent.* 95: 13-16.

Baker, H. 1744. The microscope made easy. London.*

Baker, H. 1755. On the microscope. London.*

Bassi, C. 1851. Rapport adressé à la section de zoologie, d'anatomie comparée et de physiologie du congrès de Venise, relatif au passage des substances introduites dans le système trachéen des insectes. *Ann. Sci. nat.* 15: 362-371.

Behn, F. W. G. 1835. Découverte d'un circulation de fluide nutritif dans les pattes de plusieurs insectes hemiptères. *Ann. Sci. nat.* 4: 5-12.

Bervoets, R. 1913. Notes sur la circulation du sang dans les ailes des insectes. *Ann. Soc. ent. Belg.* 57: 184-190.

Blanchard, E. 1851. Nouvelles observations sur la circulation du sang et la nutrition chez les insectes. *Ann. Sci. nat.* 15: 371-376.

Bowerbank, J. S. 1833. Observations on the circulation of the blood in insects. *Ent. Mag.* 1: 239-244.

Bowerbank, J. S. 1836. Observations on the circulation of blood and the distribution of the tracheae in the wing of *Chrysopa perla*. *Ent. Mag.* 4: 179-185.

Brocher, F. 1916. Nouvelles observations biologiques et physiologiques sur les Dyticidés. Étude anatomique et physiologique de deux organes pulsatiles aspirateurs, destinés a faciliter la circulation du sang dans les ailes et dans les élytres; utilé de l'alula. Constatation de la présence d'organes, fonctionnant d'une manière semblable, chez divers autres insectes (Hyménoptères, Diptères, Orthoptères, Lépidoptères, Névropteres). *Arch. Zool. exp. et gen.* 55: 347-373.

Brocher, F. 1917. Étude experimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. I. Le *Dyticus marginalis*. *Arch. Zool. exp. et gen.* 56: 347-358.

Brocher, F. 1919. Les organes pulsatiles méso- et métatergaux des lépidoptères. *Arch. Zool. exp. et gen.* 58: 149-171.

Brocher, F. 1920a. Étude expérimentale sur la fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. III. Le *Sphinx convolvuli*. *Arch. Zool. exp. et gen.* 60: 1-45.

Brocher, F. 1920b. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. IV. La *Vespa crabro*. *Ann. Soc. ent. France.* 89: 209-232.

Brocher, F. 1922. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. V. La *Periplaneta orientalis*. *Ann. Soc. ent. France.* 91: 156-164.

Brocher, F. 1929. Observations physiologiques sur la circulation du sang dans les ailes et dans les élytres chez la Coccinelle. *Rev. Suisse Zool.* 36: 593-607.

Burmeister, H. C. C. 1832. Handbuch der Entomologie. Berlin.*

Carus, C. G. 1827. Vorläufige Nachricht über die Entdeckung eines deutlichen Blutlaufs bei Insecten. *Isis* 20: 318.

Carus, C. G. 1828. Nachträgliche Bemerkungen über den Blut-Umlauf in den Kerfen, insbesondere den Blut-Umlauf in volkommenen betreffend. *Isis*: 21: 477-481.

Carus, C. G. 1831. Fernere Untersuchungun über Blutlauf in Kerfen. *Nov. Acta Physico-Med. Acad. Caes. Leop-Carol.* 15: 1-18.

Chapman, R. N. 1918. The basal connections of the tracheae of the wings of insects, pp. 27-51. *In* J. H. Comstock, The wings of insects. Comstock, Ithaca, N. Y.

Church, N. S. 1960. Heat loss and the body temperatures of flying insects. II. Heat conduction within the body and its loss by radiation and convection. *J. exp. Biol.* 37: 186-212.

Clare, S. and O. E. Tauber. 1940. Circulation of hemolymph in the wings of the cockroach *Blattella germanica* L. I. In normal wings. *Iowa St. Coll. J. Sci.* 14: 107-127.

Clare, S. and O. E. Tauber. 1942. Circulation of hemolymph in the wings of the cockroach *Blattella germanica* L. II. Effect of cutting hemolymph channels in the normal tegmen and hind wing. *Ann. ent. Soc. Amer.* 35: 57-67.

---

* – reference not seen.

Clare, S. and O. E. Tauber. 1942. Circulation of hemolymph in the wings of the cockroach, *Blattella germanica* L. III. Circulation in the articular membrane: The significance of this membrane, the pteralia, and wing folds as directive and speed controlling mechanisms in wing circulation. *Iowa St. Coll. J. Sci.* 16: 349-356.

Comstock, J. H. 1918. The wings of insects. Comstock Publishing Co., Ithaca, N. Y.

Davis, C. C. 1956. Experiments upon the heart of *Chaoborus albipes* (Diptera, Culicidae). *J. cell. comp. Physiol.* 47: 449-468.

Davis, N. T. 1961. Morphology and phylogeny of the Reduvioidea (Hemiptera: Heteroptera). Part II. Wing venation. *Ann. ent. Soc. Amer.* 54: 340-354.

Drenkelfort, H. 1910. Neue Beiträge zur Kentniss der Biologie und Anatomie von *Siphlurus lacustris* Eaton. *Zool. Jb. Abt. Anat.* 29: 526-617.

Dufour, L. 1841. Études anatomiques et physiologiques sur une mouche, dans le but d'éclairer l'histoire des metamorphoses et de la pretendue circulation des insectes. *Ann. Sci. nat. Zool.* 16: 5-14.

Duvernoy, G. L. 1839. Résumé sur le fluide nourricier, ses reservoirs et son mouvement dans le regne animale. *Ann. Sci. nat.* 12: 300-346.

Edmunds, G. R. Jr. and J. R. Traver. 1954. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. *J. Wash. Acad. Sci.* 44: 390-399.

Forbes, W. T. M. 1943. The origin of wings and venational types in insects. *Amer. Midl. Nat.* 29: 381-405.

Freudenstein, K. 1928. Das Herz und das Circulationssystem der Hönigbiene (*Apis mellifica* L.). *Z. wiss. Zool.* 132: 404-475.

Hamilton, M. A. 1931. The morphology of the water-scorpion, *Nepa cinerea* Linn. (Rhynchota, Heteroptera). *Proc. zool. Soc. Lond.*, 1931: 1067-1136.

Hase, A. 1927. Beobachtungen über das Verhalten, den Herzschlag soure den Stech- und Saugakt der Pferdelausfliege *Hippobosca equina* L. (Dipt. Pupipara). *Z. Morph. Ökol. Tiere* 8: 187.

Janet, C. 1906. Sur un organe non décrit du thorax des fourmis ailées. *C. R. Acad. Sci.* 143: 522-523.

Kirby, W. and W. Spence. 1826. An introduction to entomology. London.*

Kuhl, W. 1924. Der feinere Bau des Circulationssystems von *Dytiscus marginalis* L. *Zool. Jb.* 46: 75-198.

Lameere, A. 1922. Sur la nervation alaire des insectes. *Bull. Acad. roy. Belg.* s.5. 8: 138-149.

Lehr, R. 1914. Die Sinnesorgane der beiden Flügelpaare von *Dytiscus marginalis*. *Z. wiss. Zool.* 110: 87-150.

Leston, D. 1962. Tracheal capture in ontogenetic and phylogenetic phases of insect wing development. *Proc. roy. ent. Soc. Lond.*, s. A. 37: 135-144.

MacGillivray, A. D. 1906. A study of the wings of the Tenthredinoidea, a superfamily of Hymenoptera. *Proc. U. S. Nat. Mus.* 39: 569-654.

Meyer, E. 1931. Über den Blutkreislauf der Ephemeriden. *Z. wiss. Biol.* abt. A., 22: 1-52.

Moseley, H. N. 1871. On the circulation in the wings of *Blatta orientalis* and other insects, and on a new method of injecting the vessels of insects. *Quart. J. Microscop. Sci.* 11: 389-395.

Needham, J. G. 1935. Some basic principles of insect wing venation. *J. N. Y. ent. Soc.* 43: 113-129.

Newport, G. 1837. On the temperature of insects and its connection with the functions of respiration and circulation. *Phil. Trans.* 127: 259-338.

Nicolet, 1847. Note sur la circulation du sang chez les Coléoptères. *Ann. Sci. nat.* s.3, 7: 60-64.

Orr, W. 1833. Book Review: Alphabet of Insects for the Use of Beginners. By James Rennie, London, 1832. *Ent. Mag.* 1: 64-65.

Patch, Edith, M. 1909. Homologies of the wing veins of the Aphididae, Psyllidae, Aleurodidae, and Coccidae. *Ann. ent. Soc. Amer.* 2: 101-129.

Pawlowa, M. 1895. Über ampullenartige blutcirculationsorgane im Kopfe verschiedener Orthopteren. Zool. Anz. 18: 7-13.

Perttunen, V. 1955. The blood circulation and the accessory pulsatile organs in the wings of *Drosophila funebris* and *D. melanogaster* (Dipt., Drosophilidae). *Ann. Ent. Fenn.* 21: 78-88.

Portier, P. 1932. Locomotion aerienne et respiration des Lépidoptères; un nouveau role physiologique des ailes et des écailles. *Proc. V Congr. int. Ent.* 2: 25-31.

Rennie, J. 1832. Alphabet of insects, for the use of beginners. London.*

Ross, H. H. 1956. A Textbook of Entomology. John Wiley & Sons, Inc., New York.

Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Book Co., New York and London.

Stehr, G. 1947. Beziehungen zwischen der Blutzirkulation im Puppenflügel und dem Zeichnungsmuster von *Ephestia kuehniella*. *Rev. Suisse Zool.* 54: 573-608.

Tauber, O. E. and S. Clare. 1942. Circulation in the wings of the cockroach, *Blattella germanica* L. IV. Circulation in unsclerotized wings under normal and experimental conditions. *Trans. Amer. microscop. Soc.* 61: 290-296.

Thomsen, Ellen. 1938. Über den Kreislauf im Flügel der Musciden mit besonderer Berücksichtigung der Akzessorischen pulsierenden Organe. *Z. Morph. Ökol. Tiere* 34: 416-438.

Tillyard, R. J. 1917. The biology of dragon flies. Cambridge Univ. Press, Cambridge.

Treviranus, G. R. 1831. Erscheinungen und gesetze des organischen Lebens. Bremen, Bd. 1, p. 220.*

Tyrrel, J. 1835. On the circulation of the blood in insects. *Proc. roy. Soc. London* 19: 317.

Verloren, M. 1847. Mémoire sur la circulation dans les insectes. *Mem. Sav. étr. Acad. R. Belg.* 19: 1-93.

Wagner, R. 1832. Beobachtungen über den Kreislauf des Blutes und den Bau des Rückengefaesses bei den Insecten. *Isis* (1832): 320-331, 778-783.*

Whedon, A. D. 1938. The aortic diverticula of the Odonata. *J. Morph.* 63: 229-261.

Whitten, J. M. 1962. Homology and development of insect wing tracheae. *Ann. ent. Soc. Amer.* 55: 288-295.

Wille, A. 1958. A comparative study of the dorsal vessels of bees. *Ann. ent. Soc. Amer.* 51: 538-546.

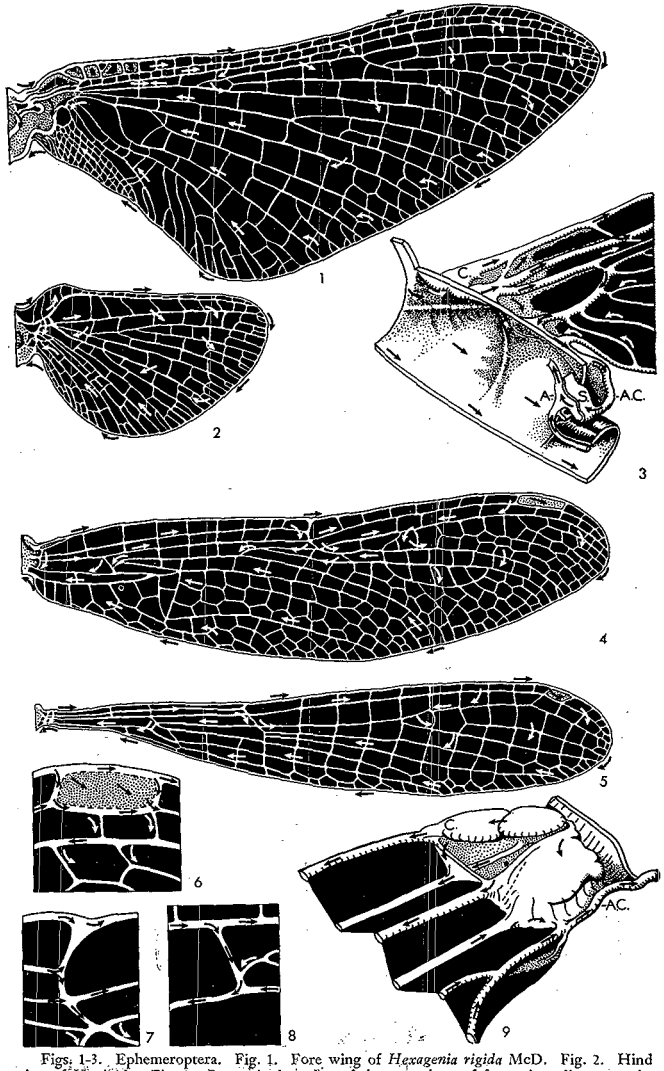
Yeager, J. F. and Hendrickson, G. O. 1933. A simple method of demonstrating blood circulation in the wings and wing-pads of the cockroach, *Periplaneta americana* Linn. *Proc. Soc. exp. Biol. Med.* 30: 858-860.

Yeager, J. F. and G. O. Hendrickson. 1934. Circulation of blood in wings and wing pads of the cockroach, *Periplaneta americana* Linn. *Ann. ent. Soc. Amer.* 27: 257-272.

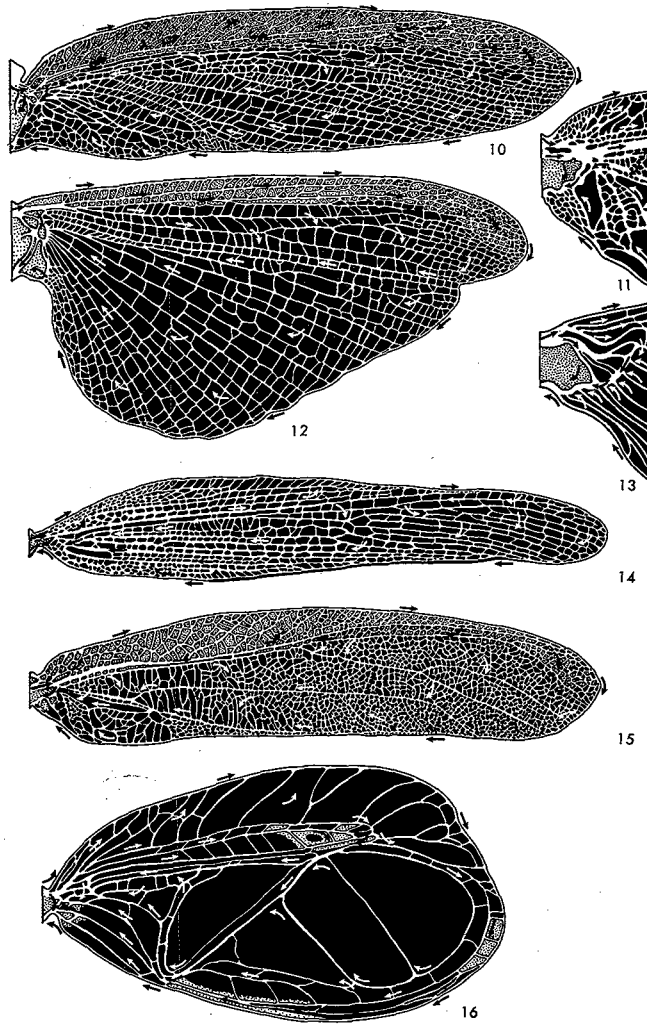
Zeller, H. 1938. Blut and Fettkörper im Flügel der Mehlmotte *Ephestia kühniella* Zeller. *Z. Morph. Ökol. Tiere.* 34: 663-738.

Illustrations

In each figure, arrows indicate the direction of blood flow. Stippled areas within the wings indicate the position of sinuses.

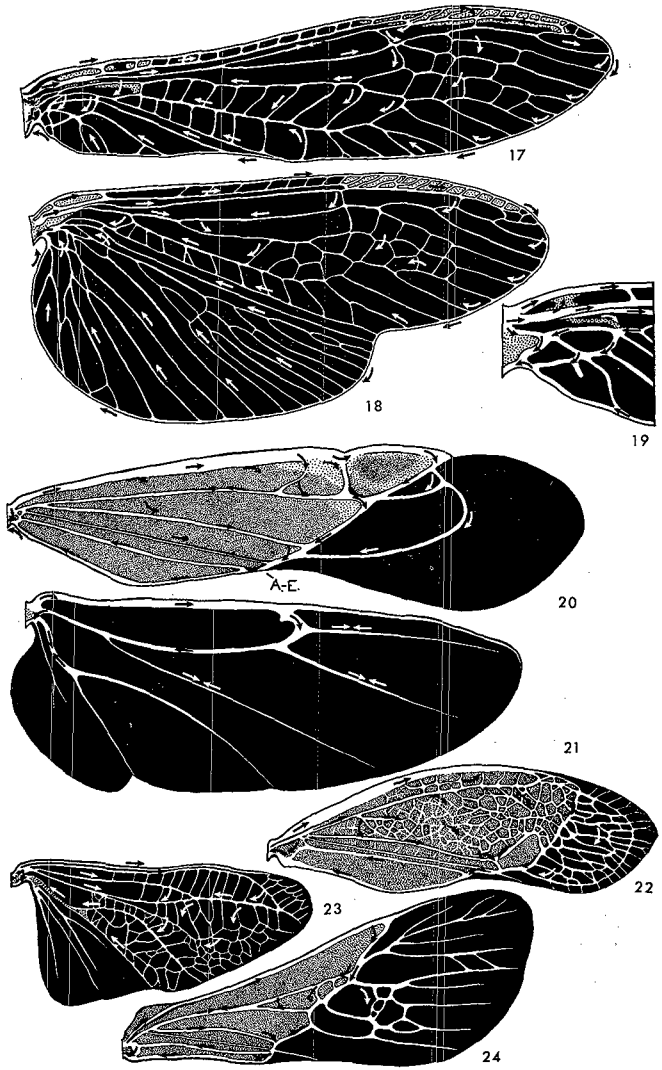


Figs. 1-3. Ephemeroptera. Fig. 1. Fore wing of *Hexagenia rigida* McD. Fig. 2. Hind wing of *H. rigida*. Fig. 3. Parasagittal section of thorax at base of fore wing, diagrammatic. Figs. 4-9. Odonata. Fig. 4. Fore wing of *Sympetrum sp.* Fig. 5. Fore wing of *Lestes unguiculatus* Hagen. Figs. 6, 7, 8. Pterostigma, nodus, and arculus respectively of *Sympetrum sp.* Fig. 9. Postero-dorsal view of wing base of *Sympetrum* sp. (dash-line indicates position of barrier to afferent-efferent flow). Abbreviations: A—aorta; A.C.—axillary cord; C—costa; S—scutellum.



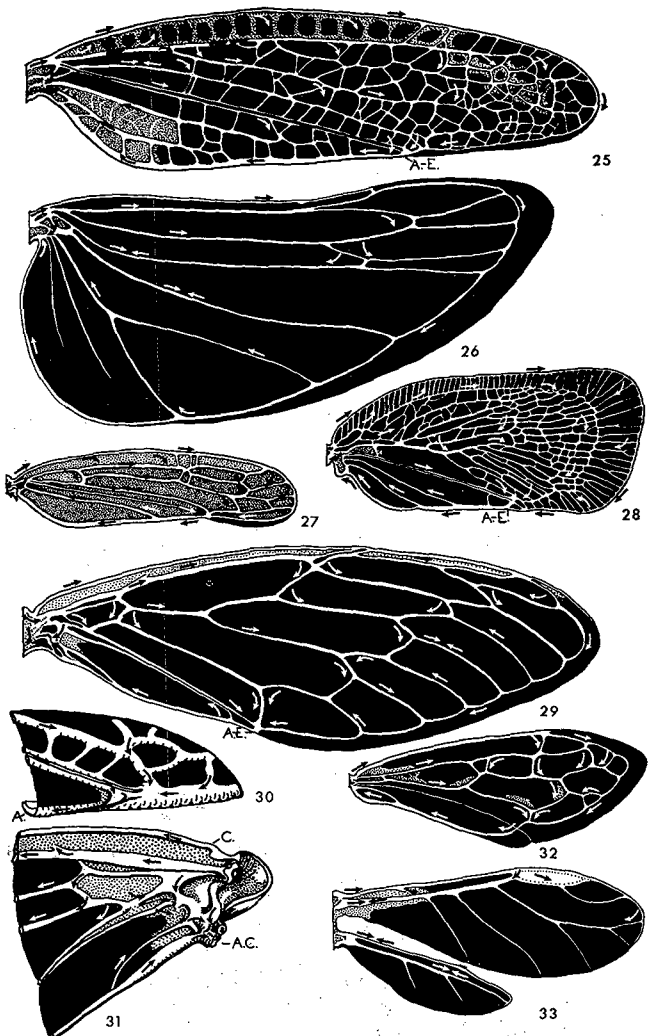
Figs. 10-13. Cursoria (Mantodea). Fig. 10. Fore wing of *Mantis religiosa* Linnaeus. Fig. 11. Base of fore wing of *M. religiosa*. Fig. 12. Hind wing of *M. religiosa*. Fig. 13. Base of hind wing of *M. religiosa*.

Figs. 14-16. Orthoptera (Saltatoria). Fig. 14. Fore wing of *Melanoplus femur-rubrum* (De Geer). Fig. 15. Fore wing of *Scudderia furcata* Brunn. Fig. 16. Fore wing of *Oecanthus* sp.



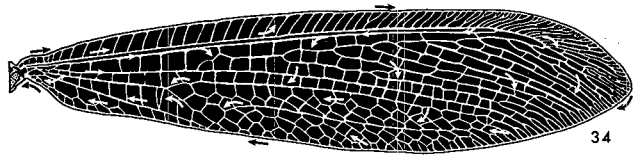
Figs. 17-19. Plecoptera. Fig. 17. Fore wing of *Acroneuria arenosa* Pictet. Fig. 18. Hind wing of *A. arenosa*. Fig. 19. Base of fore wing of *A. arenosa*.

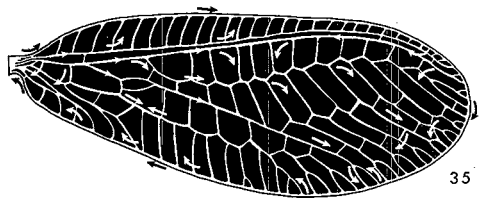
Figs. 20-24. Hemiptera (Heteroptera). Fig. 20. Fore wing of *Adelphocoris lineolatus* (Reuter). Fig. 21. Hind wing of *A. lineolatus*. Fig. 22. Fore wing of *Belostoma fluminea* (Say). Fig. 23. Hind wing of *B. fluminea*. Fig. 24. Fore wing of *Phymata fasciata* (Gray). Abbreviations: A.-E.–point of afferent-efferent exchange.

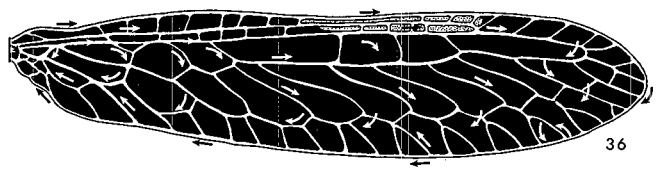


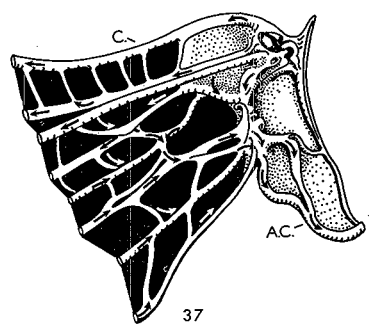
Figs. 25-33. Hemiptera (Homoptera). Fig. 25. Fore wing of *Gyponana* sp. Fig. 26. Hind wing of *Gyponana sp.* Fig. 27. Fore wing of *Graphocephala coccinea* (Forst.). Fig. 28. Fore wing of *Ormenis pruinosa* Stal. Fig. 29. Fore wing of *Okanagana* sp. Fig. 30. Enlargement of area at distal end of anal furrow in *Okanagana* sp. Fig. 31. Ventral view of wing base in *Okanagana* sp. Fig. 32. Fore wing of *Stictocephala faurina* (Harr.). Fig. 33. Wings of *Aphis viburniphila* Patch.

Abbreviations: A.–anal vein; A.C.–axillary cord; C.–costa; A.-E.–point of afferent-efferent exchange.



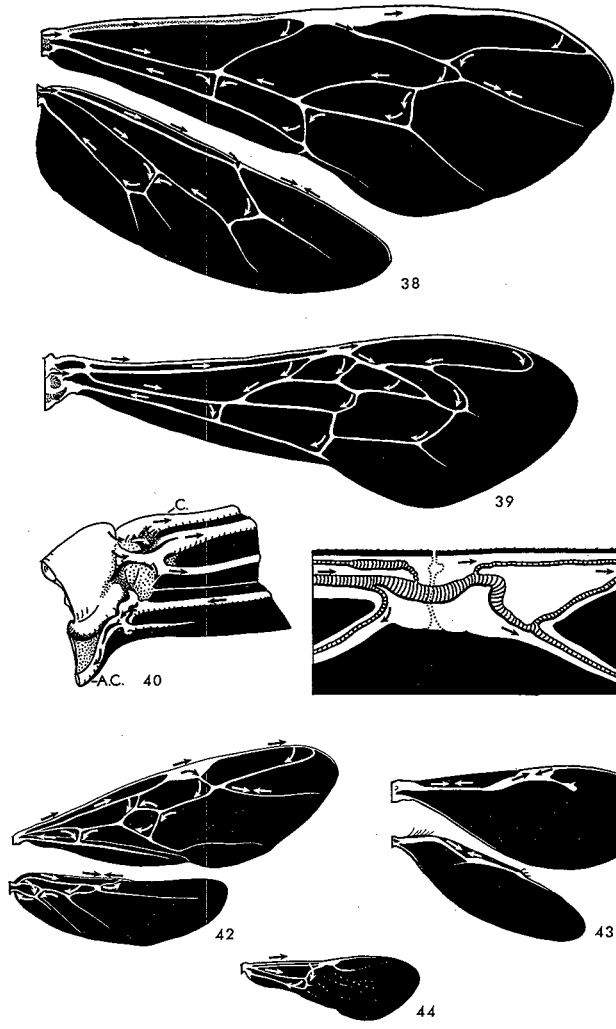






Figs. 34-37. Neuroptera. Fig. 34. Fore wing of *Myrmeleon* sp. Fig. 35. Fore wing of *Chrysopa* sp. Fig. 36. Fore wing of *Mantispa brunnea* Say. Fig. 37. Base of fore wing of *Chrysopa* sp.

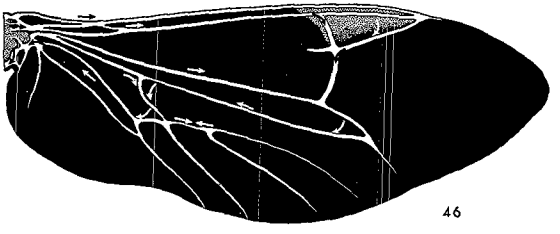
Abbreviations: A.C.–axillary cord; C.–costa.



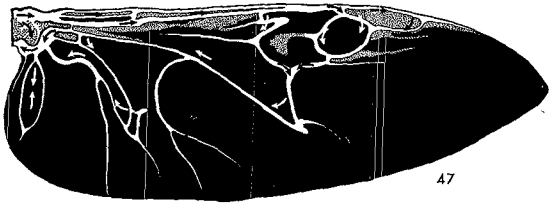
Figs. 38-44. Hymenoptera. Fig. 38. Fore and hind wing of *Mimesa* sp. Fig. 39. Fore wing of *Apis mellifera* Linnaeus. Fig. 40. Dorsal view of base of fore wing of *A. mellifera*. Fig. 41. Pterostigma in *Mimesa* sp. showing contained tracheae, and line of flexion (dotted). Fig. 42. Fore and hind wing of *Lasius* sp. Fig. 43. Fore and hind wing of *Pachyneuron* sp. Fig. 44. Fore wing of *Elampus* sp.

Abbreviations: A.C.–axillary cord; C.–costa.

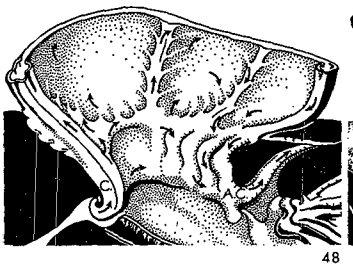
45



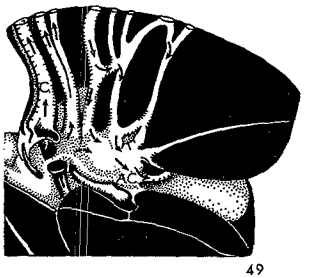
46



47



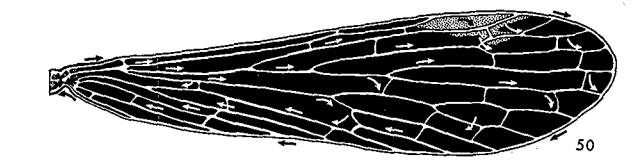
48

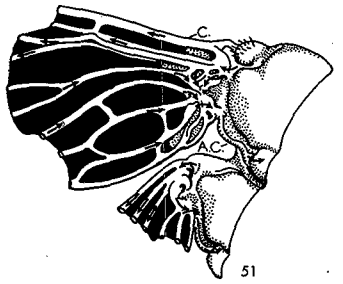


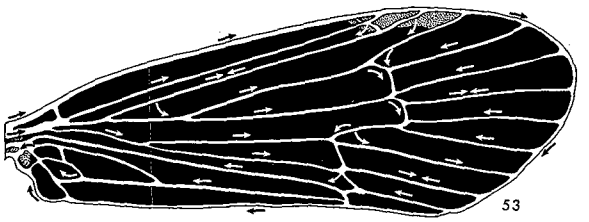
49

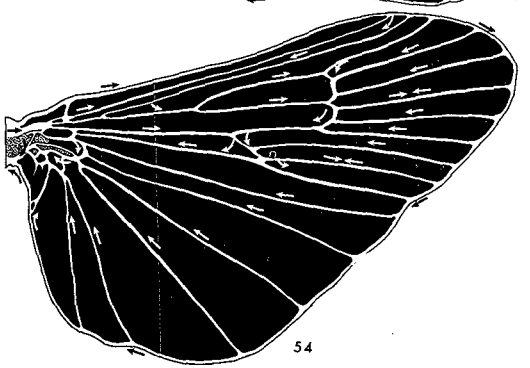
Figs. 45-49. Coleoptera. Fig. 45. Elytron of *Cantharis scitulus* Say. Fig. 46. Hind wing of *C. scitulus*. Fig. 47. Hind wing of *Cicindela punctulata punctulata* Oliv. Fig. 48. Ventral view of base of raised elytron of *Physocnemum brevilineum* Say. Fig. 49. Ventral view of base of raised hind wing of *P. brevilineum*.

Abbreviations: A.C.–axillary cord; C.–costa.



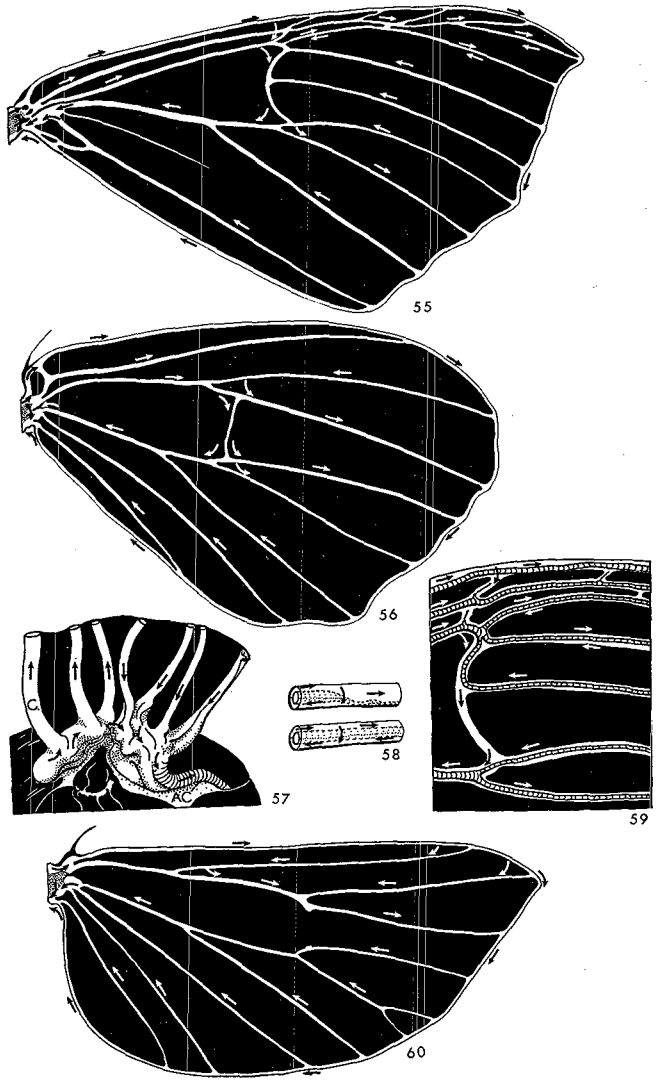






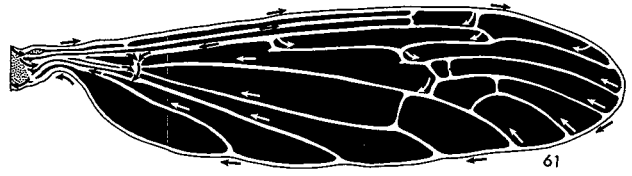
Figs. 50-51. Mecoptera. Fig. 50. Fore wing of *Panorpa* sp. Fig. 51. Dorsal view of wing bases of *Panorpa* sp.

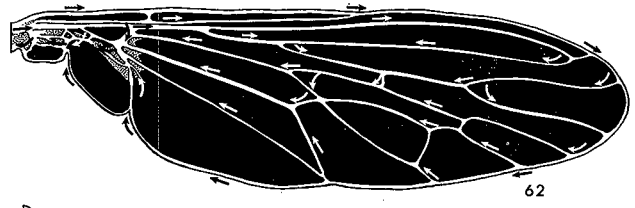
Figs. 52-54. Trichoptera. Fig. 52. Ventral view of base of raised fore wing of *Limnephilus rhombicus* (L.). Fig. 53. Fore wing of *L. rhombicus*. Fig. 54. Hind wing of *L. rhombicus*.

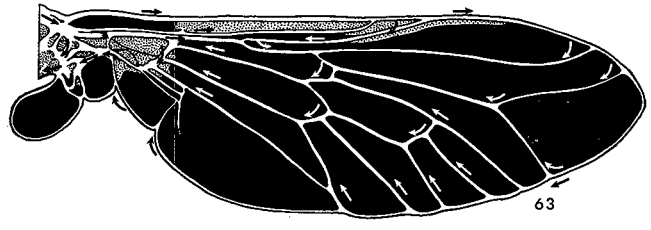


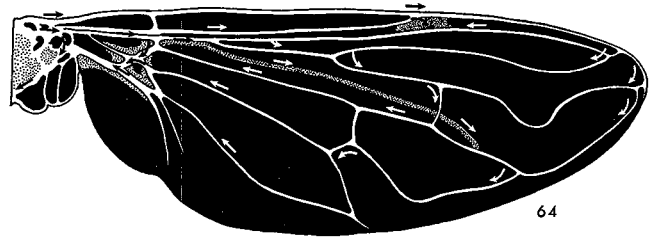
Figs. 55-60. Lepidoptera. Fig. 55. Fore wing of *Prochoerodes transversata* Dru. Fig. 56. Hind wing of *P. transversata*. Fig. 57. Ventral view of base of raised fore wing of *P. transversata*. Fig. 58. Position of tracheae (dotted lines) in wing veins of *P. transversata*, diagrammatic. Fig. 59. Tracheal system in wing veins at distal end of cell R+M in fore wing of *P. transversata*. Fig. 60. Hind wing of *Eucosma* sp.

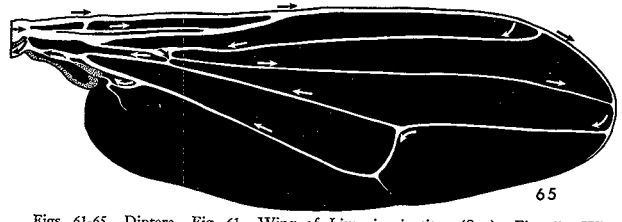
Abbreviations: A.C.–axillary cord; C.–costa.



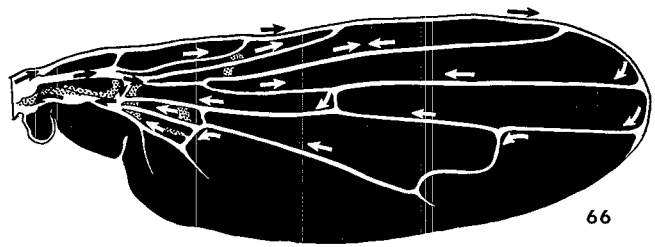


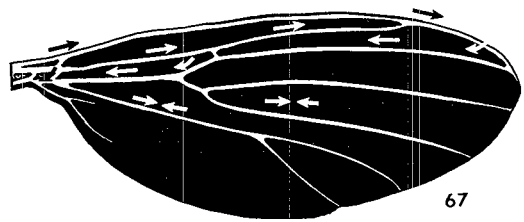


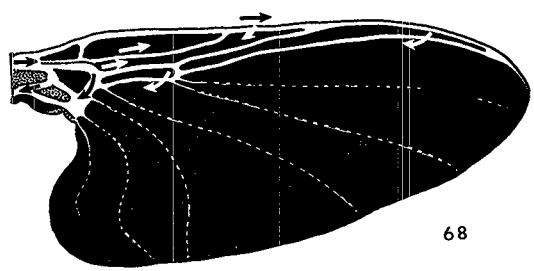




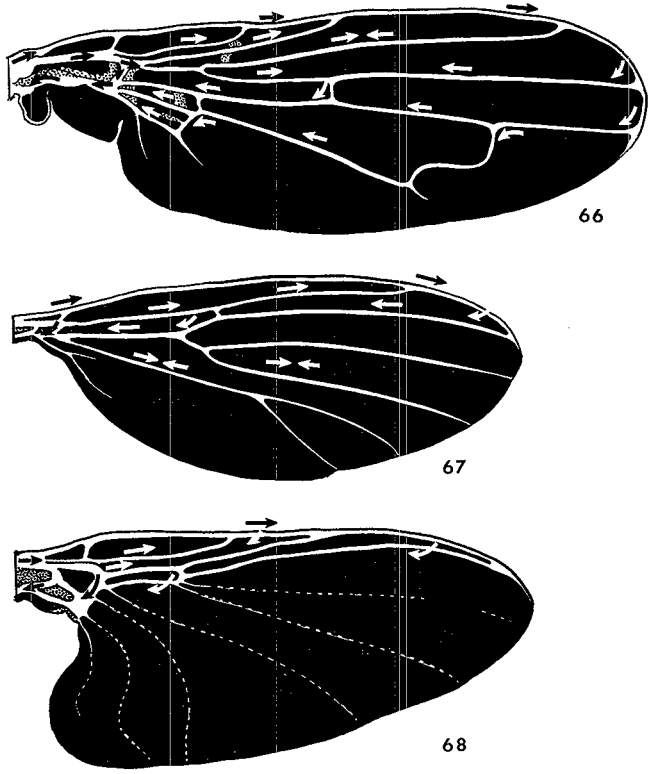
Figs. 61-65. Diptera. Fig. 61. Wing of *Limonia cinctipes* (Say). Fig. 62. Wing of *Asilus paropus* Walk. Fig. 63. Wing of *Tabanus lineola scutellaris* Wlk. Fig. 64. Wing of *Sphaerophoria robusta* Cn. Fig. 65. Wing of *Hydrophorus* sp.







Figs. 66-68. Diptera. Fig. 66. Wing of *Hedroneura rufa* (Panz.). Fig. 67. Wing of *Epicypta* sp. Fig. 68. Wing of *Simulium* sp.



Figs. 66-68. Diptera. Fig. 66. Wing of *Hedroneura rufa* (Panz.). Fig. 67. Wing of *Epicypta* sp. Fig. 68. Wing of *Simulium* sp.

Figs. 69-72. Diptera. Fig. 69. Haltere of *Limonia cinctipes* (Say). Fig. 70. Postero-dorsal view of wing base of *L. cinctipes*. Fig. 71. Postero-dorsal view of wing base of *Tabanus lineola scutellaris* Wlk. Fig. 72. Postero-dorsal view of wing base of *Musca domestica* L.

Abbreviations: A.C.–axillary cord; AM.–ambient costa; AR.–arculus; C.–costa; S.–scutellum.

LIST OF THE CANADIAN ENTOMOLOGIST SUPPLEMENTS

Volume	*No.*	*Date Printed in the Issue Itself*	*Actual Date of Issue*	*Authority*[1]	*Author*
(87) LXXXVII	Supp. 1	1955	30 Mar. 1955	WRT	Maxwell
(88) LXXXVIII	Supp. 1	Mailed 23 Nov. 1956	10 Dec. 1956	WRT	Becker
(88) LXXXVIII	Supp. 2	1956	16 Jan. 1957	WRT	Beirne
(88) LXXXVIII	Supp. 3	1956	2 Jan. 1957	Lib	Brown

After this issue the "Supplements" became, in fact, a self-contained series with a continuous numbering system independent of The Canadian Entomologist. Nevertheless, they were still issued (with later exceptions) as "Accompanying" volumes of The Canadian Entomologist.

Because 4 Supplements had already been published, the next one was called No. 5. Supplement No. 4 was never published.

No.	*"Accompanies Volume"*	*Date Printed in the Issue Itself*	*Actual Date of Issue*	*Authority*[1]	*Author*
5	89	1957	2 Dec. 1957	Lib	Thomas
6	90	1958	8 Apr. 1958	WRT	Hardwick
7	90	1958	28 Apr. 1958	Lib	Freeman
8	90	1958	12 Sep. 1958	Lib	McGuffin
9	90	1958	14 Nov. 1958	EGM	Brooks
10	91	1959	26 Mar. 1959	Lib	MacKay
11	91	1959	26 Mar. 1959	Lib	Kelton
12	91	1959	15 June 1959	Lib	Chant
13	92	1960	14 Nov. 1960	Lib	Richards
14	92	Mailed 17 Feb. 1961	16 Mar. 1961	Lib	Chillcott
15	92	Mailed 27 Jan. 1961	1 Feb. 1961	WM	Heinrich I[2]
16	92	Mailed 10 Jan. 1961	11 Jan. 1961	Lib	Freeman
17	no date or volume number		25 Oct. 1961	Lib	Munroe
18	92	Mailed 24 Mar. 1961	4 Apr. 1961	WM	Heinrich II[2]
19	93	Mailed 24 Feb. 1961	4 Apr. 1961	Lib	Watt
20	92	Mailed 24 Mar. 1961	6 Apr. 1961	Lib	Brooks
21	93	1961	13 Sep. 1961	Lib, WM	Heinrich III[2]
22	93	Mailed 12 Apr. 1961	29 May 1961	Lib	Miller
23	none	1961	21 Dec. 1961	WM	Heinrich IV[2]
24	none	1961	27 Dec. 1961	Lib, WM	Munroe
25	none	1961	28 Dec. 1961	Lib, WM	Howden
26	no date or volume number		19 Feb. 1962	WM	Heinrich V[2]
27	none	1962	20 Sep. 1962	Lib, WM	Heinrich VI[2]
28	none	1962	6 Nov. 1962	WM	MacKay
29	none	1962	27 Nov. 1962	WM	Heinrich VII[2]
30	none	1963	1 May 1963	WM	Peck

After Supplement 30, the series continued under the title "Memoirs of the Entomological Society of Canada".

MEMOIRS OF THE ENTOMOLOGICAL SOCIETY OF CANADA

31	—	1963	21 May 1963	WM	Morris *et al*
32	—	1963	4 June 1963	WM	LeRoux *et al*
33	—	1964	19 Mar. 1964	WM	Munroe
34	—	1964	1 Apr. 1964	WM	Peck *et al*
35	—	1964	14 May 1964	WM	Peck[2]

[1]The following are the authorities upon which the actual dates of issue are based:
WRT — log book of former editor W. R. Thompson
EGM — log book of former editor E. G. Munroe
WM — log book of present editor W. R. M. Mason
Lib — date stamp of the Library of the Entomology Research Institute, Ottawa

[2]The seven parts of Mr. Heinrich's *Revision of Ichneumoninae*.... and Part VIII (Indices, addenda and corrigenda) by O. Peck have consecutive pagination and are intended to be bound as a single book.

025026

Blood Circulation in Insect Wings

by

JOHN W. ARNOLD
Entomology Research Institute
Research Branch, Canada Department of Agriculture
Ottawa, Ontario.

Memoirs
of the
Entomological Society of Canada

No. 38, 1964

CONTENTS

PAGE

Introduction 5

Historical Review 6

Methods 7

Observations and Discussion 10

Features of wing circulation in insect orders 10

Ephemeroptera 10

Odonata 11

The orthopteroid complex 13

Cursoria 13

Orthoptera 15

Plecoptera 17

Hemiptera 18

Heteroptera 19

Homoptera 20

Neuroptera 22

Hymenoptera 23

Coleoptera 25

Mecoptera 27

Trichoptera 28

Lepidoptera 30

Diptera 32

Discussion and Conclusions 35

Acknowledgments 41

Appendix (list of insects) 42

References 46

Illustrations 48

Blood Circulation in Insect Wings

By JOHN W. ARNOLD

Entomology Research Institute
Research Branch, Canada Department of Agriculture
Ottawa, Ontario.

INTRODUCTION

It has long been known that blood circulates in the wings of insects. Apparently the phenomenon was reported first by Baker (1744) who observed it in the wings of a grasshopper. Since then it has been reported for numerous species in several orders and there is now little doubt that it occurs to some degree in all winged insects. It is true for definitive wings as well as for developing ones, and for modified wings such as tegmina, elytra, hemelytra, and halteres as well as for those that are specialized for flight.

The route and mechanism of blood circulation in the wings are understood in broad outline and are fundamentally alike in all species and in all forms of wings. In general, blood from the lateral intermuscular spaces of the thorax enters a wing at the humeral angle, flows distally to the wing apex through the large anterior veins and moves en route through cross veins toward the posterior margin. It returns to the body via posterior veins and empties into the pericardial sinus or the dorsal vessel by way of the axillary cord which extends from the anal angle of the wing to the scutellar region of the thorax. It is believed that the blood is propelled along this route by a combination of forces which include the aspirating action of subscutellar pulsatile organs, the pressure of blood flowing posteriorly from the head past the wing bases, the influence of respiratory and other movements, and in some insects the action of pulsatile structures within the wing itself. Nevertheless, the circulatory routes in the wings are as different in detail as the wing venation, and the forces involved in wing circulation differ in their relative importance in conjunction with structural features of the wings and of the insect.

Despite their inert appearance, the wings of insects are living evaginations of the meso- and metathoracic body wall. In this sense, and quite literally during wing development, the dorsal and ventral walls are structural duplicates of the body wall and contain between them blood, tracheae, and nerves. The definitive wings of the adult insect are of course modified by union of the two walls over much of their area so that the original condition is retained only along the veins. The latter are essentially remnants of the body haemocoel. Even here the inner layers of the original body wall, the epidermis and basement membrane, are sometimes much reduced or absent and the cuticle is thickened. The permanently appressed areas between the veins, i.e., areas of the wing membrane, appear to be entirely cuticular. However, tracheae and nerves pass through some of them and it seems likely that the union of the two walls is not always complete and may permit a slow percolation of haemolymph. Wings become dry and brittle in areas where blood circulation has ceased, and it seems evident that some exchange of materials is necessary in the wing membrane to maintain the resilience of the wing. In the main, however, tracheae and nerves lie within the wing veins and it is here also that an active circulation of blood occurs.

In view of the unique development of insect wings for flight and their modifications for functions other than flight, for example to protect, camouflage, and display, the necessity for nourishing them with a continuous supply of blood seems obvious. This requirement is also evident from a consideration of the

known and suspected physiological roles of the wings. In some insects the wings are, for example, sites of metabolic activity. This involves particularly the formation of pigments which, as in the case of the pteridines in developing wings of Lepidoptera, have fundamental roles in body metabolism. They also support numbers of sensillae which are concentrated mainly along the veins; the nerves which serve them lie within the veins. In some insects the wings are known to absorb radiant energy from the environment and transfer it to the body, presumably via the blood. In this way the internal temperature is raised in preparation for flight. A period of wing movement may precede flight for the same reason. It is logical to assume that the reverse is also true and that heat developed internally from the action of flight muscles can be dissipated by blood flowing from the thorax through the wings. This possibility is unproven and apparently was not entirely explored by Church (1960) in his excellent study of heat loss in insects. In the same way it is conceivable that waste metabolites from flight muscle action are removed rapidly from the thorax by blood flowing into the wings and may be removed from the blood in wing sinuses and deposited there in some form. Again, and contrary to some evidence, it may be suggested that the wings in some insects have at least a small respiratory function. Some contain an extensive tracheal system with loops of tracheoles suspended in the blood, particularly in sinuses near the wing bases. Finally, the existence of blood sinuses in the wings of many insects and the concentration within them of haemocytes and pigments emphasizes the suggestion of metabolic activity there and implies a role as a storage vehicle for haemocytes and as a site for their differentiation or destruction.

Flight is such a highly developed attribute of insects and is achieved in such a unique manner that each facet of its mechanism warrants study. The present work is a study of blood circulation within the wings. It attempts to compile existing information on the subject, presents circulation maps for the wings in representative species in the major insect orders, and as far as possible within the context demonstrates the mechanisms involved in wing circulation.

Historical Review

Despite the obvious need for blood to circulate in the wings as in the other appendages, and the existence of numerous publications on the subject, the fact of blood circulation in the wings is still not generally appreciated. References to the dry and lifeless nature of the insect wing can be found in recent publications and this impression is not an uncommon one. There has been a long history of doubt concerning not only circulation in the wings but of blood circulation in any form in insects. This doubt seems to have stemmed in the past from a failure to conceive of the idea of an open circulatory system and a reluctance to accept it when presented. Some of the great anatomists of the 18th and 19th centuries searched for veins and arteries in insects. Their failure to find them convinced many scholars of that era that the blood did not circulate and that the dorsal vessel, which was recognized by some as a pumping organ, had other roles. Almost one hundred years after Baker's (1744) observations on circulation in the wings were published and his further notes (1755) on pulsation of the dorsal vessel and leg hearts were recorded, James Rennie (1832), professor at King's College, London, stated "there is not, and cannot be, any real or direct circulation of blood in insects". In stating this he was knowingly refuting the several publications of Carus (1827, 1828, 1831), one of which (1831) includes the still acceptable "Carus rule" concerning the route of circulation in the insect wing. Strangely enough, Rennie's statement was not entirely unrealistic, for William Orr (1833) in reviewing Rennie's book and in quoting the statement, commented

that until lately blood circulation in insects had been considered very doubtful. In the same year Bowerbank (1833) published some general observations on blood circulation in insects including a note that he had observed blood flowing in the wing veins of *Phlogophora meticulosa.* Later (1836) he published a detailed account of circulation in the wings of *Chrysopa perla* and there is little doubt that his observations were considered by active entomologists of the day to be new discoveries. This opinion was also expressed by Tyrrel (1835) in his account of circulation in insects.

In the decade around 1830 the concept of a true blood circulation in insects was gaining general acceptance. The literature contains a variety of observations by authors such as Behn (1835), Bowerbank (1833, 1836), Burmeister (1832), Carus (1827, 1828, 1831), Duvernoy (1839), Newport (1837), Treviranus (1831), Tyrrel (1835), and Wagner (1832). Among these reports are several that record observations of circulation in the wings. Bowerbank noted it in the two insects mentioned previously. Carus detected it in the elytra, in the hind wings, or both, of a number of insects including *Semblis viridis, Eristalis apiformis, Lampyris noctiluca, Lycus sanguineus, Melolontha Frichii, Dermestes lardarius, Chrysomela menthae,* and some unnamed ephemerids and beetles. He also reported that a Professor Gruithuisen of Munich had previously (1812) observed wing circulation in *Gryllus viridissimus* and other insects. Charbrier, according to Kirby and Spence (1826), thought that insects were able to propel a fluid into and withdraw it from their wing nervures as the wings became elevated or depressed. Duvernoy merely reported that blood enters the wing veins. Ehrenberg and Hemprich, according to Verloren (1847), observed circulation in the wings of a *Mantis.* Göring and Pritchard (Verloren 1847) reported it for the elytra of *Dytiscus* and in the wings of *Semblis bilineata* and *Perla viridis.* Tyrrel saw it in species of *Hemerobius, Panorpa, Phryganea, Ephemera,* and in *Musca domesticus.* It is surprising then to find that Dufour (1841) vigorously challenged the whole concept of blood circulation in insects and supported his view by reference to the works of Cuvier, Malpighi, Swammerdam and some of the other great anatomists. In turn, Dufour's stand was assailed by Verloren (1847) who refuted the claim of support from those savants, tabled 90 species of insects and the regions within them in which blood circulation had been observed by 17 different authors, and presented a lucid account of the open system of blood circulation. Verloren's paper provides much information on the whole subject as it was understood at that time and a wealth of early references.

Although Verloren's outburst must have convinced most scholars of the efficacy of open blood circulation in insects, it apparently escaped the notice of some subsequent workers. There was still some tendency to believe in the existence of blood vessels and to try to relate blood circulation and respiration. Thus Agassiz (1851), Bassi (1851), and Blanchard (1851) became involved in exploring the possibility that certain tracheae served as blood conduits. On the other hand authors such as Moseley (1871), and Nicolet (1847) reported their observations on circulation in the wings as though the idea was not uncommon. During the last half of the 19th century interest in the subject seemed to lapse, except intermittently, and was revived early in the present century by workers such as Pawlowa and Brocher who were concerned with the mechanism of circulation. The work of authors in this recent period will be discussed in the text in conjunction with specific insect groups.

Methods

The wings of most insects are clear enough that blood circulation may be seen with the compound microscope at magnifications sufficient to reveal the

haemocytes. Sometimes the general course of blood circulation can be determined without resorting to special techniques. However, relatively few of them are clear enough for detailed observation under high magnification without some manipulation. Generally the vein walls are thick, sculptured, pigmented, or clothed in a variety of bristles or scales. In the case of modified wings such as elytra they are often heavily sclerotized and sculptured and frequently too contoured and inflexible for easy examination. Where the normal haemocyte complement in the blood is low, as in many species of Diptera for example, the complete course of flow can be determined only through long observation. The same is true for insects in which the lumens of the wing veins are narrow or the wing base is so constructed that entrance of haemocytes is limited. This is common in the hind wings of Coleoptera and Hemiptera. Positioning the wings in an unnatural fashion, or merely confining the insect for observation, in some cases causes erratic or reduced wing circulation. Nevertheless, careful examination of a number of individuals of each species will reveal routes of circulation that are acceptable as normal for the resting insect.

The methods used to observe circulation directly were relatively simple and similar to those described previously (Arnold 1959). For general scrutiny the insect was usually inverted on a glass slide and the wings were spread at a natural angle that did not interfere with normal circulation. Glass coverslips of suitable size were applied to the wings and a drop of water, to which a trace of detergent had been added, was led beneath. The wings were thus sandwiched in water between glass, and the insect's body was unrestrained and free from contact with the water. The water tension alone was sufficient to hold most insects in the inverted position and there was no evidence that circulation was affected adversely. Some of the large and active species required additional means of restraint. This was accomplished usually by stretching elastics across the body to hold the insect without undue pressure. The layer of water wetted the wing surfaces and greatly increased the clarity. Immersion oil was equally effective but tended to creep onto the insect's body. It was used to advantage only with Lepidoptera where the water mounts were unsatisfactory. Correct positioning of the insect was important and usually required the use of carbon dioxide as an anaesthetic. This frequently caused a temporary cessation of heartbeat and of circulation in the wings followed immediately on recovery by abnormally high rates of flow and erratic circulation including reversal in direction. Although this reaction was often troublesome it did nevertheless demonstrate forces involved in circulation by temporarily eliminating all or some of them and revealing them as they became reestablished in sequence and in an exaggerated condition. It also made it necessary to delay observations of the normal circulatory route until a steady pattern of flow returned. The method of Yeager and Hendrickson (1933) for examining circulation with light reflected from a white surface placed beneath the wing was found to be awkward with many species and was seldom employed.

To observe the action of the heart and pulsatile organs in relation to circulation in the wings, the insect had to be held in an upright position with the wings spread. This was accomplished by using a glass apparatus designed to accommodate the insects in this position. Standard microscope slides were fixed with transparent glue to the surface of a large glass slide in the form of an insect spreading board. The standard slides formed the supports for the wings and were separated by a space just large enough to contain the insect's body. A number of these were prepared in a variety of sizes to conform to the width and depth of the body for various species. The insects were handled as described above with the wings again held in position mainly by coverslips and water.

When necessary, the insect was further restrained by small blocks inserted before and behind it in the channel that contained the body.

Observations were made with a Leitz Ortholux microscope equipped with an Ultropak incident light illuminator. Both transmitted and reflected light were used, the choice depending entirely on the effectiveness of the illumination for the particular insect under observation. The Ultropak was employed mainly because the lenses with the aperture most commonly employed had a long working distance and were suitable for observing large insects and those with thick or contoured wings. Coloured filters were used as required to aid in detecting the moving haemocytes which in some insects are quite hyaline. It was also found useful to vary the position of the substage condenser and its magnifying lens for the same reason. In general, phase contrast was not useful because of the short working distance that its lenses allow and the confusing visual effects created by sculptured wing surfaces.

In an effort to determine the causes of circulation in the wings and of its variability within individual insects and between species, counts were made of various movements and pulsations that might be involved. These were visual counts, using a mechanical counter and timer, and included the heart-beat at different regions of the body, contractions of accessory pulsatile structures, waves of peristalsis in the thorax and abdomen, respiratory movements, and pulsations of the blood when evident at different regions in the wings. For the same reason and also to determine whether certain veins regulated the direction of blood flow within the wings, individual veins were severed in some species and the resultant course recorded. The veins were severed with a micro-scalpel with the wing held only at the apex.

For the most part the insects used were newly obtained in the field by sweeping with a net or by collection at lights. They were examined as soon as possible after collection. Where an appreciable delay in examination was unavoidable, the insects were held in screen cages in the presence of water. Whenever possible several specimens of each species were collected and examined to appreciate variations in the circulatory route, obtain an average of pulse rates, and to provide specimens for identification and the preparation of permanent wing mounts. Some were also used for dissection and for sectioning by standard histological methods. Generally the age of the insects was unknown, but those that showed signs of senescence were not used in the main studies. A few species were reared in the laboratory or obtained at the time of adult emergence and served to determine the effects of age on circulation. A number of insect orders are of course not considered in the present work. Some of them may be of special interest and it is hoped that future studies will include them.

The permanent whole mounts of wings were used to prepare the illustrations of wing venation by direct projection-tracing with a photographic enlarger. The illustrations incorporate details which are only recognizable in the living wings, such as the position of sinuses, from sketches made at the time of observation.

The vein nomenclature and general wing terminology used here is mainly that of Comstock (1918). His treatise seems to be the most extensive and generally accepted one on the subject of venation. Some use is also made of terms from Snodgrass (1935) and reference is made to taxonomic studies for particular insect groups. Ross' (1956) taxonomic grouping of insects at the order level is adhered to. The terms "afferent" and "efferent" concerning the direction of blood flow are used here as they are by Clare and Tauber (1940) to conform with their meaning in vertebrate studies: "afferent" refers to flow toward the distal part of the appendage; "efferent" refers to flow from the appendage toward the body.

Observations and Discussion

Although certain features of wing circulation vary considerably among the insects, and are reported hereafter for several orders, a basic route of circulation tends to be stable throughout the class and the mechanism of circulation is usually the same. At the risk of being repetitious, it seems useful to summarize the common or generalized features of circulation before describing characteristics peculiar to the phenomenon in different groups of insects. In this way some clarity may be contributed to the text.

In general, the anterior basic wing veins, costa, subcosta, radius, and media are afferent channels for the blood, and the posterior basic wing veins, the cubito-anal group, are efferent. Cross-veins anterior to the radius usually carry blood toward the costal margin and the others carry it posteriorly. In other words, blood flows from the insect body toward the wing apex through longitudinal veins in the anterior portion of the wings, moves posteriorly through cross-veins, and returns to the body through longitudinal veins in the posterior region of the wings; it re-enters the body via the axillary cord. This route will be referred to in the text as the basic pattern or basic route of circulation. Some of the blood that enters the wings avoids this route by flowing immediately to the axillary cord through the wing base or in cross-veins just beyond the base.

Also in general, two forces cooperate to cause the circulation of blood in the wings. A propulsive force, created mainly by the heart, pushes blood into the anterior portion of the wings through an opening near the humeral angle, and an aspiratory force draws blood out of the wings through the axillary cord. The aspiratory force is attributable mainly to accessory pulsatile organs that lie beneath the scutellum in the thorax. The two forces are not well coordinated, however, and the system is influenced continuously and may be intermittently dominated by pressure changes within the body; as parts of the haemocoel, the wing veins are subject to whatever fluctuations in pressure occur in the body as a result of respiratory or other movements.

Features of Wing Circulation in Insect Orders

Order: Ephemeroptera

The mayflies have long been favourite insects for the demonstration of blood circulation because of the transparency of their cuticle. Much of the published work deals entirely with the larvae, and the few papers that do include observations on the adults refer to wing circulation only in a general way. Such is the case, for example, in the previously mentioned early papers of Carus and of Tyrrel. Similarly, Drenkelfort (1910) noted circulating blood in cubital veins and suggested that meso- and metathoracic heart diverticula were somehow involved in wing circulation. Other authors referred to special features of ephemerid wing circulation without describing the system as a whole.

Materials

Species from several genera were examined but detailed studies of wing circulation were limited to *Hexagenia rigida* McD. and of an unidentified species of *Stenonema*. Consistent with the slight differences in venation, the circulatory route and features of circulation were basically alike in the fore and hind wings of individuals and in the various species examined. Circulation was always more vigorous in the fore than in the hind wings.

Observations and Discussion

The irregularity of circulation was a feature in the wings of all individuals of the species examined. It received comment from other authors as well.

Bervoets (1913) observed the passage of blood cells in the subcosta and radius and mentioned the intermittent refluxing of the blood there and the pulsations caused by heart systole. He suggested that blood circulated through the wings but that much of it returned to the body by the same route it entered. Meyer (1931) commented similarly but he also described the aspiration of blood from the wings by thoracic pulsatile organs to complete a regular circuit.

The irregularity of circulation occurred as an intermittent gushing of blood into and out of the wings and periodically as a complete and steady reversal of the normal direction of flow. It was true for adults of different age, for anaesthetized and for untreated individuals, for restrained and for unrestrained ones, and for those with the wings spread or with the wings held vertically in the normal resting position. There is little doubt that it is a normal occurrence which reflects unusual structural features at the junction of the wing base with the thorax, the pliable nature of the body wall, or perhaps a lack of efficiency on the part of the thoracic pulsatile organs. One might suspect that the development of wing tracheae from a single trunk in Ephemeroptera (Chapman 1918; Whitten 1962) rather than from two trunks as in other insects is somehow involved. Also in these primitive insects the wings are not flexed at rest but are held vertically above the body. The articular areas, especially the axillary sclerites are less well-defined than in wing-folding insects and less obstructive to blood movement. The wing bases are relatively open sinuses which connect broadly to the thorax (Fig. 3) and are especially subject to pressure changes within the body.

Despite the variability of wing circulation a basic circulatory route does occur (Figs. 1, 2 and 3). It is the course frequently followed by the blood when respiratory movements and heart activity are slow and steady. The costa, subcosta and radius are the principal afferent veins. The extensive sinuses at the wing bases and the prominent radio-medial cross-vein influence the flow in the media which tends to be efferent along with the cubital and anal veins. Some alternation in the direction of flow occurs in successive distal branches of the afferent veins but is not a dependable feature.

Order: Odonata

Although blood circulation in the developing wings of naiads of Odonata has been reported by a number of authors, scarcely any reference is made to circulation in the wings of adults. Carus (1831) noted circulation in the wings of newly-emerged adults of *Libellula depressa* and Bervoets (1913) reported that blood flowed from the cut extremities of the wings of a dragonfly. Otherwise, even among authors who worked almost exclusively with Odonata, the opinion was held that the adult wings were devoid of blood. Tillyard (1917) mentioned the remnant of blood sinus around the wing tracheae but did not suggest an active circulation of blood therein. Indeed the thought was discouraged by a subsequent statement that the tracheae withdrew from the wing and shrivelled up at metamorphosis. More recently Whedon (1938) described the meso- and metathoracic aortic diverticula in nymphs and adults of aeschnids and libellulids. He described their function of aspirating blood from the nymphal wings and from the basal sinuses of the adult wings but he considered that the adult wing distal to its thoracic junction was bloodless.

The impression of a bloodless condition in odonatan wings is not entirely surprising. Although the wings are transparent the veins are thick-walled and frequently pigmented. The lumens of the veins are narrow and to some extent limit the passage of the haemocytes, which is usually the most obvious visual evidence of circulation. Nevertheless a comparatively strong and regular circulation occurs throughout the wings and follows a relatively constant route. It

is quite different from the situation in Ephemeroptera, despite the primitive position of the group, and reflects the great differences in the structure of the thorax and wing bases as well as of the wings themselves.

Materials

A number of species were examined from five genera, mainly from *Cordulia* in the Anisoptera and from *Lestes* in the Zygoptera (see Appendix). There were no major differences in wing circulation among the species or between the fore and hind wings of individuals.

Observations and Discussion

The wings of Odonata, like those of the Ephemeroptera, are not flexed at rest but the wing bases are dissimilar in the two groups. The significant differences in blood circulation include the presence in Odonata of one true axillary sclerite (Snodgrass 1935) and of a thin cuticular wall which partially separates the afferent and efferent portions of the bases (Fig. 9). These structures limit the posterior flow of blood through the bases and direct it mainly outwards into the veins. They undoubtedly contribute to the strong and comparatively steady circulation in the wings. Some blood moves posteriorly in the wing bases but mainly in close proximity to the thoracic wall and in the adjacent cross-veins which form a structural part of the bases.

Comstock (1918) pointed out the uniqueness of odonatan wing venation and particularly of what he termed the invasion of the area of the radial sector by one or more branches of the media. Whether or not his interpretation of the vein homologies is correct, the venation in this area is unique and one might expect to find commensurate changes in the circulatory route. This however is not the case and the route of circulation (Figs. 4 and 5) is not significantly different from the basic route in most insects. It seems clear that the position of the veins and not their origin is the governing principle in establishing the circulatory route. Unusual conditions occur mainly at the nodus, the arculus, and the stigma.

The nodus, which is essentially a prominent cross-vein situated midway along the wing and joining the afferent veins, is peculiar to the odonatan wing and is significant in blood circulation. It diverts a portion of the blood from the afferent into the efferent streams and thereby provides a short route for the blood through the wings. In the antenodal region the route is typical and blood flows afferently in the costa, subcosta, and in the combined radius-media. Postnodally the route is also typical but it is accomplished via veins that occupy unusual positions according to Comstock's view. There the costa continues to support an afferent current which hesitates only slightly as it crosses the nodus. The subcosta terminates at the nodus. Blood that issues from it into the nodus separates into two streams (Fig. 7), one deflecting anteriorly to join the postnodal current in the costa and the other posteriorly to join the stream in radius-one. Radius-one reportedly occupies the position usually held by the subcosta in this region and assumes its function of carrying blood afferently. Similarly, media-one in its new position tends to accept the normal role of radius-one and is usually efferent. The short radius-media probably carries the greatest volume of blood afferently but part of it is deflected almost immediately into the arculus and the remainder continues in the radius to the nodus. Here its stream again divides, part of it crossing the nodus and proceeding afferently in radius-one, and the remainder moving posteriorly in the subnodus to join the efferent stream in media-one.

Structurally the arculus appears to be a cross-vein that extends from the radius to the cubitus near the wing base; the media appears to extend from it. The arculus is a constant feature in the odonatan wing, it occurs also in some other

groups and is significant in wing circulation wherever it occurs. In addition to diverting blood from the radius or radius-media (Fig. 8) it accepts efferent streams from the medial veins and from the radial sector. The radial sector here is a functional part of the medial system and is efferent. The arculus empties into the cubito-anal veins which unite in the axillary cord and like the nodus, provides a short route through which the blood may return quickly to the body and avoid the distal veins. The nodus and arculus together, because of their position and configuration, may be responsible for the noticeable reduction in the strength of the blood current in the wing extremities and for the tendency for those areas to become dry and to fragment in the late stages of adult life.

The pterostigma (Fig. 6) which joins the costa and radius-one near the wing apex is a constant feature in most species of Odonata and occurs in certain other orders. It is a box-like sinus which accepts blood from the surrounding veins but does not significantly alter the course of circulation. Its structure and possible origin and significance have already been discussed (Arnold 1963).

The Orthopteroid Complex

The taxonomic composition of the Orthopteroid complex is highly controversial and little help in resolving the arguments is gained from a consideration of blood circulation within the group. Although basic similarities exist in wing structure and in circulation in the wings in each of the component orders, there are also unique features in some of them and a general diversity in details of circulation, especially in the fore-wings. The main similarities do not usually extend above the suborder level and some distinctions occur at lower levels. As a result, the complex cannot be discussed readily as a unit.

By chance, the portions of the complex reported upon here, Cursoria (Blattaria and Mantodea) and Orthoptera (Saltatoria), have the fore-wings modified as tegmina. The orders Isoptera, Dermaptera, and Embioptera, along with the suborders Phasmida and Grylloblattodea usually included in the complex, were not studied. In some of them the fore-wings are not tegmina and should prove interesting from a comparative viewpoint.

Order: Cursoria

Suborder: *Blattaria*

Circulation in the wings has been studied more extensively in orthopteroids than in any other group of insects, and species from the suborder Blattaria have served for the bulk of experimental work in this field. The blattids are especially suitable for several reasons. Their wings are flat, not usually obscured by pigment or structural features, and support a strong current of blood which is clearly visible under the microscope by reason of its large complement of haemocytes. The insects are relatively easy to handle and generally do not respond unfavourably to manipulation. These features are much less true of the other orthopteroids, but many species within the complex provide excellent demonstrations of circulation.

Moseley (1871) was the first author to seriously study the wing circulation in a cockroach. His observations were confined to *Blatta orientalis* and mainly to the hind wings but he presented a reasonably clear account of the circulatory route with few references to conditions that might now be considered abnormal; e.g. reversal of direction of flow, and fluctuation in the wing base.

The principal investigations of wing circulation in blattids have come from the associated authors Yeager, Hendrickson, Tauber, and Clare. Yeager and Hendrickson (1933) in presenting a method for the study of wing circulation in

Periplaneta americana Linn. commented on the circulatory route and the efferent streams through meso- and metatergal pulsatile organs into the heart. They also included in their observations *P. orientalis* L., *B. fulginosa*, and *Blattella germanica* (L.). Later (1934) they gave a detailed account of circulation in the wings of *P. americana*. Clare and Tauber (1940) described circulation in *B. germanica*, studied the effect of cutting certain of the blood channels on the circulatory route (Tauber and Clare 1942), and examined circulation in the articular membrane (Clare and Tauber 1942). Some of their findings warrant special comment below in connection with similar studies on another species.

Materials

The giant cockroach *Blaberus giganteus* (L.) was used almost exclusively. *P. americana* and *B. germanica* were examined only briefly to ensure that the circulatory route conformed generally to the accepted pattern.

Observations and Discussion

The circulatory route for *B. giganteus* was described and illustrated previously (Arnold 1959). It conforms generally to the route described for *P. americana* and *B. germanica* by the previously mentioned authors. Structural differences in the tegmina of various species are the main cause of variation in details of circulation. In *B. giganteus* for example the proximal area of the tegmen anterior to the subcosta is essentially a sinus where the vein walls are represented only by pillars of cuticle and unlike those of other blattids. There the blood moves freely outwards for a short distance before it becomes confined to the veins. In the same insect the cubitus arises close to the base of the media and on occasion is afferent. According to Comstock the costa is not a readily definable vein in blattids. However a prominent blood channel always occurs in the position normally occupied by that vein and represents it functionally at least. Unlike the condition in *P. americana* (Yeager and Hendrickson 1934), the costal streams in tegmina and hind wings of *B. giganteus* flowed around the wing apex. There is however a tendency for circulation to become retarded at the apex and for the wing tip to desiccate and fragment in old age. The ambient extension of the costa continues along the posterior margin of the tegmina, but in the hind wing does not occur beyond the median fold. Consequently the posterior margin of the hind wing desiccates and fragments early in adult life.

A portion of the blood that enters the wing bases in *B. giganteus* re-enters the body without penetrating the veins. This is unlike the situation reported for *B. germanica* where the articular membrane in the tegmen was completely fused in the jugal area and prevented blood from re-entering the body except via the veins (Clare and Tauber 1942). The same authors found that folds in the hind wings retarded circulation and that flow was increased when the wings were extended in the position of flight. This is not true in *B. giganteus* where a taenidia-like structure characterizes the vein walls at the main wing folds and prevents their collapse when folded.

Suborder: Mantodea

Although circulation in the wings of the mantids is strong and easily visible there seems to be only a single brief reference to its observation in the literature. Verloren (1847) cites the authors Ehrenberg and Hemprich as having observed blood circulating in the wings of a mantid.

Materials

Only three specimens of *Mantis religiosa* Linnaeus were examined in the present study. However, in each individual the circulation was strong, the route was clear, and the features of circulation were alike.

Observations and Discussion

Circulation is more vigorous in the fore than in the hind wings but the route is similar in each except for differences imposed by structure. The route (Figs. 10 and 12) is generally similar to that in the blattids but is less controlled and less confined to the veins. In these respects it is more closely akin to circulation in wings of some of the saltatorial orthopterans. Afferent flow occurs in the costa, subcosta, radius, and the proximal part of the media. The cubitus is normally efferent and contributes blood to a large basal cross-vein from the media (Figs. 11 and 13). Although the afferent veins support vigorous currents many of them are not completely closed and there is a continual leakage of blood from them into the surrounding areas. Consequently much of the remigium of the tegmen and a less extensive area in the anterior part of the hind wing are, in effect, sinuses. They contain layers and clumps of tissue, apparently composed largely of haemocytes intermingled with deposits of pigment. The areas are obviously sites of metabolic activity and warrant further study. Efferent flow is confined in closed veins. In the tegmina an ambient extension of the costa carries blood efferently from the apex along the posterior margin of the wing and donates blood en route to the efferent veins and proximally to the jugal veins. A similar vein occurs in the hind wing but, as in all orthopteroids, it extends from the apex only for a short distance beyond the vannal fold. The hind wing is highly pleated in the vannal area but there is no evidence of interruption to blood flow when it is in the folded condition. The illustration (Fig. 12) serves as well for the other orthopteroids.

Although the mantid wings are flexed at rest and contain the normal complement of articular sclerites, the bases are nevertheless flexible and contain sinuses which are relatively open to the body cavity (Figs. 11 and 13). In this respect they resemble the simpler wing bases of the ephemerids. Part of the blood that enters the bases passes directly through the sinuses and re-enters the body. Heart pulsations are frequently evident in the bases and in the proximal part of the remigium. There is also some tendency for the blood to gush and to flow in the reverse direction in response to struggling and exaggerated respiratory movements.

Order: Orthoptera

Suborder: Saltatoria

The suborder Saltatoria includes several families in which there is a great diversity in the form and venation of the tegmina, both within and between families, and what seems to be a corresponding diversity in the circulatory routes. This diversity however is only in minor features, and the basic scheme of venation or of circulation is unaltered. Comstock considered that there were no distinguishing characters separating the wings of saltatorial Orthoptera and the Blattaria, and his view is supported in general by the present studies of circulation. In both groups and also in the Mantodea, which Comstock did not study, the afferent and efferent routes are very similar. Also in each a transverse proximal vein plays a prominent role in circulation by diverting blood from the bases of the afferent costo-radial veins to the axillary cord and receiving blood from the efferent cubito-anal veins. The media, because of its position, may be either afferent or efferent in each group of insects depending on the blood pressure.

It tends to be afferent when the pressure is high and efferent when low. Blood circulation in the hind wings is almost identical in all of these insects.

The literature contains very few references to circulation in the wings of the Saltatoria. Aside from the early ones of Baker (1744) and Gruithuisen (Carus 1831) previously referred to, only Brocher (1916) has contributed and then only briefly. He merely noted that thoracic pulsatile organs similar to those of *Dytiscus marginalis* occur in crickets.

Family: Locustidae
Materials

Circulation was studied in wings of a number of specimens of the following locustids: *Melanoplus femur-rubrum* (DeGeer) *Encoptolophus sordidus* (Burm.), and *Chorthippus curtipennis* (Harris). It was examined briefly in a number of other species (see Appendix) to determine the consistency of the route within the family. There was close similarity in the routes and of the features of circulation in all of them.

Observations and Discussion

The tegmina of locustids (Fig. 14) feature numerous intercalary veins which seem to complicate the circulatory route. However the intercalary veins merely add to the number of channels through which blood flows in the same general direction as in the principal veins between which they are located. The basic route remains the same, with the costa, subcosta and radius as the main afferent channels and with the cubito-anal group as efferent veins. The direction of blood flow in the media is variable depending upon pressure. The costa is not identifiable as a vein in the usual sense but exists as a channel that is apparently formed by the union of the distal ends of veins from the subcosta. The ambient extension of the costa along the posterior margin of the tegmen is well defined. Perhaps because of the large number of intercalary veins in the tegmen circulation near the wing apex is less forceful than elsewhere and the veins there tend to become occluded with haemocytes early in adult life. Consequently the apex becomes dry and brittle. There are frequent examples of this in the wings of many insects, principally at the apex and along the posterior margin. They demonstrate clearly that the formed cuticle is not simply an inert substance but is rather a metabolizing system.

Circulation in the hind wings is almost identical to that in other orthopteroids and as illustrated for Mantodea. Veins near the apex are incompletely closed and result in the formation of a stigma-like sinus. The ambient extension of the costa extends only as far as the vannal fold. Again, folding of the hind wings does not retard circulation in them, but characteristically the flow there is slower, steadier, and less obvious than in the tegmina. It also seems less affected by exaggerated respiratory or other movements.

Family: Tettigoniidae
Materials

Circulation was studied in wings of *Scudderia furcata* Brunn., *S. pistillata* Brunn., and *Conocephalus fasciatus* (DeGeer). There were no major differences between them.

Observations and Discussion

As in the Locustidae, the tegmina of tettigoniids feature large numbers of intercalary veins (Fig. 15) and the circulatory route in the two groups is very

similar. Unlike the former, however, circulation here is relatively strong throughout the tegmina, apparently as a result of assistance from respiratory movements of the thorax which seem to be especially prominent. A pulse that averaged about 30 beats per minute and was attributable only to respiratory movements was usually evident in the afferent veins. Pulsations in the efferent veins averaged about 78 beats per minute and were directly attributable to the mesothoracic pulsatile organs. There appeared to be no relationship between the afferent and efferent pulse and the efferent one remained fairly constant despite variations in the other. The veins anterior to the large subcosta are mainly open. The main blood current and most of the haemocytes remain within them but there is a continual leakage into the surrounding broad sinus. The costa, like that of the locustids, occurs as a union of tips of veins from the subcosta. Its ambient extension forms a prominent conduit along the posterior margin to the jugal area.

The circulatory route in the hind wings is basically similar to that in the other orthopteroids. Again open veins create a stigma-like sinus near the apex. The ambient extension of the costa is somewhat shorter than in the preceding families and reaches only a short distance beyond the apex. The current is slower and more constant in the hind wings than in the tegmina and much less affected by respiratory movements.

Family: *Gryllidae*

Materials

The studies were restricted mainly to species of *Oecanthus*, primarily because of their availability and ease of handling. A number of other crickets were examined but their short, contoured tegmina were not well suited for microscopic examination and the insects did not accept confinement. Despite their unusual structural features, the wings showed no peculiar conditions of circulation.

Observations and Discussion

Although the tegmina in species of *Oecanthus* appear to differ widely from those of other orthopteroids, the system of venation in Comstock's view is basically the same. Circulation is not altered from the normal pattern (Fig. 16), but it is simpler than in the preceding families because of the comparative scarcity of intercalary veins. As in the tettigoniids, afferent flow in the tegmina is strongly influenced by respiratory movements. An afferent pulse of about 25 beats per minute was usually evident in veins near the base of the remigium and coincided with thoracic movements. An efferent pulse in the axillary cord and in flexible portions of the anal veins averaged about 112 beats per minute and was attributable to thoracic pulsatile organs. Unlike the tettigoniids however most of the veins are closed, and leakage into sinuses is restricted to small areas near the apex in both the tegmina and hind wings. Circulation in the hind wings is identical to that in the other orthopteroids.

Order: Plecoptera

Few insects provide a better demonstration of circulation in the wings than do the stoneflies, but strangely enough there are scarcely any references to them in the literature in this regard. Their mention in the early works of Carus and of Goring and Pritchard, already referred to, seem to stand alone. The order is a primitive one allied to the orthopteroids (Ross 1956) and this is evident in features of circulation which in many respects resemble those of the family Gryllidae.

Materials

Only two species from the order were studied extensively here, a small unidentified species of *Perla,* and a large one, *Acroneuria arenosa* Pictet. The route and features of circulation were similar in the two species despite the great difference in size and it seems likely that they fairly represent the order. *A. arenosa* served for most of the detailed observations and can be highly recommended as an experimental animal for studies of this kind. Wing circulation is vigorous, the vein walls are clear, the blood contains a high complement of large haemocytes, and the insect is relatively easy to handle under the microscope.

Observations and Discussion

Wing venation in Plecoptera approximates that of the hypothetical primitive wing, and the circulatory routes (Figs. 17 and 18) conform closely to the basic pattern. The costa, subcosta, and radius are the main afferent veins in both wings. The media is usually afferent only in the proximal region but may be largely afferent when the blood pressure is especially high. A prominent basal transverse vein (Fig. 19) allows blood to proceed directly from the humeral angle to the axillary exit without entering the veins and receives blood from efferent veins, including the media. Blood may also move through the sinuses of the wing bases and avoid the veins. Here it is directly subject to pressures from the body and fluctuates in response to thoracic movements. Excessive movements are also expressed in the flow in the veins, and may cause a complete or partial reversal of the direction of flow.

In both wings a relatively extensive stigma-like sinus occurs in the region where the costa and subcosta join. These areas, as in orthopteroids, result from leakage of blood from open veins. The ambient extension of the costa is an important efferent channel in both wings. In the hind wings it continues around the circumference of the large vannal area to the axillary cord and is therefore a much more extensive and important channel than it is in orthopteroids.

Perhaps the most unusual feature of wing circulation in Plecoptera is the apparent lack of independent pulsatile organs beneath the scutellum. They were not detected by direct observation or by dissection. Direct observation showed that blood from the wing flowed through the axillary cord and entered the thorax beneath the scutellum. There it was joined by blood from lateral spaces of the thorax and entered the heart directly through ostia. Evidently circulation through the wings is effected by the action of the heart and with assistance from respiratory movements. The heart in these insects is unusually strong and its action is characterized by violent peristaltic contractions. Its pulse is evident in the proximal regions of the remigium and in flexible portions of the anal veins. Histological studies may reveal the organs, or some reduced representative of them, joining the axillary cords to the heart. However it seems reasonable that the system can function without them where the aspirative force of the heart is strong and operates close to the exit from the axillary cords. A slow circulation of blood occurs in the wings of many other insects during periods when their accessory pulsatile organs are not functioning.

Order: Hemiptera

The order Hemiptera includes many diverse insects which are grouped into the two suborders Heteroptera and Homoptera partly on the basis of wing structure. The structural differences in the wings also impose some circulatory distinctions between the two groups even though the main features are alike.

Circulation in the wings of Hemiptera has been scarcely mentioned in the literature, and not without reason. In many species the circulation is slow, and

in most of them it is difficult to detect because of the nature of the wings and of the blood. This is particularly true of Heteroptera but applies to some extent also in Homoptera. In the former, the dense pigment and heavy cuticle in the corium of the hemelytra obscures direct observation, while in the distal membrane circulation is very limited. In the hind wings the lumens of the veins are narrow and restrict the entrance of haemocytes which are the principal indicators of circulation. The complement of haemocytes in the blood is also relatively low in Hemiptera and often the main evidence of circulation is obtained from observing the flow of particulate matter rather than cells in the haemolymph. Only two references of significance were located: Bervoets (1913) stated that blood occurred in the hemelytra of *Notonecta*, *Corixa*, and *Nepa*, but did not mention a circulatory route; similarly Patch (1909) failed to observe circulation in Homoptera but recognized that blood occurred in the costal vein as far as the stigma. Nevertheless, circulation occurs in all members of the order and is quite efficient in some.

Suborder: Heteroptera

Materials

Circulation was examined in the wings of one or more species (see Appendix) in the families Belostomatidae, Corixidae, Miridae, Nabidae, and Phymatidae. In these widely different insects the course followed by the blood in the wings was similar except for minor variations resulting from differences in venation. Likewise, features of circulation such as the rate of flow, the extent of sinuses, and the rate of afferent and efferent pulsations showed common characteristics but varied somewhat between species.

Observations and Discussion

The conditions of circulation in the wings of species from the family Miridae are fairly representative of the suborder and are the ones discussed particularly here. The circulatory route in wings of *Adelphocoris lineolatus* (Reuter) is illustrated (Figs. 20 and 21). Unlike the conditions in the insect orders already discussed, the structure and venation of the fore and hind wings are quite different and the circulation likewise is dissimilar.

The whole corium of the hemelytra is a thin sinus through which blood trickles slowly. The main current is confined within the open veins which continually leak blood into the surrounding areas. Sinuses that are relatively free from obstructions and support a full current of blood occur at the base of the hemelytra and in the region where the embolium and cuneus join. Blood flows afferently in all of the veins of the corium to its junction with the distal membrane. A channel at this junction carries the blood posteriorly to the termination of the anal furrow where the course becomes directly efferent. This is the only point of afferent-efferent change and is a unique feature of the hemipteran wing. Efferent flow from this point occurs mainly in the large vein that extends along the posterior margin of the clavus. This vein seems to be considered a united postcubitus and first anal (Davis 1961). Some efferent flow occurs also in the smaller cubitus and there is generally a slow trickling of blood throughout the clavus which contains, like the corium, a thin sinus. The membrane of the hemelytra is poorly served by the blood and its margin tends to become dry and brittle. The flow there is restricted to two venal loops, presumably extensions of the media and cubitus, but some leakage of blood occurs into the closely adjacent areas.

Although some of the blood that enters the humeral sinus of the hemelytra finds its way through the basal sinuses and avoids the veins, most of it follows a

complete course through the wings. There is little evidence of an afferent pulse in the corium, except during periods of struggling, and the blood moves outward from the body in a slow, steady fashion. Efferent flow however, being restricted largely to one vein, moves rapidly and is strongly aspirated by the thoracic pulsatile organs. Their action appears to be assisted by tissue located in the common junction of veins at the distal end of the anal furrow. Although the tissue is reminiscent of the tibial pulsatile organs common to insects in this order, its mechanism is less clear and it acts always in rhythm with the thoracic pulsatile organs. Its movement diminishes with age and it is seldom evident in old adults, even where circulation is still vigorous. Its characteristics suggest that it is a flexible area of the vein wall that responds vigorously to the action of the thoracic pulsatile organs and affords some advantage in aspirating blood from the corium. A histological investigation of the area seems warranted.

The hind wings are entirely membranous and the venation is much reduced from the hypothetical primitive condition and from the system in the hemelytra. The volume of blood circulation in them is also reduced and the route is much simplified. Part of the blood that enters the wing bases by-passes the veins via the broad basal transverse vein (Fig. 21) and re-enters the body. Within the wing, afferent flow is entirely confined to the large vein at the costal margin. This vein, the homology of which seems to be obscure or controversial, forms a loop with one that is generally accepted as the composite medio-cubital and carries the blood efferently to the basal transverse vein. Thus the blood flows through a simple circular path in the wing without the deviations through branches and cross-veins that characterize the wings of the insects already discussed. Veins that radiate from this loop are "blind", i.e. not otherwise connected, and are not involved in the circuit even though they contain blood. Haemocytes may be seen to flow into them periodically and to remain for a time and be drawn out again during a period of accelerated flow in the main circuit. Although it might be considered that reduction of circulation to this extent would expose the wing to desiccation, they nevertheless remain flexible during most of the adult life. Possibly leakage of haemolymph occurs from the veins and much of the wing area is actually served by blood. Perhaps the fluid traverses the relatively wide areas of membrane in a circular route and utilizes the "blind" veins to rejoin the regular circuit. Few haemocytes enter the hind wings but there is a slow and steady circulation of haemolymph without prominent pulsations.

The preceding discussion, as mentioned, pertains especially to members of the family Miridae but is generally true for the whole suborder Heteroptera. In some other families however the venation is more extensive in both pairs of wings and warrants some mention. The circulatory system in the wings of two other families is therefore illustrated, Phymatidae (Fig. 24) where venation is only slightly more elaborate, and Belostomatidae (Figs. 22 and 23) where numerous accessory veins occur. In each of them the course of circulation is similar but the blood is more closely confined to definite channels.

Suborder: Homoptera

Materials

Circulation was examined in the wings of species from the families Cicadellidae, Cicadidae, Membracidae and Aphididae (see Appendix). It was similar in the first three families, which are allied also by a number of other features, but quite different in the last one.

Observations and Discussion

In the family Cicadellidae the structure of the fore wings and their venation is highly varied. They range from a Heteroptera-like condition, subcoriaceous and with simple venation (Fig. 27), through those where the venation is increased (Fig. 25) to some that are strangely modified, delicate, and Lepidoptera-like (Fig. 28) with numerous accessory veins. Although the details of circulation are appropriately varied the basic scheme remains the same in all of them. Afferent flow is confined to the area anterior to the anal furrow and efferent flow occurs posterior to it. As in the Heteroptera, most of the blood that enters the wings passes through a common channel at the distal end of the anal furrow at the start of its efferent course. Also, whereas the afferent flow is usually slow and steady, efferent flow is characterized by a strong and rapid pulse directly attributable to the action of the thoracic pulsatile organs. The pulsations here are more obvious than in Heteroptera and are evident not only in the rapid movement of the haemocytes but also as strong contractions of the entire vein walls at the flexible distal end of the anal furrow, in flexible parts of the efferent veins, and in the axillary cords. Although these separate pulsating areas suggest the presence of independent pulsatile tissues within the wing, they act in rhythm with the thoracic organs and reflect their activity. In species where the venation is simple (Fig. 27) most of the veins are open and blood moves slowly through the entire wing while the main flow remains in the veins. In species where the venation is more complex (Fig. 25) there is a tendency for the sinuses to be reduced in area and restricted mainly to the costal and anal regions. Where accessory veins are very numerous (Fig. 28) the sinuses are insignificant or entirely absent. Thus by one means or another, through leakage from open veins or by the presence of numerous veins, blood permeates the fore wings.

In the other two families of the so-called "needle-horned series" of Homoptera examined here, circulation in the fore wings was quite similar to the above but the blood was more confined. In Cicadidae (Fig. 29) the blood flows in thick-walled veins except in two sinuses, one between the open costa and the combined subcosta-radius, and the other located around the arculus. The arculus is a prominent feature in all members of the series and provides a short course for the blood to flow from the proximal regions of afferent veins to the anal angle while receiving blood from the distal regions of the wing through efferent veins. A short course is also provided by the transverse basal vein (Fig. 31). Also in Cicadidae, the common vein at the distal end of the anal furrow (Fig. 30) is typical of the structure in the other families but somewhat more rigid; pulsations of the thoracic organs are evident there but less obvious than in families with more flexible wings. In members of the family Membracidae (Fig. 32) no sinus occurs at the costal margin, but open veins are present elsewhere in the wing and blood leaks from them into small surrounding areas.

In the same series of insects the structure and venation of the hind wings is quite different from that of the fore wings and blood circulation likewise is different. The hind wings are fully veined and the branches are joined terminally by the ambient costa or its equivalent. This vein undulates parallel to the outer margin of the wing and approaches the edge along the inner margin. Comstock considered it to be a characteristic of the wings of most membracids and cicadas and termed it the "marginal vein". Apparently he was unaware that a similar vein unites the tips of the longitudinal veins in many other insects but is usually less obvious and located at the edge of both the outer and inner margins. It is always an important vein for blood circulation and there seems little reason to distinguish it particularly in this group of insects. From discussions with a num-

ber of taxonomists it is clear that the vein is generally recognized only as the costa, and it is termed here the "ambient costa" to indicate its continuation around the circumference of the wing. The circulatory route in the hind wing of a cicadellid (Fig. 26) is fairly representative for the entire group. Circulation is comparatively slow and steady and the blood contains relatively few haemocytes. Most of the haemocytes appear to be excluded at the entrance to the wing base, and the few that enter pass through the veins singly and sluggishly. A portion of the blood that enters the wing base always avoids the circuit through the veins by flowing directly to the anal angle via an open transverse basal vein.

In the family Aphididae the venation is highly modified (Patch 1909). In the fore wings only two principal veins extend outward from the base and unite at a pterostigma. In the hind wings the pterostigma is absent, but two similar veins unite at the wing apex. In both the fore and hind wings these veins (Fig. 33) form a complete loop, reminiscent of the condition in the hind wings of Heteroptera; branches from the loop, except those near the apex, are not connected terminally. It might therefore be expected that blood would flow afferently in the anterior vein and return via the posterior one, thus completing a circuit; this happens only irregularly. Generally the wing circulation is weak and intermittent, without regular pulsations. Often the blood moves afferently in both of the main veins, stops for an interval and returns in the same way. Its movement seems to depend almost entirely on changes in pressure within the body haemocoel, apparently with little if any assistance from thoracic pulsatile organs. The apparent absence of pulsatile organs and the lack of separation between the bases of the two main veins likely account for the irregularity in the volume and the course of circulation. Few haemocytes enter the veins and then only singly. In the fore wings they seldom travel beyond the pterostigma. Circulation in that structure has already been described (Arnold 1963).

Order: Neuroptera

The wings of Neuroptera usually have numerous accessory veins and the radial sector is often pectinately branched. As a result, the venation in most species is extensive and unusual but is basically similar to the hypothetical primitive condition.

The literature contains no recent references to circulation in wings of Neuroptera. Among early accounts however are the noteworthy ones of Tyrrel (1835) and Bowerbank (1836). The former mentions briefly the movement of globules in the wing veins of some species of *Hemerobius*. The latter provides a detailed description of circulation in the wings of *Chrysopa perla*. It contributed much to the general acceptance of the reality of blood circulation by entomologists of that time.

Materials

Circulation was studied in one or more species from the families Chrysopidae, Hemerobiidae, Mantispidae and Myrmelionidae (see Appendix). Circulation was moderately vigorous in each of them and the circulatory route was generally similar. Species of *Chrysopa* served for most of the detailed observations.

Observations and Discussion

A general description of circulation in any one of the insects examined would serve for all of them and for either the fore or hind wings which are almost identical. The route adheres closely to the basic pattern of circulation in the wings despite the characteristically large numbers of accessory veins. They merely increase the number of channels through which the blood flows in the

same general direction as in the main longitudinal veins from which they are derived. This is evident from a comparison of the route in *Myrmeleon* sp. (Fig. 34) where accessory and cross-veins are very numerous as compared with the number in *Chrysopa* sp. (Fig. 35). The venation seems particularly well suited to carry blood throughout the wings. For example the pectinately branched radial sector gives a more positive direction to the blood currents than the more familiar dichotomous arrangement in other insects; the gradate veins which are especially prominent in *Hemerobius* sp. provide clear channels for efferent flow in the distal regions of the wings; the numerous accessory marginal veins in conjunction with the ambient costa ensure complete circulation around the periphery and there is seldom any evidence of wing deterioration even in old adults. Variations in details of venation account for differences in the circulatory routes between species, but these are seldom great. Variations in venation near the wing base, which were stressed in Comstock's interpretations of vein homologies in different families, are mechanically similar at least and provide a recurrent course for the blood from afferent to efferent veins. An obvious feature of wing circulation that is not present in all members of the order is the stigma-like sinus illustrated for the wing of *Mantispa brunnea* Say (Fig. 36) and discussed previously (Arnold 1963).

Although the current in the veins is moderately strong in all of the species examined, a noticeably large portion of the blood passes directly through the basal sinuses and the recurrent configuration of basal veins (Fig. 37) and re-enters the body. Fluctuations in haemocoelic pressure within the body are reflected in the wings by changes in the strength of the current and in the direction of flow. Reversal of flow is not uncommon during periods when the insect struggles or when respiratory movements are exaggerated. Obviously these occurrences influence circulation in the wings, but the flow is usually regular and maintained through the efficient action of the thoracic pulsatile organs. Their pulsations are evident in identical contractions of flexible portions of the axillary cords, of proximal regions of the anal veins, and in movements of loose tissues in the basal sinuses. Relatively few haemocytes enter the wing veins. Most of them are almost as wide as the lumen of the veins and are forced to move singly through them.

Order: Hymenoptera

In the Hymenoptera wing, venation is much reduced and altered from the hypothetical primitive condition and there is no firm agreement on the homologies. Comstock noted that wing venation precedes tracheation in these insects and that the courses of tracheae could not be depended upon for determining vein homologies. Undoubtedly this is true also for other groups of insects where discrepancies between wing venation and wing tracheation are less obvious. It points to a limitation of the system of homologizing veins broadly on the basis of tracheation but does not discredit its general usefulness. Comstock's concept of the venation in the forewings of Hymenoptera was derived mainly from studying similar developments in the Diptera where the various modifications could be followed more clearly. In the hind wings of Hymenoptera venation is so reduced that he was unable to determine homologies except by interpretation from the work of MacGillivray (1906) with the suborder Chalastogastra where venation is the most generalized. Nevertheless, the venation in most Hymenoptera is basically alike and so also is the route of blood circulation.

It is not surprising that the literature contains few references to wing circulation in Hymenoptera; the walls of the veins are thick and often pigmented, and the haemocytes are not easily detected in the swift current as they are relatively

few in number and mostly hyaline. The earliest reference is that of Moseley (1871) where mention is made of three pulsating dilated areas in vessels of the hind wings of some small, unidentified Hymenoptera. Janet (1906) described thoracic pulsatile organs in the ant *Lasius niger* but apparently did not fully understand their role in wing circulation. Similarly, Brocher (1920b) demonstrated rudimentary pulsatile organs in the mesothorax of *Vespa crabro* and suggested their presence also in the metathorax. He was well aware of their role from his earlier discoveries of similar structures in other insects. Their rudimentary aspect in *V. crabro* led him to suggest that their original function of aspirating blood from the wings had been assumed largely by abdominal respiratory movements and that the pulsatile organs open into the body cavity and not into the heart. Freudenstein (1928) also made mention of pulsatile organs in the thorax of *Apis mellifera* and suggested their involvement in wing circulation. Wille (1958) however in his comparative studies on the hearts of bees made no mention of accessory structures in the thorax.

Materials

Observations were limited to the suborder Apocrita and included species from eight families (see Appendix). The honey bee, *Apis mellifera* L., and several species of Ichneumonidae served for most of the detailed studies and much of the discussion will pertain directly to them. In all of the families however the route and features of circulation were remarkably similar, except in highly specialized forms, and require little separate comment.

Observations and Discussion

In the Hymenoptera the lumens of the veins are remarkably free of obstructions. The tracheae and nerves, where they occur, are mainly small and simple and the surfaces of the vein walls are free of cells and membranes. Blood circulation is generally swift. Bullae occur where the veins cross furrows; they are clear and corrugated and permit circulation to continue unobstructed when the wing is folded. The current that passes directly through the wing bases (Fig. 40) is generally insignificant. The veins in the hind wings are structurally similar to those in the fore wings but appreciably smaller in diameter. In them the circulation of haemocytes is restricted by the narrow lumen and the few that enter the veins move through singly. The pterostigma of the fore wings is unlike the similarly termed structure in the wings of Odonata and some other insects (Arnold 1963); it is simply an enlarged junction of several veins. Nerves and tracheae branch out within it (Fig. 41) but it is otherwise unobstructed. Blood passes through it without hesitation.

In the fore wings of species in most families of Hymenoptera, four longitudinal veins extend outward from the wing base. An afferent outflow of blood occurs in each of the three anterior ones, and efferent flow is limited to the single posterior one. The crossover from the afferent veins to the efferent one is accomplished through one or at most two veins which have the function of cross-veins with regard to blood circulation but are apparently considered to be branches of the media and cubitus. The first and second afferent veins pour blood into the pterostigma where streams are directed onwards into the veins that emerge distally from it. In one of the largest families, Ichneumonidae, the first and second afferent veins are joined longitudinally as a wide costal channel (Fig. 38). The two veins retain their separate identities superficially but the wall between them is incomplete and blood passes freely from one to the other. In most other families, e.g. Apidae, (Fig. 39), the two veins are clearly separate. In either case a portion of the blood in the second afferent vein is directed posteriorly

to the third afferent vein as illustrated. In the former case it is directed there through a vein which branches from the entrance to the stigma. In the latter it flows through a comparable vein which leaves the second afferent before it reaches the stigma. This stream merges with the one in the third afferent vein and crosses to the single efferent vein through the more proximal of the two "cross-veins". The more distal cross-vein, where it occurs, receives blood mainly from the vein complex which lies distal to the stigma. Circulation in that complex is circuitous and somewhat variable in different families, in conjunction with variations in the configurations of the veins and the size and form of the wing cells. The vein at the costal margin seldom extends beyond the apex, and the outer margin of the wing is consequently devoid of blood. It tends to become dry and brittle and is seldom entire in the late stages of adult life. In some families, e.g. Formicidae, the distal vein complex is reduced (Fig. 42) and the distal cross-vein to the efferent channel is absent. The condition is more striking in species of Chrysididae (Fig. 44) where the distal complex is absent. This pattern of venation and of circulation which features a single efferent channel and only one or at most two routes of access to it is reminiscent of the Hemipteran wing despite the wide differences that otherwise separate the two orders.

Some of the principles governing circulation in the wings were revealed when individual veins were blocked. Where blood is carried from the afferent veins to the efferent vein through two channels, destruction of either one of them causes the blood to flow entirely through the other but does not alter the main course of flow in other areas of the wing. Destruction of both of them or of the efferent vein itself reduces wing circulation to a comparatively passive and unregulated mechanism which functions only intermittently and not very effectively. Under these circumstances the third afferent vein may intermittently accept the efferent role. It performs this function more effectively in families such as Vespidae where the third afferent vein emerges separately from the wing base than in those such as Apidae and Formicidae where it branches from the base of the second afferent vein. Destruction of the third afferent vein without injuring the others does not alter the course of circulation.

Throughout the order there is considerable variation in the venation and route of circulation in the hind wings. In many families the hind wings are simplified versions of the fore wings and the circulatory routes are comparable. Simplification is mainly in the distal area, but the first afferent vein may also be reduced and cease to carry blood. The simple route of circulation is illustrated for Ichneumonidae (Fig. 38) and for Formicidae (Fig. 42). Circulation is never strong in the hind wings and in some Hymenoptera, e.g., Chrysididae, the venation is so reduced that a complete circuit of blood cannot occur. In such cases blood occurs in two simple and unconnected veins and presumably moves inwards and outwards only in response to pressure changes in the body. Also in Chrysididae, the venation of the fore wings is much reduced and the circulatory route (Fig. 44) is similar to that in the hind wings of the families already illustrated.

In the family Chalcididae the venation is very much reduced in both fore and hind wings and here again a complete circuit of blood cannot occur. The single vein in each wing (Fig. 43) contains blood which apparently enters and leaves periodically as a result of pressure changes in the body and is unassisted by accessory pulsatile organs.

Order: Coleoptera

The extreme modifications in form and structure of the wings of Coleoptera impose some unusual circulatory problems. However the problems are much

the same throughout the order and there is remarkable constancy in the circulatory route and features of circulation among the different families.

Despite the rather obvious difficulties in observing blood circulation in coleopteran wings a number of authors have reported upon it. They are mainly among the early workers referred to previously and their observations were not extensive. Neither were the more recent observations of Bervoets (1913) on *Dytiscus* and *Meloë* and of Lehr (1914) on *Dytiscus marginalis*. Undoubtedly the most extensive work in Coleoptera was that of Brocher (1916). It was concerned mainly with the anatomy and function of the accessory pulsatile organs, but included a number of pertinent observations on circulation within the wings of *D. marginalis* and *D. punctulatus*. Particularly, Brocher's observations led him to believe that circulation in the hind wings occurred only on certain occasions, as during flight, despite the presence of pulsatile organs. Later (Brocher 1929) he carried out similar studies with *Coccinella conglobata* and *Galeruca crataegi* and decided that the pulsatile organs were mainly responsible for wing circulation but were assisted by respiratory movements. Similar studies by Kuhl (1924) with *D. marginalis* confirmed the anatomy of the pulsatile organs and their connections but gave no indication of the importance of the organs in circulation.

Materials

Circulation was studied in the wings of members of nine families of Coleoptera (see Appendix) where the wings were much different in size and form. Circulation was of course much different in the fore and hind wings but was otherwise similar throughout the group. These insects are among the most trying for observations of this kind. They are generally less sensitive to carbon dioxide than other insects and are consequently more difficult to handle. Many of them are hard to confine because of the shape of the body and elytra, and most of them resist confinement vigorously. Their resistance inevitably causes irregular circulation and the blood gushes into and out of the wings in response to pressure changes in the body haemocoel. Nevertheless, on occasion the blood can be seen to follow a complete circuit in the wings and in a steady fashion. On such occasions the regular pulsations in the axillary cords provide convincing evidence of the role of the accessory pulsatile organs in normal wing circulation.

Observations and Discussion

Essentially the elytra are sinuses (Fig. 45) through which the veins are open, longitudinal channels, extending from base to apex with few and incomplete branches. The veins are unobstructed and blood moves through them more swiftly than in the surrounding areas. This is especially true of the costal or marginal vein which conducts blood around the circumference from the humeral angle to the axillary cord and accepts blood en route from the afferent portion of the wing; it also contributes blood to the efferent portion of the wing. There is no clear distinction between afferent and efferent areas but the blood moves in a circular path outward in the anterior half of the elytron and back toward the base in the posterior half. At the wing base (Fig. 48) this path is accomplished relatively swiftly via a basal transverse channel. The areas around the veins receive blood from them but its flow is impeded by indentations and by pillars of cuticle that join the dorsal and ventral surfaces and are more or less concentrated in different regions in different species. These areas tend to become repositories for haemocytes which settle from the slow current and create further obstructions to flow. In general the lack of closed veins does not interfere with the main course of circulation but it undoubtedly dissipates the force of the current. During periods of rest the only evident pulsations are in the axillary cord and

these reflect the action of the pulsatile organs in the thorax. The normal changes in the substance of the elytra during early adult life are undoubtedly provided for by the ample blood supply.

In the hind wings the venation is also highly modified and primarily, it would seem, to permit the transverse folding which is characteristic of the wings in this order. Despite specific differences in the plan of folding, the basic system of veins is relatively constant in form, if not in extent, and the blood circulates through a relatively simple route (Figs. 46 and 47). During periods of rest the current in the veins is slow and steady and pulsations are evident only in the axillary cord. Haemocytes are relatively scarce in the veins and the route is often obscure. Periodically the blood gushes through the veins in conjunction with obvious respiratory movements or struggling. Then the route is clear and sinus areas become apparent around the distal junction of veins proximal to the main transverse fold. At the same time the route through the basal transverse channels (Fig. 49) is also clear. These observations support Brocher's aforementioned suggestion that respiratory movements are important for wing circulation in these insects, but suggest that the less vigorous circulation is regulated by the thoracic pulsatile organs.

Considering the degree of flexibility required for the wings to fold beneath the elytra it seems almost essential that haemolymph should circulate outside the veined area. No direct evidence of this was obtained during the usual periods of observation or from dye injections, and the indirect evidence is not strong. Nevertheless, in newly emerged adults the position of the definitive veins is occupied by wide channels which are open to the unveined areas of the wing. Blood moves through the channels swiftly in the normal circuit and also escapes into the unveined areas which at that time are thin sinuses. The entire wing is filled with circulating blood and this condition may persist for some hours after wing extension and folding. This is the case at least in *Coccinella transversoguttata quinquenotata* Kby., where these observations were made. The two wing surfaces gradually become appressed and the apparent extent of circulation is reduced to the lumen of the veins and to a few small sinuses. Probably the apposition of the two surfaces is incomplete and spaces remain and support a slow percolation of haemolymph.

Order: Mecoptera

In Mecoptera the two pairs of wings are similar in size, form, and venation. The arrangement of the veins closely approximates the hypothetical primitive condition and the route of circulation conforms to the basic pattern.

Only two references to circulation in this order were located in the literature and these were very brief. Tyrrel (1835) included *Panorpa* among the insects in which he observed wing circulation, and Brocher (1916) mentioned that the same genus had accessory pulsatile organs similar to those which he described for *Dytiscus*.

Materials

Observations were limited to only a few individuals of *Panorpa* sp. and in these the circulatory routes were distinct and alike. Presumably it is similar in other members of the order.

Observations and Discussion

For several reasons species of *Panorpa* are better subjects for demonstrating a simple, basic system of circulation in the wings than many of the more primitive insects: there is an even distribution of blood and a comparatively clear separation

between afferent and efferent portions of the system (Fig. 50): the ambient extension of the costa joins the ends of the longitudinal veins so that an uninterrupted marginal circuit is provided from the humeral sinus to the axillary cord; open veins are a feature of the wings around the distal junction of the costa and subcosta where a stigma-like sinus is formed. The mechanism involved in circulation in the wings is also comparatively clear: the thoracic pulsatile organs are more clearly visible than in most other insects and can be seen to aspirate blood from the wing with sufficient force to cause movements of the axillary cord and of flexible areas at the basal junction of the anal veins; at the same time blood in the thorax can be seen flowing past the wing bases uninfluenced by the action of the pulsatile organs. Along with these features, the insects are relatively placid, the few pigmented areas in the wings do not obscure the veins, and circulation is moderately strong and clearly visible due to its high complement of haemocytes.

As in almost all other insects, a portion of the blood that enters the wing base avoids the circuit through the veins and passes directly to the axillary cord. In *Panorpa* this route is via a basal medio-cubital channel (Fig. 51) which joins directly with the flexible union of the cubitus and the anal veins at the axillary cord. A more distal medio-cubital cross-vein also directs blood from the afferent stream in the proximal part of the media to the efferent one in the cubitus. When the current in this cross-vein is swift, the distal portion of the media is efferent and contributes blood to the same stream.

The activity of the thoracic pulsatile organs and its effect on the efferent current in the wing veins is comparatively clear in these insects. The flexible areas in the axillary cord and in the basal junction of the cubitus and anal veins pulsate in rhythm with the organs and the action is expressed in the pulsing movement of the blood in the neighboring veins. There is considerable fluctuation in the activity of the organs and the rate of pulsation may vary from approximately 65 to 100 beats per minute. It is usually more rapid than the beat of the heart in the same region. The rate is the same in the two wings of each pair but is usually slightly different between the two pairs. There is little doubt that the nervous control for the pulsatile organs is distinct from that for the heart, and that there is no regulatory mechanism operating to maintain equivalent action in the two.

Order: Trichoptera

Blood circulation is seldom strong in the wings of Trichoptera but the current is comparatively steady and the route distinct and constant. The fore and hind wings are somewhat different in the species studied here, mainly in the greater extent of the anal area in the hind wings. The only reference to wing circulation in these insects is a brief one by Tyrrel (1835) where *Phryganea* is included among the insects in which he observed the phenomenon.

Materials

Observations were made on species from the families Hydropsychidae, Limnophilidae, and Phryganeidae (see Appendix). The observations included some on the effects of blocking certain veins to determine the resultant routes and thereby the mechanical principles involved in the pattern of flow. The paucity of tracheae in the veins of Trichoptera make them especially suitable for studies of this nature.

Observations and Discussion

Although the wing venation in Trichoptera is basically similar to the hypothetical primitive system and not unlike the system in Mecoptera, it is sufficiently

different to cause significant changes in the route of blood circulation, particularly in the fore wings. The changes involve mainly the distal branches of the radius and media where a series of cross-veins, close to the final bifurcations, form an interrupted channel across the wing proximal to the outer margin (Figs. 53 and 54). This channel, despite its lack of continuity, carries a stronger current than the more distal ambient costa and attracts blood from the latter through all, or almost all, of the terminal longitudinal veins. In the fore wings this route crosses to the posterior edge of the wing and finally contributes blood to the cubitus and the distal portions of the anal veins via a short channel reminiscent of the common afferent-efferent cross-vein in the fore wing of Hemiptera. In the hind wings it terminates at a branch of the media and is not closely associated with the afferent-efferent cross-veins. In both wings the ambient costa provides a direct marginal route for the blood from the humeral angle to the axillary cord; from it the anal veins of the hind wings receive all of their blood supply. Among the species examined, only *Limnophilus rhombicus* (L.) had a stigma-like sinus from open veins around the costa-subcosta junction, but it probably occurs in other species. In all cases a constant stream of blood passes directly from the humeral sinus to the axillary cord via the arculus-like transverse basal channel (Fig. 52) without entering the veins. A portion of the blood in the media is also directed almost immediately into the efferent stream of the cubitus via the proximally situated medio-cubital cross-vein. Infrequently in most individuals there occur periods of fluctuating blood pressure in the wings and reversal of the normal direction of flow in association with struggling movements of the insect.

The comparatively weak, steady current of blood in the wings is concomitant with rapid, shallow pulsations of the thoracic pulsatile organs and this relationship seems to be somewhat characteristic of the order. The organs were only vaguely visible in a few of the insects examined but their pulsations were usually evident in the axillary cords. In the majority of specimens the rate of pulsation was greater than the heart beat at the same region and often it was approximately double the heart rate. In *Pycnosyche* sp. for example, the relationship of heartbeat to pulsatile organ activity for five individuals averaged 51 to 98 beats per minute respectively. In *Limnephilus* sp. it was 41 to 82. In *Macronema zebratum* however the relationship was reversed (63 to 33) even though circulation in the wings was no less efficient than in the others.

The experimental blockage of individual veins caused only local changes in the circulatory route and these changes were predictable from principles of haemodynamics. For example, blockage of any of the unbranched veins such as the costa, subcosta, or radius-one caused the stoppage of flow only within themselves because the remainder of the system is a complete circuit without them (see Fig. 53). Blockage of the main stem of a branching vein, such as the radial sector or the media, resulted in cessation of flow within the vein and removed the original afferent force from its branches. The branches then accommodated a reduced current of blood from other sources and in directions that continued to complete the circuit without the stem vein. Thus in the case of the blockage of the radial sector, the anterior branch of its bifurcation (radius-two plus three) received blood from veins anterior to it (e.g. radius-one or radius-two or both) and became efferent. The blood flowed slowly toward the point of blockage. At the bifurcation it necessarily reversed direction and flowed afferently in the posterior branch (radius-four plus five) as it had done originally. The whole sector continued to receive blood at a reduced rate with only slight modification of the circulatory route.

Order: Lepidoptera

Wing venation in the Lepidoptera corresponds closely to Comstock's hypothetical primitive type. The main divergence from it in certain families is in the reduction of the media and its branches. The route of circulation conforms generally to the basic pattern for such a system of veins and with appropriate changes where such divergences occur. However, the amount of blood in the wings and the force of the current are markedly less than in most other insect orders. This is due to the large wing tracheae which almost fill the lumens of the main veins and occupy a considerable portion of many of their branches (Fig. 59). In some veins the blood channel is little more than a thin space around the tracheae and is scarcely wide enough for haemocytes to pass singly. The haemocytes also have difficulty in entering the wings, because of the large tracheal trunks in the bases, and comparatively few occur in the veins at a given time. In many cases their scarcity and the obstructions to their movement make it difficult to detect circulation in the wings even when the surface scales have been removed or cleared. Nevertheless, circulation is moderately strong in young adults of some species and follows a complete circuit. It becomes noticeably reduced with age, and this undoubtedly accounts for the progressive fraying of the distal margins of the wings and the eventual cessation of wing circulation when cross channels are broken.

Early workers apparently failed to see circulation in wings of Lepidoptera although some suggested that it must occur. Recent authors have mentioned it sparingly. Bervoets (1913) noted blood in the hind wings of a pierid. Brocher (1916, 1919) demonstrated the function of the thoracic pulsatile organs, mainly in *Sphinx convolvuli,* without commenting particularly on circulation within the wings themselves. His work was recognized by Portier (1932) who suggested, with some experimental evidence, that wing circulation assisted respiration during flight. This suggestion has not been confirmed by recent studies. Zeller (1938) described circulation in the pupal wings of *Anagasta* (*Ephestia*) *kuhniella* Zell. but observed that circulation in the adult wings was slight even in young individuals. He felt that the thoracic pulsatile organs drew blood only from the wing bases and his observations were supported by those of Stehr (1947) with the same insect. In the present studies *A. kuhniella* was not included among the pyralids examined but it seems unlikely that it would differ significantly from others. In the ones examined, wing circulation was perhaps weaker and less obvious than in species from other families but it was nevertheless complete and generally typical of the order.

Materials

Observations were confined to members of the suborders Frenatae and Rhopalocera but there is little reason to suspect major differences among the Jugatae which were neglected here. Species from five families were represented (see Appendix), and special attention was given to those from Geometridae and Noctuidae, where circulation was most vigorous.

Observations and Discussion

The circulatory route in a geometrid (Figs. 55 and 56) is basically representative of the Lepidoptera. There, as in the species examined from other families, the main stem of the media is absent and there is no blood channel in its position. Presumably, in species where the media persists it will carry an afferent current as it does, basically, in other insects with similar venation. In the absence of the media the afferent and efferent veins in different species are more or less widely separated by the cell R + M. The main afferent flow occurs in the veins anterior

to the cell and efferent currents characterize those posterior to it; there is, of course, some efferent movement of blood in certain distal branches of the afferent system near the apex and some afferent flow in one or more of the veins leading from the end of the cell to the outer margin. In the fore wings the change-over from the afferent to the efferent veins is accomplished through two channels: one is the cross-vein or series of short veins which join the radius and cubitus at the end of the cell R + M and unites the bases of the medial branches; the other is the ambient costa which carries blood marginally to the axillary cord. In the hind wings, as described below, the change-over may or may not occur in the same way according to the family.

A peculiar feature of circulation in the fore wings of geometrids is the movement of blood in opposite directions on the two sides of a trachea suspended centrally in the lumen of certain veins (Fig. 58). It was not observed in members of other families but it may not be uncommon; similar double circulation occurs in short portions of some veins in the tegmina of cockroaches. In the geometrids it occurs principally in the distal branches of the radius and media. Blood flows afferently in the anterior half of the veins to their termination in the ambient costa at the outer margin of the wings. Midway along the veins however part of the blood passes around the trachea and flows efferently behind it to join the current in the aforementioned radio-cubital channel. The reversal occurs at about the same region of the veins whether the trachea continues in its suspended position or becomes adherent to the vein wall. Apparently the blood flows through openings in the membrane that suspends the trachea and divides the veins longitudinally. The change in the direction of flow behind the tracheae demonstrates a haemodynamic principle and reflects the difference in the size of the two afferent-efferent cross channels and the force of the currents within them. The radio-cubital channel is the larger, is closer to the wing base, and carries the stronger current. It therefore attracts more blood from the distal regions than the ambient costa which, because of its small size, cannot accept the normal outflow from the afferent veins. In so doing it allows circulation to continue in the main area of the wings in old adults where the outer margins, including the ambient costa, are broken.

The venation in the hind wings is quite different from that of the fore wings, in Comstock's view, but distinctions between them in the route of circulation are not great. The main stem of the media was absent from the hind wing of all of the species examined here, and, as in the fore wings, the main afferent veins were separated from the main efferent ones by a long discal cell. In some families, as in Geometridae (Fig. 56), the cell is terminated by a discal cross-vein extending from the radius to the cubitus or their corelatives and the afferent-efferent exchange of blood is then the same as in the fore wings. In others however, as in Olethreutidae (Fig. 60), the cross-vein is absent and the only course of exchange is via the ambient costa in the outer margin. Consequently, complete circulation in the wings is limited and depends upon the persistence of this single vein. This limitation is presumably responsible for modifications in the route of circulation in the region anterior to the discal cell where blood flows afferently only in the vein at the costal margin and in the main trunk of the other compound vein. The anterior branches of the latter carry blood to it from the costal vein in an efferent direction. The names of these veins seem to be controversial, partly because the costa is considered to be reduced or absent. The present studies show that it is present as a blood channel, but not heavily sclerotized.

There is some direct flow of blood through the wing bases (Fig. 57) but, as in the veins, its movement is hindered by the large tracheae. The suggestion by

aforementioned authors that this is the main passageway for the blood is untenable. Pulsations are rarely observed in the wings or their bases despite the presence of active thoracic pulsatile organs. Their action was faintly visible in some species, particularly of geometrids and pterophorids, and coincided with shallow pulsations of the axillary cords. The rate of pulsation was variable but usually greater than that of the heart.

Order: Diptera

In the generalized members of the Diptera the wing venation is said to be only slightly modified from the hypothetical primitive type. However the route of circulation is quite different from the basic pattern. At the same time the route is simple, direct, and easily observed, and the current is usually vigorous. In the specialized members of the order, the venation is variously reduced and the route of circulation conforms to it while maintaining the basic circuit of the generalized members; it is more difficult to observe, partly because the current is not usually strong, and partly because the haemocytes are hyaline and comparatively few in number.

A number of authors have published accounts of wing circulation in the order, mainly of species that may be considered specialized. Tyrrel (1835) commented briefly on blood circulation in the wings of *Musca domestica.* Bervoets (1913) recognized the presence of blood in the wings of the "bluebottle" fly and noted that less blood flowed from cuts made at the wing tip than from those made at the base. Brocher (1916) noted the pulsatile organs in tipulids and remarked on their similarity to those of *Dytiscus.* Comprehensive studies of wing circulation were later carried out by three authors. Hase (1927) described circulation in the wings of *Hippobosca equina* L. and noted variations in the rate of pulsation of "wing hearts". Thomsen (1938) worked similarly with *Musca domestica* L. and reported subscutellar pulsatile organs and four separate pulsatile organs within the wings. Perttunen (1955) studied circulation in the wings of *Drosophila funebris* and *D. melanogaster* and counted five accessory pulsatile organs within the wings.

Materials

Wing circulation was studied in members of each of the suborders Nematocera, Brachycera, and Cyclorrhapha. Representatives from 17 families were included: six families were among the Nematocera, six also from the Brachycera, and five from the Cyclorrhapha (see Appendix). Experimental studies to determine circulatory paths following the blockage of certain veins were carried out mainly with species from Tipulidae.

Observations and Discussion

There are significant differences at the family level in the route of blood circulation in the wings of the Diptera. These differences are mainly attributable to the presence or absence in combination of two features of the venation, the ambient or marginal extension of the costa, and the arculus or a functionally equivalent sinus in its position; although the arculus is generally recognized only in the family Tipulidae, the term is used here in its broadest sense, as by Comstock, to indicate a cross-vein (or blood channel) extending from radius to cubitus near the wing base. Less significant differences also occur concomitantly with minor variations in the venation and in the structure of the bases of the wings, and there are some rather exceptional variations in families such as Simuliidae where venation is highly modified.

There are three main routes of circulation in the different families of Diptera, each basically similar but with certain distinctive features. For comparison, the families may be separated into two groups, those in which the ambient costa extends around the entire margin of the wing, and those in which it terminates a short distance beyond the apex. Among the families examined here, the first group included Tipulidae, Asilidae, and Tabanidae, in each of which the wings also feature a prominent arculus. The second group may be subdivided into families in which the arculus or an equivalent sinus is prominent, and those in which it is insignificant or absent. It was prominent in the families Syrphidae, Sciomyzidae, Stratiomyiidae, and Simuliidae, among those examined, and absent in the remainder. The three categories have little or no taxonomic significance, except perhaps the third one which characterizes the Cyclorrhapha.

The ambient costa, in its position around the entire wing margin and as the terminus of the afferent and efferent longitudinal veins, provides for the circulation of blood throughout the wing. This is true of the vein in whatever insect it occurs, but among the Diptera it is especially effective and important as a channel for afferent-efferent exchange. This is partly because it is comparatively large and partly, or perhaps mainly, because of its association with a prominent arculus. The arculus carries a strong current of blood posteriorly near the wing base and the current in adjoining veins is directed toward it. This is a unique occurrence in a system of veins that approximates the hypothetical primitive condition. It is exemplified in the wings of Tipulidae.

In the Tipulidae (Figs. 61 and 70) a broad arculus crosses the wing near the base and joins the intervening veins from the radius to the cubitus. It occurred as a blood channel in each of the species examined, but was not always as heavily sclerotized as the other veins. This would account for the fact that it is not recognized in all members of the family and is used as a taxonomic character. Afferent flow occurs in the costa and subcosta to the wing apex and in the radius and media only as far as the arculus. Beyond the arculus and posterior to the subcosta all of the veins are efferent. They carry blood from the distal regions to the arculus which acts as a common channel directing blood into the axillary cord. Only the ambient costa by-passes the arculus completely and joins the axillary cord more or less separately. The current in the arculus is strong and combines the force of the afferent streams from the bases of radius and media with the aspirating force of the thoracic pulsatile organs. The latter is the more significant; this is evident from pulsations of flexible portions of the arculus wall and of contained tracheae and associated tissues in synchrony with movements of similar areas and structures in the wing base, of the axillary cords, and of the pulsatile organs themselves. The average rate of pulsation for ten individuals was 116 per minute and exceeded the heart-beat, which was 83 per minute, at the same region. Both were variable, however, and periodically the rate of the pulsatile organs was less than that of the heart or exceeded it greatly. There was no evidence to indicate that separate pulsing areas and tissues, that occur particularly in the wing bases and arculus of several species, were independent pulsatile structures. Their activity was usually attributable to pulsations of the thoracic organs or the heart and they appeared to be flexible areas of the vein walls or portions of connective strands that attached tracheae or nerves to the walls. This is contrary to the findings of aforementioned authors with species other than the ones studied here.

In Tipulids, as mentioned previously, the efferent flow of blood from the outer margin of the wings to the arculus and thence to the axillary cord is effected mainly by the aspirative force of the strong current in the arculus. This

current was studied experimentally by blocking separately, and in combination, the veins that enter the arculus and by blocking the arculus separately at its entrance and exit. Blockage of one or more of the efferent veins stopped the flow only in the affected vein and resulted in local re-routeing of the streams through distal cross-veins without changing the main course of circulation. Blocking the afferent veins to the arculus, particularly the radius, resulted in an appreciable decrease in the force of circulation in the wing without altering the main course. Blocking the entrance to the arculus also failed to change the main course of circulation, except that the radius became afferent for its whole length. Finally, blocking the arculus at its exit into the first anal vein caused a temporary complete stoppage of wing circulation followed by a slow return with the current much reduced in strength and with the course somewhat altered and variable. The entire wing continued to be served by blood which now flowed from the outer margin to the axillary cord via the anal veins and ambient costa. Blood also continued to flow from the outer margin to the arculus, but slowly and only in the anterior veins, radius and media; it moved slowly away from the arculus in the posterior veins. Obviously the afferent veins that enter the arculus contribute significantly to the current there but the main force is derived from the thoracic pulsatile organs. When this force is eliminated from the arculus the efferent movement of blood to that vein is reduced to a passive condition and the main course of flow is peripheral.

Although in Diptera the arculus and the ambient costa are associated with relatively vigorous circulation throughout the wing, they are not as closely interrelated functionally in all forms as they are in the tipulids. In the Asilidae, for example (Fig. 62), the arculus accepts only part of the blood from the radius and the main current continues afferently to the outer wing margin. The afferent-efferent exchange is then obtained through three channels, the arculus, the radio-medial cross-vein, and the ambient costa. Efferent flow in the cubito-anal veins converges to the common union at the base of the arculus and thence to the axillary cord. The main force is still derived from the thoracic pulsatile organs but it acts less through the arculus and more directly in the cubito-anal veins. The same course is followed in Tabanidae (Fig. 63) but there the current is somewhat dissipated in sinuses around open veins at the stigma area and at the arculus.

In the absence of the ambient costa the outer and inner margins of the wings are not served by the blood, the longitudinal veins are not all joined terminally, and the afferent-efferent exchange of blood in the distal regions occurs entirely through cross-veins or by unions of the longitudinal veins in other ways. Some changes in the route of circulation are necessarily involved and the area of the wings included in the direct route of circulation is reduced by different amounts in various families. There is also usually a reduction in the relative vigor of wing circulation, not necessarily attributable to the absence of the ambient costa. In its absence however circulation is generally more effective where an arculus is prominent than where it is small or absent. In the former case, for example in members of the family Syrphidae (Fig. 64), the route of circulation is only slightly modified from that in tipulids. The basic distinction between the two is in the extent of confluence of the radius and arculus. Whereas in tipulids all of the blood from the radius enters the arculus, in Syrphidae only part of it does and the remainder continues to flow afferently. The unique "'spurious vein" of the syrphids is also afferent. Although the ambient costa is lacking, the longitudinal veins approach the outer and inner margins at several points and most of the wing is included in the direct route of circulation. This is not the case in members of other families such as Sciomyzidae (Fig. 66) where the confluence of

anal veins is removed from the margins. It is still less so in Mycetophilidae (Fig. 67) and in Simuliidae (Fig. 68) where the outer region is more or less devoid of circulating blood. In Mycetophilidae, blood occupies the cubito-anal veins but they are not a part of the direct circuit. Blood enters and leaves them intermittently in conjunction with gushing of blood in the wings. In Simuliidae, circulation is limited to the anterior margin and the wing base; the basic mechanism is unchanged but radius-one and the radial sector serve as efferent channels for blood from the costa near the wing apex.

In Diptera where both the arculus and ambient costa are absent, as in the family Dolichopodidae (Fig. 65), most of the blood that enters the wing follows a complete course through the veins. The only short course available to it proximally from the afferent to the efferent sectors is through the small radio-medial cross-vein. Alternation of the direction of flow is common in successive veins, apparently to compensate for the few available channels, and the anal area is poorly served. Circulation tends to be less vigorous than in wings where the arculus is prominent but it is nevertheless comparatively steady.

In all Diptera some of the blood that enters the wings follows a rather tortuous course through the wing base to the axillary cord without entering the veins. In those without an alula (Fig. 70) the basal stream joins directly at the anal angle with blood flowing from the vein complex and the current is relatively swift. It is less swift but the route is similar in forms such as tabanids (Fig. 71) where the anal veins are not prominent and are removed from the inner margin at the anal angle. Where alulae are well developed, as in muscids (Fig. 72), the route is similar again but less direct; part of the blood is directed through the margins of the alulae before entering the axillary cord.

The halteres also support a circulation of blood (Fig. 69) but the flow is generally slow and irregular. The route followed is basically the same as in the normal wing. Blood enters the anterior channel, circles through the knobbed extremity, and returns to the body through a posterior channel that terminates in the facsimile of the axillary cord. The irregularity of the pulse suggests that the flow is not controlled by pulsatile organs, but responds to heart activity and respiratory and other movements.

Discussion and Conclusions

Blood circulation in one form or another was a constant feature in the wings of all the insects examined during the course of this study. Approximately 100 species from fourteen orders were included, and they represent a fair sampling from the class, with the wings widely varied in size, form, and venation. They add to the already large number and variety of species in which wing circulation has been reported, and confirm the opinion that circulation occurs in the wings of all pterygotes, however modified these appendages may be.

In a very general sense, the route of blood circulation in insect wings is described in Carus' (1831) rule which states that blood flows from the insect body through the anterior margin of the wings and returns to the body in the posterior margin. For most insects, the route may be described more precisely than this, as in the preamble to the preceding section, but it is difficult to conceive of comprehensive rules or laws of circulation that would apply to all species. Probably the closest facsimile to these would be a synopsis of circulation that gives the normal direction of blood flow in the basic wing veins and their main branches along with notations on the most frequent deviations.

The following synopsis of wing circulation applies most readily to wings that approximate Comstock's (1918) interpretation of the hypothetical primitive

condition, but may be interpreted also for those where the number of veins is increased or moderately reduced; extreme reduction in venation may completely alter the basic course of circulation in the wings. Specialization of the wings by addition of veins increases the number of accessory or intercalary veins, not the number of basic veins, and merely provides more channels through which blood is carried in the same direction as it is in the basic veins from which they branch or between which they are inserted. Similarly, a moderate reduction in venation implies that neighboring veins within one of the basic groups have coalesced, or at least that one or more members of a group are absent. In either case, the original direction of blood flow is maintained in the remaining veins of the group. Comstock's system of wing venation is based on the premise that the main wing tracheae are constant in number and that the principal veins form along the courses of tracheae. It has been shown by several authors, and recently by Whitten (1962), that certain aspects of this premise are questionable and certain of its corollaries, particularly with regard to tracheal homologies at broad taxonomic levels and to tracheal fusion and migration, are untenable. The present study demonstrates further that some principal veins occur in the adult wing where apparently no tracheae existed during wing development. In some instances these veins are not evident in dead specimens and were considered by Comstock to have fused with neighboring veins; his interpretations of the structural composition of some veins was consequently mistaken. Regardless of the significance of these findings in phylogenetic and other studies however, they do not seriously affect vein terminology, and the present synopsis uses Comstock's system.

Costa: this vein, or the channel or sinus that occupies its position along the costal margin of the wing, is invariably afferent during normal circulation and usually supports a strong current of blood, at least in the proximal region. Despite its prominence as a blood channel it is not always evident in dead wings and was overlooked by Comstock in some insects. In many insects it extends around the entire margin of the wing, receives blood from the other afferent veins, contributes blood to terminal efferent veins, and is a direct conduit for blood around the circumference of the wing to the anal region. Comstock considered this to be a thickening of the wing margin and termed it the *ambient vein;* here it is termed the *ambient costa.*

Subcosta: the subcosta is normally afferent throughout its length. Frequently it supports a stronger flow of blood than the costa and contributes some of it to the latter via cross-veins or sinuses. The current in the *humeral cross-vein*, which commonly joins the bases of the costa and subcosta, may be in either direction depending on its position in different species and on the relative force of the current in the two main veins.

Radius: the main trunk of the radius is normally afferent and usually carries the major outflow of blood from the body. The direction of flow in its branches is less definite, but it too is basically afferent. There is a tendency, however, for successive branches of the radius to carry blood in opposite directions. Ideally this creates an extensive alternating movement of blood in the distal part of the wing. In species where this does occur, *radius-one* is efferent; it accepts blood from the costa or its equivalent and directs it inward toward the radial sector; some of it becomes diverted posteriorly through the *radial cross-vein* and the remainder continues inward and becomes reversed in direction as it joins with the strong afferent current in the radial sector. The *radial sector* is afferent and so are both branches from its initial bifurcation. However its terminal branches, *radius-two, -three, -four,* and *-five* tend to be consecutively efferent and afferent, as mentioned above. This tendency is seldom dependable over a period of time

and the blood may flow in either direction intermittently while following a course that is mainly toward the posterior. This direction is obtained by means of the *sectoral* and the *radio-medial cross-veins* or their equivalents and by the ambient costa. In some insects, and especially during periods when the blood pressure is high, all of these branches are afferent.

Media: fundamentally the media is an afferent vein and the blood course in it and its branches is similar to that in the radius. However, the current in it is seldom as strong as that in the radius and the direction of flow is consequently more variable. In insects where the base of the media is more closely associated with the cubitus than with the radius, or where the basal *medio-cubital cross-vein* is prominent, the course is mainly efferent, especially when the blood pressure is low.

Cubitus: the cubitus and its branches are typically efferent; generally they accept blood from the ambient costa or from cross-veins from the radio-medial system, or both, and contribute it directly into anal veins or into the wing base at the anal angle. Occasionally the course of flow is variable.

Anal: the anal veins are invariably efferent; they accept blood from the ambient costa, where it exists, and from cubital cross-veins and carry it directly into the basal region of the axillary cord.

Not all of the blood that enters the wings continues through the veins. Part of it may immediately flow posteriorly through the wing base or through channels just beyond the base and reenter the body directly. The proportion which thus by-passes the main area of the wings is probably small in most insects but it is variable and seems to be governed partly by structural features such as the size and position of the axillary sclerites, the completeness of membranes in the wing bases, the nature of the wing veins, and partly by the blood pressure. Axillary sclerites and membranes in the wing bases tend to obstruct the current. On the other hand, where the lumen of a vein is narrow and the walls inflexible the blood tends to follow the easier course through the base or near it. Similarly, this course tends to be followed when the blood pressure is low.

The above synopsis of the circulatory route refers briefly to a common feature of wing circulation, the variability in the course of flow that results from fluctuations in blood pressure. Periodically in any insect, circulation in the wings may falter, reverse its direction of flow completely or in part, or stop entirely for short intervals. These periods of change tend to increase in frequency and duration with age, but they are normal occurrences at any age. They are unquestionably expressions of the unconfined nature of the circulatory system as a whole, and of inefficiency on the part of the mechanism for wing circulation.

The open circulatory system in insects permits the occurrence of shifts in pressure within areas of the haemocoel as a result of muscular contractions. This is a useful feature and serves a variety of functions, but it also interferes with the normal course of circulation in the wings; the wing veins are extensions of the haemocoel and the blood there is subject to pressure changes in the body. When these changes are marked, they dominate the regular forces involved in wing circulation. In some insects, for example, blood may be forced back and forth through the wings in rhythm with pressure changes accompanying exaggerated respiratory movements, even though the heart and accessory pulsatile organs are apparently functioning in normal fashion. Similarly, contraction of the abdomen in certain insects may cause a steady reversal of the normal direction of blood flow in the wings. Such extreme cases are more common among insects where the wings approximate the hypothetical primitive condition than among special-

ized forms, but they are not confined to them. Undoubtedly the rate and direction of blood flow varies in the wings during periods of activity such as flight when pressure changes in the thorax are probably extreme and rapid. The decline in circulation in the wings with age reflects the general retardation of circulation and, in wings with extensive venation, of occlusion of increasing numbers of veins by haemocytes.

The degree of constancy of circulation in the wings varies in different taxonomic groups. In some orders, such as Ephemeroptera, fluctuations are almost continual, whereas in others, such as Hymenoptera, they are comparatively rare. Similarly, the strength or rate of wing circulation is broadly characteristic of taxonomic groups. In Plecoptera and Hymenoptera, for example, the flow is vigorous and seldom falters, whereas in certain members of Trichoptera and Lepidoptera it is comparatively slow and feeble. These distinctions are easily recognized but difficult to interpret precisely. Undoubtedly the constancy and vigour of circulation in the wings are related to features of general morphology and particularly to the structure of the thorax and the wing bases. Certainly they are also related to the nature, extent, and complexity of the blood channels in the wings as well as to the efficiency of the circulatory system as a whole. A simple analogy would suggest that a more efficient pumping mechanism is required to provide equal circulation in a wing with extensive venation or one with large sinuses than in one where the venation is in the form of a simple circuit. It does not necessarily follow, however, that circulation is vigorous in wings where the venation is simple. Other factors, as mentioned above, complicate the situation. For example, where the entrance to the wings at the humeral angle is narrow or largely occupied by tracheae the flow of blood may be limited, regardless of the simplicity of venation. The same may be true where the veins are narrow or their lumens obstructed. In any case, the circulation may be slight during periods of rest and swift during periods of activity when the blood pressure is high, depending upon the efficiency of the heart and the accessory pulsatile organs.

There is some evidence of a relationship between wing circulation and flight, but it is only partly convincing. In Ephemeroptera and Odonata, for example, flight is more efficient in Odonata where circulation also is more controlled. Similarly, in many Hymenoptera and Diptera where flight is rapid and can be sustained for long periods blood circulation in the wings is noticeably more efficient than in some Cursoria or Orthoptera where flight is feeble. Other examples of a direct relationship may be selected, but it seems much more likely that structural differences, rather than circulatory ones, are primarily involved, along with such factors as the ratio of body weight to wing area or to volume of flight muscles, and with physiological distinctions. Moreover, if certain related insects are compared, such as tipulids and syrphids, circulation seems equally strong in the wings of each but flight efficiency is quite different; in this case the syrphids are much the stronger fliers. Further speculation might suggest that the volume or weight of blood in the wings in relation to wing area is an inverse function of flight efficiency. This too is not very convincing. It is true that tegmina, hemelytra, and elytra, which are not effective in flight, contain more blood than flight wings in the same insects that bear them, and also that the wings of many feeble fliers, such as plecopterans and neuropterans, are extensively veined and must contain relatively large quantities of blood per unit area. On the other hand, the flight wings of flightless cursorians apparently contain no more blood than those of some arboreal orthopterans which are capable of sustained flight, and the strongly flying syrphids have relatively more blood in the

wings than the weaker simuliids. Obviously, these relationships are difficult to equate, but it seems unlikely that circulation in the wings is directly significant in the mechanics of flight. Indirectly, however, it is undoubtedly important in maintaining the structural integrity of the wing and in nourishing sensory structures that are directly or indirectly involved in orientation and stabilization of flight.

The mechanism for circulating blood in the wings is complex, and a complete explanation of it awaits further study. It is basically the same in all insects but varies in detail and is influenced by different factors in the various groups. In general, the main forces involved come from the heart, which indirectly propels blood into the anterior portion of the wings, and the thoracic accessory pulsatile organs which draw blood from the posterior portion and return it to the body. These two forces working together maintain the circular route of flow which is generally characteristic of the wings in all orders. There is no doubt that the blood enters the wings under pressure, for pulsations of the heart are often apparent in the afferent veins, and changes in pressure within the body affect the flow in the wings. The pulsations from the heart are not normally discernible at the apex of the wing, and apparently the original propulsive force is dissipated in the afferent system of veins. The force required to move the blood through the efferent system of veins and thus complete the circuit is the one, already mentioned, provided by the accessory pulsatile organs acting through the axillary cord. It is reportedly supplemented in some insects by pulsatile tissues within the wings, but this was not confirmed in this study. Some of the force may also develop from the heart which is connected with the pulsatile organs and acts in a similar fashion; it normally aspirates blood from the pericardial sinus in many insects, and in the same way may draw blood from the pulsatile organs. In some insects it is difficult to distinguish the action of heart and pulsatile organs because of the close degree of their association and the synchronization of their pulsations. In a few, distinctive pulsatile organs are not evident but seem to be represented by lateral extensions of the heart. Generally, however, the beat of the heart and of the pulsatile organs are not synchronous, and it is the beat of the organs that is expressed in the flexible portions of the axillary cord and anal veins. Occasionally, pulses that are attributable only to respiratory movements register also in these flexible areas and suggest that normal, rhythmical, respiratory movements also assist in drawing blood from the wings. On the other hand, the rhythmical contractions of connective tissue which cause the constant undulation of viscera and contribute to the movement of blood in the body cavity evidently do not affect wing circulation; at least no comparable pulse is evident in the wings. The effectiveness of the whole mechanism depends on the efficiency of the organs involved and on structural features of the thorax, wing bases and veins. In insects where the wings are highly modified the mechanism may be rudimentary or absent and circulation in the wings is reduced to a relatively passive condition; blood gushes into and out of the wings intermittently in response to changes in pressure in the body haemocoel and may or may not follow a circular path.

There is a general tendency for blood circulation to be less extensive and slower in the hind wings than in the fore wings, especially where there is an appreciable discrepancy in the size or nature of the two pairs. Circulation in the hind wings tends also to be less affected by changes in pressure within the body haemocoel. Presumably these distinctions are due to structural differences, including the smaller size of pulsatile organs of the metathorax. There may be some slight advantage to this tendency in keeping the weight of blood in the wings low while a constant supply is assured to maintain flexibility and sensitivity.

Differences in the circulatory route in the wings of various taxonomic groups are due mainly to the influence of distinctive features of wing structure and venation on the manner in which the blood can be accommodated. Features which alter the route significantly are usual at the order level of the taxonomic system, occur commonly at the family level, and may be evident at the generic level in some families. Specific differences are usually insignificant. Whatever these features may be, whether they are extensive structural characteristics of the entire wing as in tegmina or elytra, less obvious structural details of the wing bases, peculiarities in size or configuration of the veins, etc., they can modify the circulatory route only within the framework of haemodynamic principles which govern the flow. Undoubtedly, the movement of blood in the wings is governed by those physical laws which apply to the flow of liquids in any system of connected cylindrical tubes and is comparable, with certain reservations, to flow in the mammalian vascular system. It is complicated by the aforementioned and other peculiar structural features and by a number of unestimated and variable factors such as the combined volume output of the heart and accessory pulsatile organs, blood viscosity, blood volume, elasticity of the wing veins, leakage from the veins, and resistance to flow. It is also complicated by the physical separation between the two pumping mechanisms involved, the heart and the pulsatile organs, and the fact that their action may not be synchronous and result in some damming back of the blood in parts of the system; the same result may develop from shifts in pressure within the body haemocoel. It is in this aspect, the damming back of blood, probably more than in the others that the system in insects differs from the mammalian; in the latter, both sides of the heart eject the same quantity of blood in a given time and the problem is avoided.

In spite of these complicating factors, certain recognized haemodynamic principles are seen to operate in the wings, at least during periods when the circulation is stable. Probably the most obvious principle involved, and perhaps the most important, is the inverse relationship between lateral pressure and velocity of outflow. It accounts for the movement of blood toward veins wherein the flow is swiftest, and accordingly for its direction into main channels which lead most directly from the entrance to the exit from the wing. It is evident, for example, in the movement of blood toward the arculus in certain dipterans, in the flow through cross-veins between parallel, longitudinal veins of different size, e.g. from subcosta to costa or radius, and in the flow of blood in opposite directions in the two branches at a bifurcation where one branch is larger than the other; the latter is exemplified by the efferent current in radius-one toward the afferent stream in the radial sector. The same principle probably accounts for the greater precision and constancy of circulation in wings where the venation is reduced than in those where it is similar to or more extensive than the hypothetical primitive condition. Where the venation is reduced, as in the Hymenoptera, the pressure gradient in the relatively direct circuit from entrance to exit is great and the current is swift; blood in the distal portion of the vein complex is caused to flow toward the exit in a precise route also. Where the venation is extensive, as in Orthoptera, the route from entrance to exit is indirect and pressure is dissipated en route; pressure gradients are comparatively slight, the currents are relatively slow, and the direction of flow may be somewhat imprecise and variable.

Undoubtedly, a number of other haemodynamic principles are involved in wing circulation but their effect is entirely speculative. Some are mentioned here to show possible causes for variability in the course and velocity of flow and to suggest areas for further study. The principle that resistance to flow varies

directly with the length of a cylinder is likely involved in the reduction of circulation that is commonly found near the wing apex. This effect probably also involves another principle, the inverse proportionality of velocity of flow to sectional area of a cylinder; presumably this operates as a result of the change in the diameter of veins as they proceed distally. Again, cross-veins introduce another principle of flow and another factor in directing wing circulation; longitudinal veins are divided into areas of relatively high pressure proximal to a cross-vein and low pressure distal to it, thereby complicating the route where venation is extensive, and again tending to keep circulation most vigorous near the wing base. These principles, and probably others, are involved in a complex interrelationship that directs blood through a surprisingly constant course in the wings. The degree of their involvement and a full understanding of the mechanism of wing circulation will come from measurements of pressure at various points in the system of veins.

The subject of the development of wing venation and of the homologies of veins continues to be controversial, and a knowledge of circulatory routes in the wings does not contribute convincingly to its solution. Obviously, the routes of circulation conform to the peculiarities of venation, not the reverse, and they can scarcely serve as criteria for establishing vein homologies. Nevertheless, they merit consideration, particularly in a role of demonstrating the existence of some veins which are not evident in the wings of dead specimens, and from which a concept of venation and vein homologies has been derived. Very often, for example, the costa has been considered absent where a clear blood channel exists in the normal position of that vein. Similarly, blood channels show the position of veins in the hemelytra of Heteroptera, and demonstrate the existence of an arculus in certain Diptera, where they are not detectable in dead specimens. These and certain other discrepancies that are mentioned in the text do not alter the basic concept of wing venation, but they may contribute to a correct interpretation of the composition of the vein complex in a number of insects. Present concepts of wing venation rest on either structural bases, derived from comparisons of modern with fossil insects, or on tracheal pathways in developing wings. Some of the main contributors include Tillyard (1917), Comstock (1918), Lameere (1922), Needham (1935), Forbes (1943), and Edmunds and Traver (1954). Few have mentioned the blood and nerve supply to the wings as potential adjuncts to the other criteria for determining vein homologies. Forbes (1943) mentioned the nerve supply but felt that knowledge of it was insufficient for interpretation. This is probably justified, but at the same time, the criteria already used are not entirely sound; there is still much to be learned of wing structure, and there is increasing evidence (Whitten 1962) that tracheal pathways are not as reliable as previously considered. This is not meant to imply that the criteria which have been used in the past are invalid or that present concepts of wing venation and vein homologies are unsound. It merely suggests that other criteria may be usefully included in future studies and in re-examinations of the subject.

Acknowledgments

I am indebted to officers of the Insect Systematics Section of the Entomology Research Institute, Ottawa, for identifying specimens and for contributing useful advice on aspects of the study that relate to taxonomy. Acknowledgment is also due to G. B. Wiggins, Royal Ontario Museum, Toronto, for determinations of Trichoptera, and to W. E. Ricker, Fisheries Research Board of Canada, Nanaimo, B. C. for determinations of Plecoptera. I wish also to thank J. A. Downes for critical comments which added materially to the manuscript.

APPENDIX

List of identified insects used in the present study of wing circulation.

Order: Ephemeroptera
- Family: Hexageniidae
  - *Hexagenia rigida* McD.
  - *Stenonema* sp.

Order: Odonata
- Family: Agrionidae
  - *Enallagma ebrium* (Hagen)
  - *Ischnura verticalis* (Say)
  - *Lestes unquiculatus* Hagen
- Family: Libellulidae
  - *Cordulia* sp.
  - *Sympetrum* sp.

Order: Cursoria
- Family: Blattidae
  - *Blaberus giganteus* (L.)
  - *Blattella germanica* (L.)
  - *Periplaneta americana* (L.)
- Family: Mantidae
  - *Mantis religiosa* Linnaeus

Order: Orthoptera
- Family: Gryllidae
  - *Oecanthus* sp.
- Family: Locustidae
  - *Melanoplus femur-rubrum* (DeGeer)
  - *Melanoplus bivittatus* (Say)
  - *Chorthippus curtipennis* (Harris)
  - *Chortophaga viridifasciata* (DeGeer)
  - *Dissosteira carolina* (Linnaeus)
  - *Encoptolophus sordidus* (Burm.)
- Family: Tettigoniidae
  - *Conocephalus fasciatus* (DeGeer)
  - *Scudderia furcata* Brunn.
  - *Scudderia pistillata* Brunn.

Order: Plecoptera
- Family: Pteronarcidae
  - *Acroneuria arenosa* Pictet
- Family: Perlidae
  - *Perla* sp.

Order: Hemiptera (Heteroptera)
- Family: Belostomatidae
  - *Belostoma fluminea* (Say)
- Family: Corixidae
  - *Corixa* sp.
- Family: Miridae
  - *Adelphocoris rapidus* (Say)
  - *Adelphocoris lineolatus* (Reuter)
  - *Liocoris* sp.

Family: Nabidae
Nabis ferus (Linnaeus)
Family: Phymatidae
Phymata fasciata (Gray)

Order: Hemiptera (Homoptera)
Family: Aphididae
Aphis viburniphila Patch
Family: Cicadellidae
Draeculacephala producta (Wlk.)
Graphocephala coccinea (Forst.)
Gyponana sp.
Idiocerus sp.
Ormenis pruinosa Stal.
Philaenus spumarius (L.)
Family: Cicadidae
Okanagana sp.
Family: Membracidae
Acutalis tartarea (Say)
Campylenchia latipes (Say)
Gargara genistae Am. & Serv.
Stictocephala faurina (Harr.)

Order: Neuroptera
Family: Chrysopidae
Chrysopa sp.
Family: Hemerobiidae
Hemerobius sp.
Family: Mantispidae
Mantispa brunnea Say
Family: Myrmeleonidae
Myrmeleon sp.

Order: Hymenoptera
Family: Apidae
Apis mellifera Linnaeus
Colletes sp.
Family: Bombidae
Psithyrus sp.
Family: Chalcididae
Pachyneuron sp.
Family: Chrysididae
Elampus sp.
Family: Formicidae
Formica sp.
Lasius sp.
Myrmica sp.
Family: Ichneumonidae
Enicospilus sp.
Mimesa sp.
Pimplopterus sp.
Temelucha sp.

Family: Sphecidae
Ammophila sp.
Family: Vespidae
Polistes sp.

Order: Coleoptera
Family: Cantharidae
Cantharis scitulus Say
Family: Cerambycidae
Physocnemum brevilineum Say
Family: Chrysomelidae
Diabrotica duodecimpunctata F.
Oedionychis vians Ill.
Family: Cicindelidae
Cicindela punctulata punctulata Oliv.
Family: Coccinellidae
Coccinella transversoguttata quinquenotata Kby.
Family: Hydrophilidae
Tropisternus sp.
Family: Lampyridae
Ellychnia sp.
Family: Staphylinidae
Gyrohypnus sp.
Quedius sp.

Order: Mecoptera
Family: Panorpidae
Panorpa sp.

Order: Trichoptera
Family: Hydropsychidae
Macronema zebratum Hagen
Family: Limnephilidae
Anabolia bimaculata Walk.
Limnephilus rhombicus (L.)
Limnephilus submonilifer Walk.
Pycnopsyche sp.
Family: Phryganeidae
Phryganea cinerea Walk.

Order: Lepidoptera
Family: Geometridae
Deuteronomos magnarius Gn.
Prochoerodes transversata Dru.
Family: Noctuidae
Oligia mactata Gn.
Family: Olethreutidae
Eucosma sp.
Family: Pyralididae
Crambus trisectus Wlk.

Order: Diptera
- Family: Bibionidae
  - *Bibio* sp.
- Family: Mycetophilidae
  - *Epicypta* sp.
- Family: Psychodidae
  - *Psychoda* sp.
- Family: Simuliidae
  - *Simulium* sp.
- Family. Tipulidae
  - *Limonia cinctipes* (Say)
  - *Limonia parietina* (O.S.)
  - *Ormosia* sp.
  - *Tipula* sp.
- Family: Asilidae
  - *Asilus paropus* Walk.
- Family: Dolichopodidae
  - *Hydrophorus* sp.
- Family: Stratiomyiidae
  - *Sargus decorus* Say
- Family: Tabanidae
  - *Tabanus lineola scutellaris* Wlk.
- Family: Heleomyzidae
  - *Allophylla laevis* Lw.
- Family: Muscidae
  - *Coenosia tigrina* (Fab.)
  - *Musca domestica* L.
- Family: Sciomyzidae
  - *Hedroneura rufa* (Panz.)
- Family: Sphaeroceridae
  - *Leptocera* sp.
- Family: Syrphidae
  - *Eristalis arbustorum* (L.)
  - *Sphaerophoria robusta* Cn.

References

Agassiz, L. 1851. Note sur la circulation des fluides chez les insectes. *Ann. Sci. nat.* 15: 358-362.

Arnold, J. W. 1959. Observations on living hemocytes in wing veins of the cockroach *Blaberus giganteus* (L.) (Orthoptera: Blattidae). *Ann. ent. Soc. Amer.* 52: 229-236.

Arnold, J. W. 1963. A note on the pterostigma in insects. *Canad. Ent.* 95: 13-16.

Baker, H. 1744. The microscope made easy. London.*

Baker, H. 1755. On the microscope. London.*

Bassi, C. 1851. Rapport adressé à la section de zoologie, d'anatomie comparée et de physiologie du congrès de Venise, relatif au passage des substances introduites dans le système trachéen des insectes. *Ann. Sci. nat.* 15: 362-371.

Behn, F. W. G. 1835. Découverte d'un circulation de fluide nutritif dans les pattes de plusieurs insectes hemiptères. *Ann. Sci. nat.* 4: 5-12.

Bervoets, R. 1913. Notes sur la circulation du sang dans les ailes des insectes. *Ann. Soc. ent. Belg.* 57: 184-190.

Blanchard, E. 1851. Nouvelles observations sur la circulation du sang et la nutrition chez les insectes. *Ann. Sci. nat.* 15: 371-376.

Bowerbank, J. S. 1833. Observations on the circulation of the blood in insects. *Ent. Mag.* 1: 239-244.

Bowerbank, J. S. 1836. Observations on the circulation of blood and the distribution of the tracheae in the wing of *Chrysopa perla*. *Ent. Mag.* 4: 179-185.

Brocher, F. 1916. Nouvelles observations biologiques et physiologiques sur les Dyticidés. Étude anatomique et physiologique de deux organes pulsatiles aspirateurs, destinés a faciliter la circulation du sang dans les ailes et dans les élytres; utilé de l'alula. Constatation de la présence d'organes, fonctionnant d'une manière semblable, chez divers autres insectes (Hyménoptères, Diptères, Orthoptères, Lépidoptères, Névropteres). *Arch. Zool. exp. et gen.* 55: 347-373.

Brocher, F. 1917. Étude experimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. I. Le *Dyticus marginalis*. *Arch. Zool. exp. et gen.* 56: 347-358.

Brocher, F. 1919. Les organes pulsatiles méso- et métatergaux des lépidoptères. *Arch. Zool. exp. et gen.* 58: 149-171.

Brocher, F. 1920a. Étude expérimentale sur la fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. III. Le *Sphinx convolvuli*. *Arch. Zool. exp. et gen.* 60: 1-45.

Brocher, F. 1920b. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. IV. La *Vespa crabro*. *Ann. Soc. ent. France.* 89: 209-232.

Brocher, F. 1922. Étude expérimentale sur le fonctionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. V. La *Periplaneta orientalis*. *Ann. Soc. ent. France.* 91: 156-164.

Brocher, F. 1929. Observations physiologiques sur la circulation du sang dans les ailes et dans les élytres chez la Coccinelle. *Rev. Suisse Zool.* 36: 593-607.

Burmeister, H. C. C. 1832. Handbuch der Entomologie. Berlin.*

Carus, C. G. 1827. Vorläufige Nachricht über die Entdeckung eines deutlichen Blutlaufs bei Insecten. *Isis* 20: 318.

Carus, C. G. 1828. Nachträgliche Bemerkungen über den Blut-Umlauf in den Kerfen, insbesondere den Blut-Umlauf in volkommenen betreffend. *Isis*: 21: 477-481.

Carus, C. G. 1831. Fernere Untersuchungun über Blutlauf in Kerfen. *Nov. Acta Physico-Med. Acad. Caes. Leop-Carol.* 15: 1-18.

Chapman, R. N. 1918. The basal connections of the tracheae of the wings of insects, pp. 27-51. *In* J. H. Comstock, The wings of insects. Comstock, Ithaca, N. Y.

Church, N. S. 1960. Heat loss and the body temperatures of flying insects. II. Heat conduction within the body and its loss by radiation and convection. *J. exp. Biol.* 37: 186-212.

Clare, S. and O. E. Tauber. 1940. Circulation of hemolymph in the wings of the cockroach *Blattella germanica* L. I. In normal wings. *Iowa St. Coll. J. Sci.* 14: 107-127.

Clare, S. and O. E. Tauber. 1942. Circulation of hemolymph in the wings of the cockroach *Blattella germanica* L. II. Effect of cutting hemolymph channels in the normal tegmen and hind wing. *Ann. ent. Soc. Amer.* 35: 57-67.

---

* – reference not seen.

Clare, S. and O. E. Tauber. 1942. Circulation of hemolymph in the wings of the cockroach, *Blattella germanica* L. III. Circulation in the articular membrane: The significance of this membrane, the pteralia, and wing folds as directive and speed controlling mechanisms in wing circulation. *Iowa St. Coll. J. Sci.* 16: 349-356.

Comstock, J. H. 1918. The wings of insects. Comstock Publishing Co., Ithaca, N. Y.

Davis, C. C. 1956. Experiments upon the heart of *Chaoborus albipes* (Diptera, Culicidae). *J. cell. comp. Physiol.* 47: 449-468.

Davis, N. T. 1961. Morphology and phylogeny of the Reduvioidea (Hemiptera: Heteroptera). Part II. Wing venation. *Ann. ent. Soc. Amer.* 54: 340-354.

Drenkelfort, H. 1910. Neue Beiträge zur Kentniss der Biologie und Anatomie von *Siphlurus lacustris* Eaton. *Zool. Jb. Abt. Anat.* 29: 526-617.

Dufour, L. 1841. Études anatomiques et physiologiques sur une mouche, dans le but d'éclairer l'histoire des metamorphoses et de la pretendue circulation des insectes. *Ann. Sci. nat. Zool.* 16: 5-14.

Duvernoy, G. L. 1839. Résumé sur le fluide nourricier, ses reservoirs et son mouvement dans le regne animale. *Ann. Sci. nat.* 12: 300-346.

Edmunds, G. R. Jr. and J. R. Traver. 1954. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. *J. Wash. Acad. Sci.* 44: 390-399.

Forbes, W. T. M. 1943. The origin of wings and venational types in insects. *Amer. Midl. Nat.* 29: 381-405.

Freudenstein, K. 1928. Das Herz und das Circulationssystem der Hönigbiene (*Apis mellifica* L.). *Z. wiss. Zool.* 132: 404-475.

Hamilton, M. A. 1931. The morphology of the water-scorpion, *Nepa cinerea* Linn. (Rhynchota, Heteroptera). *Proc. zool. Soc. Lond.*, 1931: 1067-1136.

Hase, A. 1927. Beobachtungen über das Verhalten, den Herzschlag soure den Stech- und Saugakt der Pferdelausfliege *Hippobosca equina* L. (Dipt. Pupipara). *Z. Morph. Ökol. Tiere* 8: 187.

Janet, C. 1906. Sur un organe non décrit du thorax des fourmis ailées. *C. R. Acad. Sci.* 143: 522-523.

Kirby, W. and W. Spence. 1826. An introduction to entomology. London.*

Kuhl, W. 1924. Der feinere Bau des Circulationssystems von *Dytiscus marginalis* L. *Zool. Jb.* 46: 75-198.

Lameere, A. 1922. Sur la nervation alaire des insectes. *Bull. Acad. roy. Belg.* s.5. 8: 138-149.

Lehr, R. 1914. Die Sinnesorgane der beiden Flügelpaare von *Dytiscus marginalis*. *Z. wiss. Zool.* 110: 87-150.

Leston, D. 1962. Tracheal capture in ontogenetic and phylogenetic phases of insect wing development. *Proc. roy. ent. Soc. Lond.*, s. A. 37: 135-144.

MacGillivray, A. D. 1906. A study of the wings of the Tenthredinoidea, a superfamily of Hymenoptera. *Proc. U. S. Nat. Mus.* 39: 569-654.

Meyer, E. 1931. Über den Blutkreislauf der Ephemeriden. *Z. wiss. Biol.* abt. A., 22: 1-52.

Moseley, H. N. 1871. On the circulation in the wings of *Blatta orientalis* and other insects, and on a new method of injecting the vessels of insects. *Quart. J. Microscop. Sci.* 11: 389-395.

Needham, J. G. 1935. Some basic principles of insect wing venation. *J. N. Y. ent. Soc.* 43: 113-129.

Newport, G. 1837. On the temperature of insects and its connection with the functions of respiration and circulation. *Phil. Trans.* 127: 259-338.

Nicolet, 1847. Note sur la circulation du sang chez les Coléoptères. *Ann. Sci. nat.* s.3, 7: 60-64.

Orr, W. 1833. Book Review: Alphabet of Insects for the Use of Beginners. By James Rennie, London, 1832. *Ent. Mag.* 1: 64-65.

Patch, Edith, M. 1909. Homologies of the wing veins of the Aphididae, Psyllidae, Aleurodidae, and Coccidae. *Ann. ent. Soc. Amer.* 2: 101-129.

Pawlowa, M. 1895. Über ampullenartige blutcirculationsorgane im Kopfe verschiedener Orthopteren. Zool. Anz. 18: 7-13.

Perttunen, V. 1955. The blood circulation and the accessory pulsatile organs in the wings of *Drosophila funebris* and *D. melanogaster* (Dipt., Drosophilidae). *Ann. Ent. Fenn.* 21: 78-88.

Portier, P. 1932. Locomotion aerienne et respiration des Lépidoptères; un nouveau role physiologique des ailes et des écailles. *Proc. V Congr. int. Ent.* 2: 25-31.

Rennie, J. 1832. Alphabet of insects, for the use of beginners. London.*

Ross, H. H. 1956. A Textbook of Entomology. John Wiley & Sons, Inc., New York.

Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Book Co., New York and London.

Stehr, G. 1947. Beziehungen zwischen der Blutzirkulation im Puppenflügel und dem Zeichnungsmuster von *Ephestia kuehniella*. *Rev. Suisse Zool.* 54: 573-608.

Tauber, O. E. and S. Clare. 1942. Circulation in the wings of the cockroach, *Blattella germanica* L. IV. Circulation in unsclerotized wings under normal and experimental conditions. *Trans. Amer. microscop. Soc.* 61: 290-296.

Thomsen, Ellen. 1938. Über den Kreislauf im Flügel der Musciden mit besonderer Berücksichtigung der Akzessorischen pulsierenden Organe. *Z. Morph. Ökol. Tiere* 34: 416-438.

Tillyard, R. J. 1917. The biology of dragon flies. Cambridge Univ. Press, Cambridge.

Treviranus, G. R. 1831. Erscheinungen und gesetze des organischen Lebens. Bremen, Bd. 1, p. 220.*

Tyrrel, J. 1835. On the circulation of the blood in insects. *Proc. roy. Soc. London* 19: 317.

Verloren, M. 1847. Mémoire sur la circulation dans les insectes. *Mem. Sav. étr. Acad. R. Belg.* 19: 1-93.

Wagner, R. 1832. Beobachtungen über den Kreislauf des Blutes und den Bau des Rückengefaesses bei den Insecten. *Isis* (1832): 320-331, 778-783.*

Whedon, A. D. 1938. The aortic diverticula of the Odonata. *J. Morph.* 63: 229-261.

Whitten, J. M. 1962. Homology and development of insect wing tracheae. *Ann. ent. Soc. Amer.* 55: 288-295.

Wille, A. 1958. A comparative study of the dorsal vessels of bees. *Ann. ent. Soc. Amer.* 51: 538-546.

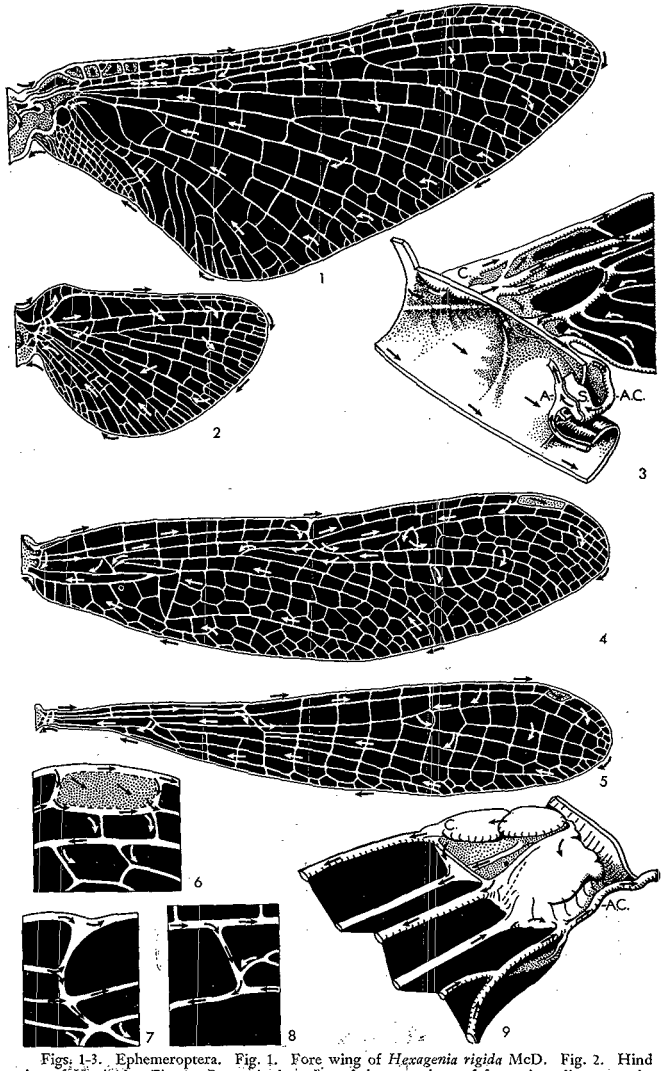
Yeager, J. F. and Hendrickson, G. O. 1933. A simple method of demonstrating blood circulation in the wings and wing-pads of the cockroach, *Periplaneta americana* Linn. *Proc. Soc. exp. Biol. Med.* 30: 858-860.

Yeager, J. F. and G. O. Hendrickson. 1934. Circulation of blood in wings and wing pads of the cockroach, *Periplaneta americana* Linn. *Ann. ent. Soc. Amer.* 27: 257-272.

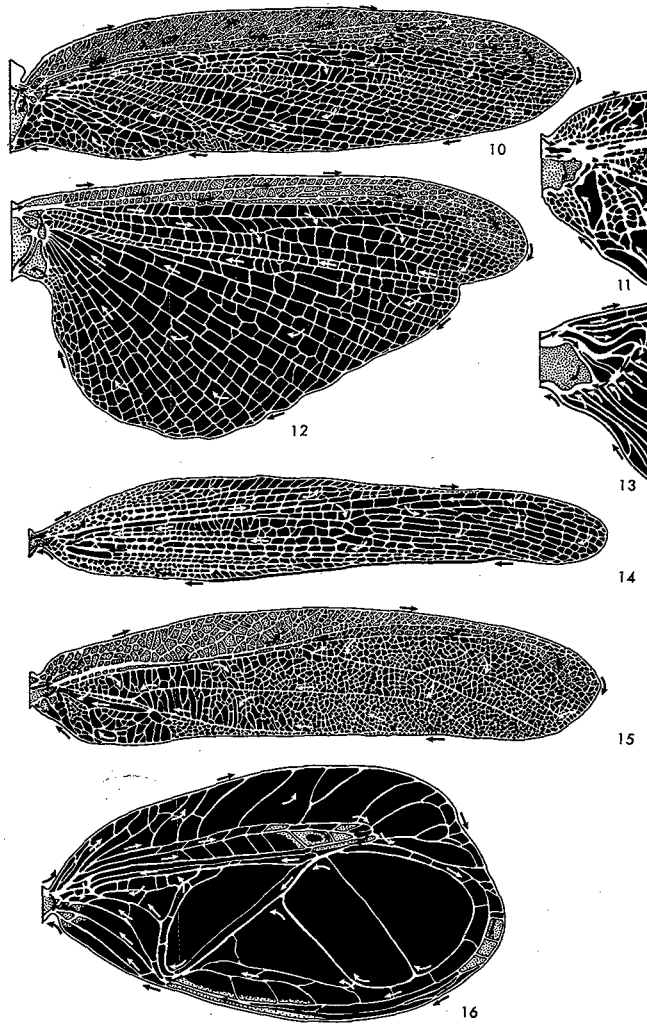
Zeller, H. 1938. Blut and Fettkörper im Flügel der Mehlmotte *Ephestia kühniella* Zeller. *Z. Morph. Ökol. Tiere.* 34: 663-738.

Illustrations

In each figure, arrows indicate the direction of blood flow. Stippled areas within the wings indicate the position of sinuses.

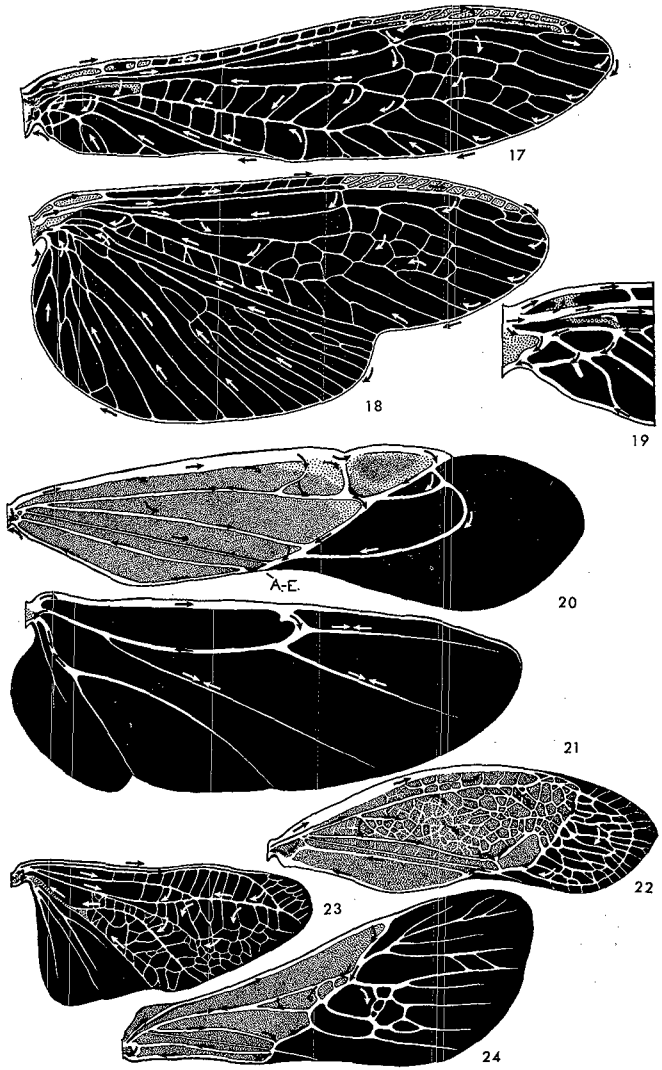


Figs. 1-3. Ephemeroptera. Fig. 1. Fore wing of *Hexagenia rigida* McD. Fig. 2. Hind wing of *H. rigida*. Fig. 3. Parasagittal section of thorax at base of fore wing, diagrammatic. Figs. 4-9. Odonata. Fig. 4. Fore wing of *Sympetrum sp.* Fig. 5. Fore wing of *Lestes unguiculatus* Hagen. Figs. 6, 7, 8. Pterostigma, nodus, and arculus respectively of *Sympetrum sp.* Fig. 9. Postero-dorsal view of wing base of *Sympetrum* sp. (dash-line indicates position of barrier to afferent-efferent flow). Abbreviations: A—aorta; A.C.—axillary cord; C—costa; S—scutellum.



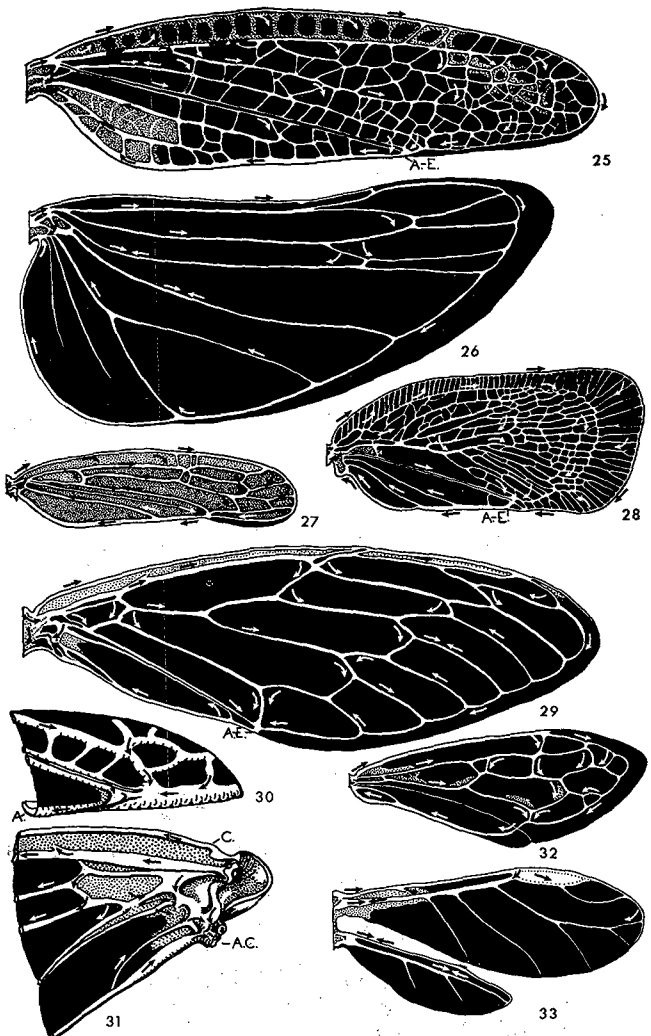
Figs. 10-13. Cursoria (Mantodea). Fig. 10. Fore wing of *Mantis religiosa* Linnaeus. Fig. 11. Base of fore wing of *M. religiosa*. Fig. 12. Hind wing of *M. religiosa*. Fig. 13. Base of hind wing of *M. religiosa*.

Figs. 14-16. Orthoptera (Saltatoria). Fig. 14. Fore wing of *Melanoplus femur-rubrum* (De Geer). Fig. 15. Fore wing of *Scudderia furcata* Brunn. Fig. 16. Fore wing of *Oecanthus* sp.



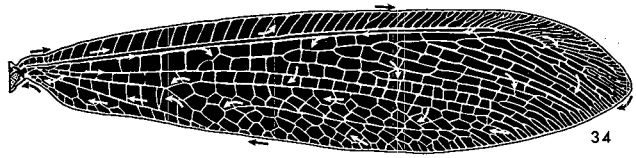
Figs. 17-19. Plecoptera. Fig. 17. Fore wing of *Acroneuria arenosa* Pictet. Fig. 18. Hind wing of *A. arenosa*. Fig. 19. Base of fore wing of *A. arenosa*.

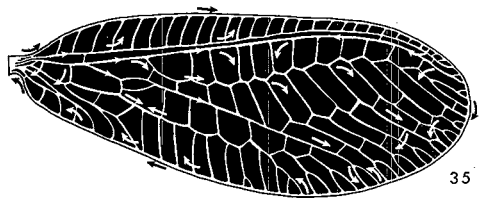
Figs. 20-24. Hemiptera (Heteroptera). Fig. 20. Fore wing of *Adelphocoris lineolatus* (Reuter). Fig. 21. Hind wing of *A. lineolatus*. Fig. 22. Fore wing of *Belostoma fluminea* (Say). Fig. 23. Hind wing of *B. fluminea*. Fig. 24. Fore wing of *Phymata fasciata* (Gray). Abbreviations: A.-E.–point of afferent-efferent exchange.

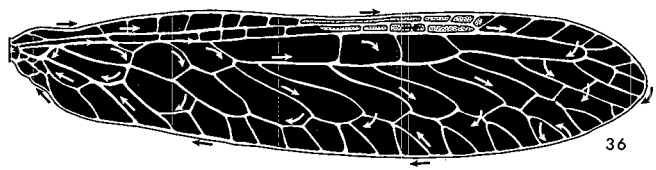


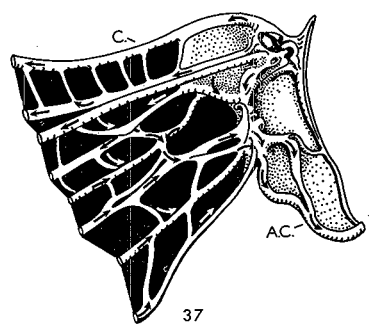
Figs. 25-33. Hemiptera (Homoptera). Fig. 25. Fore wing of *Gyponana* sp. Fig. 26. Hind wing of *Gyponana sp.* Fig. 27. Fore wing of *Graphocephala coccinea* (Forst.). Fig. 28. Fore wing of *Ormenis pruinosa* Stal. Fig. 29. Fore wing of *Okanagana* sp. Fig. 30. Enlargement of area at distal end of anal furrow in *Okanagana* sp. Fig. 31. Ventral view of wing base in *Okanagana* sp. Fig. 32. Fore wing of *Stictocephala faurina* (Harr.). Fig. 33. Wings of *Aphis viburniphila* Patch.

Abbreviations: A.–anal vein; A.C.–axillary cord; C.–costa; A.-E.–point of afferent-efferent exchange.



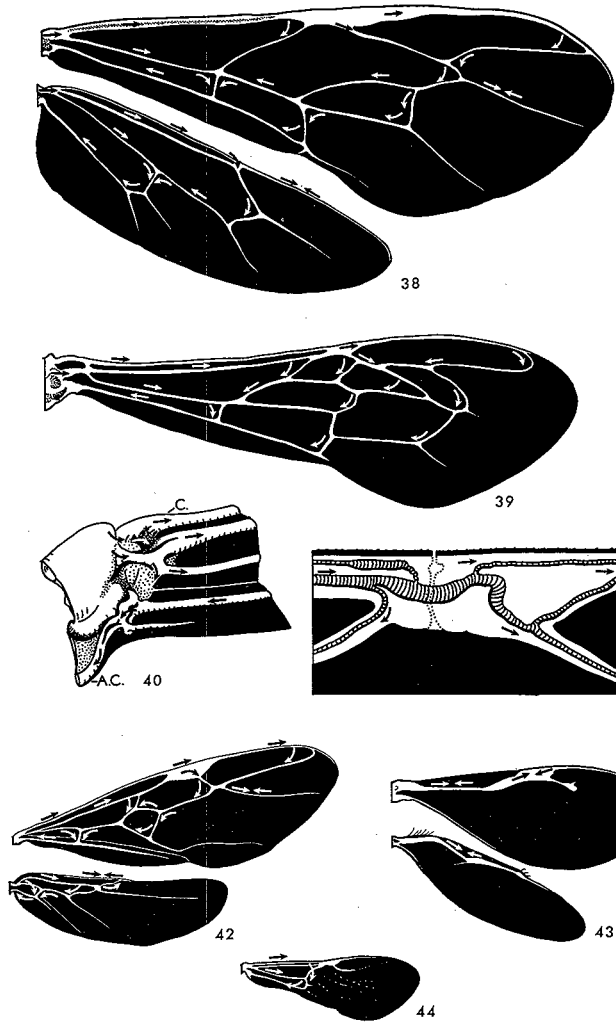






Figs. 34-37. Neuroptera. Fig. 34. Fore wing of *Myrmeleon* sp. Fig. 35. Fore wing of *Chrysopa* sp. Fig. 36. Fore wing of *Mantispa brunnea* Say. Fig. 37. Base of fore wing of *Chrysopa* sp.

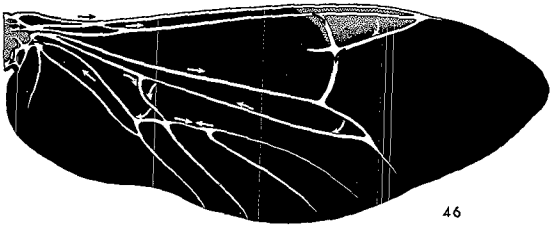
Abbreviations: A.C.–axillary cord; C.–costa.



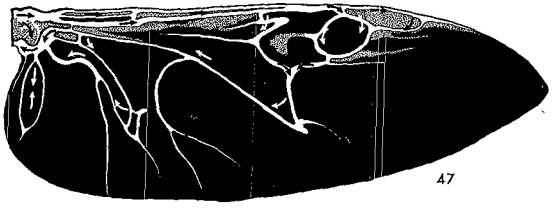
Figs. 38-44. Hymenoptera. Fig. 38. Fore and hind wing of *Mimesa* sp. Fig. 39. Fore wing of *Apis mellifera* Linnaeus. Fig. 40. Dorsal view of base of fore wing of *A. mellifera*. Fig. 41. Pterostigma in *Mimesa* sp. showing contained tracheae, and line of flexion (dotted). Fig. 42. Fore and hind wing of *Lasius* sp. Fig. 43. Fore and hind wing of *Pachyneuron* sp. Fig. 44. Fore wing of *Elampus* sp.

Abbreviations: A.C.–axillary cord; C.–costa.

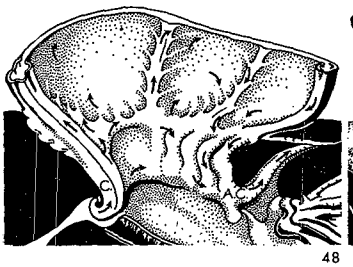
45



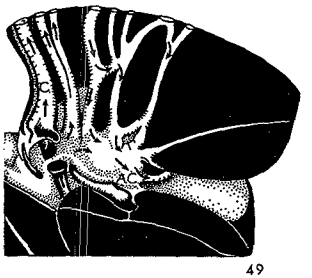
46



47



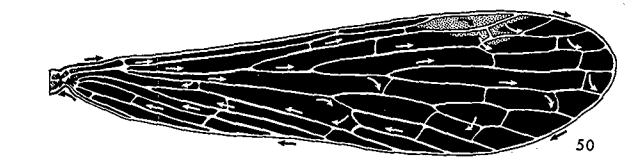
48

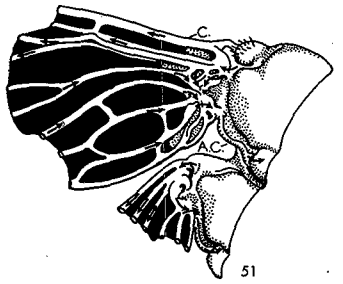


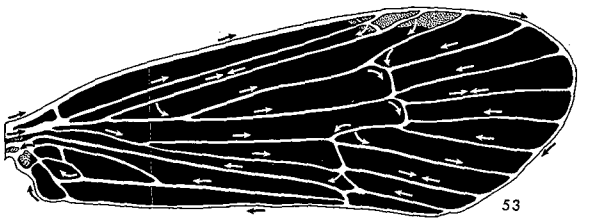
49

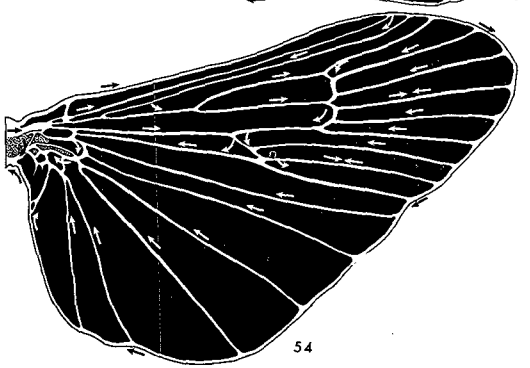
Figs. 45-49. Coleoptera. Fig. 45. Elytron of *Cantharis scitulus* Say. Fig. 46. Hind wing of *C. scitulus*. Fig. 47. Hind wing of *Cicindela punctulata punctulata* Oliv. Fig. 48. Ventral view of base of raised elytron of *Physocnemum brevilineum* Say. Fig. 49. Ventral view of base of raised hind wing of *P. brevilineum*.

Abbreviations: A.C.–axillary cord; C.–costa.



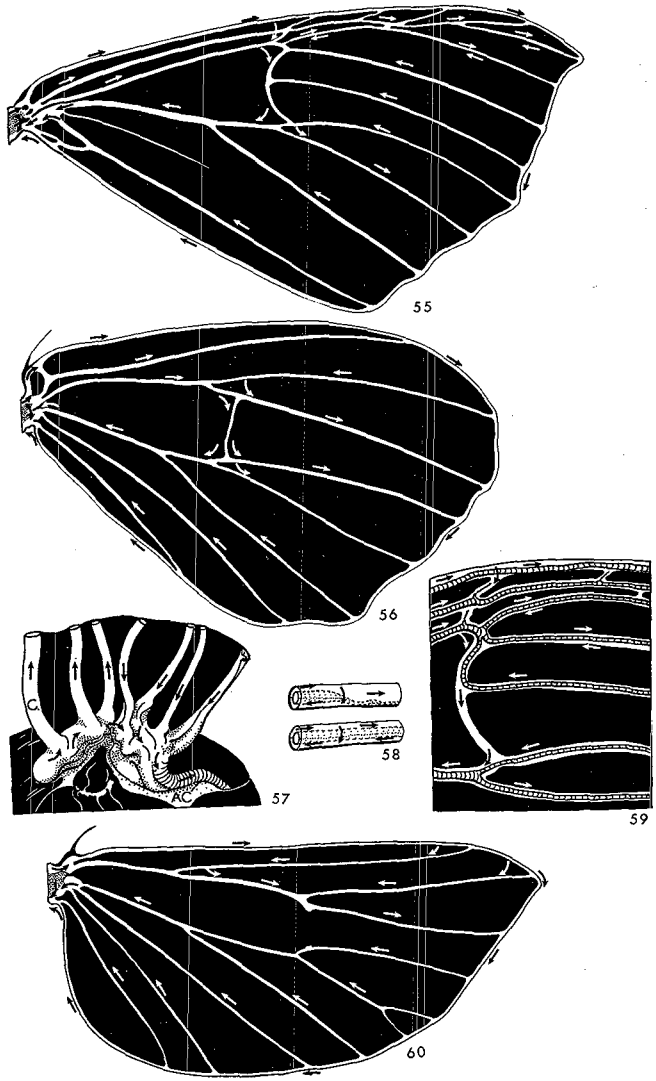






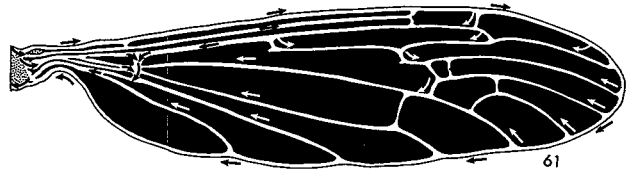
Figs. 50-51. Mecoptera. Fig. 50. Fore wing of *Panorpa* sp. Fig. 51. Dorsal view of wing bases of *Panorpa* sp.

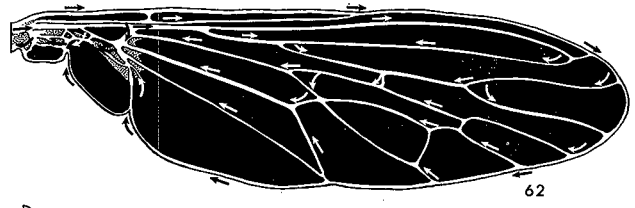
Figs. 52-54. Trichoptera. Fig. 52. Ventral view of base of raised fore wing of *Limnephilus rhombicus* (L.). Fig. 53. Fore wing of *L. rhombicus*. Fig. 54. Hind wing of *L. rhombicus*.

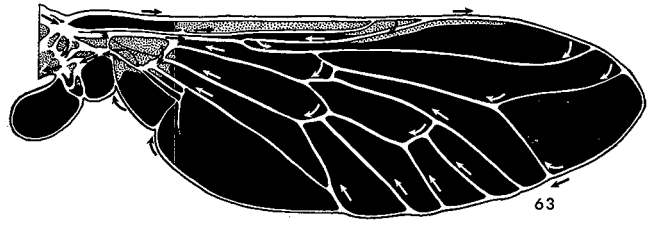


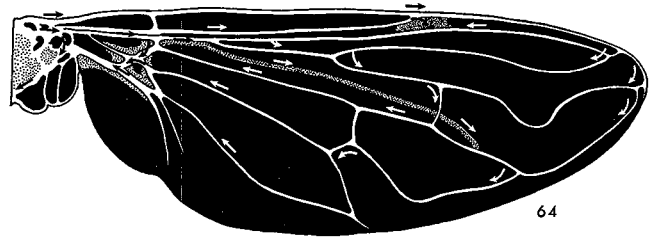
Figs. 55-60. Lepidoptera. Fig. 55. Fore wing of *Prochoerodes transversata* Dru. Fig. 56. Hind wing of *P. transversata*. Fig. 57. Ventral view of base of raised fore wing of *P. transversata*. Fig. 58. Position of tracheae (dotted lines) in wing veins of *P. transversata*, diagrammatic. Fig. 59. Tracheal system in wing veins at distal end of cell R+M in fore wing of *P. transversata*. Fig. 60. Hind wing of *Eucosma* sp.

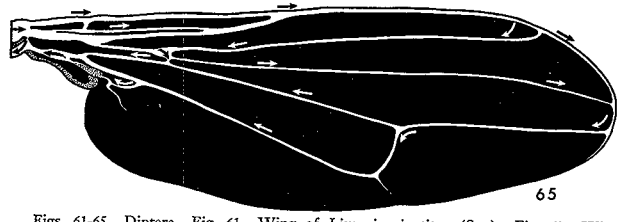
Abbreviations: A.C.–axillary cord; C.–costa.



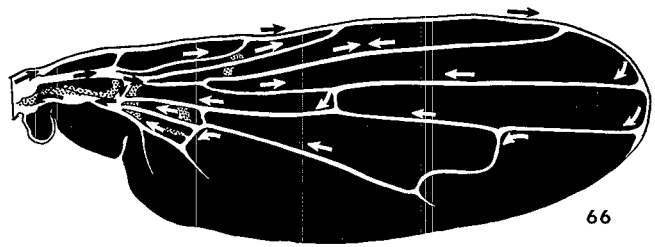


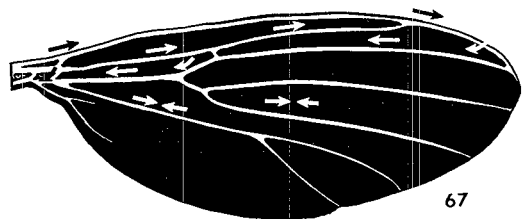


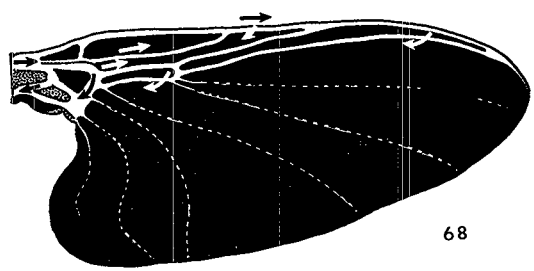




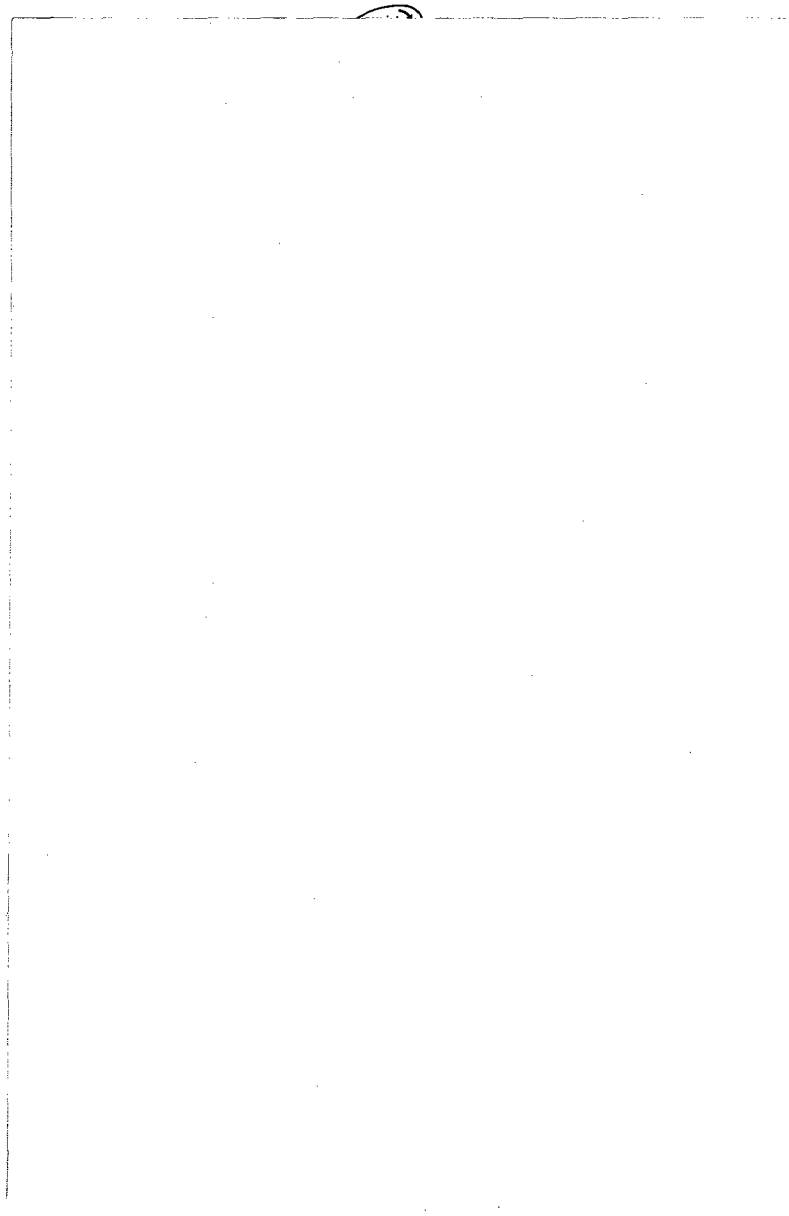
Figs. 61-65. Diptera. Fig. 61. Wing of *Limonia cinctipes* (Say). Fig. 62. Wing of *Asilus paropus* Walk. Fig. 63. Wing of *Tabanus lineola scutellaris* Wlk. Fig. 64. Wing of *Sphaerophoria robusta* Cn. Fig. 65. Wing of *Hydrophorus* sp.

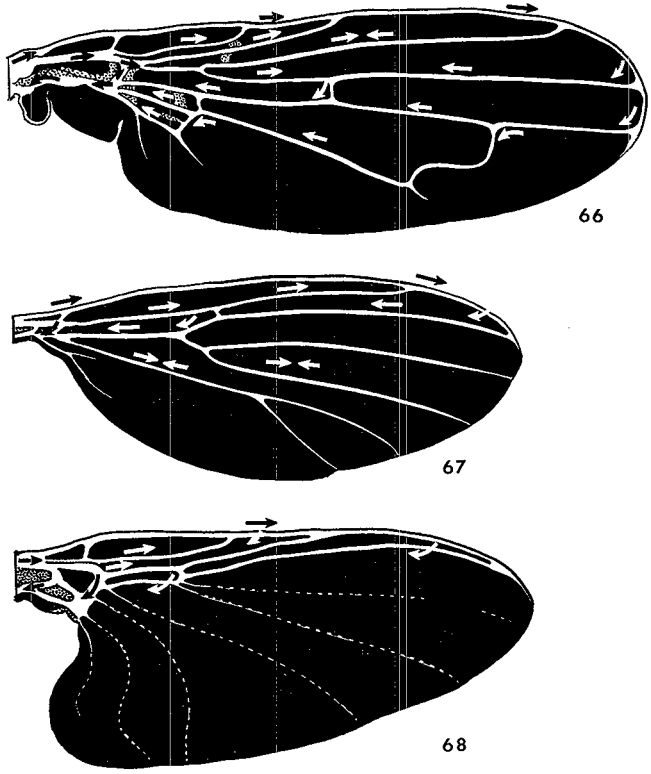






Figs. 66-68. Diptera. Fig. 66. Wing of *Hedroneura rufa* (Panz.). Fig. 67. Wing of *Epicypta* sp. Fig. 68. Wing of *Simulium* sp.





Figs. 66-68. Diptera. Fig. 66. Wing of *Hedroneura rufa* (Panz.). Fig. 67. Wing of *Epicypta* sp. Fig. 68. Wing of *Simulium* sp.

Figs. 69-72. Diptera. Fig. 69. Haltere of *Limonia cinctipes* (Say). Fig. 70. Postero-dorsal view of wing base of *L. cinctipes*. Fig. 71. Postero-dorsal view of wing base of *Tabanus lineola scutellaris* Wlk. Fig. 72. Postero-dorsal view of wing base of *Musca domestica* L.

Abbreviations: A.C.–axillary cord; AM.–ambient costa; AR.–arculus; C.–costa; S.–scutellum.

LIST OF THE CANADIAN ENTOMOLOGIST SUPPLEMENTS

Volume	*No.*	*Date Printed in the Issue Itself*	*Actual Date of Issue*	*Authority*[1]	*Author*
(87) LXXXVII	Supp. 1	1955	30 Mar. 1955	WRT	Maxwell
(88) LXXXVIII	Supp. 1	Mailed 23 Nov. 1956	10 Dec. 1956	WRT	Becker
(88) LXXXVIII	Supp. 2	1956	16 Jan. 1957	WRT	Beirne
(88) LXXXVIII	Supp. 3	1956	2 Jan. 1957	Lib	Brown

After this issue the "Supplements" became, in fact, a self-contained series with a continuous numbering system independent of The Canadian Entomologist. Nevertheless, they were still issued (with later exceptions) as "Accompanying" volumes of The Canadian Entomologist.

Because 4 Supplements had already been published, the next one was called No. 5. Supplement No. 4 was never published.

No.	*"Accompanies Volume"*	*Date Printed in the Issue Itself*	*Actual Date of Issue*	*Authority*[1]	*Author*
5	89	1957	2 Dec. 1957	Lib	Thomas
6	90	1958	8 Apr. 1958	WRT	Hardwick
7	90	1958	28 Apr. 1958	Lib	Freeman
8	90	1958	12 Sep. 1958	Lib	McGuffin
9	90	1958	14 Nov. 1958	EGM	Brooks
10	91	1959	26 Mar. 1959	Lib	MacKay
11	91	1959	26 Mar. 1959	Lib	Kelton
12	91	1959	15 June 1959	Lib	Chant
13	92	1960	14 Nov. 1960	Lib	Richards
14	92	Mailed 17 Feb. 1961	16 Mar. 1961	Lib	Chillcott
15	92	Mailed 27 Jan. 1961	1 Feb. 1961	WM	Heinrich I[2]
16	92	Mailed 10 Jan. 1961	11 Jan. 1961	Lib	Freeman
17	no date or volume number		25 Oct. 1961	Lib	Munroe
18	92	Mailed 24 Mar. 1961	4 Apr. 1961	WM	Heinrich II[2]
19	93	Mailed 24 Feb. 1961	4 Apr. 1961	Lib	Watt
20	92	Mailed 24 Mar. 1961	6 Apr. 1961	Lib	Brooks
21	93	1961	13 Sep. 1961	Lib, WM	Heinrich III[2]
22	93	Mailed 12 Apr. 1961	29 May 1961	Lib	Miller
23	none	1961	21 Dec. 1961	WM	Heinrich IV[2]
24	none	1961	27 Dec. 1961	Lib, WM	Munroe
25	none	1961	28 Dec. 1961	Lib, WM	Howden
26	no date or volume number		19 Feb. 1962	WM	Heinrich V[2]
27	none	1962	20 Sep. 1962	Lib, WM	Heinrich VI[2]
28	none	1962	6 Nov. 1962	WM	MacKay
29	none	1962	27 Nov. 1962	WM	Heinrich VII[2]
30	none	1963	1 May 1963	WM	Peck

After Supplement 30, the series continued under the title "Memoirs of the Entomological Society of Canada".

MEMOIRS OF THE ENTOMOLOGICAL SOCIETY OF CANADA

31	—	1963	21 May 1963	WM	Morris *et al*
32	—	1963	4 June 1963	WM	LeRoux *et al*
33	—	1964	19 Mar. 1964	WM	Munroe
34	—	1964	1 Apr. 1964	WM	Peck *et al*
35	—	1964	14 May 1964	WM	Peck[2]

[1]The following are the authorities upon which the actual dates of issue are based:
WRT — log book of former editor W. R. Thompson
EGM — log book of former editor E. G. Munroe
WM — log book of present editor W. R. M. Mason
Lib — date stamp of the Library of the Entomology Research Institute, Ottawa

[2]The seven parts of Mr. Heinrich's *Revision of Ichneumoninae*.... and Part VIII (Indices, addenda and corrigenda) by O. Peck have consecutive pagination and are intended to be bound as a single book.