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Review article

Beyond aerodynamics: The critical roles of the circulatory and tracheal systems in maintaining insect wing functionality

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ABSTRACT

Insect wings consist almost entirely of lifeless cuticle; yet their veins host a complex multimodal sensory apparatus and other tissues that require a continuous supply of water, nutrients and oxygen. This review provides a survey of the various living components in insect wings, as well as the specific contribution of the circulatory and tracheal systems to provide all essential substances. In most insects, hemolymph circulates through the veinal network in a loop flow caused by the contraction of accessory pulsatile organs in the thorax. In other insects, hemolymph oscillates into and out of the wings due to the complex interaction of several factors, such as heartbeat reversal, intermittent pumping of the accessory pulsatile organs in the thorax, and the elasticity of the wall of a special type of tracheae. A practically unexplored subject is the need for continuous hydration of the wing cuticle to retain its flexibility and toughness, including the associated problem of water loss due to evaporation. Also, widely neglected is the influence of the hemolymph mass and the circulating flow in the veins on the aerodynamic properties of insect wings during flight. Ventilation of the extraordinarily long wing tracheae is probably accomplished by intricate interactions with the circulatory system, and by the exchange of oxygen via cutaneous respiration.

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1. Introduction

Hardly any structure of insects has generated more fascination and research than the wings. It is amazing how such delicate body appendages enable these little creatures to rise into the air and skillfully maneuver themselves in an environment where locomotion obeys completely different physical conditions than on the ground or under water. The constraints on the development of insect wings are extremely narrow, and the selective forces have probably been very keen, all of which make the topic of outstanding interest from both functional and evolutionary points of view (reviews: Pringle, 1957; Brodsky, 1994; Dudley, 2000; Nachtigall, 2003; Alexander, 2015). The emergence of wings is unequivocally a key event in the evolutionary history of insects and is considered one of the main reasons behind their massive diversification and ecological success (Grimaldi and Engel, 2005). The origin of winged insects, the Pterygota, is estimated by molecular approaches to have occurred approximately 400 million years ago in the early Ordovician (Misof et al., 2014). Strangely, early pterygotes must

have had some kind of protowings yet are entirely lacking in the fossil record, and only pterygotes with fully developed wings are known, the earliest of which are dated about 90 million years later in the Carboniferous period (Engel et al., 2013). A much older fossil of a head capsule with mandibles that is suspected to belong to a pterygote insect (Engel and Grimaldi, 2004), has recently been re-analyzed and is more likely to be from a myriapod (Haug and Haug, 2017). Overall, we have to recognize that the origin of insect wings remains enigmatic, and a variety of hypotheses has been proposed on how the protowings would have looked and the functional changes they could have undergone in the early phase of their evolution prior to being organs suitable for flight (review: Alexander, 2018, this issue).

Apart from the controversies these discussions have incited, we know that each wing develops from a simple folding of the integument. After imaginal ecdysis, the initially folded wings are expanded and transformed into definitive airfoils in a complex maturation process. The wing expansion is affected by increased hemolymph pressure in the thorax due to complex interactions of abdominal contractions and pumping activities of the various circulatory organs (Moreau and Lavenseau, 1975; Wasserthal, 1976; Elliott, 1981). Then,

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the epidermis within the wings is apoptotically dissolved (Kimura et al., 2004), and the resulting cell fragments are sucked out of the developing wing by accessory circulatory organs in the thorax (Tögel et al., 2008). Hemolymph volume subsequently decreases, which causes the dorsal and ventral cuticular lamellae to draw closer to each other. In most parts of the wing, the two lamellae are then tightly glued together with an extracellular matrix produced by special hemocytes (Kiger et al., 2001). However, they remain separate in the areas where later the wing veins emerge. The fully developed veins are hollow tubes that form the stabilizing scaffold of the wing between which the delicate wing membrane is stretched (review: Wootton, 1992). The structure and architecture of the veins are crucial for the biomechanical properties of the wings and determine wing deformation during flight (Combes and Daniel, 2003; Appel et al., 2015; Rajabi et al., 2016a). The veins also enhance the fracture toughness of heavily stressed wings (Dirks and Taylor, 2012; Rajabi et al., 2015), and mitigate collision damages (Mountcastle and Combes, 2014). In addition, it should be remembered that insect wings generally serve for more than flight. They may be involved in many other biological functions, such as protection and defense, thermoregulation, as well as territorial or sexual signaling and display (Chapman et al., 2013).

Mature wings are not just “dead” cuticle, as often is believed. Their veins host living components, such as neurons of a complex sensory apparatus and other tissues that need supply of oxygen, water, nutrients, hormones, and other substances; in turn, their final metabolic products must be removed from the immediate environment. The provision of these essentials and the removal of wastes occur via the wing veins, which are filled with hemolymph and may contain tracheal tubing as well. Aside from the living tissue, the wing cuticle must receive a constant supply of water to maintain its elasticity and toughness.

Although meeting these requirements is of vital importance to maintain the proper functioning of insect wings, surprisingly little attention has been paid to the supply of hemolymph to these appendages. Thus far, research has mainly concentrated on the patterns of hemolymph circulation in the veins (Arnold, 1964; Wasserthal, 1982), as well as on the structure and function of the wing circulatory organs (reviews: Pass, 1998, 2000, Pass et al., 2015). Largely ignored until recently are the consequences of the mass and flow dynamics of the hemolymph for the aerodynamic properties of the wings (Wang and Zhong, 2014; Hou et al., 2015a; b). The need for continuous hydration of the wing cuticle is a known but virtually unresearched fact, as well as the question how the extraordinarily long wing tracheae are ventilated.

The goal of the present review is to provide a comprehensive and integrative view of the wings as “living” body appendages. The article is organized into two main parts: the first part (section 2) provides an overview of the structures that require hemolymph and a supply of oxygen, whereas the second part (sections 3 and 4) focuses on the structure and function of the supplying organs and their multiple functions in maintaining the various tasks of insect wings.

2. Target structures and tissues receiving supply

Among the various living components on insect wings, the complex multimodal sensory apparatus clearly stands out, and a brief overview of these organs is given. The other living cells that require supply of hemolymph and oxygen are the epidermis and some glandular tissues. The important subject of wing cuticle hydration will be treated here from a more general perspective due to its neglect as a topic of research.

2.1. Wing sensory apparatus

The sensory organs on insect wings are primarily mechanoreceptors that are involved in the control of wing movement and body stabilization during flight. In some insects, specialized sound pressure mechanoreceptors are associated with wing veins and serve for predator detection and/or intraspecific communication. Furthermore, chemo- and thermoreceptors are present in insect wings. The nerves of these sensory organs run through the wing veins and project into the thoracic ganglia with some fibers ascending to the head ganglia (Ando et al., 2011).

2.1.1. Mechanoreceptors

Of the multimodal sensory inputs required to achieve flight stability, mechanosensation is crucial, since it permits a tremendously rapid acquisition and processing of information (Sherman and Dickinson, 2003). Although the study of the sensory biology of insect wings focuses primarily on flight control, one must keep in mind that insects spend the greater part of their existence in a resting position. Even during periods of inactivity, wing mechanoreceptors serve a number of vital functions, e.g. toward the perception of stimuli for orientation in their environment, for discovery of potential predators, and to initiate defense reactions. For all these tasks, insects have a number of different mechanoreceptors on various parts of the body, especially on the head and thorax, but also on the wings. Most of the wing mechanoreceptors are localized at the joint region between the thorax and wing base, but some are also on the wing blade. Various types of these receptors are present in the wings, including hair sensilla, campaniform sensilla, as well as stretch and chordotonal proprioceptors.

Hair sensilla. As almost everywhere on the insect body, there are numerous hairy structures on the wings. Only some of these are sensory hairs; most are non-innervated spines or microtrichia. On the locust hindwing, for example, only about 800 of the 12,400 hair structures are innervated (Altman et al., 1978). Most of the sensory hairs are located at the margins of the wings and are touch-sensitive (Vogel, 1911; Albert et al., 1976; Hartenstein and Posakony, 1989; Yoshida and Emoto, 2010). For example, mechanical stimulation of certain hair sensilla on the wings of the locust elicits hindleg scratching (Page and Matheson, 2004), or a kicking defense behavior in the fruit fly (Li et al., 2016). Other hair sensilla are specialized to encode air-borne vibrations and possibly play a role in the stabilization of wing beat frequency (Fig. 1A and B; Ai, 2013).

Campaniform sensilla. These mechanoreceptors are recognizable exteriorly as very small, more or less circular, domed cuticular elevations (Fig. 1A). They encode strain forces that impinge on the cuticle making them particularly suitable to measure positional changes at wing joints and deformations of the wing blade (review: Taylor and Krapp, 2007). The distribution and number of the campaniform sensilla associated with the wings differ significantly among insects (reviews: Pringle, 1957; Chapman et al., 2013). In cockroaches and locusts, campaniform sensilla are only present on the underside of the wing and are relatively few in number (Zacwilichowski, 1934; Gettrup, 1966), while in some holometabolans they occur on both sides of the wing and can be quite numerous (Fig. 1C and D). The blowfly, *Calliphora vicina*, for example, possesses approximately 1200 campaniform sensilla throughout the body that are usually arranged in functional groups (Gnatzy et al., 1987). Nearly 85% of them are associated with the flight apparatus; about a third are on the wings and the rest are on the halteres, which are modified hindwings. These proportions indicate the outstanding importance of the campaniform sensilla for flight control. The organs on the wing base and the halteres provide information important for stabilization of body posture (Dickerson et al., 2014; Eberle et al., 2015; Agrawal et al., 2017; Pratt et al., 2017), whereas the few

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