Chapter 4
Flight Morphology and Flight Muscles

N. Chari, A. Ravi, Ponna Srinivas, and A. Uma

Abstract Structure of flying segments—thorax, associated chitinous membranous wings and their morphology have been explained including venation. Venation of wing helps in identifying species and also in classifying insects. Direct and indirect flight muscles, which help wing movements have been described. Flight parameters of body and wing contribute to basic understanding of wing movements in insect flight. Flight parameters of some insects have been studied in greater detail so that this may help in understanding the design of biomimicking MAVs. Differences between Neurogenic and myogenic muscles and the basis of muscle contraction have been explained. Oxidation of biomolecules has been summarised in the form of a table.

Keywords Wing venation · Wing muscles · Flight parameters · Wingbeat frequency · Pterothorax · Myofibrils · Neurogenic and myogenic fliers

Introduction

The study of the flight morphology of insects helps in understanding basic and derived flight parameters which are responsible for the flight performance of a flier. In insect flight, the mass is small and the aerodynamic forces such as lift, thrust and drag developed are proportional to wing area and wingspan. The morphological parameters of the insect body and associated wings help in flight. Basic flight parameters and their development are under genetic control. Therefore, the detailed study of basic and derived parameters and their correlation is necessary to understand the aerodynamic

---

N. Chari (✉)
Kakatiya University, Warangal, India

A. Ravi
Adilabad, Telangana, India

P. Srinivas
Dr. B.R. Ambedkar Open University, Hyderabad, India

A. Uma
Department of Bio-Technology, JNTUH, Hyderabad, India

N. Chari et al. (eds.), *Biophysics of Insect Flight*, Springer Series in Biophysics 22,
https://doi.org/10.1007/978-981-16-5184-7_4

forces of insect flight. Biological flight is highly complex and still remains to be elucidated fully; hence, the research is being carried out in different laboratories [1].

Structure of Thorax and Wing Morphology

The insect body is differentiated into three distinct regions such as head, thorax and abdomen as shown in Fig. 4.1. The thorax is considered as a locomotory apparatus having three pairs of legs ventrally and two pairs of wings laterally for flight. A detailed description of the morphology of insect thorax has been documented after [2] and others [1].

Thorax has three segments: prothorax (pro is first), mesothorax (meso is second) and metathorax (meta is third). Prothorax has no wings. However, meso and metathorax have a pair of lateral flying wings which are known as the first and second pair of flying wings. The dorsal portion of the thorax is covered by a sclerite which is known as tergum. While the V-shaped ventral portion covered by a plate is known as the sternum and the lateral portion (where tergum and sternum meet) is called as pleuron. The pleuron forms the semi-elastic lateral wall of the thorax and surrounds the base of the leg. Each of the thoracic segments has a pair of legs ventrally. Insects are also named as hexapoda since they possess six legs as compared to spiders, millipedes, centipedes and crabs.

The wings are thin chitinous membranes attached to the sides of the thorax by an elastic membrane (resilin). Each wing has a geometric structure and is traversed by longitudinal veins, which support the membrane and contribute to the flapping flexible behaviour of the wing resulting in the lift, thrust and drag due to aeroelasticity and structural deformation of the wing.

Each segment of pterothorax (flying segments) has a pair of parallel muscles running longitudinally below the tergum. They also have a pair of vertical muscles connecting the sternum to the tergum, which help in up and down movements of the wings indirectly. Thorax also has other muscles attached to the base of the wings for effective turning/rotation of the wings when the insect is flying. During the rest time,

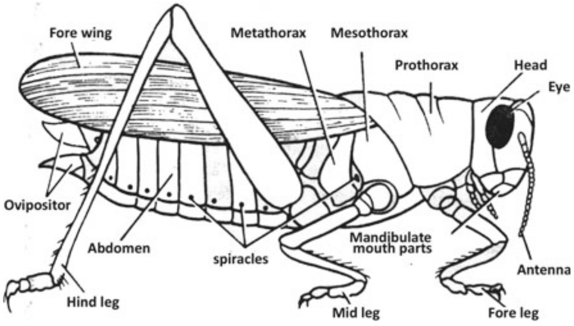


Fig. 4.1 Outline features of Grasshopper (a typical insect)

the wings are usually folded on the back and the body rests on three pairs of jointed legs on the substratum.

The main flight muscles in the thorax can be classified as direct and indirect flight muscles. Direct flight muscles are present in primitive insects and are attached to the wing base directly. Hence, they can move their wings by contraction either downward or upward. However, in insects with indirect flight muscles, the wings are attached to the thorax and by their contraction, they deform the thorax. As the wings are the continuation of thoracic chitin, the contraction of the flight muscle causes the deformation of the thorax which in turn leads to down and up movements of the wings which usually trace a figure of eight.

Based on the number of contractions made by the thoracic muscles, we have low-frequency and high-frequency fliers. Low-frequency fliers are known as neurogenic (synchronous) and high-frequency fliers are known as myogenic (asynchronous). Flight motor construction in insects has evolved independently. Wing venation also might have evolved from a single ancestor. The study of flight morphology helps in understanding the body and wing geometry, scaling laws, mimicking models, wingbeat frequency and flight at low Reynolds number at a moderate velocity.

The Vein

Each of the wings consists of a thin membrane supported by many longitudinal veins. The membrane is formed by two layers of integument closely fused, while veins are formed where two layers remain separate and the lower cuticle is thicker. Within each of the major veins, there is a nerve and trachea. Since the cavities of veins are connected with the haemocoel, haemolymph (the colourless blood) can flow into the wings from the base of the wing to the tip of the wing (Fig. 4.2).

The Transverse Section (TS) of the longitudinal vein of the wing has a covering of wing membrane running along the epidermis. The study of Fig. 4.2 shows the cut

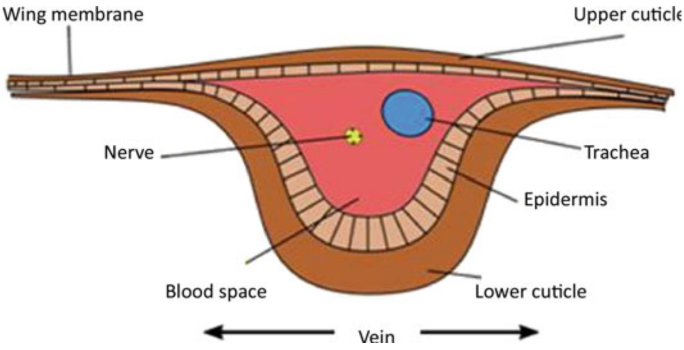


Fig. 4.2 Transverse section of a longitudinal vein (illustrative)

trachea and nerve floating in blood space. This clearly indicates that the insect wing is a living membrane covered by a cuticle on both sides.

Wing Venation [3]

1. In small insects, the venation is greatly reduced as in chalcid wasps.
2. In the wings of grasshopper and crickets, branching of the veins produces accessory veins or intercalary veins between the original veins.
3. Large numbers of cross veins are found in dragonflies and damselflies forming a reticulum.
4. All winged insects are supposed to have evolved from a common ancestor, the “archedictyon”. The hypothetical scheme of wing venation represents (Fig. 4.3) the “template” that has been modified by natural selection for more than 200 million years in different orders of insects.
5. Wing venation helps in the classification of insect orders which is listed below in Table 4.1.

The basic longitudinal veins which can be distinguished from the leading edge of the wing are shown in Figs. 4.3 and 4.4. The veins are named after the Comstock–Needham System.

The wing also has some folds. The wing venation helps in the classification of insects and contributes to the aeroelastic properties of the wing in flight. The geometry of the wing is variable in many orders. The fundamental basic plan of

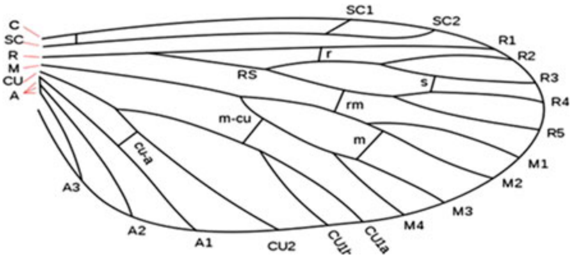
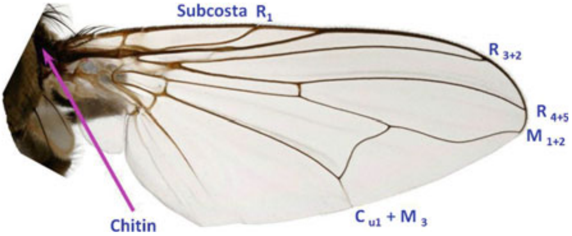


Fig. 4.3 Wing venation (The Comstock–Needham System)

Table 4.1 The classification of veins

Costa	(C)	First longitudinal vein, the leading edge of the wing
Subcosta	(Sc)	Second longitudinal vein (behind the Costa), typically un-branched
Radius	(R)	Third longitudinal vein, one to five branches reach the wing margin
Media	(M)	Fourth longitudinal vein, one to four branches reach the wing margin
Cubitus	(Cu)	Fifth longitudinal vein, one to three branches reach the wing margin
Anal veins	(A_1, A_2, A_3)	Un-branched Veins behind the cubitus

Fig. 4.4 Wing and venation of a housefly



the wing venation has been shown in Fig. 4.3 and that of a housefly which differs significantly in Fig. 4.4.

Wing Joints

1. A majority of insects can flex their thin wings over the back when at rest.
2. There is a complicated articular structure at the wing base than a mere hinged joint of the wing with the body.
3. Each wing is attached to the body by a membranous basal area. The membrane contains a number of small articular sclerites, collectively called "pteralia".
4. Pteralia includes a group of "axillaries" which are specially developed only in the wing flexing insects.
5. The axillaries contribute to the flexor mechanism. There are first, second and third axillary sclerites that support the wing.
6. There are special sclerotized plates such as humeral plate at the base of the costal vein, distal plate at the base of the cubic vein and proximal plate at the base of anal veins, and thus, it supports the venation of the wing (Fig. 4.5).

Wing Muscles

1. The insect flight muscles are highly oxidative in their metabolism and constitute 10–30% of total body mass.
2. Insect muscles are strictly aerobic and maintain high levels of energy required during flight. Fuel is carried by the blood to the muscles and O_2 through minute tracheoles by diffusion. Flight muscles have many mitochondria which act as miniature powerhouses of the cells.
3. Many wing muscles are large measuring about 10 mm in length and 2 mm in width.

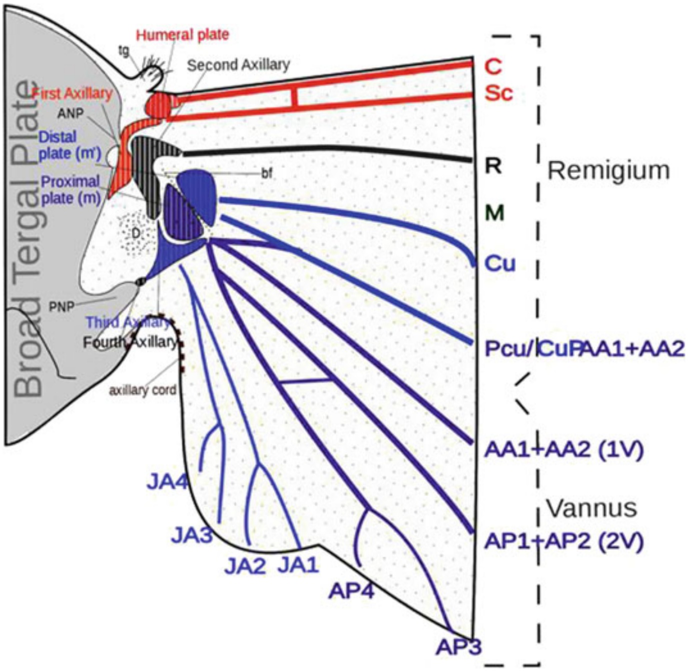


Fig. 4.5 Wing joints of an insect

Direct Muscles

In all insects, the upward movement of the wings is due to the contraction of indirect dorsoventral muscles or vertical muscles. As a result of this contraction, the wing membrane moves up and with the pleural process act as a fulcrum. These muscles may not be always homologous in different insect groups. Direct Flight Muscles are found typically in Odonata (Dragonfly) and Blattaria (Cockroach) (Fig. 4.6).

Indirect Muscles

The up and down movements of the wing are produced by indirect muscles due to changes in the shape of the notum (tergum plate), which is not directly attached to the wing base. Indirect Flight Muscles are typically found in Diptera (Housefly) and Hymenoptera (Honey bees). The wing movements, Transverse Sections (TS) and structure of thorax are shown in Figs. 4.7 and 4.8 in a semi-diagrammatic fashion modified from various sources.

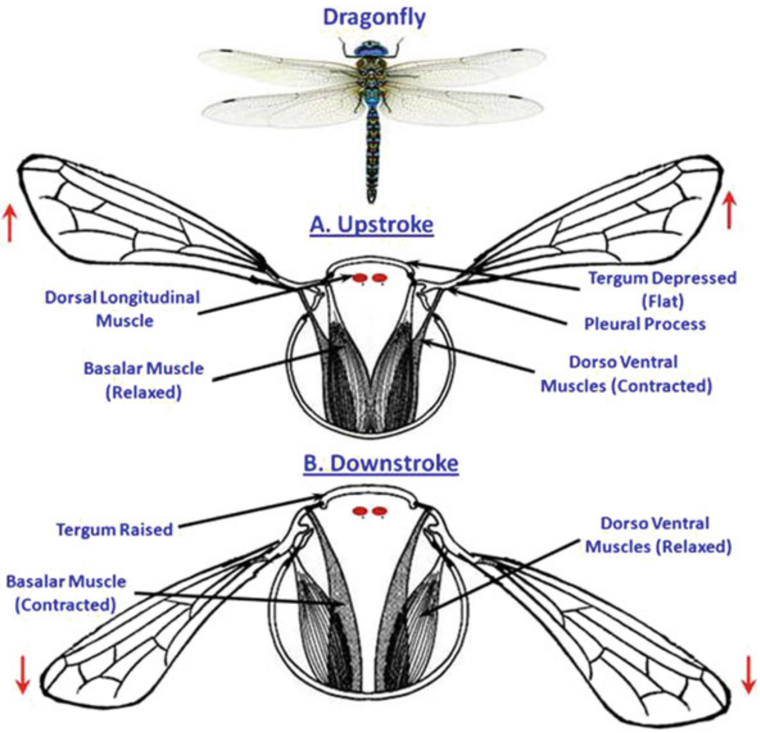


Fig. 4.6 Illustrating the direct muscle action in an insect

Wing Coupling, Folding and Wing Movements

1. In many insect species, the fore and hind wings are coupled together on each side, which improves the aerodynamic efficiency of flight.
2. In Hymenoptera (Bees and Wasps) and Trichoptera (Caddis flies), a row of small hooks called "hamuli" located at the front margin of hind wings lock on to the forewing; thus, both the wings are held together.
3. In some other insects such as butterflies, the jugal lobe of the forewing covers a portion of the hind wing.
4. Also, in other insects, margins of the fore and hind wing overlap or the hind wing bristles or frenulum hook up in the forewing.
5. When at rest, wings are held over the back in most insects causing longitudinal or transverse folding of the wing membrane.
6. Normally, there will be radial fold lines to the base of the wing allowing the adjacent wing to be folded over or under each other.
7. In cockroaches and locusts, the anal part of wings is folded like a fan along the veins.

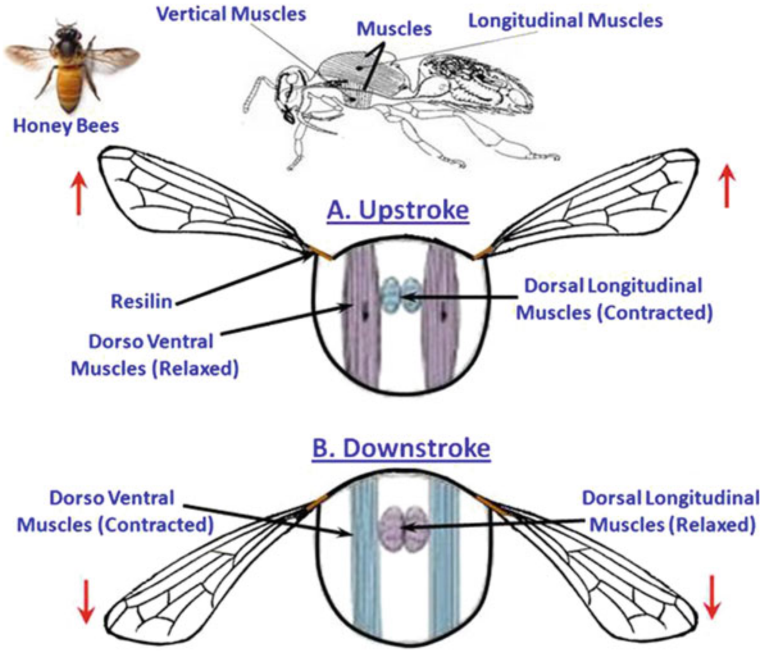


Fig. 4.7 Illustrating the indirect muscle action in an insect

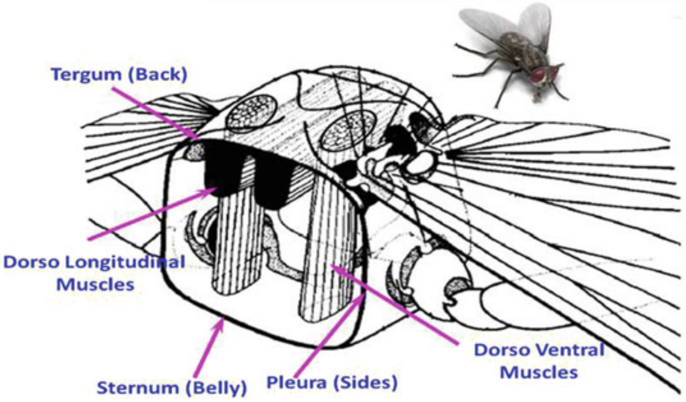


Fig. 4.8 Transverse section of thorax—housefly (Illustrative)

8. Folding of the wing is produced by a muscle arising on pleuron and inserted into the third axillary sclerite of the wing; interestingly, the activity of the same muscle in insect flight affects the power output of the wing. Thus, it is also important in flight control.

9. The wing movements consist of the upstroke, downstroke, flexion and forward and backward movements. Rotational movements along the longitudinal axis of the wing contribute to forming an approximate figure of eight “8” at the wing tip. The downstroke of the wing is brought about due to the elevation of the tergum.
10. The downstroke is also accompanied by a forward movement. The upstroke is associated with the backward movement of the wing.

Flight Parameters

The basic and derived flight parameters of an insect are as follows:

Basic Parameters:

a. Body Mass (M)
b. Wing Length (l)
c. Wingspan (L)
d. Wing area (A)
e. Area of two wings ($2A$)
f. Disc Area (S_d).

Derived Parameters:

a. **Average Breadth of Wing**: Average breadth of the wing is calculated as 2A/2 l. B_{eff} is an important wing characteristic parameter in calculating wing area and wingbeat frequency of the flier. It may be mentioned here that a change in camber through a differential change in the value of B_{eff} will contribute to additional lift in insect flight. B_{eff} is also calculated by the strip analysis method which is also used in the study of Moment of Inertia (MI).
b. **Wing Loading (W_L)**: It is the ratio of body mass to total flight surface area (2A) and is expressed in gm/cm^2.
c. **Disc Loading**: It is the ratio of mass to disc area. It is expressed in gm/cm^2. W_L helps in calculating frequency and other related power calculations. The weight of the flier gets distributed over the flight surface as wing loading during flight. It may be mentioned that the effective wing area will be changing during flapping of the wing due to which the wing loading values also vary.
d. **Aspect Ratio (AR)**: It is the ratio of the square of wingspan (L^2) to total flight surface area (2A). The aspect ratio in insects usually ranges from 3 to 5. The aspect ratio has an important impact on flight performance. Insects having a high aspect ratio can fly more efficiently as compared to those with a low aspect ratio. MAVs designed on flight principle have low AR.
e. **Airfoil (Aerofoil)**: Transverse Section (TS) of the wing is known as the Airfoil section. In insects, TS is very small and airfoils are very thin. The section varies along the wingspan in terms of the chord, thickness distribution and camber. The wing is flexible and hence, the camber can be changed and get altered during different strokes, and hence can modify the aerodynamic forces as well.

f. **Wingspan Loading (WSL)**: It is the ratio of mass to the square of wingspan and is represented as M/L^2. M/L^2 is also a ratio of wing loading to aspect ratio. M/L^2 is an important aerodynamic parameter that helps in the calculation of wingbeat frequency and other related parameters. M/L^2 represents the flight efficiency better than W_L and the aspect ratio is considered separately. Earlier researchers have not realized the significance of the wingspan loading parameters in bio-aerodynamic studies involving flapping wing motion. M/L2 becomes important in comparative aerodynamic studies [1].

Some Useful Definitions

a. **Flight Velocity**: The speed and direction of a flier in the air are known as flight velocity. For insects, it is usually expressed in metres per second (m/s).
b. **Relative Wind (RW)**: The speed and direction of air impinging on a flier are known as relative wind. It may be stated that it is equal and opposite to the direction of the flight path velocity.
c. **Angle of Attack (AOA or α)**: The *acute angle* between the relative wind and the chord line of an airfoil is known as the Angle of Attack. With an increase in AOA, lift also gradually increases until the stalling angle of attack is reached.
d. **Lift (L)**: The component L of the aerodynamic force, which is perpendicular to the relative wind, is known as Lift.
e. **Drag (D)**: The component D of the aerodynamic force, which is parallel to the relative wind, is known as Drag. It may be noted that drag always opposes the flight motion. There are various types of drag acting on fliers such as surface drag, body drag and induced drag at wing tip which is responsible for the formation of wing tip vortices.
f. **Centre of Pressure (CP)**: The point on the chord line where the aerodynamic forces intersect is known as centre of pressure.
g. **Laminar Flow**: Smooth airflow with a little transfer of momentum or energy between parallel layers is known to be laminar flow.
h. **Turbulent Flow**: Flow where streamlines move fast and break up and there is a considerable mixing up of the layers is known as turbulent flow. There will be an exchange of momentum between different layers. Unsteady flows can be an example of turbulent flow.

Wingbeat frequency: It is expressed as the number of wingbeats or oscillations per second (cps/ Hz). The wingbeat frequency may be empirically calculated as follows:

$$\text{Wing beat frequency}(\vartheta_h) = \frac{\text{Mass of the flier}}{(\text{Wing span})^2 \times \mathrm{B_{eff}}} \times \text{Constant}$$

Table 4.2 Comparision[b] of typical wingbeat frequencies of different insects

S. No	Primitive fliers (Neurogenic-Synchronous)		Advanced fliers (Myogenic-Asynchronous)	
	Type of flier	Wingbeat frequency (cps/Hz)	Type of flier	Wingbeat frequency (cps/Hz)
1	Large butter fly	**10**	Soapnut bug (*T.j*)[a]	**50**
2	Damselfly	**16**	Chrysocoris	**100**
3	Cockroach	**20**	Bumblebee	**130**
4	Locust	**25**	Housefly	**190**
5	Scorpionfly	**28**	Honey bee	**250**
6	Dragonfly	40	Mosquito	600
7	Humming Moth	85	Forcipomia	1000

[a] Low ϑ_h observed in *T.j* due to secondary adaptations since primarily ***T.j*** is a myogenic flier hence the frequency is 50Hz

[b] From various sources

The small insects are observed to have a higher frequency in contrast to bigger fliers. The wingbeat frequencies of some of the fliers given in Table 4.2 are modified after [2] and [1]. The wingbeat frequency of some of the fliers is as follows:

Table 4.3 reads detailed flight parameters measured and calculated for ***Tessaratoma javanica*** (***T.j***) and ***Chrysocoris purpureus*** (***C.p***) for a better understanding and comparison. The parameters selected here also may form the quantitative basis for the experimental design of Insect Mimicking MAVs based on bio-mimicking principles.

Typical forward velocities of some common insects have been shown in Table 4.4.

Based on Table 4.5 of the flight parameters, the derived flight features of the above insects can be understood and calculated which help in understanding the natural flight of these fliers.

Moment of Inertia studies have been carried on insect wings by using the strip analysis method, which may give a general idea of lift, thrust and distribution of mass and area in relation to wing strips as counted from the fulcrum. The study of MI helps in understanding the properties of moving bodies including insects (more details are discussed in Chap. 6). Insect flapping flexible wing is peculiar in the sense that the upper part of the wing develops lift, the lower part thrust because of bending and the tip develops induced drag (tip vortices). It is a thin tapering chitinous membrane supported by longitudinal veins, which make it anisotropic and contribute to the aeroelastic properties of the wing. The bending of the insect wing is a resultant of uneven distribution of mass which decreases from fulcrum to the wing tip.

Table 4.3 Flight parameters of two pentatomid (Heteroptera) insects [1]

Sl. No	Parameters	Notation	Units	*Tessaratoma javanica*	*Chrysocoris purpureus*
1	Mass	M	gm	0.860	0.170
2	Wing length	*l*	cm	2.20	1.20
3	Wing breadth	Beff	cm	1.15	0.65
4	Wingspan	L	cm	6.00	3.16
5	Wing area	2A	cm^2	5.00	1.60
6	Fineness (*l/b*) Ratio		–	2.00	2.00
7	Wing loading	W_L	g/cm^2	0.20	0.11
8	Wingspan loading M/L^2 (WSL = WL/AR)	WSL	g/cm^2	0.03	0.018
9	Aspect ratio	AR	–	6.8	6.3
10	Wingbeat frequency	ϑ_h	cps	50	90
11	Stroke period $\frac{1}{\vartheta_h} x 1000$	T	ms	20–22	10–12
12	Reynolds number	*Re*	–	4000	1000
13	Disc area	–	cm^2	27	8.0
14	Disc loading	–	g/cm^2	0.034	0.021
15	Wing swept area	–	cm^2	9.5	3
16	Velocity	V	m/s	3.5	0.11
17	Weight of two wings	–	gm	17.33×10^{-3}	2.01×10^{-3}
18	Angular velocity	–	rad/sec	325	700
19	Angular acceleration	–	rad/s^2	1.03×10^5	4.5×10^5
20	Angular momentum	–	$g\ cm^2/s$	–	1.12
21	Moment of inertia	MI	$g\ cm^2$	0.03	–

Table 4.4 Typical forward velocity of insects during flight (*from various authors)

Type of flier	Speed in mph
Locust	20.5
Dragonfly	15.6
Humming bird moth	11.1
Bumblebee	6.4
Honey Bee	5.7
Housefly	4.4

Table 4.5 Comparision of[a] Flight Parameters of Various Insects

Parameter	Units	Primitive insects	Advanced insects		
		Dragon fly	*Chalcid wasp*	*C.purpureus*[a]	*T.javanica*[a]
B_{eff} (Chord)	cm	1		0.65	1.15
l	cm	4	0.5 – 0.7	1.2	2.2
L	cm			3.16	6.0
ϑ_h	Hz	40	400	90	50
Forward velocity (V)	m/s			1.8–2	3–4
Re	–	103	25	1000	4000
Mass	gm			0.17	0.86
Angle of attack($\propto$)	deg	25–45	25–45	25–45	25–45

[a] This work is carried out at SNIST, Hyderabad, others from various sources

Insect Flight Muscles

The arrangement of direct and indirect flight muscles in the thorax and their contribution to up and down movements of the wings in both primitive and advanced insects have been discussed. However, the wingbeat frequency is an important parameter that helps in classifying the insects as Neurogenic (Synchronous) and Myogenic (Asynchronous) fliers. The differences between these two types of fliers have been listed below in Table 4.6.

Table 4.6 Differences between neurogenic and myogenic fliers

S. No	Neurogenic fliers (Synchronous)	Myogenic fliers (Asynchronous)
1	Frequency of wingbeat (ϑ_h): 2–200cps	Frequency of wingbeat (ϑ_h): 200–1000cps
2	Primitive insects such as dragonflies, cockroaches and locust	Advanced insects such as houseflies, mosquitoes and drosophila
3	Metabolism of flight muscles—oxidative type	Metabolism of flight muscles—highly oxidative and depends on fat metabolism
4	Number of mitochondria (cristae)—more (++)	Number of mitochondria (cristae)—more (++++)
5	Wing tip mutilation frequency does not increase	Wing tip mutilation frequency increases by 50% or more
6	Resilin elastomer at wingbase is moderately developed	Resilin elastomer at wingbase is more efficiently developed
7	Flight muscle contraction—Twitch-like (Direct muscles)	Flight muscle contraction—Tetanus-like oscillations (Indirect muscles)
8	Sarcoplasmic Reticulum (SR)—Highly developed for storing calcium	Sarcoplasmic Reticulum (SR)—developed for storing calcium
9	Small myofibrils	Large myofibrils

Table 4.7 Energetics of catabolism (Bio-molecules Oxidation)*

Type of biomolicules and metabolic pathway	Number of ATPs produced	Total energy (kJ)
Glucose and glycolysis and TCA cycle	26–38	780–1140
TAG (fatty acid C16)	129 + 16	4350
Proline (Oxidative Deamination, TCA)	15	450

*ATP upon hydrolysis yields 7.3 k cal/mol or 30.5 kJ/mol
*Insect spends 57 J of energy/gram body weight/hour of flight

Myofibrils are made up of fine actin filaments (I-band) and thick myosin (A-band) filaments. Actin filaments are isotropic and myosin filaments are anisotropic. Troponin and tropomyosin proteins block the myosin head from coming in contact with actin. Due to nerve impulse action, the calcium is released from the SR and this in turn removes the TN-TM blocking. In the presence of ATP, the ATP hydrolysis takes place leading to muscle contraction. Regulation of oscillatory contraction in flight muscle by troponin is rather well known. The sarcomere is the basic unit of muscle contraction within the sarcomere, with the arrival of a nerve impulse at Motor-end-plates (MEP), I-filaments slide against free ends of A-filaments leading to muscle contraction. Flight muscles shorten by about 1%. The asynchronous flight muscles produce remarkable amounts of tension in muscle fibres, in the presence of large amounts of free calcium available in the cytoplasm in contrast to synchronous muscles.

Insect flight muscles are metabolically highly active such as they have more of oxidative enzymes, mitochondrial respiration and aerobic capacity. Insect flight muscles depend on trehalose, proline and lipids as fuels in the metabolism. Carbohydrates like trehalose and proteins like proline are used during short flights. After carbohydrates, amino acids also provide a major source of energy in many insect flight muscles. Fatty acids are the fuels for long-duration and long-distance flight. Locusts, hawk moths and beetles depend on fatty oxidation. Fats are stored as triglycerides and they are released as diglycerides. Fat produced double the energy as compared to the unit weight of carbohydrate.

Since this book is dealing with the bio-aerodynamics of insect flight, instead of going into the details of metabolic pathways such as Glycolysis and Citric acid cycle, the energetics of these pathways are given the form of Table 4.7.

Summary

The structure of the thorax including the flying segments (pterothorax) and associated wings and their morphology have been considered in detail. Wing venation, which forms the supporting structural basis for the wing and its significance in the classification of insect orders, has been elucidated. The wing is attached to the thorax by a membranous basal area having sclerites, also known as pteralia, which along with their attached muscles help in flapping and rotation. Direct and indirect muscles have been described in detail, which help in wing movements.

Flight parameters of body and wing contribute to the basic understanding of insect flight and its novelty. Some aerodynamics terms have been defined clearly for the sake of convenience and clarity. Wingbeat frequencies of insects, forward velocity and flight parameters have been summarized. It has to be emphasized that flight parameters of two pentatomid bugs such as ***Tessaratoma javanica*** and ***Chro purpureus*** have been studied in all the possible details so that this may possibly help and inspire for the design of bio-mimicking MAVs [1].

Differences between neurogenic and myogenic fliers, the basis of muscle contraction and energetics have been explained briefly. Oxidation of bio-molecules has been briefly summarized in the form of a (Table 4.7).

Insect flight muscle and cardiac muscle appear to contract rhythmically but differently. The Ca^{2+} sensitivity of cardiac and flight muscle (water bug, Lethocerus) can be manipulated experimentally. The cardiac and flight muscle have thick and thin filaments adapted for oscillatory mechanical movements (Belinda Bullard and Analisa Pastore, JA Muscle Res. Cell Motil, 2019). This has been further supported by recent research articles (2021).

References

1. Chari. (2014). Bio-aerodynamics of Avian Flight. NDRF, Banglore, India.
2. Chapman, R. F. (1998). *The insects: Structure and function*, 3rd edn. Cambridge University Press.
3. Chadwick, L. E. (1953). Aerodynamics and flight metabolism. In K.D. Roeder (Ed.), *Insect physiology*. New York: Wiley.