Flight I: Structure & Function of Wings

• Wings in living insects serve a number of functions, including active flying, gliding, parachuting, altitude stability while jumping, thermoregulation, and sound production. Today’s lecture covers the structure and function of wings in modern insects.

• Understanding the evolution of wings requires an understanding of the adaptive value of the intermediate or transitional stages in their development. The next lecture covers the evolution of wings and problems associated with its study.
**Structure of wings**

- **Cross section through the wing.** Membrane is two layers of integument. Veins including nerve, blood space and tracheae. Wings do not contain muscle.

- **Venation.** Irregular network of veins found in primitive insects. Longitudinal veins with limited cross-veins common in many pterygote groups. Extreme reduction of all veins common in small insects. Longitudinal veins concentrated and thickened toward the anterior margin of the wing. This gives increased efficiency and support.
Structure of wings

- **Pterostigma.** Darkened area on forewing in Hymenoptera, Pscoptera, Megaloptera and Mecoptera and on both wings in Odonata. Functions as inertial mass in flight. Reduces wing flutter during gliding in odonates, thereby increasing flight efficiency. Provides passive control of angle of attack in small insects, which enhances efficiency during flapping flight.

- **Wing folding.** Flexion lines reduce passive deformation and enhances wing as an aerofoil. Fold lines used in folding of wings over back.
Mechanisms of wing movement

• **Wing coupling.** Orthoptera and Odonata wings are not anatomically coupled. Coordination of forewings and hindwings in flight is accomplished by pattern-generator neurons in the central nervous system. Details of anatomical wing-coupling varies among taxonomic groups, suggesting that it evolved independently several times.

• **Halteres in Diptera.** Derived from the hindwings. Functions to maintain stability in flight.
Two general mechanisms of wing movement

- **Direct mechanism.** Downward movement of the wing is the result of the contraction of muscles attached directly to the wing. This flight mechanism is under control of **synchronous flight muscle.** Because each wingbeat is control by a nervous impulse, the direct mechanism of insect flight is said to be **neurogenic** in origin.

- **Indirect mechanism.** Downward movement of the wing is the indirect result of the contraction of muscles attached to the thorax. This flight mechanism is under the control of **asynchronous flight muscle.** Because several to many wingbeats occur for every nervous impulse, the indirect mechanism of insect flight is said to be **myogenic** in origin.
Two general mechanisms of wing movement

- **Taxonomic distribution of direct and indirect flight mechanism.** Direct mechanism of wing movement is found in the Palaeoptera and the Blatteria. Indirect mechanism of wing movement is found in the Hymenoptera (bees), Diptera, some Coleoptera and some Hemiptera. Other groups (some Coleoptera and Orthoptera) use a combination of direct and indirect mechanisms to move wings.

- **Efficiency of flight production.** Muscles used in flight arise in the coxa in many insects and also function in leg movement during terrestrial locomotion. Elastic properties of wing hinges, wing muscles and thorax greatly enhance flight efficiency. Elasticity of these structures is due to the presence of the protein resilin. In locust, 86% of the energy used in the upstroke can by recovered during the downstroke. Elasticity of the thorax means that wings are in stable position only at the top of the upstroke or at the bottom of the downstroke.
Movement of the wings

- **Stoke plane** is the plane in which wings move relative to the long axis of the body. Stroke plane determines the rate of forward movement during flight. Insects control turning movements by changing the stroke plane on one side of the body relative to that on the other side of the body. Stroke plane in locust averages about $30^\circ$. Hovering requires an average stroke plane of $0^\circ$.

- **Amplitude** of wingbeat is the distance in degrees travelled by the wing tip from the top of the upstroke to the bottom of the downstroke. Greater amplitude produces greater power output. Insect control turning movements by varying the amplitude of the wingbeat on both sides of the body.
Movement of the wings

- **Wingbeat frequency** is the number of wingbeats per second (Hz). Insects with synchronous flight muscles have low wingbeat frequencies ($\leq 50$ Hz) relative to insects with asynchronous flight muscle (100-1000 Hz). Wingbeat frequency is also negatively correlated with body size. The greater the wingbeat frequency the greater the power output and the greater the lift production.

- **Wing twisting** occurs when the relative position of the leading and tailing edges of the wing changes during the wingbeat. Both passive and active (=muscular) forces are responsible for changing wing twisting. Wing twisting controls the angle of attack which control lift and forward movement of the insect in space.
Aerodynamics

- **Relative wind** is the movement of air relative to the wing. Its two components are due to 1) the airspeed of the insect and 2) the velocity of the wing in the stroke plane.

- **Angle of attack** is the angle at which the relative wind strikes the chord of the wing. Insects control the angle of attack by active and passive twisting of the wing. Changes in the angle of attack are used to control the force of relative wind.

- **Force of relative wind** has two components. **Lift** is the vertical force produced by relative wind. This force is what gets insects into the air and keeps them there. **Thrust** is the horizontal force produced by relative wind. This force moves insects forward through the air. Forward thrust is resisted by **profile drag** (the cross-sectional area the insect presents to the air) and mostly by **induced drag** (development of vortices at the wing tips.)
Variations in forward flight

- **Hovering** in flight is accomplished by changing the stroke plane to nearly horizontal and maintaining a positive angle of attack throughout the wingbeat.

- **Gliding** requires a high lift-to-drag ratio. This is accomplished mostly by changing the angle of attack to maximize thrust and minimize drag and negative lift.

*Fig. 147* Hovering by *Manduca*. A. Dorso-lateral view, body almost vertical, strokeplane almost horizontal. B. Lift production on the morphological 'up' and 'down' strokes. Notice that the wing has twisted through almost 180° on the 'up-stroke' to bring the morphological lower surface uppermost. C. Sequence from a film taken from directly above a hovering insect showing positions of the wings. Under surfaces of wings shown stippled, leading edge of forewing thicker (after Weis-Fogh, 1973)
Control of flight