Insect Locomotion and Wing Evolution

[Images of insects and their anatomical structures, including close-ups of muscles and exoskeletons.]

- Flexible muscle
- Extensor muscle
- Exoskeleton (cuticle)
- Joint

[Links to related resources such as websites and images of insects and their anatomy.]
INSECT MUSCLES

All muscles are striated (intracellular bands)

Muscles with few striae/cell = slow rhythmic contraction
many striae/cell = vigorous contractions

All insect muscles possess striae (unlike mammals)

Adult Acrididae - ~900
Caterpillar (Lepidoptera) - ~ 4000
Humans ~800
INSECT MUSCLES

FOUR TYPES (functional categories)


2. Segmental – necessary for contraction of segments (molting, breathing, locomotion, increase in body temp, etc.)

3. Appendicular - Appendages moved (as unit) by muscles originating either on tergum or sternum and inserted on the coxae.

4. Flight – direct and indirect

Each Segment operated by muscles originating in the previous segment (anterior)
Fig. 3.2  Muscle attachments to body wall: (a) tonofibrillae traversing the epidermis from the muscle to the cuticle; (b) a muscle attachment in an adult beetle of *Chrysobothrus femorata* (Coleoptera: Buprestidae); (c) a multicellular apodeme with a muscle attached to one of its thread-like, cuticular ‘tendons’ or apophyses. (After Snodgrass, 1935.)
Fascinating Facts about Insect Locomotion

- Cockroaches (Blattodea) can run 2.9 mph (=70 mph if scaled to size of lion)
- Fly (Diptera) wings can beat 200x/s
- Bumble bee (Hymenoptera) wings can beat 160x/s
- Average flight speed of a fly is 4.5 mph
- Houseflies move 300x their body length/s; a jet at the speed of sound moves 100x its length/s
- Fastest flier is the desert locust (*Schistocerca gregaria*) @ 33 km/h
- Fastest runner is the tiger beetle (*Cicindela hudsoni*) @ 5.57 mph
Walking & Running

External leg morphology
Motion

- Contractions/relaxations of pairs of agonistic/antagonistic muscles attached to cuticle allow walking

- Tripod motion at low-moderate speed

- Tripod maintains center of gravity/stability

- To go faster: 1) shorten retraction period to increase frequency of movement
  2) quadrupedality
  3) hind-leg bipedality
Friction and Leverage

- Claws
- Aroluim/Pulvilli (flies)
- Lubricated hairs

- Empodium
- Pulivilliform empodium
Jumping

Common mechanism:
- Slow contraction of femoral muscles

Adaptations:
- Enlarged hind femora
- Cuticular elasticity (high resilin content)

Examples:
- Fleas (Siphonaptera) jump 33 cm high = 200x the length of flea
- Locusts (Acrididae) jump 30 cm high and 70 cm forward

Grasshopper jump: [http://www.st-andrews.ac.uk/~wjh/jumping/perform.htm](http://www.st-andrews.ac.uk/~wjh/jumping/perform.htm)
Specialized Examples:

- Collembola (Springtails): jump w/ fucula-tenaculum mechanism

- Elateridae (Click beetles): right themselves w/ prosternal spine, flexible union of pro and mesothorax
Wings may have evolved on jumping insects as a gliding mechanism. Flying jumpers may benefit by getting into the air before opening wings to avoid damage from the surrounding substrate.
Crawling/Larval Locomotion

Morphology:
- Thin, flexible cuticle w/o necessary rigidity to anchor muscles
- Hemolymph forms **hydrostatic skeleton**
- Turgidity maintained by criss-crossed body wall ‘turgor’ muscles
- Turgor muscles contract against incompressible **haemocoel**

-Caterpillar legs on thoracic segments and **prolegs** on abdominal segments
- Abdominal prolegs have **crochets** (schlerotized hooks)

http://www.sdnhm.org/exhibits/monarca/teachers/images/caterpillar-body-answers.gif
Larval Locomotion:

Figure 7.6  Locomotion in a crane fly larva. Redrawn with modifications from Kevan, 1962, after Gilyarov.

Direction of progression
Direction of peristaltic waves
Figure 1: Main locomotory gaits in *Pleurotya* caterpillar. In **a** the insect is walking from left to right; in **b** and **c** it is retreating from right to left. Stippling indicates when leg-bearing segments (6–9, 13) are off the ground. The black arrow in **b** and **c** signifies the rapid recoil stage of locomotion. Speed, stride frequency and stride length during normal forward walking were 1.0±0.2 cm s⁻¹, 1.7±0.2 Hz and 0.6 cm, respectively. Measurements were made from video images (Panasonic, 50 frames per second, shutter speed 0.001 s, and NAC200, 200 frames per second with strobe synchronization).

Swimming--surface

Cohesion and surface tension important

Morphology and Motion:
- Contact w/ water maintained during protraction
- So, more thrust put into retraction by expanding the leg area w/ fringes of hair and spines
- Hair/spines collapse onto leg during recovery stroke

http://www.cirrusimage.com/bugs_water_strider.htm
Swimming—sub-surface

Air stores increase buoyancy

Motion:
- undulate body
- jets of water through anus (Odonata nymphs push water out @ 50 cm/s)
- walk on underwater substrate
Examples:

- Dytiscidae (predaceous diving beetles, p 405): submerge w/ air in chamber under elytra, swim by moving opposite legs simultaneously, like frog

- Hydrophilidae (water scavenger beetles, p 406): swim by moving opposite legs alternately, carry air in silvery film over ventral surface

- Notonectidae (Hemiptera, backswimmer, p 291): swim upside down

- Corixidae (Hemiptera, water boatmen, p 290): use ground eggs in flour, front tarsi scooped

- Belostomatidae (giant water bug, p 289): largest Hemiptera

- Trichoptera (caddisflies, p 558): caterpillar-like larvae, gills, some make cases w/ silk or cement
Flight

- Evolved 330-40 mya

- Pterygotes are now the most species rich group on Earth—60% of all described spp

- Gravity and drag (air resistance) must be overcome for flight

http://www.ucmp.berkeley.edu/arthropoda/uniramia/odonatoida.html
Morphology:

- Wings are outgrowths of body wall located dorsolaterally between nota and pleura
- Arise as saclike outgrowths, when fully developed are flaplike with sclerotized veins
- Most pterygotes have 2 pairs of wings, one on mesothoracic and one on metathoracic segment
Morphological Problem:

- Turbulance created by forewings hinders hindwings (makes Orthoptera, Neuroptera, Isoptera poor fliers)

- In many Odonata, hindwings move before forewings

- In some Odonata and most Orthoptera, only slight phase difference w/ front wings moving a little ahead

- Pairs of wings may be overlapped at base or hooked together so they move as one (Lepidoptera, Hymenoptera, Trichoptera, Hemiptera)

- Hindwings may be reduced (Diptera—halteres)
Mechanisms:

- Direct and indirect flight muscles present

- Direct: connected to wings

- Indirect: no muscle-wing connection. Muscles deform thoracic box to move wings.

- Direct used in old groups: Odonata and Blattodea. Some recovery muscles still indirect.

- Indirect used in advanced groups, and direct used just for wing orientation.
Direct flight:

- Muscles are attached to 2 sclerites at wing base (basalare and subalare) and the axillary sclerite and coxa and sternum.

- Upward stroke by contraction of muscles attached to wing base inside pivotal point.

- Downward stroke by contraction of muscles that extend from the sternum to wing base outside pivotal point.
Indirect flight:

- Flight muscles attached to tergum and sternum

- Wing depression process:
  1) Dorsal longitudinal muscles cause notum to bow;
  2) raising notal wing processes in relation to pleural wing processes;
  3) causing depression of wing.
Wing elevation process:

1) Tergosternal muscles contract;
2) pulling down on notum;
3) notal wing processes move down in relation to pleural wing processes;
4) wing is elevated.

In addition:

Direct wing muscles used for controlling angle of flight and wing flexion (folding wings back in neopterygotes).
-Flight is:

1) elevation and depression
2) fore (promotion) and aft (remotion) movement
3) twisting w/ direct muscles—pronation (leading edge down) and supination (trailing edge down)
4) changes in shape by folding and buckling

-Wing traces out a figure 8 relative to the body at its base.
<table>
<thead>
<tr>
<th>Insect</th>
<th>Speed, km/h</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mayflies, small field grasshoppers</td>
<td>1.8</td>
</tr>
<tr>
<td>Bumble bees, rose chafers</td>
<td>3.0</td>
</tr>
<tr>
<td>Malaria mosquitoes</td>
<td>3.2</td>
</tr>
<tr>
<td>Stag beetle, damselfly, <em>Ammophila</em> (a fossorial wasp)</td>
<td>5.4</td>
</tr>
<tr>
<td>House fly</td>
<td>6.4</td>
</tr>
<tr>
<td>Cockchafer, cabbage white butterfly, garden wasp</td>
<td>9.0</td>
</tr>
<tr>
<td>Blow fly</td>
<td>11.0</td>
</tr>
<tr>
<td>Desert locust</td>
<td>16.0</td>
</tr>
<tr>
<td>Hummingbird hawk moth</td>
<td>18.0</td>
</tr>
<tr>
<td>Honeybee, horse fly</td>
<td>22.4</td>
</tr>
<tr>
<td><em>Aeschna</em> (a big dragonfly), hornet</td>
<td>25.2</td>
</tr>
<tr>
<td><em>Anax</em> (one of the biggest of European dragonflies)</td>
<td>30.0</td>
</tr>
<tr>
<td>Deer bot fly</td>
<td>40.0</td>
</tr>
</tbody>
</table>

*Data from Nachtigall (1974b) based on various sources.*
Neural control of flight:

- 1 nerve impulse/wing beat = **synchronous muscles** in slow fliers (Odonata)
- In fast fliers, there is not a 1:1 neural impulse:muscle contraction = **asynchronous muscles**

- **Click mechanism:** wings have 2 stable positions, up and down. As wing moves from one extreme to other, passes through intermediate unstable position = **click point.** At click, thoracic elasticity snaps the wing through to the alternate stable position.
- Release of muscle tension at click causes next muscle contraction.
- Allows muscles to oscillate, contracting much faster than neural impulses
Wing Evolution

- Several competing theories attempt to explain evolution of wings

- All hypotheses have common assumption that winglets originally had a non-flight function

- Insects evolved after hexapod ancestors were terrestrial, but bc/ primitive pterygote orders have aquatic nymphs, primitive condition for pterygotes may have been immature development in fresh water

- Wings likely evolved only once bc/ veins and articulated sclerites at wing base are homologous and imply monophyly

- Wings likely evolved in Devonian
Preadaptive functions of protowings:

- protection of legs
- covers for spiracles
- thermoregulation
- sexual display
- aids in concealment by breaking-up outline
- predator avoidance by extension of escape jump with gliding

Aerodynamic function gained only after enlargement.
Advantages of flight:
- Sexual outcrossing among unrelated mates
- Dispersing to new habitats
- Escaping enemies
- Locating specific feeding and oviposition sites
- Dispersal by wind

Routes to flight:

- Floating
- Paragliding
- Running-jumping to flying
- Surface sailing
  - requires articulated winglets
  - accounts for loss of abdominal winglets, which would be downwind of thoracic ones
  - occurs in some Plecoptera
  - could have driven evolution of wing length
Hypotheses for the origin of wings/flight

Paranotal Lobe Hypothesis:

- Long-standing hypothesis
- Wings derived from postulated lobes, outgrowths of thoracic terga called paranota
- Lobes not articulated, so tracheation, innervation, venation, and musculature were of secondary origin
- Posits gliding origin for flight
- Similar extensions widespread in non-hexapod arthropods. Lateral lobes present in trilobites, even articulated in crustaceans and myriapods

http://www.nature.com/nature/journal/v427/n6975/fig_tab/nature02291_F1.html
Exite-endite Hypothesis:

- Displaces PLH
- Wings evolved from serially repeated, pre-existing mobile structures on pleuron
- Likely from outer appendage, exite, and inner appendage, endite, of basal leg segment, the expicoxa
- Each ‘proto-wing’ was formed by fusion of exite and endite lobes of ancestral leg
- Exites and endites had tracheation and articulation
- Fossil and molecular development studies support articulated winglets on all body segments, best developed on thorax
Gills to Wings Hypothesis/Exite Origin of Wings:

- Fits w/ above hypothesis
- Earliest pterygotes had aquatic immatures
- Wings as derivations fr/ tracheal gills in ancestral aquatic ‘protopterygote’
- Winglets postulated to be used in gas exchange and swimming, w/ terrestrial adult co-opting them for aerodynamic function
- Unknown whether proto-wings originally used for aerodynamic or thermoregulatory function
- Fossil, neurological, and developmental support


-Showed ancestral aquatic insects with small wings, rudimentary thoracic muscles, low muscle power could have been effective surface skimmers and evolved flight via selection for faster skimming (’94)

-Support with intermediate flying form of *Leuctra* spp (Plecoptera) = **surface skimming with hind legs** (’97)

http://cac.psu.edu/~jhm10/movies/stonefly.mov
Thermoregulatory Hypothesis:


-Used models of Paleozoic insects to measure aerodynamic and heat transfer characteristics of these models as functions of physical characteristics of wings.

-Wings evolved from an ancestor with small winglets: selection for increased thermoregulatory capacity (preadaptation for flight)

-After this initial selection, selection could act for increased aerodynamic capacity
- Also relevant for evolution of flapping flight because:

1. Effectiveness of wings in regulating body T enhanced if wings move

2. Thermoregulation and flight associated in modern insects—high and narrow range of body T needed for flight
Conclusions:

1. Short wings don't change any aerodynamic properties of the insect compared to wingless forms. Large wings had significant aerodynamic effects.

2. Short wings do have a large thermoregulatory effect relative to wingless models.

3. This suggests a gradual transition from thermal to aerodynamic roles in the evolution of longer winglets.