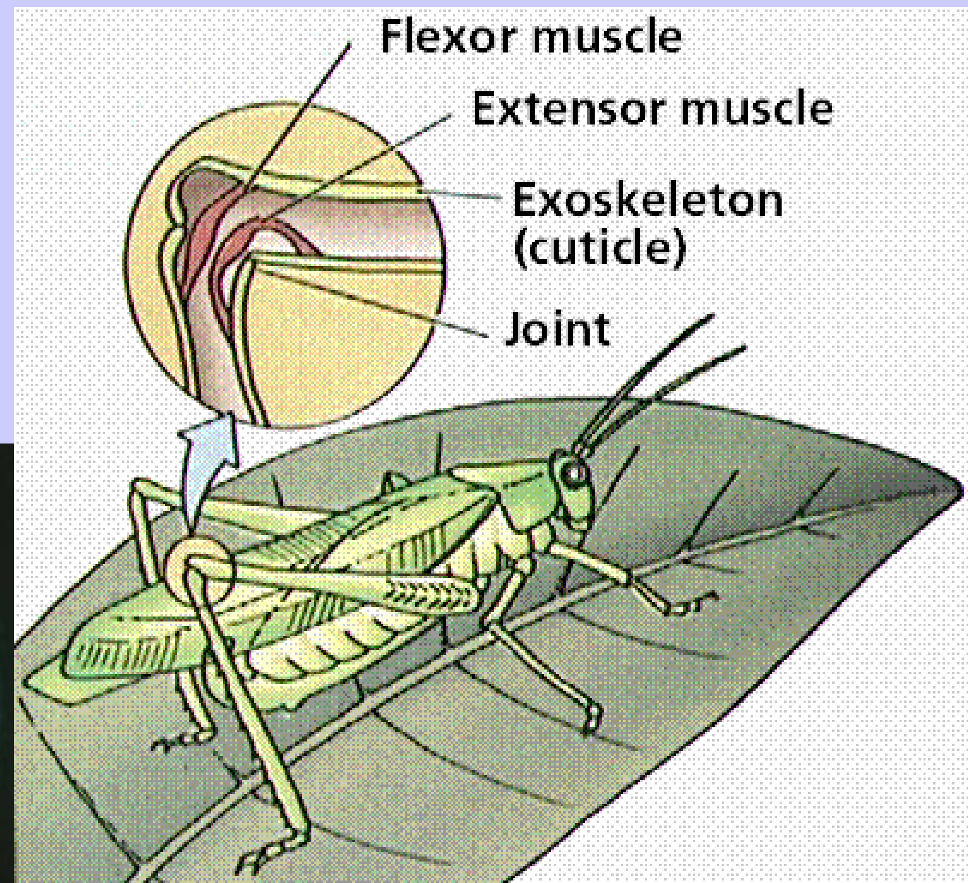
Insect Locomotion and Wing Evolution



www.hawaii.edu/zoology/ faculty/taylor.htm http://stammhirn.biologie.uni-ulm.de/w4fly/LehmannLabProjects.html http://www.emc.maricopa.edu/faculty/farabee/BIOBK/exoskel.gif

INSECT MUSCLES

All muscles are striated (intracelular bands)

Muscles w/ few striae/ cell = slow rhythmic contraction
w/ a lot = vigorous contractions

All insect muscles posses striae (vs humans)

Adult Acrididae - ~900
Caterpillar (imm Lepidoptera) - ~ 4000

Humans ~800

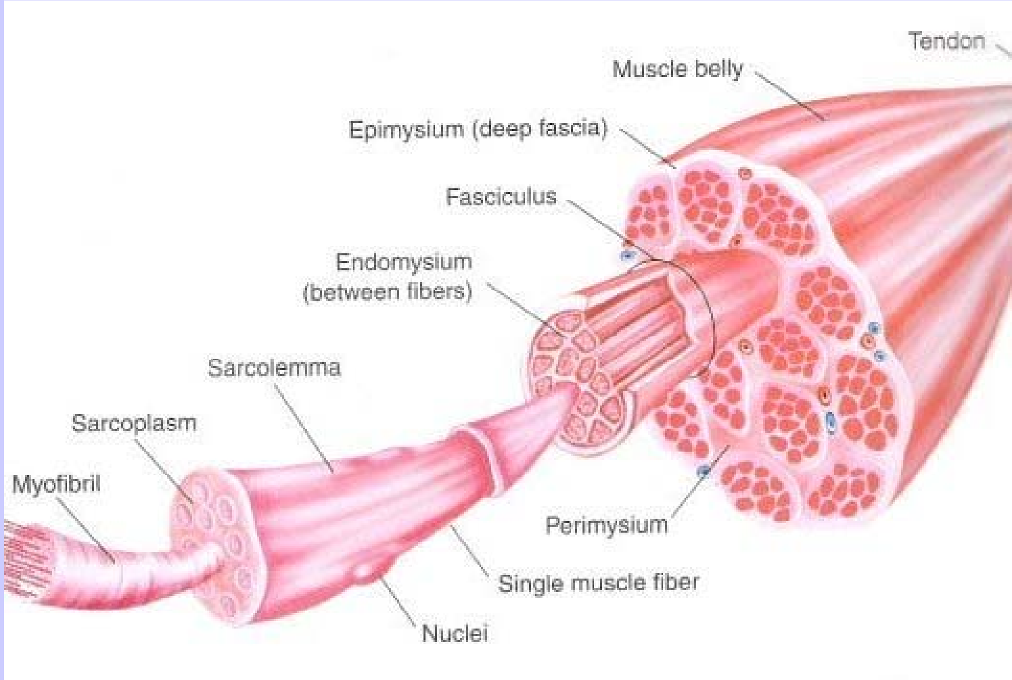


Figure 1: Muscle belly split into various component parts (from Essentials of Strength Training & Conditioning, National Strength & Conditioning Association)

INSECT MUSCLES

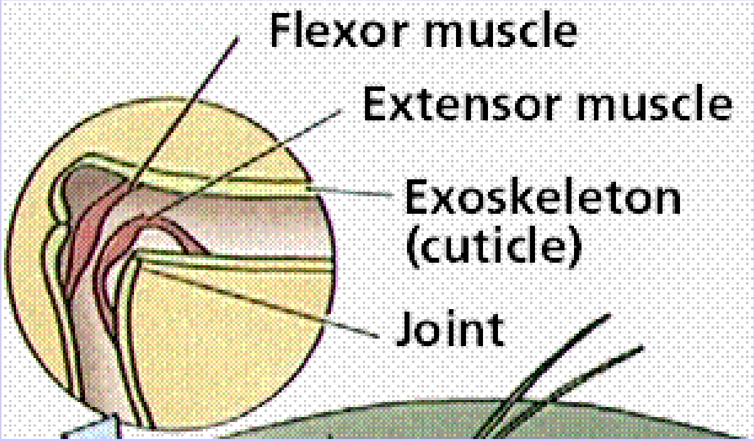
FOUR BASIC TYPES (artificial groupings, rather – functional groupings

1. Visceral – surrounds ducts and tubes produce directional waves /peristalsis for moving “products”

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

Muscle Attachment

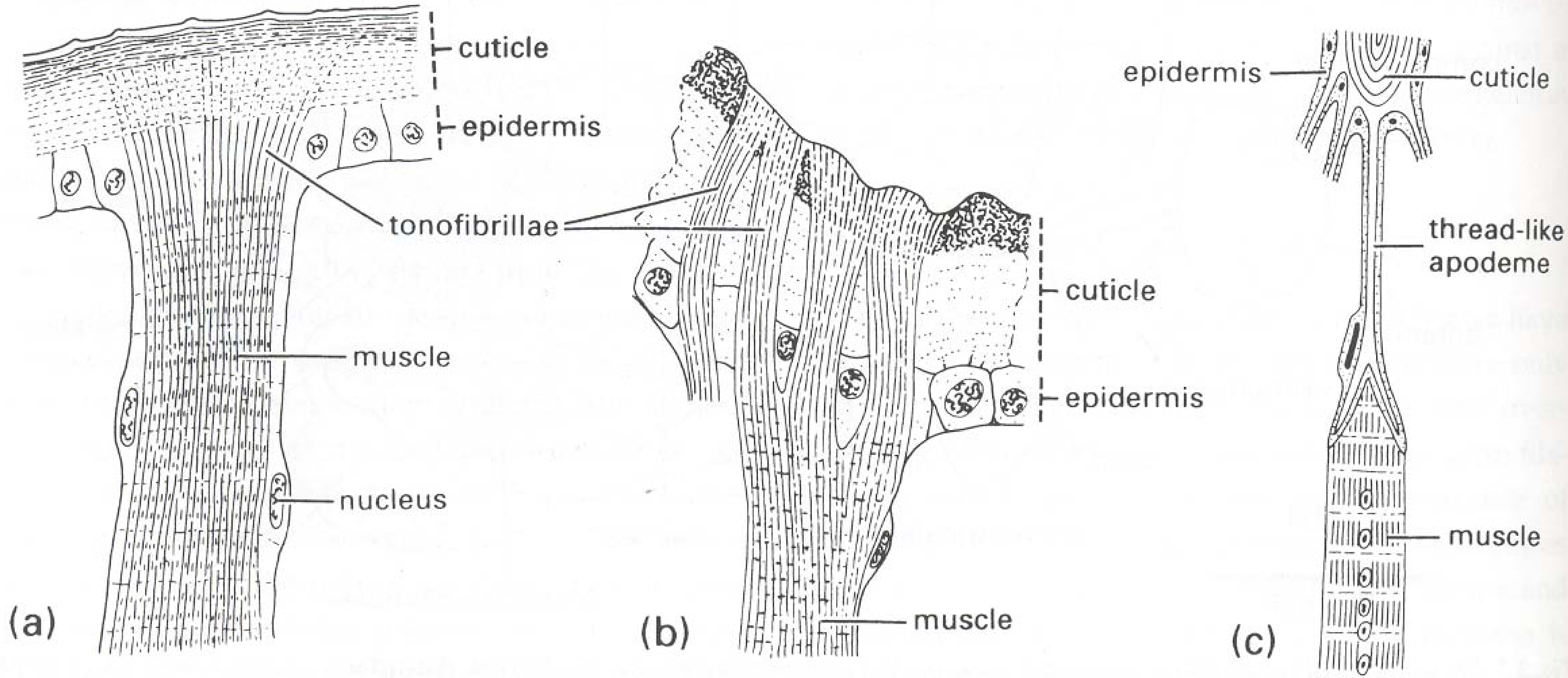


Fig. 3.2 Muscle attachments to body wall: (a) tonofibrillae traversing the epidermis from the muscle to the cuticle; (b) a muscle attachment in an adult beetle of *Chrysobothrus femorata* (Coleoptera: Buprestidae); (c) a multicellular apodeme with a muscle attached to one of its thread-like, cuticular 'tendons' or apophyses. (After Snodgrass, 1935.)

See: http://entochem.tamu.edu/MuscleStrucContractswf/index.html

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

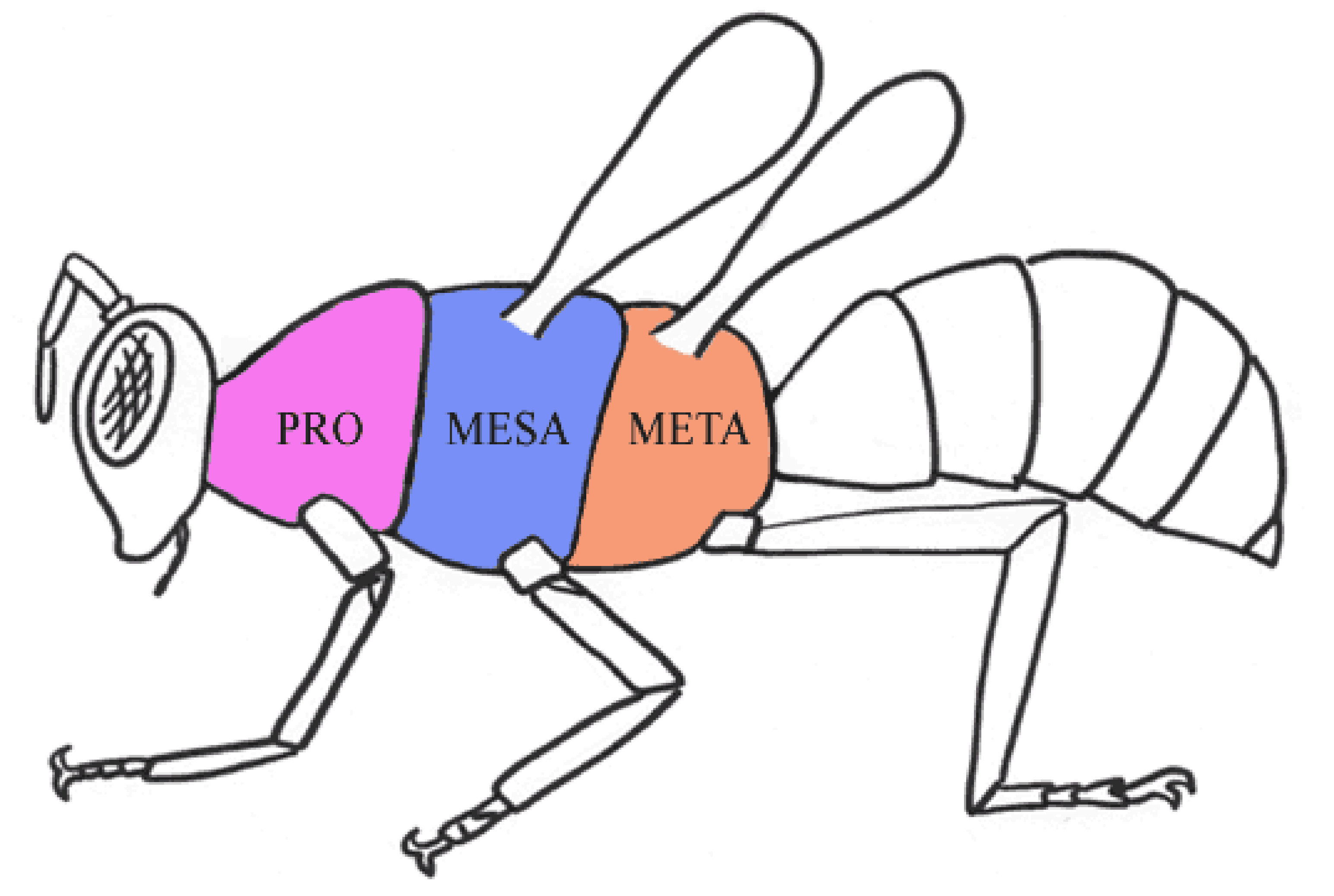
-Fastest flier is the desert locust (*Schistoccerca gregaria)* @ 33 km/h

-Fastest runner is the tiger beetle (*Cicindela hudsoni*) @ 5.57 mph

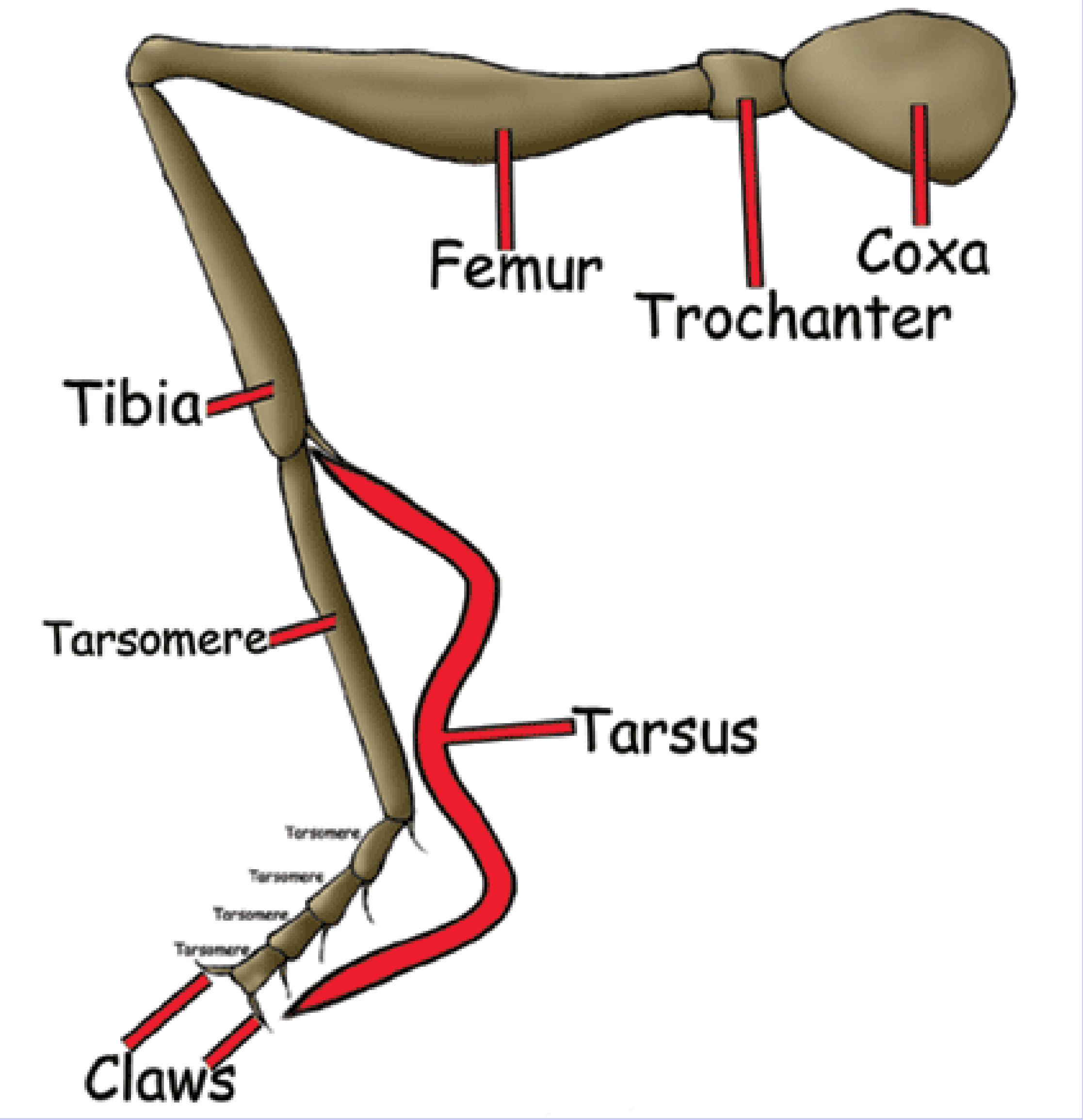
www.news.cornell.edu/.../ insect_flight.html

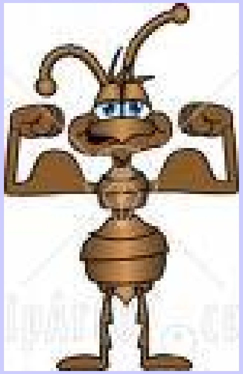
Walking & Running

External leg morphology



bugs.bio.usyd.edu.au/.../ extMorphology.html





http://bugs.bio.usyd.edu.au/Entomology/images/Topics/extMorphology/leg_master.gif

Motion

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

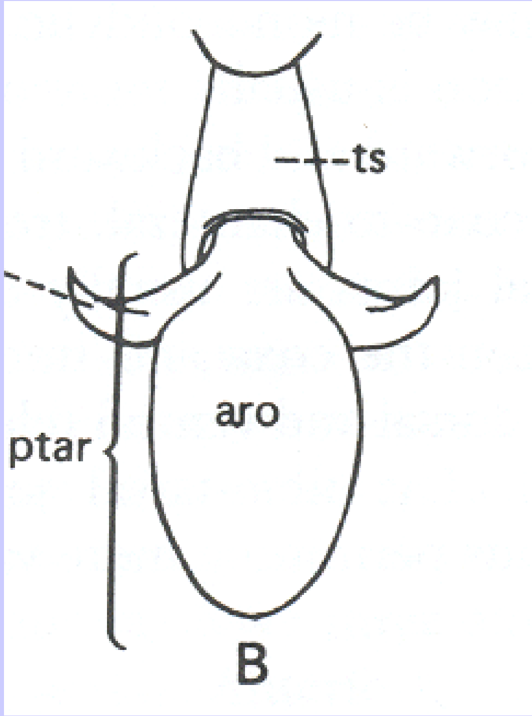
-Tripod motion at low-moderate speed

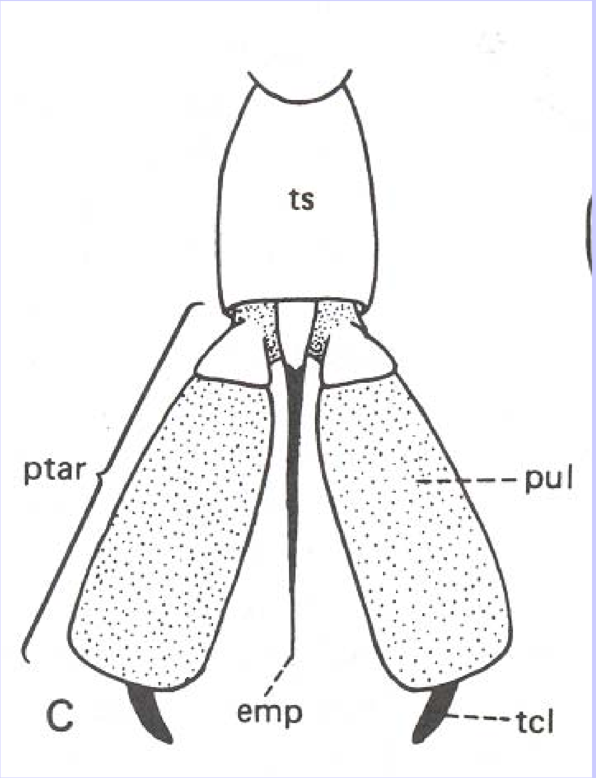
-Tripod maintains center of gravity/stability

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

http://www.life.uiuc.edu/delcomyn/RSSimAnimation.html

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:

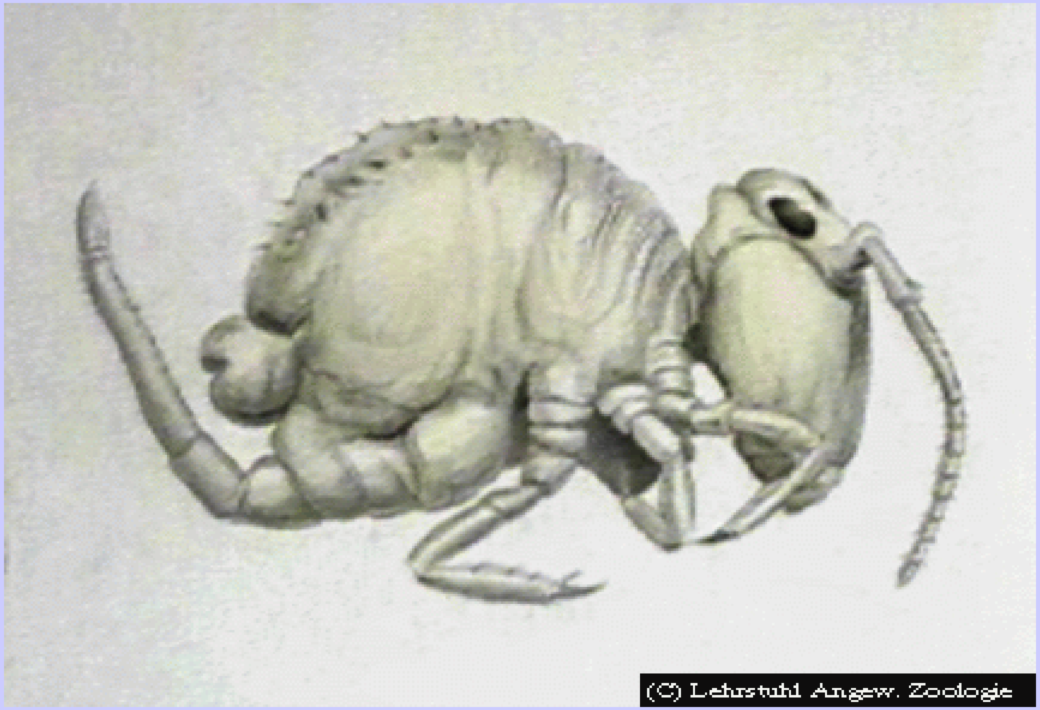
- **-Fleas (Siphonaptera) jump 33 cm high=200x the length of flea**
- **-Locusts (Acrididae) jump 30 cm high and 70 cm forward**
- **-Grasshopper jump: http://www.st-andrews.ac.uk/~wjh/jumping/perform.htm**

http://www.geocities.com/brisbane_grasshoppers/images/wpe20.jpg

Specialized Examples:

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

-Elateridae (Click beetles): right themselves w/ prosternal spine, flexible union of pro and mesothorax



http://collections.ic.gc.ca/biodiversity/photos/coleoptera/elateridae.jpg

www.faunistik.net/DETINVERT/ COLLEMBOLA/col01.html

Link to Flight…

-Wings may have 1st evolved on jumping insects as a gliding mechanism

-Flying jumpers may benefit by getting into the air before opening wings to avoid damage fr/ surrounding substrate

Crawling / Larval Locomotion

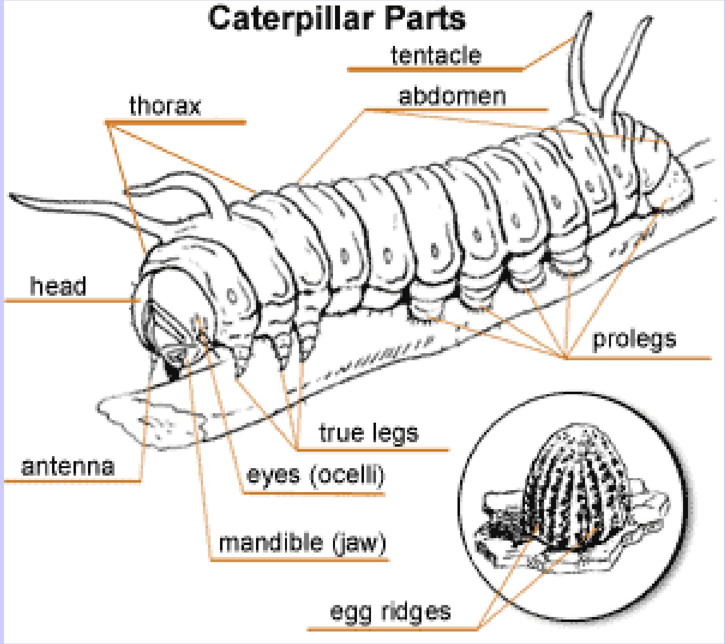
Morphology:

-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**

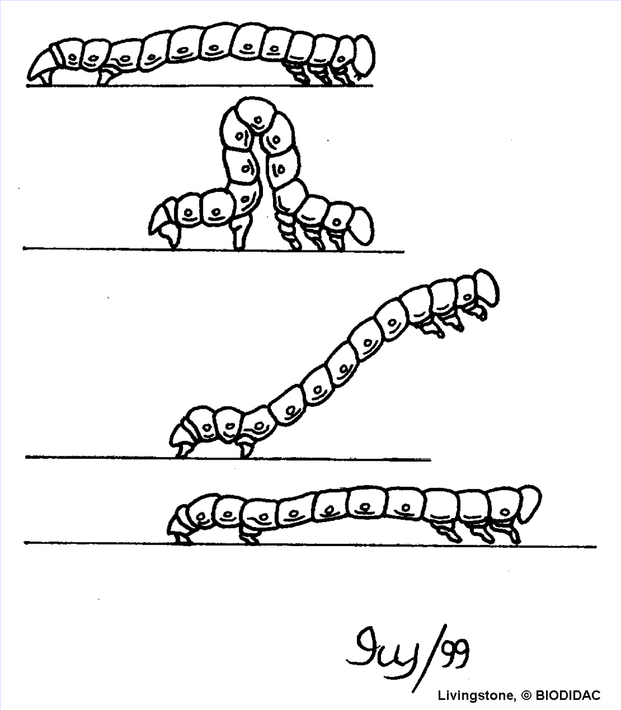


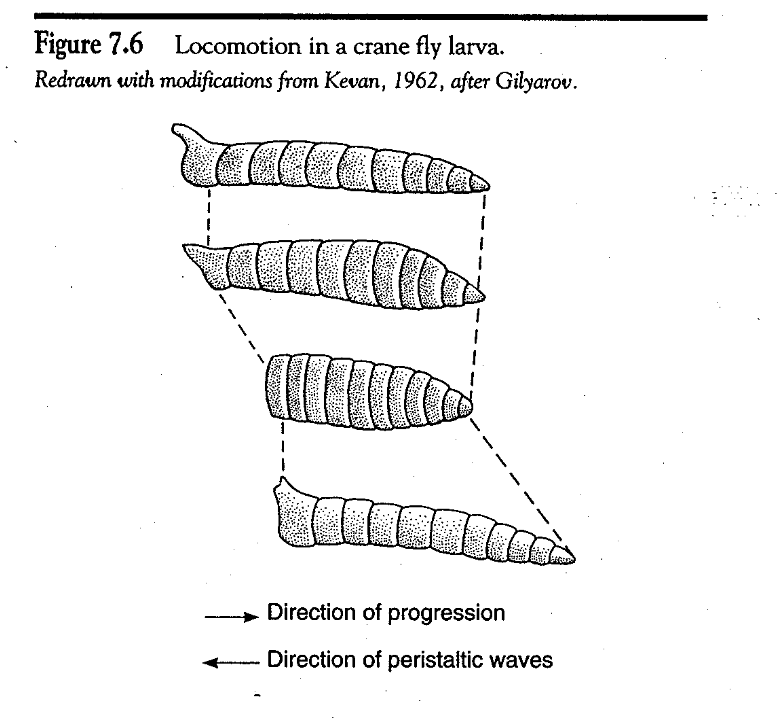
-Caterpillar legs on thoracic segments and **prolegs** on abdominal segments

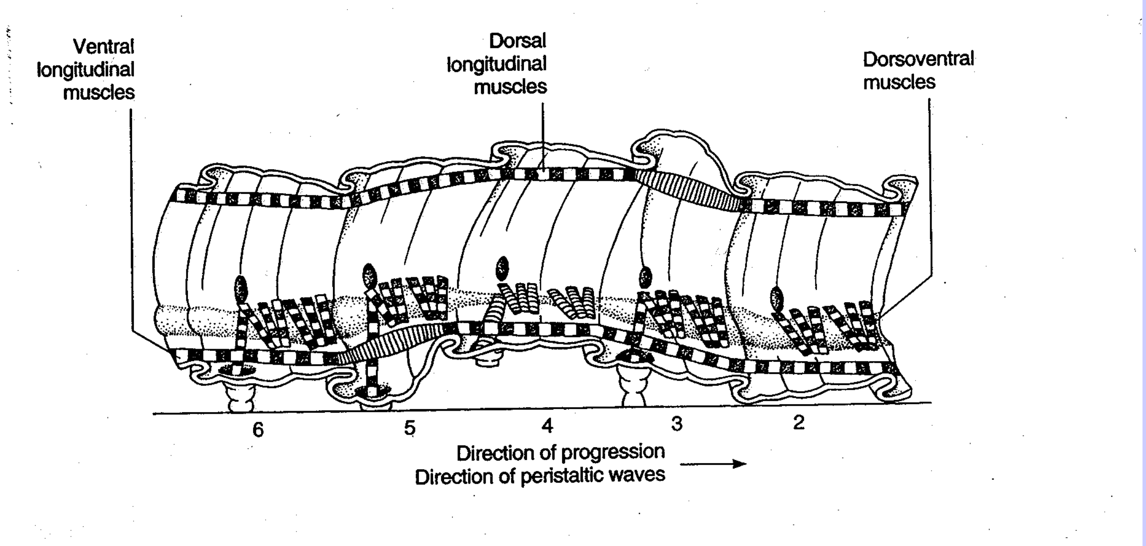
-Abdominal prolegs have **crochets** (schlerotized hooks)

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

Larval Locomotion:







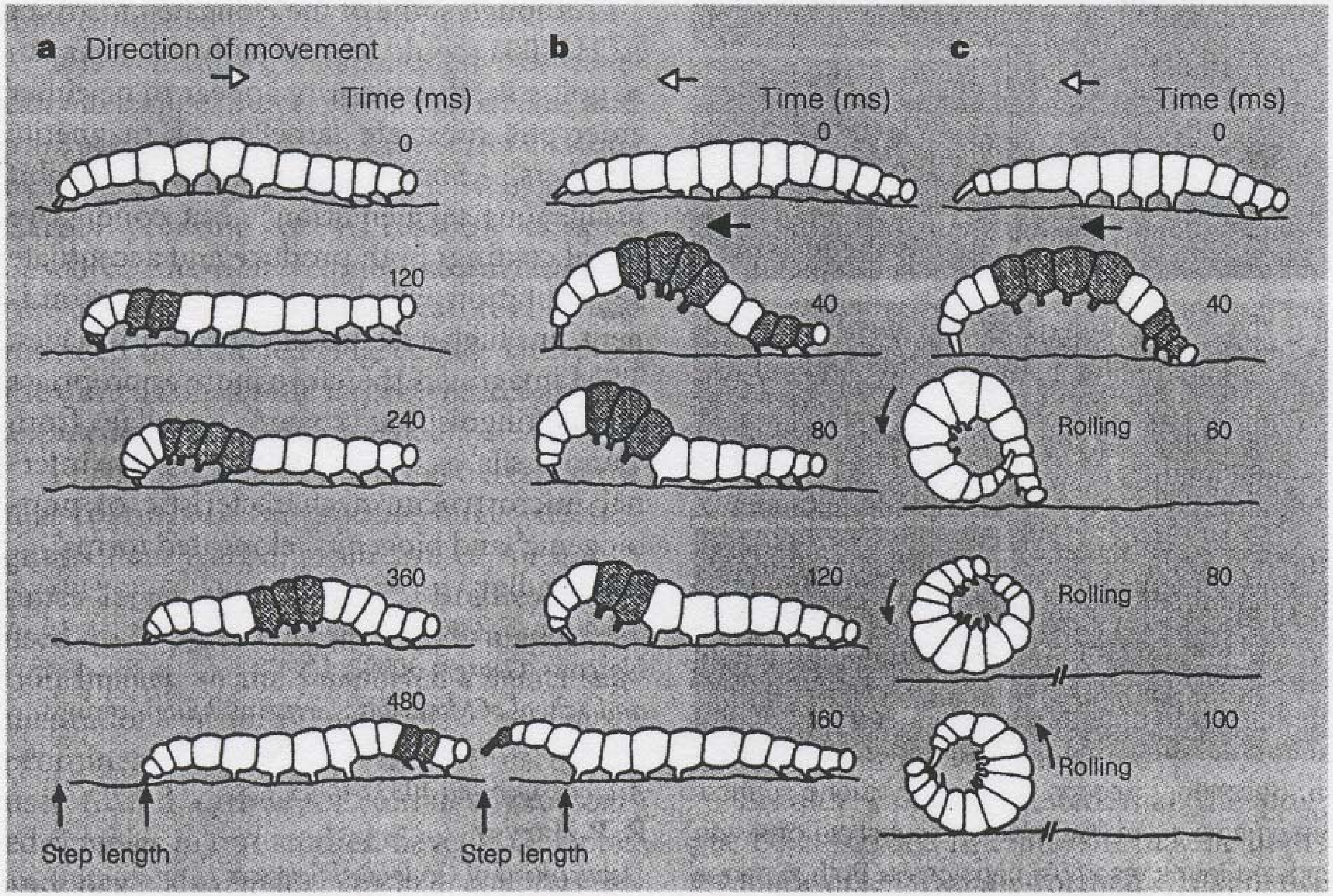


Figure 1 Main locomotory gaits in *Pleurotya* caterpillar. In **a** the insect is walking from left to right; in **b** and **c** it is retreating from right to left. Stippling indicates when leg-bearing segments (6–9, 13) are off the ground. The black arrow in **b** and **c** signifies the rapid recoil 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).

Brakenbury, J. 1997. Caterpillar kinematics. Nature 390:453.

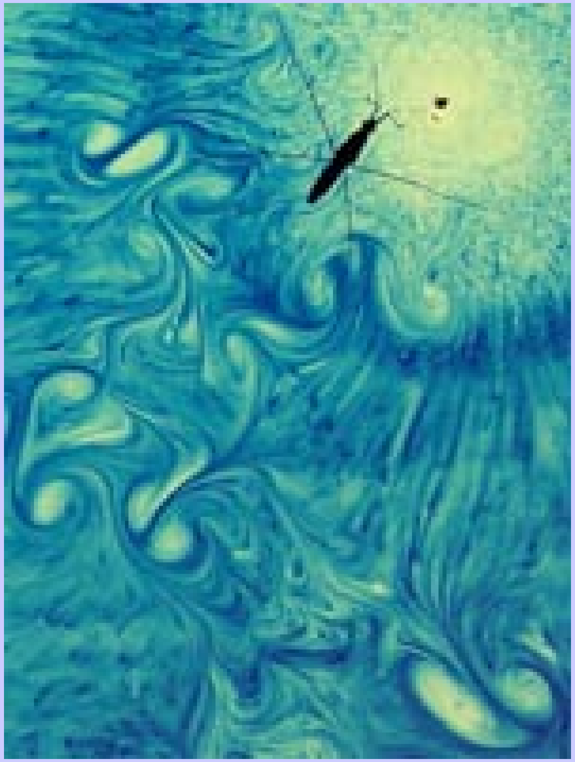
Swimming--surface

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



web.mit.edu/newsoffice/ nr/2003/robostrider.html

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**

www.btinternet.com/.../ dragonflylarvae.htm

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

http://www.troutnut.com/naturals/other/index5.php

Flight

-Evolved 330-40 mya

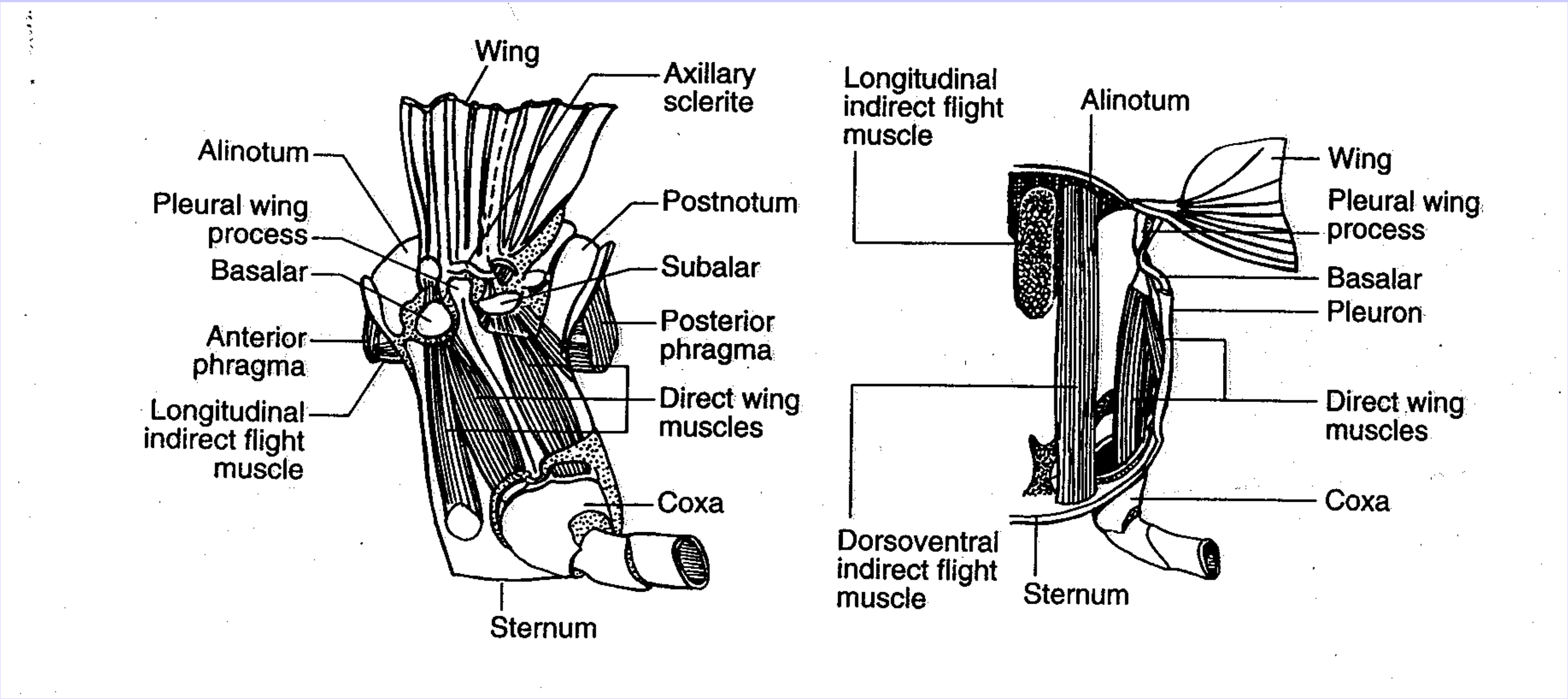
-Pterygotes are now the most species rich group on Earth—60% of all described spp

-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 f laplike w/ sclerotized veins
-Most pterygotes have 2 pairs of wings, one on mesothroacic 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 Orthoperta, 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)

http://www.ento.csiro.au/education/insects/hymenoptera.html

http://instruct1.cit.cornell.edu/courses/bionb424/students/acp13/Phylogenyandevolution.htm

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.

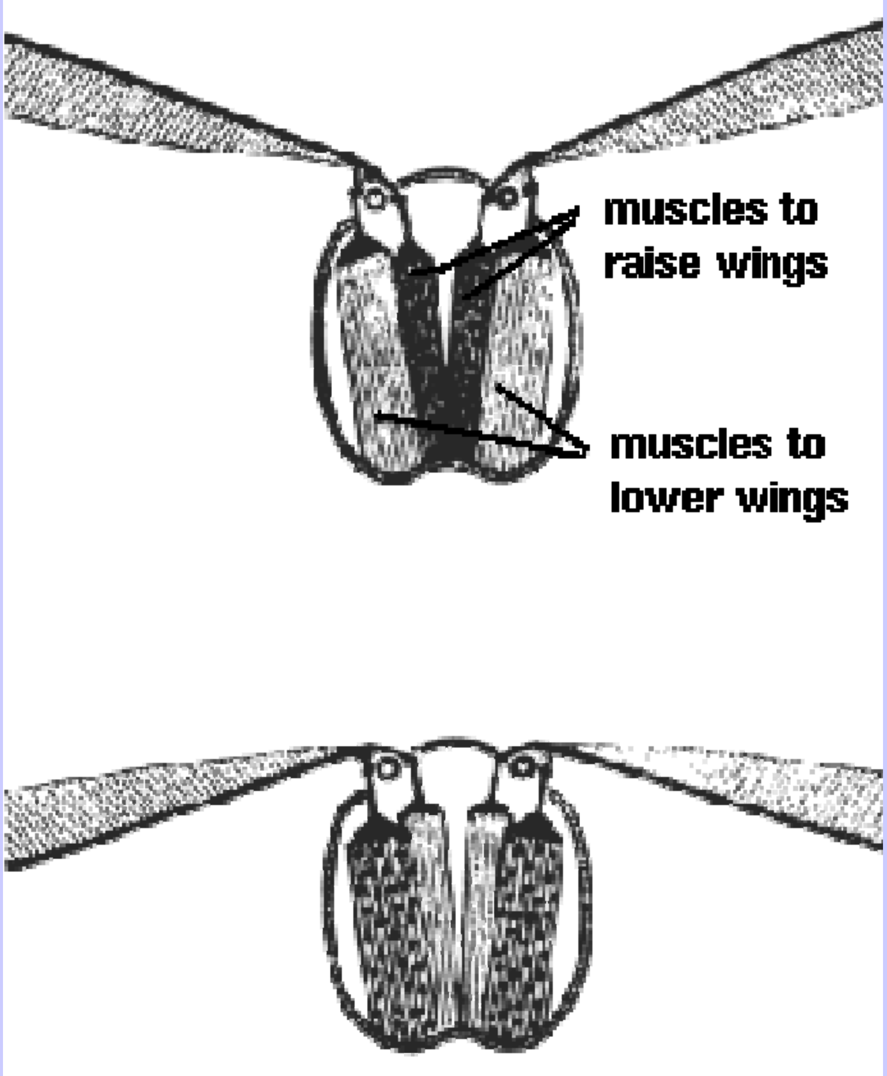
-Indirect used in advanced groups, and direct used just for wing orientation.

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 fr/ the sternum to wing base outside pivotal point.



Indirect flight:

-Flight muscles attached to tergum and sternum

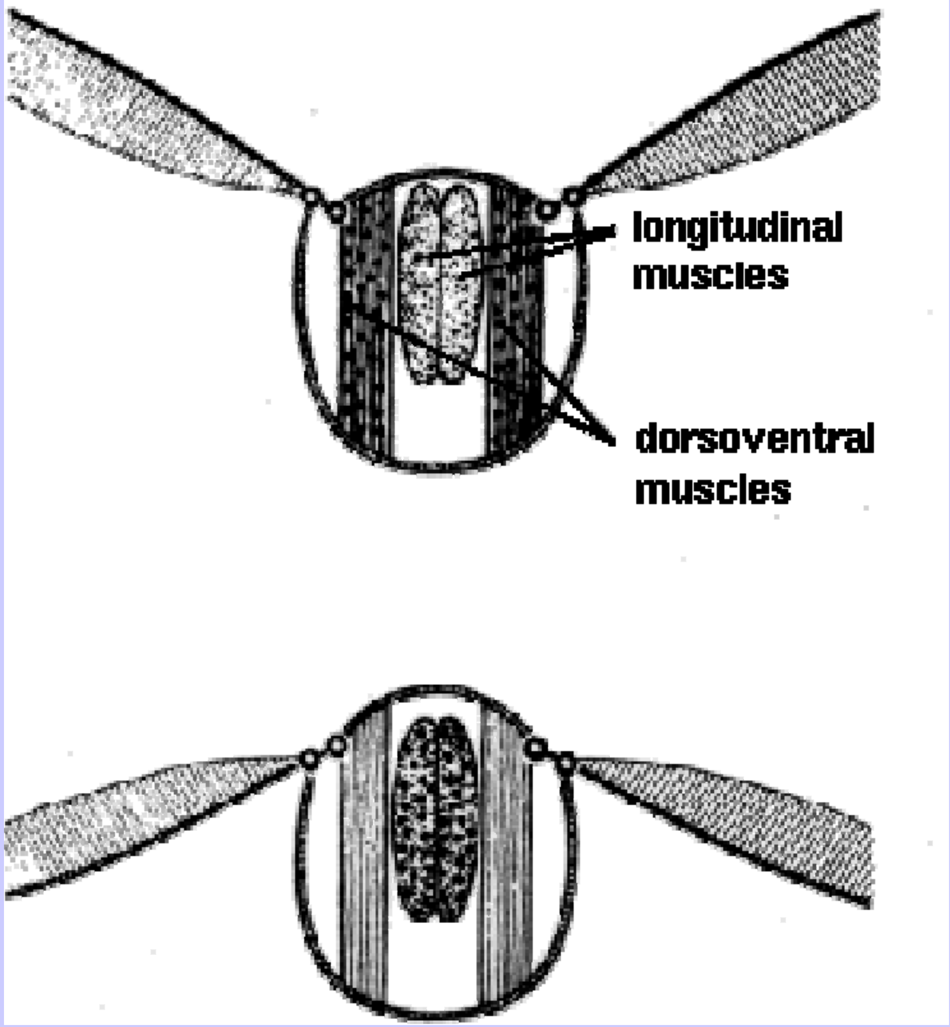
-Wing depression process:

1) Dorsal longitudinal muscles cause notum to bow;

2) raising notal wing processes in relation to pleural wing processes;

3) causing depression of wing.

Indirect



-Wing elevation process:

1) Tergosternal muscles contract;

2) pulling down on notum;

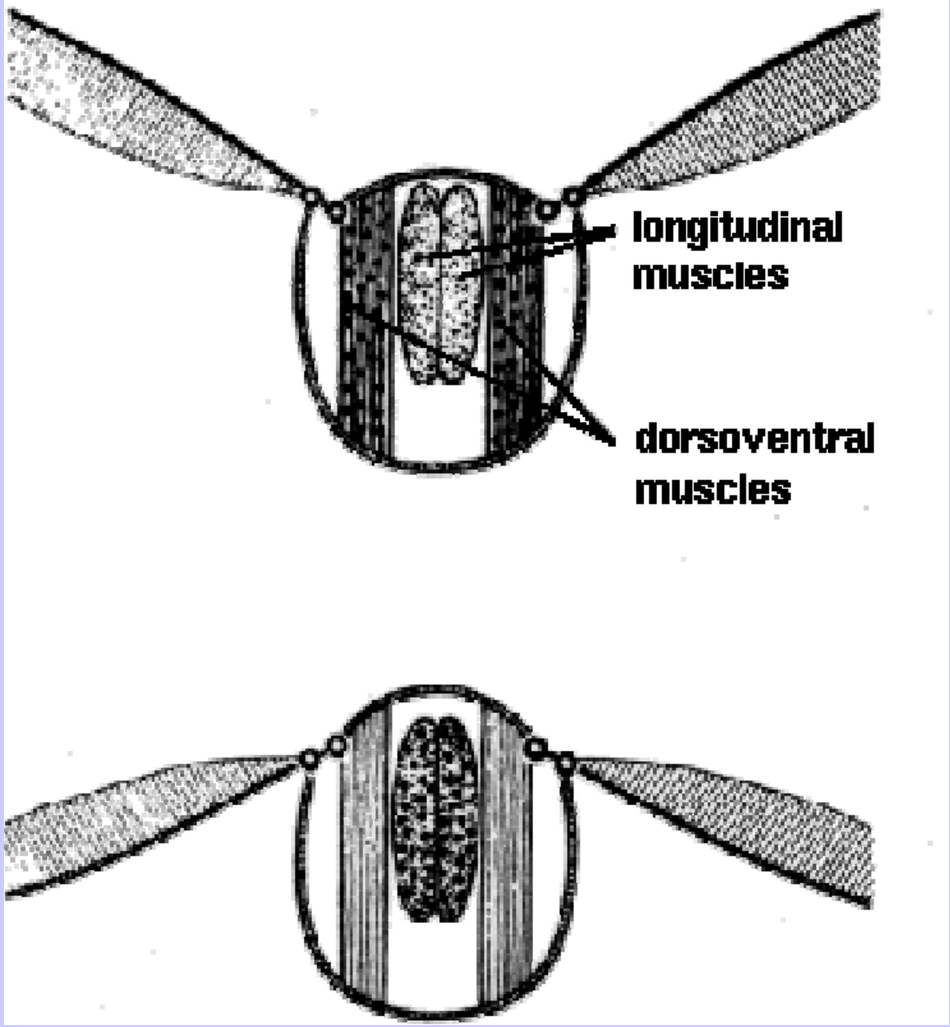
3) notal wing processes move down in relation to pleural wing processes;

4) wing is elevated.

-In addition:

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

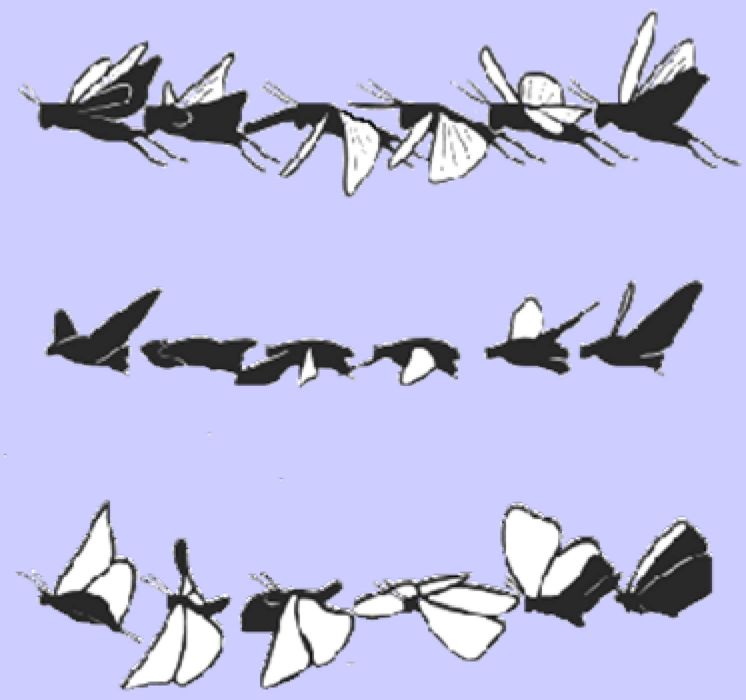
Indirect



-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.



hannover.park.org/.../ flight/flapping.html

Table 7.2 Average Speed of Sustained Flight in Various Insects[a]

Insect	Speed, km/h
Mayflies, small field grasshoppers	1.8
Bumble bees, rose chafers	3.0
Malaria mosquitoes	3.2
Stag beetle, damselfly, *Ammophila* (a fossorial wasp)	5.4
House fly	6.4
Cockchafer, cabbage white butterfly, garden wasp	9.0
Blow fly	11.0
Desert locust	16.0
Hummingbird hawk moth	18.0
Honeybee, horse fly	22.4
Aeschna (a big dragonfly), hornet	25.2
Anax (one of the biggest of European dragonflies)	30.0
Deer bot fly	40.0

[a]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 fr/ 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 hyp 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 w/ gliding**

Aerodynamic function gained only after enlargement.

http://animalpicturesarchive.com/animal/Description/insect/mate/mate04-cabbage.jpg

http://www.mongabay.org/images/thai/moth_bark_close-th.jpg

Advantages of flight:

-Sexual outcrossing among unrelated mates

-Dispersing to new habitats

-Escaping enemies

-Locating specific feeding and oviposition sites

-Dispersal by wind

http://upload.wikimedia.org/wikipedia/en/2/29/Honeybee_pollen_basket_5233.jpg

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:

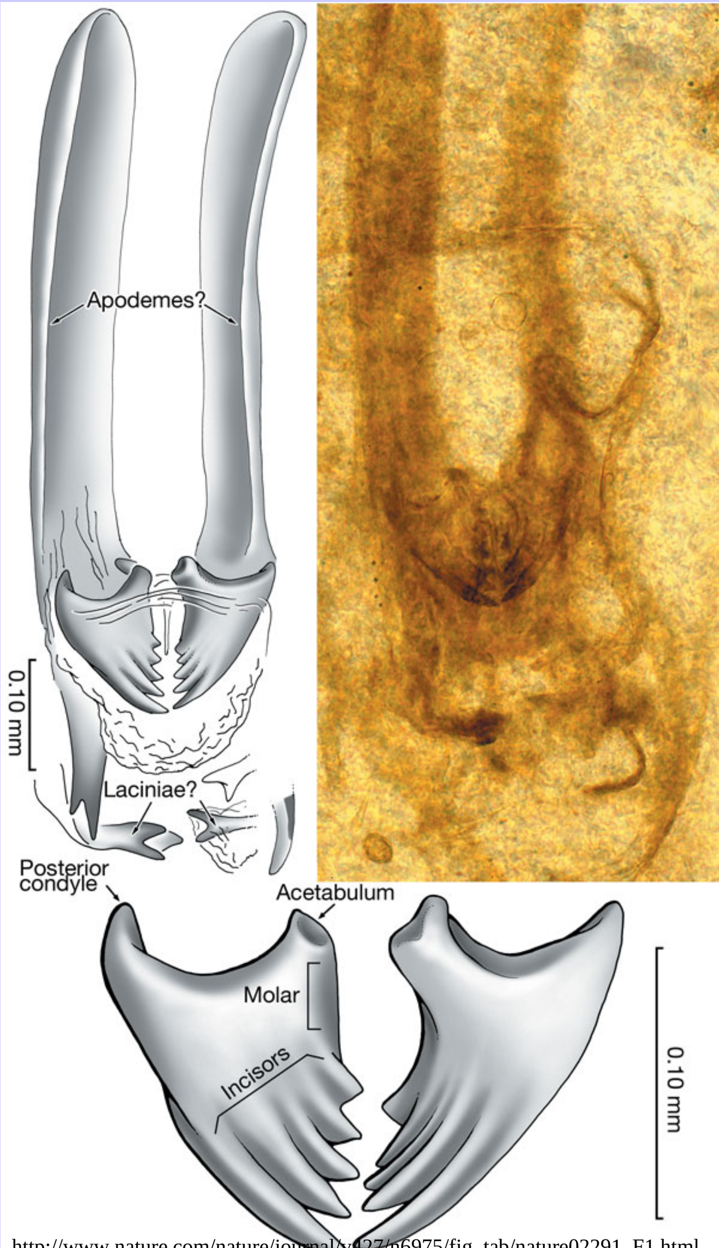
-Long-standing hypothesis

-Wings derived fr/ 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

-Wing origination fr/ 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 for hyp

www.lesinsectesduquebec.com/.../ Plecoptera.htm

-Marden J.H., and M.G. Kramer. 1994. Surface-skimming stoneflies: a possible intermediate stage in insect flight evolution. Science 266: 427-430.

-Kramer, M.G., and Marden, J.H. 1997. Almost airborne. Nature 385: 403-404

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

-Support w/ intermediate flying form of *Leuctra* spp (Plecoptera) = **surface skimming w/ hind legs** ('97)

http://cac.psu.edu/~jhm10/movies/stonefly6.mov

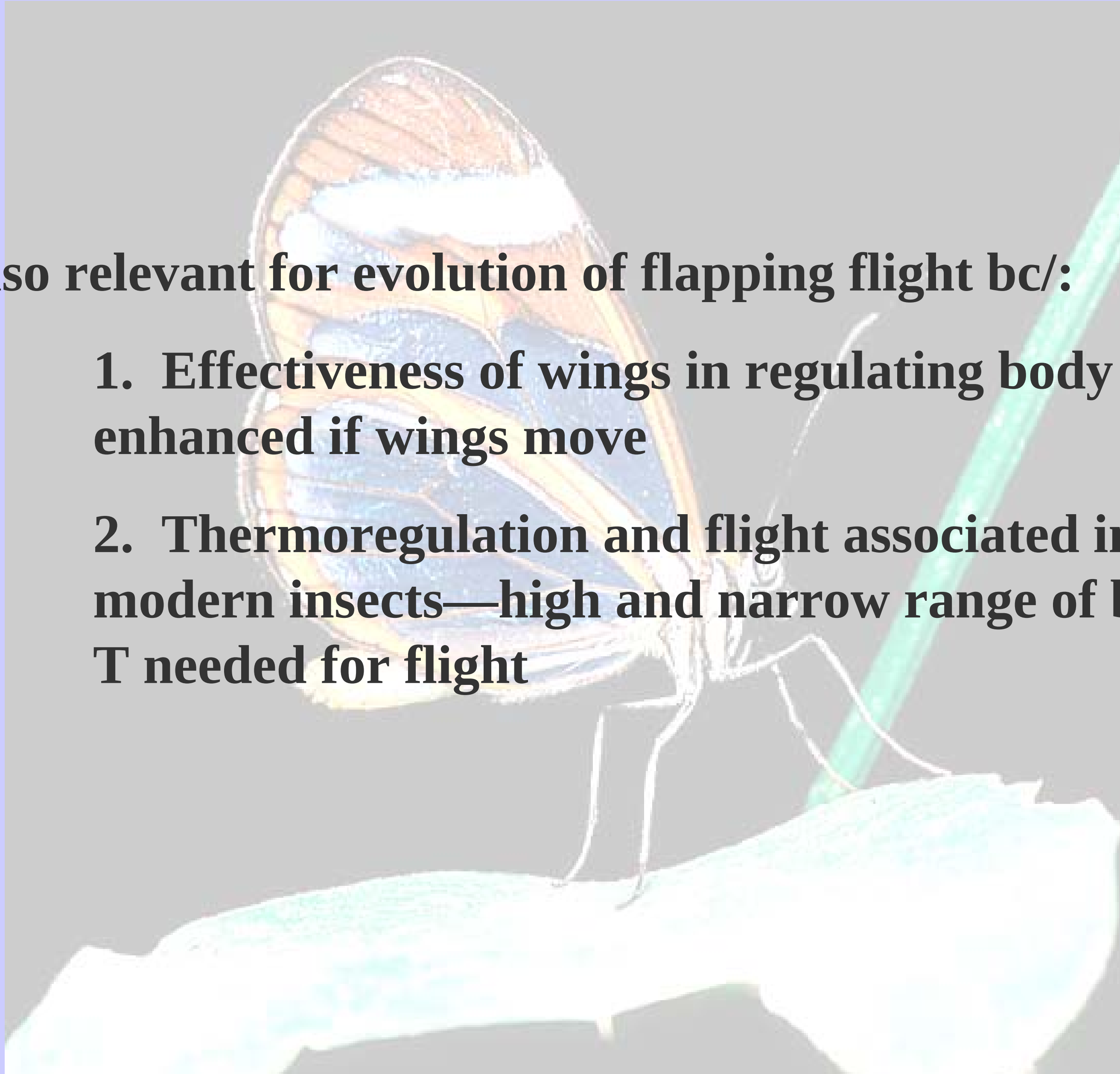
Thermoregulatory Hypothesis:

-Kingsolver, J.G. and M.A.R. Koehl. 1985. Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. Evolution 39:488-504.

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

-Wings evolved fr/ ancestor w/ small winglets related to 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 bc/:

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

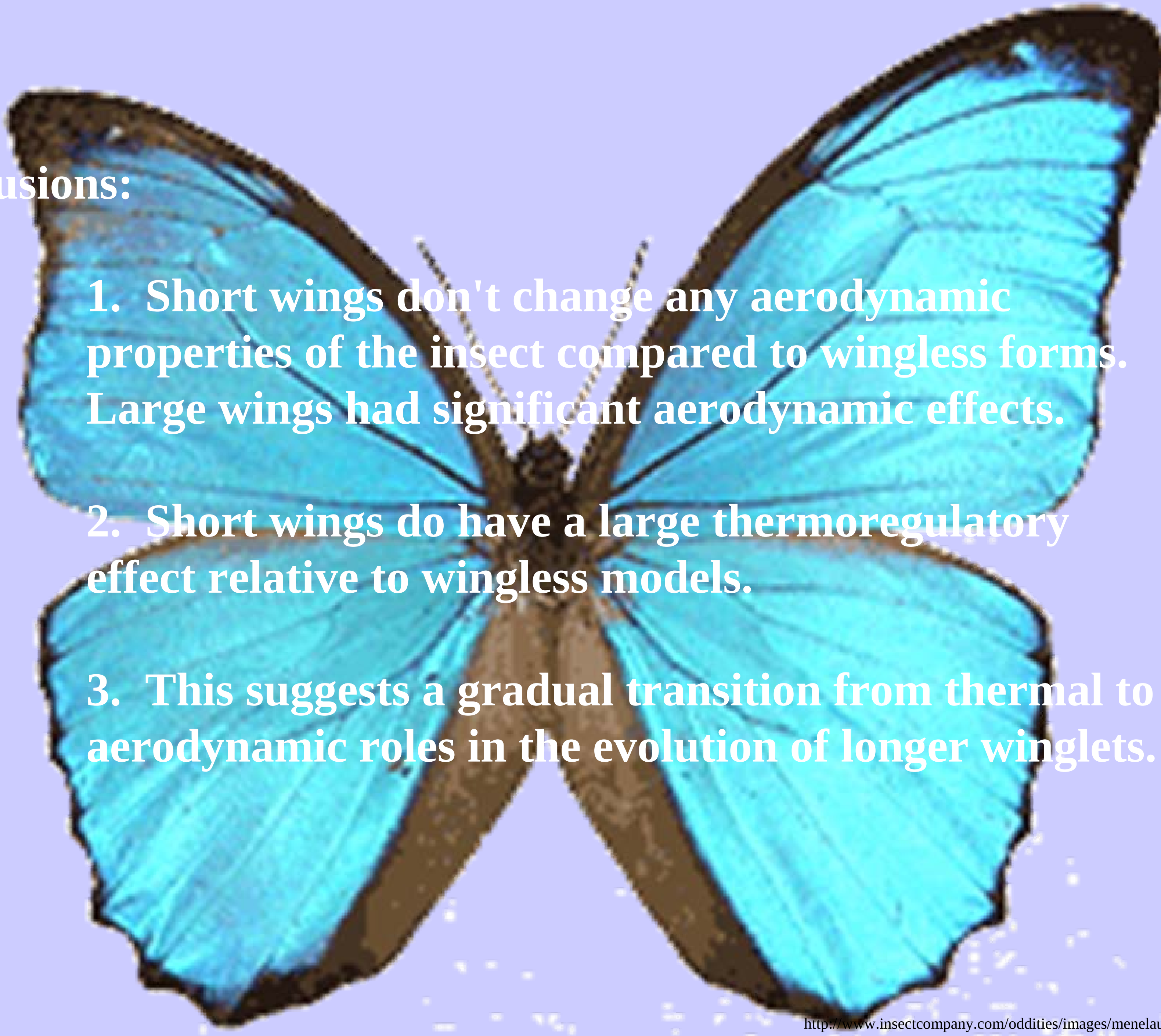
www.geneise.com/insects/ pages/glasswing.htm

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.



http://www.insectcompany.com/oddities/images/menelaus%20deformed.gif