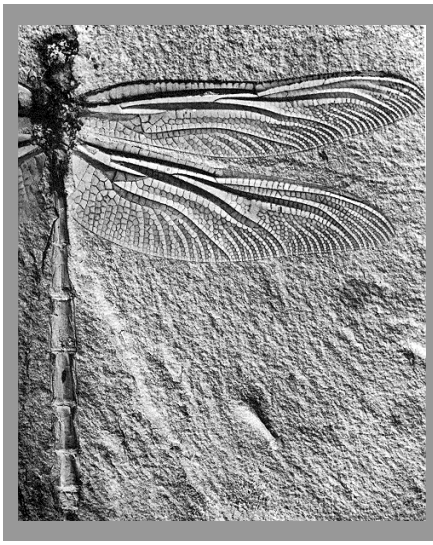


ENTOMOLOGY 322
LABS 10 & 11
Wings

Insect wings are complex yet elegantly simple structures consisting of wing "membrane," exceedingly thin and flexible cuticle, stretched between rigid, longitudinal wing veins that provide support in flight. Structurally they are similar to the wings of early airplanes: canvas "membrane" stretched over a rigid framework of wooden struts and stays. Wings are formed during development from two layers of epidermal cells that later secrete overlaying cuticle. While insect wings may appear dry and lifeless in a dead insect, in living insects the wings contain circulating hemolymph (in the wing veins), sensory neurons associated with wing sensillae, and tracheae, which provide oxygen to the living cells of the wing. Only recently have insect wings been studied from the perspective of aerodynamics, and the results (summarized in papers by R.J. Wooton and colleagues) are intriguing!

The systems of nomenclature that have developed around identifying wing veins can appear confusing, and the criteria used of identifying homologous wing veins across the insect orders obscure at best. We will adopt a slightly modified version of the most widely used system, the Comstock-Needham system (Comstock, 1918), shown below from Snodgrass (1935; Fig. 10.1). According to this system the wing veins are named, from anterior to posterior: Costa (C), Subcosta (Sc), Radius (R; usually consists of mutiple branches, R1 to R5 [R2 through R5 ofter referred to as the radial sector, Rs]), Media (M; usually consists of two to four branches), Anterior Cubitus (CuA; usually two-branched), Posterior Cubitus (CuP; one-branched), and finally the anal veins, A1, A2, A3, and so on.

You should learn the generalized insect wing vein pattern shown in Fig. 10.1, but keep in mind that this wing venation pattern is an archetype, based on comparisons among the living insect orders, and not an ancestral wing vein pattern.

1.

Obtain a specimen of *Romalea*, the lubber grasshopper. Although it cannot fly, it has a relatively generalized wing articulation. The specimen can be examined dry or under alcohol.

While we have already examined the wing base in *Romalea* (labs 6 and 7), we will take a closer look this time and learn how the sclerites at the wing base (the pteralia) relate to the wing veins.

Spread the right tegmen (forewing) and examine its articulation with the thorax from dorsal

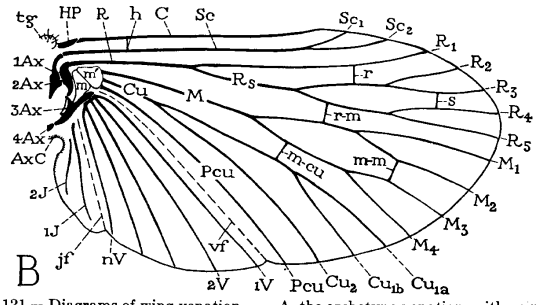


FIG. 121.—Diagrams of wing venation. A, the archetype venation, with veins named according to the Comstock-Needham system. (*Adapted from Bradley*, 1931, *to include three branches of cubitus.*) B, the usual wing veins and axillaries as designated in the accompanying text. *A*, anal veins; *Ax*, axillary sclerites (first, second, third, and fourth); *AxC*, axillary cord; *C*, costa; *Cu*, cubitus; *h*, humeral cross-vein; *HP*, humeral plate; *J*, jugal veins; *jf*, jugal fold; *M*, media; *m*, *m'*, median plates; *MA*, media anterior; *m-m*, median cross-vein; *m-cu*, mediocubital cross-vein; *MP*, media posterior; *Pc*, precosta; *Pcu*, postcubitus (first anal); *R*, radius; *r*, radial cross-vein; *Rs*, radial sector; *s*, sectorial cross-vein; *tg*, rudiment of tegula; *V*, vannal veins (anal veins except the first); *vf*, vannal fold.

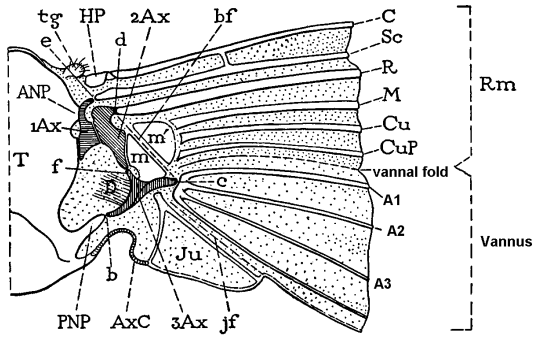


FIG. 122.—Diagram showing the articulation of the wing with the alinotum, and the basal relations of the veins to the humeral plate and the axillary sclerites. (Lettering as on Fig. 121.)

Figure 10.1 Wing venation [left] and axillary sclerites [right] according to the Comstock-Needham system (from Snodgrass 1935. p. 219. some labels modified).

view. With the aid of Fig. 10.2, identify the first axillary sclerite (1Ax). The anterior end of the first axillary sclerite meets the anterior notal wing process (ANP) and it is hinged posteriorly to the mesoscutal lateral edge. Now locate the second (2Ax) and third (3Ax) axillary sclerites as well as the median axillary sclerite (m in Fig. 10.2; pmp in Fig. 10.3). The second axillary sclerite acticulates proximally with the bases of the anal veins (A1, A2, A3...). The median axillary sclerite articulates with the fused, enlarged bases of the media (M) and cubitus (Cu), called the median plate (m in Fig. 10.2; dmp in Fig 10.3). The base of the third axillary sclerite articulates with the posterior notal wing process (PNP) by means of a small, poorly defined fourth axillary sclerite (4Ax) that is absent in most insects. Between the base of the costal vein an the thorax lies a small tegula (tg). The posterior margin of the wing forms the axillary cord (ac) that joins the posterior edge of the scutellum.

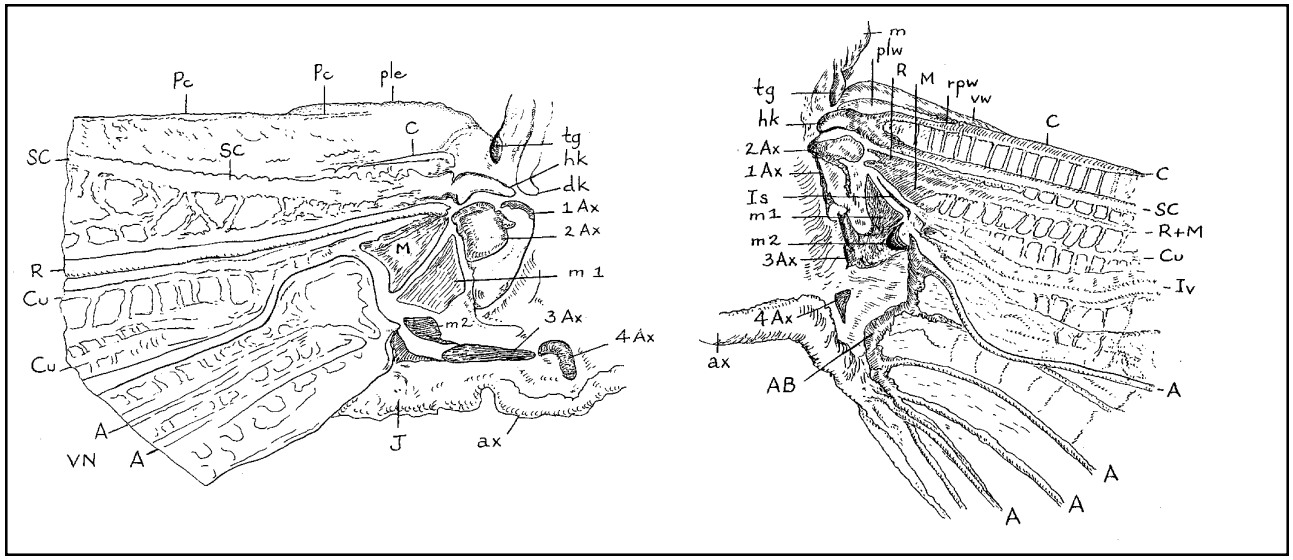


Figure 10.2 Forewing [left] and hingwing [right] of *Romalea microptera* (from Jones, 1981).

View the grasshopper ventro-laterally and spread the tegmen upwards so that the ventral surface of its articulation with the thorax can be observed (Fig. 10.##). Note that the ventral surface of the second axillary sclerite rests upon the pleural wing process (WP). Locate the two basalares (Ba) above the mesepisternum, connected by ligaments to the subcostal region of the wing. The subalare (Sa) lies above the mesepimeron and behind the second axillary sclerite. Examine how the anterior notal wing process (ANP), the posterior notal wing process (PNP), and the pleural wing process (WP) are related to each other spatially. How do their positions change when the dorso-ventral indirect flight muscles contract? How do their positions change when the dorsal longitudinal indirect flight muscles contract? (This would be a good time to review how the indirect flight muscles act on the thorax to cause wing movement.)

Examine the hindwing and compare it to the forewing. In grasshoppers (and beetles) the hindwing is far larger and plays a more important role in flight than does the forewing. The hindwing can be roughly divided into several functional regions -- the anterior region, supported by relatively rigid wing veins is the remigium (Fig. 10.3). The posterior region of the wing is the vannus (Fig. 10.3). This greatly expanded and fan-like region is supported by relatively flexible, longitudinal veins and is extremely important aerodynamically. The veins in the vannal region are the anal veins and (generally) include: 1A, 2A, 3A, etc. The precise limits of the remigium and the vannus are still debated (cf. Wooton, 1979).

Fold both wings over the abdomen and view the lines along which the alar region and axillary region fold (see Fig. 10.3: U-X and U-W-Y). Pay attention to how the axillary sclerites move with respect to each other, especially the third axillary sclerite, which pivots beneath the wing during folding. The principle wing hinge in flight is along the line U-V, at the junction of the pteralia and the notal wing process.

Remove the hindwing at its base (leaving the axillary sclerites attached to the wing for reference) and spread it out in a petri dish with some 70% alchohol. Observe the mechanism of wing folding. Note how the vannal region folds up underneath the remigium along a fold line called the vannal fold. The vannal fold lies just posterior to the first anal vein (1A; Fig. 10.3). How would the wing look in cross section when folded over the back? Is the vannal fold convex or concave? Note that the folds of the vannal region alternate between convex and concave, and that each fold line runs parallel to an anal vein. How many fold lines do you count in the vannus?

With the wing in a folded position (and looking downward on the dorsal surface of the wing), identify the claval furrow. This flexion line should appear as a transparent line running parallel to CuP and immediately behind (posterior to) it (see Fig. 10.3). Note that the crossveins between CuP and 1A are weak where they cross the claval furrow, indicating that the wing flexes at these points. The claval furrow is a flexion line along which the wing bends in flight and is present in most neopterygote insects (Figs. 10.3 & 10.4). The claval furrow allows the anterior portion of the wing to pronate and supinate before the posterior portion during the stroke cycle. Another important flexion line is the median flexion line, however, its location is more variable than that of the claval flexion line (Fig. 10.4).

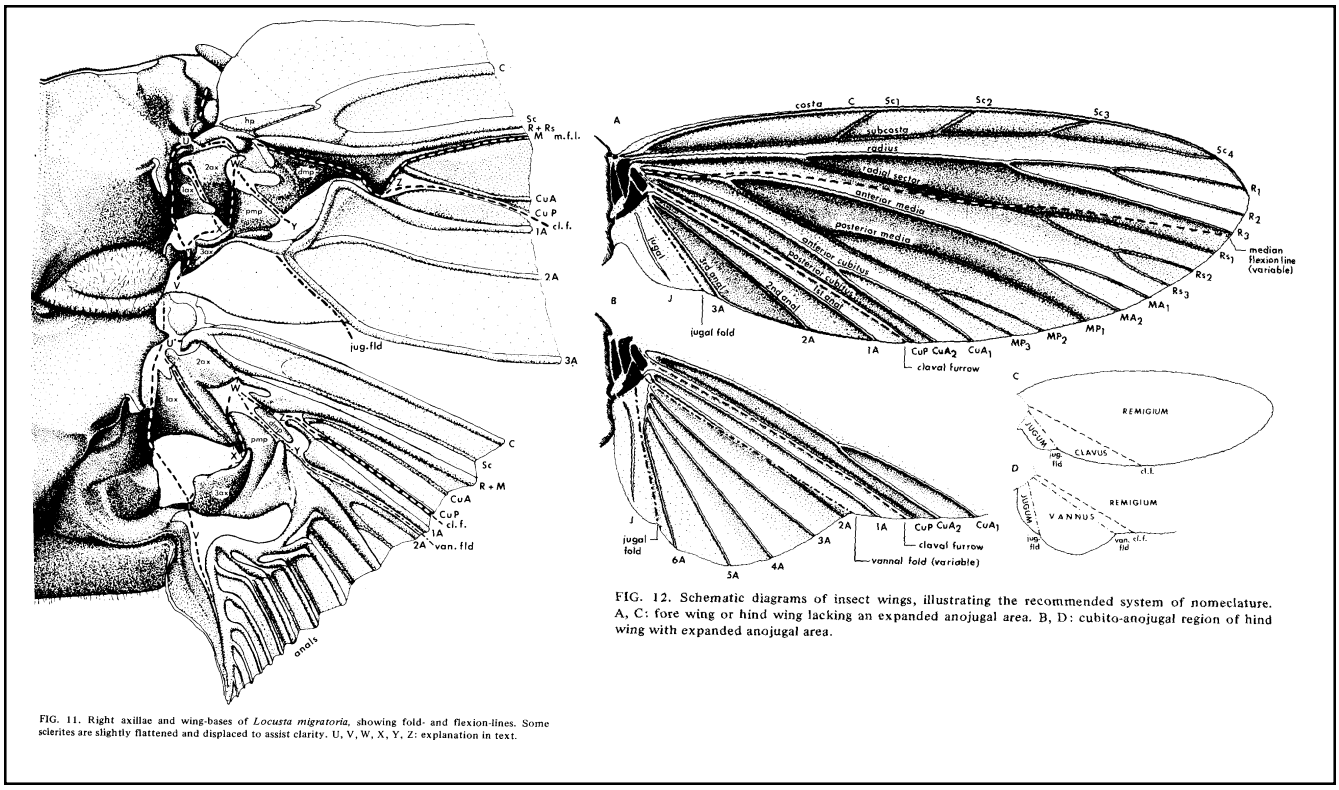


FIG. 11. Right axillae and wing-bases of *Locusta migratoria*, showing fold- and flexion-lines. Some sclerites are slightly flattened and displaced to assist clarity. U, V, W, X, Y, Z: explanation in text.

FIG. 12. Schematic diagrams of insect wings, illustrating the recommended system of nomeclature. A, C: fore wing or hind wing lacking an expanded anojugal area. B, D: cubito-anojugal region of hind wing with expanded anojugal area.

Figure 10.3 (Wootton, 1979)

Using Figs. 10.2 to 10.3, identify the following veins and regions of the hindwing:

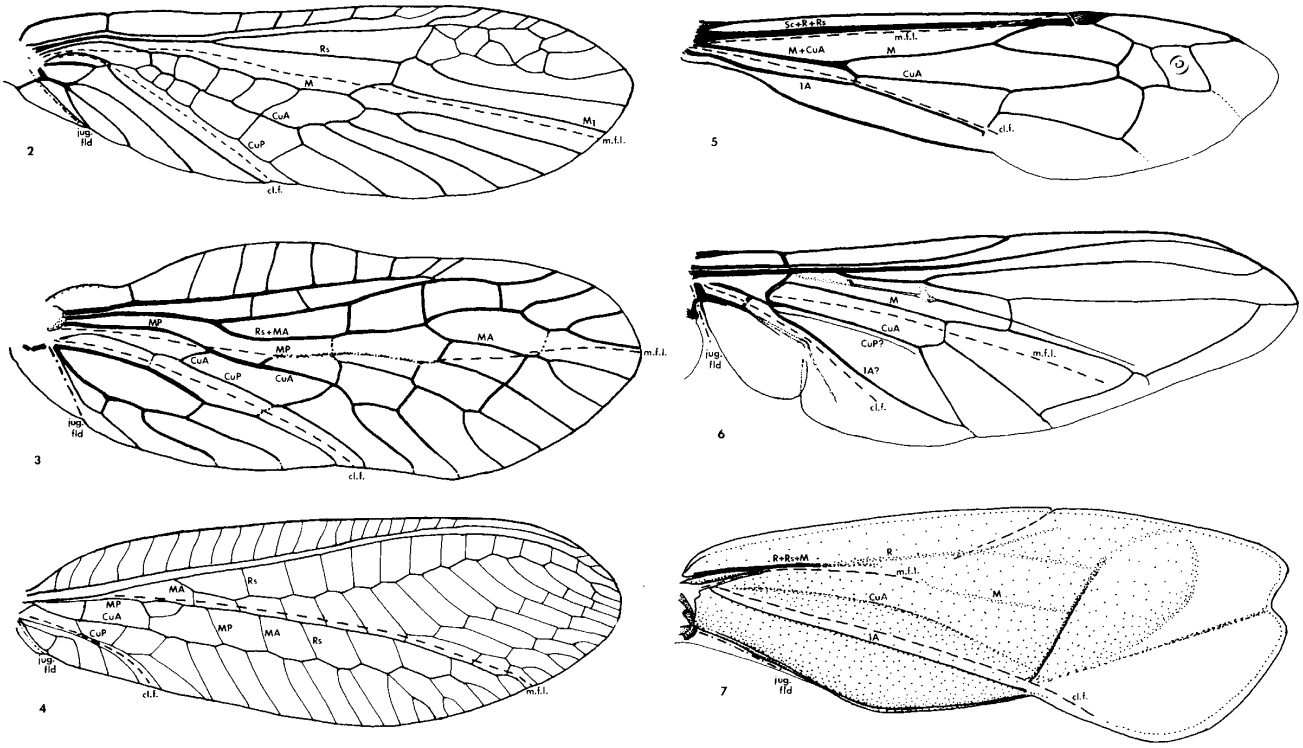
Veins:	**Regions:**
costa (C)	**remigium**
subcosta (Sc)	**vannal fold**
radius+ media (R + M)	**vannus**
cubitus (Cu)	**jugum**
anal veins (1A, 2A...)	

2.

Obtain a cicada (Homoptera: Cicadidae) and spread the wings to one side of the body. Examine the forewings (Fig. 10.5A). Is there a consistent trend in the diameter of the longitudinal veins from the base to the apex of the wing? If so, what is it?

Notice that the longitudinal veins of the forewing appear to be "broken" at certain points along their length. These lines of weakness correspond to a flexion line called the nodal line. Is there a discernable difference in the form of the veins and/or membrane on either side of this nodal line? Is there a trend in the diameter of the longitudinal veins from the anterior to the posterior edge of the wing? How might these differences relate to variation in the ability of the different parts of the wing to deform in response to aerodynamic forces?

Using the highest magnification available, examine the veins that run parallel to the outer edge of the wing. Can you see any difference in the structure of these veins compared to the main longitudinal and cross veins? Most insects do not have veins in this position. What does the structure of these unusual veins suggest about their possible function?



FIGS. 2–7. Representative fore wings, showing the positions of the median flexion-line, claval furrow and jugal fold. Not to scale. (2) *Perlodes mortoni* (Plecoptera); (3) *Sialis lutaria* (Megaloptera); (4) *Chrysopa carnea* (Neuroptera); (5) *Vespula germanica* (Hymenoptera); (6) *Syrphus ribesii* (Diptera); (7) *Notonecta glauca* (Heteroptera). jug. fld: jugal fold.

Figure 10.4 (Wootton, 1979)

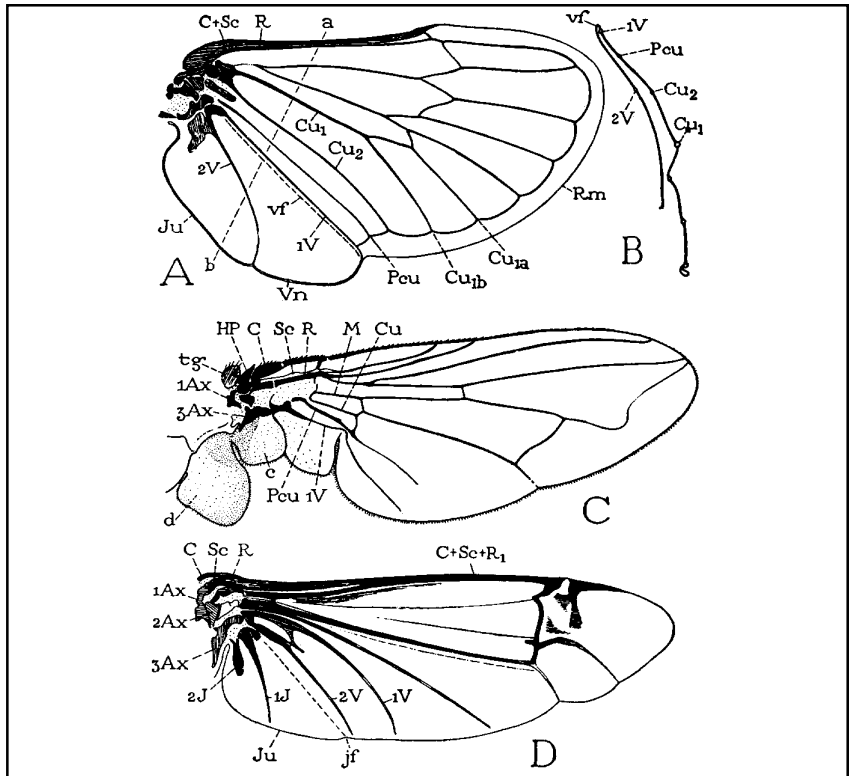


FIG. 127.—Examples of wing venation. A, *Magicicada septendecim*, hind wing, extended. B, section of same along line *a-b* when folded. C, *Musca domestica*, wing and calypteres. D, *Epicauta pennsylvanica*.

Figure 10.5 (Snodgrass. 1935. p.228)

Given the difference in size and shape of the two wings, would you expect both pairs of wings to be equally musculated? Can you account for the difference in structure of the hind margins of the fore vs the hind wings? Looking at the structure of the wings, do you think they are hooked together in flight and, if so, how? Where are the longitudinal veins strongest?

Examine the hind wing. Locate the basal axillary region. Is there a nodal line in the hind wing? Is the basic pattern of variation in strength of the longitudinal veins the same as in the forewing, or different? Fold the wings back over the abdomen and note the method of folding. How is this different from that of orthopteroid insects as seen in the grasshopper. Identify the remigium (Rm), vannus (Vn), vannal fold (vf), jugum (Ju) and jugal fold (using Fig. 10.5A).

3.

Observe the demonstrations of the junction of the dragonfly wing to the thorax. Identify the forked pleural wing process and the humeral plate (HP) and the fused basal plates (=axillary plate, Axp, of Snodgrass, 1935; Fig. 10.6B). If a fresh specimen is available, move the wing up and down and observe its action on the pleural wing process from side view. Note that the wing is fluted through an alternation of convex and concave veins.

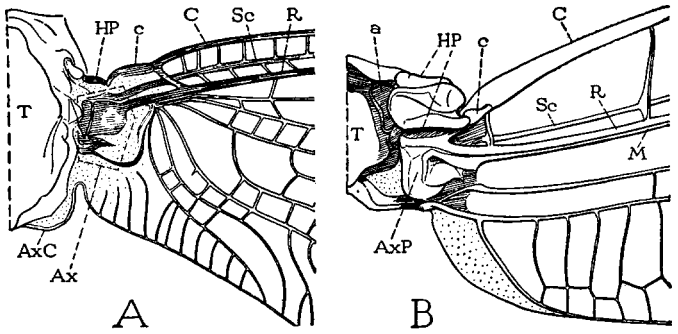


FIG. 123.—The wing articulation in insects that do not flex the wings. A, wing base of a mayfly. B, wing base of a dragonfly. *Ax*, axillary region; *AxP*, axillary plate; *HP*, humeral plate.

Figure 10.6 (Snodgrass 1935, p.220)

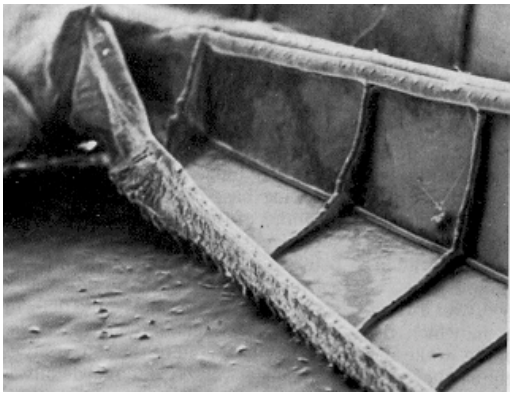


Figure 10.7 SEM of wing base showing vein fluting and cross veins; *Calopteryx splendens* (Wootton, 1990. Sci. Amer. p.117)

4.

Throughout the more advanced orders of insects (i.e., the Holometabola), there is a tendency for only one pair of wings to power flight. This can arise in a number of different ways, including extreme reduction of one pair of wings (Diptera), modification of one pair of wings for functions other than flight (e.g., defense; Coleoptera), or coupling of the two pairs of wings together (Hymenoptera [Fig. 10.8] and Lepidoptera [Fig. 10.9]).

Examine the demonstrations of the following orders and note the characteristics called for (using Figs. 10.8 and 10.9):

Coleoptera (elytra)
Diptera (halteres)
Hymenoptera (hamuli)
Lepidoptera (frenulum, jugum)

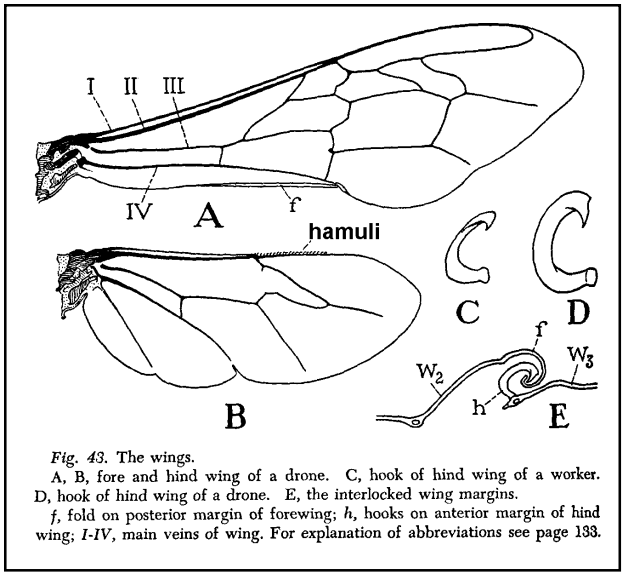


Fig. 43. The wings.
A, B, fore and hind wing of a drone. C, hook of hind wing of a worker. D, hook of hind wing of a drone. E, the interlocked wing margins.
f, fold on posterior margin of forewing; *h*, hooks on anterior margin of hind wing; *I-IV*, main veins of wing. For explanation of abbreviations see page 133.

Figure 10.8 Hamuli -- in the Hymenoptera (Snodgrass 1956, p. 116)

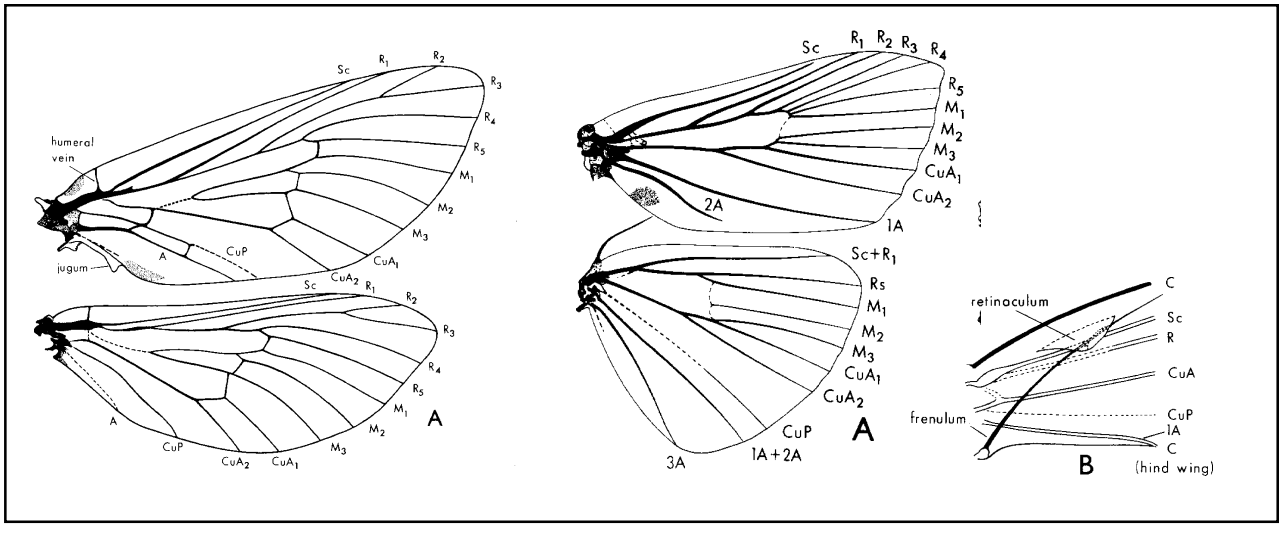


Figure 10.9 Jugum (left) and frenulum (right)-- in the Lepidoptera (Insects of Australia, 1979)

5.

Obtain a live muscoid fly and kill it in a jar with a kimwipe soaked in carbon tetrachloride (or chloroform). While observing the fly under the stereo-microscope, compress its thorax with forceps in such a way as to move the wings through the upstroke and downstroke. Do not manipulate the wings themselves. You should be able to guess how to squeeze the thorax from your knowledge of the flight mechanism. Notice that the wing has only two stable positions: up and down.

Observe how the wing rotates and how the click mechanism operates. The wing appears to have just two stable positions: up and down. How does this mechanism work? Look at the fly under the microscope and identify the mesoscutum, mesoscutellum, "scutellar lever" (lateral portion of the mesoscutellum), and pleural wing process. Note that the pleural wing process is located laterad (outside) the anterior and posterior notal wing processes. Notice also that the second axillary sclerite rotates over the pleural wing process and is stable in only two positions: when rotated outward and when rotated inward (Fig. 10.10). Other insect orders have been shown to have click mechanisms, including Orthoptera, Diptera, Coleoptera, and possibly Odonata.

The hind wings in Diptera are modified to form halteres, which function as gyroscopes in flight. Rotate the forewing and observe the movement of the haltere. What does this suggest about their musculature? For more details on the click mechanism of Diptera and other insects see Chapman (1982; pp. 220-221) and Pringle (1957).

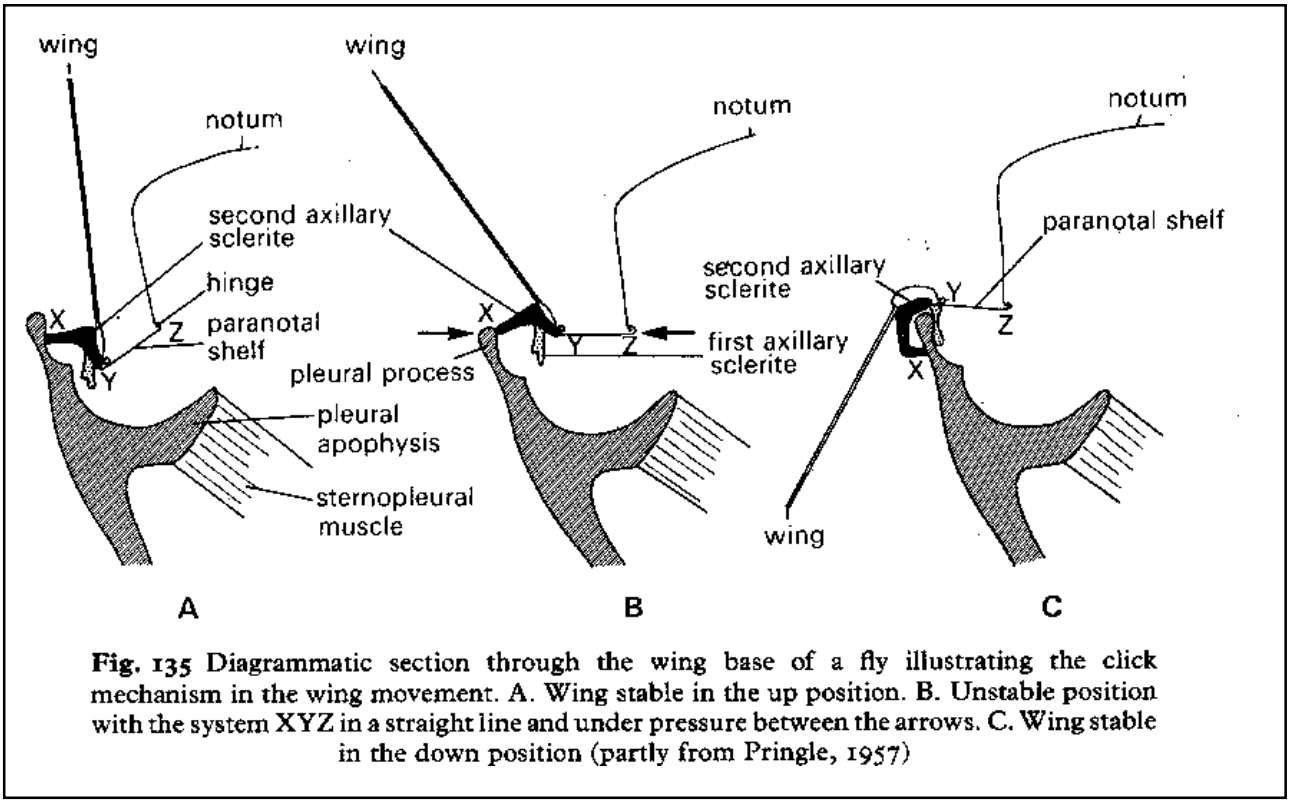


Fig. 135 Diagrammatic section through the wing base of a fly illustrating the click mechanism in the wing movement. A. Wing stable in the up position. B. Unstable position with the system XYZ in a straight line and under pressure between the arrows. C. Wing stable in the down position (partly from Pringle, 1957)

Figure 10.10 Click mechanism in the wing base of *Sarcophaga* (from Chapman, 1982)

6.

Procure a dried (or fresh) specimen of "your" insect. Carefully excise the right wings from the thorax so as to completely remove the axillary sclerites with the wing. Cut off the alar region near its base, and boil the axillary region in KOH. This may be stained in chlorazol black E if transparent and will aid in the interpretation of the axillary sclerites.

Obtain another fresh (preferably) or preserved specimen and examine its wing articulation intact. Locate the following, if possible:

anterior notal wing process
posterior notal wing process
1st, 2nd, and 3rd axillaries
4th axillary (Hymenoptera, Orthoptera)
tegula
bases of wing veins (identify)
axillary cord
pleural wing process
basalare
subalare

7.

Preparation of wing slides for venation study: Under the dissecting microscope, carefully remove both wings of the right side of your insect, including the axillary sclerites. If the wings of your insect are large, it will probably be necessary to then separate some or all of the axillary sclerites by carefully cutting between them under the dissecting scope -— this is to allow the wing to lie flat. If your wings are highly folded, brief immersion in hot 10% KOH will help flatten them. Place both wings in a bath of 95% alcohol. After a few minutes, transfer to a second bath of 95% alcohol and allow to sit for about 10 minutes.

7a. (for smaller wings)

Obtain a microscope slide and a large cover slip. The wings may need to be mounted on separate slides if they will not both fit on one slide. Do not attempt to mount the elytra of beetles. Quickly smear a light coat of diaphane mounting medium (=euparal) over the right 2/3 of the slide, and place the wing, top surface up, onto the medium. Spread the wing so all areas are visible. Cover with additional diaphane if necessary, and the cover slip. If air spaces remain at the edges of the cover slip, use the glass rod in the diaphane bottle to place diaphane on the slide at the edge of the cover slip. Mark the slide with your initials in marking pencil, and place in the oven or slide warming tray. Clean forceps, hands, desk top, etc., with 95% ethanol. Prepare a slide label, indicating genus and family, right front and/or hind wing(s), date, preparator. Apply this label to the left side of the slide when dry.

7b. (for larger wings)

An alternative for wings too large to fit on a microscope slide is to mount them in 2 × 2 transparency mounts for viewing with a slide projector. For many insects, wings need only to be removed from a dry specimen and bound between the glass covers of the mount. Label the mount as above for slides. If the insect is preserved in alcohol or has folded wings, follow the instructions below:

If the wing is folded on a dry specimen, briefly immerse it in hot 10% KOH. Transfer to distilled water to rinse, then to dilute (30-50%) ethanol. Remove the wing in spread configuration by sliding a microscope slide under it and slowly lifting the wing out of alcohol. Adjust the wing to spread position and place another slide on top to flatten. Allow to dry. Then transfer to slide mount.

Colored or scale-covered wings may have obscured venational patterns. The following will bypass this problem.

Remove dry wing and wet in 95% ethanol. Place wing in full strength Clorox (or 50:50 aqueous mixture of sodium chloride and sodium hypochlorite) to bleach. Use intermittent washes of 10% hydrochloric acid to speed bleaching. Do not overbleach. Pass through at least 3 rinses of distilled water (5 minutes each) to remove acid and bleach. Stain in 1% eosin-Y in 70% ethanol for 24 hours. Rinse thoroughly in 70% ethanol. Mount dry in projection slide mount or transfer to 95% ethanol, then to diaphane for microscope slide mount.

8.

Examine the wings of "your" insect. In what ways are the wings of your insect specially modified? Examine the wings under high power. Locate the folds and flexion lines in the wing, which may "break" the wing veins where they cross at alar fenestrae. The wings are usually partially covered with setae, at least on the veins. Are the veins equally protuberant on both sides of the wing?

A particular advantage of wing slides is that they may be projected upon a drawing pad and traced. This is useful for identifying (and remembering) the veins. Use either a microprojector (for microscope slides) or a slide projector. Identify the longitudinal veins and principal crossveins, using Borror, Triplehorn & Johnson (1989), or other references. Allow the slide to dry before viewing.