ENTOMOLOGY 322
LABS 8 & 9
Thoracic Musculature & Flight Mechanisms

Muscle-powered flight is a remarkable adaptation that has arisen only four times in animals: in pterodactyls, birds, bats and insects. Insects were the first to evolve flight. Winged insects appear in the fossil record in the Upper Carboniferous Period (>270 million years ago) more than 60 million years before birds or pterodactyls. How insects evolved flight is still unkown and remains a subject of considerable debate, experimentation and speculation in the entomological literature. The vast majority of living insects (Pterygota) are capable of some form of flight. In fact, the relative success of the Insecta, in terms of species diversity as well as shear biomass, is often attributed to the evolution of flight. Flightlessness (termed brachyptery when the wings are greatly reduced, and aptery when they are lost altogether) has arisen in several insect lineages, though it is usually associated with specific life histories such as parasitism (e.g., fleas & lice) or living at high elevations where strong winds predominate (e.g., many high elevation beetles and flies).

In the next two labs, we will examine the thoracic modifications (both external and internal) that allow insects to fly. There is a huge diversity in both flight behavior as well as the anatomy responsible for it. We will begin this lab by examining the flight motor in one exceptionally good flyer, the cicada. Then we will focus on some of the variation in thoracic morphology displayed in other insect groups. Ultimately, this should provide you with a strong comparative basis to examine and understand the internal and external anatomy of the particular insect you've chosen.

Flight musculature in the majority of insects consists of two sets of muscles: the direct flight muscles and the indirect flight muscles. Direct flight muscles (as the name implies) act directly on the wing base via small sclerites, the basalare (BA) and subalare (SA) (Fig. 8.1). In dragonflies these muscles cause wing depression and hence dragonflies are said to have direct flight musculature. However, in the majority of insects the direct flight muscles have assumed a different role. Because of the close association of the basalare and subalare with the wing base, the basalar and subalar muscles exert subtle control over wing shape, camber, and angle of attack. Contraction of the basalar muscles (Fig. 8.1) causes the leading edge of the wing to tilt downward (pronate) while contraction of the subalar muscles (Fig. 8.1) causes the leading edge of the wing to tilt upward (supinate). These small movements in wing shape are clearly visible in high speed photographs of insects in flight (cf. Brackenbury, 1992 for example)

The real powerhouse of the insect flight motor is the indirect flight musculature. These important

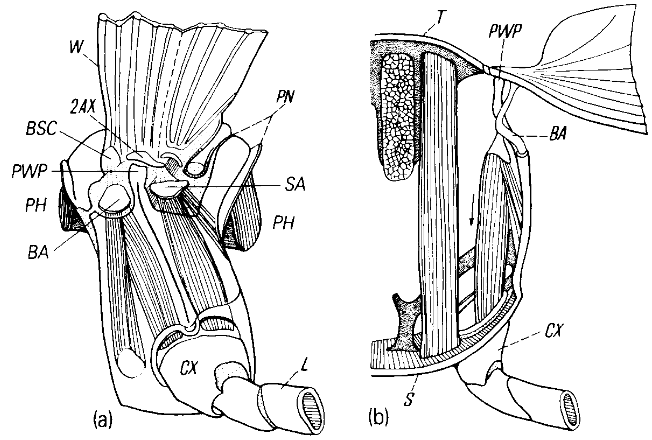


Fig. 1.4 The insect thorax, illustrating the action of the direct wing muscles. (a) Lateral view of the thorax showing basalar and subalar muscles. The pleural region is drawn as if transparent. (b) Cross-section of the thorax showing the mode of action of the basalar muscles (after Snodgrass 1935).

Figure 8.1 (from Snodgrass, 1935)

muscles have a relatively humble origin: small intersegmental muscles that we first studied in lab 3. You will remember from lab 3 (insect abdomen) that the primitive condition for arthropods is for adjoining segments of the body to be connected by dorsal and ventral longitudinal muscles. These muscles attach to the leading edge of each tergum and sternum (the antecosta) and cause adjoining segments to move ("telescope") with respect to each other. In the thoracic segments of pterygote insects the homologs of these muscles are greatly expanded, as are the associated antecostae (Fig. 8.2), to give rise to the dorsal longitudinal indirect muscles and their associate phragmata. The first phragma (1Ph) is the antecosta of the mesonotum, the second phragma (2Ph) is the antecosta of the metanotum, and the third phragma (3Ph) is the antecosta of the first abdominal tergum.

The antagonistic set of indirect flight muscles are the dorso-ventral indirect flight muscles. These muscles also have homologs in the abdomen: small muscles called tergo-sternal muscles. In the meso- and metathorax these muscles have become greatly enlarged to form dorso-ventral muscles responsible for causing wing elevation.

Alternating contraction and relaxation of the indirect flight muscles produces the upstroke and downstroke of the wing. Contraction of the dorso-ventral muscles (C in Fig. 8.3) causes the notum to move downward between the lateral walls of the pleura (Fig. 8.3A), resulting in wing *elevation*. Contraction of the dorsal longitudinal muscles (A in Fig. 8.3) forces the notum to bulge upwards, causing wing *depression* (Fig. 8.3C).

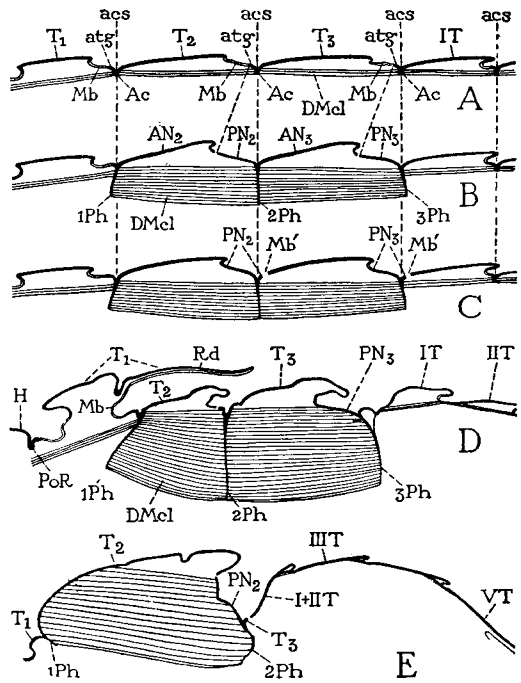


Fig. 97.—Evolution of the postnotal plates of the mesothorax and metathorax from the acrotergites of the segments following, and the development of the phragmata and dorsal muscles. A, generalized condition. B, postnotal plates formed as extensions of the acrotergites. C, postnotal plates with phragmata cut off by secondary membranes (*Mb′*) from tergal plates following. D, section of *Dissosteira*, showing postnotum developed only in metathorax. D, section of *Calliphora*, showing postnotum in mesothorax, and metathoracic tergum almost obliterated on median line.

Figure 8.2 (Snodgrass, 1935)

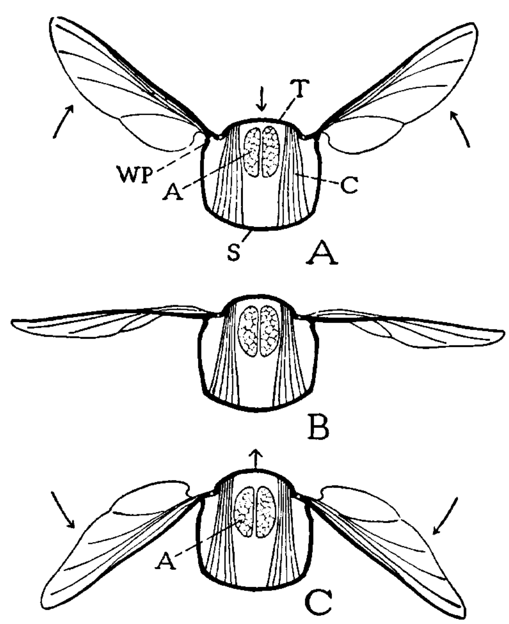


Fig. 131.—Diagrams of successive positions of the wings in flight and the corresponding movements of the tergum.

Figure 8.3 (Snodgrass, 1935)

1.

Obtain a preserved cicada (Homoptera: Cicadidae). Trim the wings down to about 1/2 cm in length to make it easier to view the thorax. In dorsal view identify the pronotum, mesonotum and metanotum. The mesonotum is considerably larger than the metanotum, suggesting that the mesothorax bears the principle indirect flight muscles. Now identify the mesopleuron and the metapleuron and identify the pleural suture extending from the pleural wing process to the dorsal articulation of the coxa. The pleural suture marks the position of the pleural apophyseal arms (or pleural apophysis) which you will identify internally when you do the dissection.

Now cut the body in sagittal section and mount it in a dissecting pan so that you can view the flight musculature. Identify the mesonotum (AN_2), mesopostnotum (PN_2) and metanotum in cross section. Note that the mesopostnotum is small and hidden from view dorsally by the posterior margin of the mesonotum (the scutellum, to be exact). Identify the second phragma (2Ph), the large, sclerotized plate connected to the mesopostnotum and extending into the thorax. Notice also that, as expected based on your observation of the external anatomy, the metathorax has no obvious indirect flight muscles. In flight the hindwings are linked to the forewings and the metathoracic flight musculature has been almost totally lost.

The large, horizontal muscles are the dorsal longitudinal indirect flight muscles connecting the second phragma (2Ph) to the anterior margin of the mesonotum (1Ph). The position of these muscles is indicated in Fig. 8.4 by dashed lines because in this illustration they have been removed to reveal the underlying muscles (see below). The contraction of the dorsal longitudinal muscles causes the mesonotum to shorten and bulge upward, thus *depressing* the wing. Carefully remove the median dorsal longitudinal muscles.

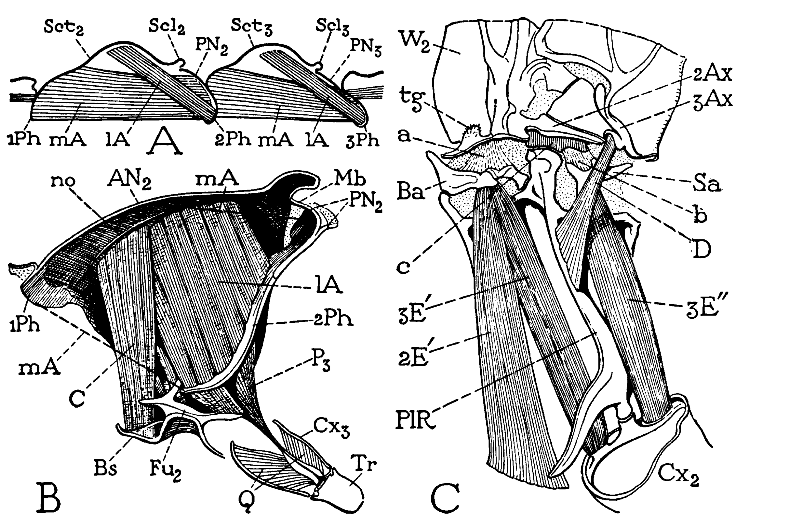


FIG. 128.—The wing muscles. A, dorsal muscles of pterothorax of *Panorpa*, lateral view. B, mesothorax of *Magicicada*, median dorsals (*mA*) removed, showing almost vertical position of large lateral dorsals (*lA*). C, mesothorax of *Dissosteira* with basalar (*E′*), subalar (*E″*), and wing flexor muscles (*D*) of right side, mesal view.

Figure 8.4 (Snodgrass, 1935)

You will now see two sets of muscles running dorso-ventrally (Fig. 8.4). The anterior set are the tergo-sternal muscles (labelled C in Fig. 8.4), which are the primary elevators of the wing in most insects with indirect flight musculature. These muscles cause the tergum to move downward with respect to the pleural wing processes and hence cause the *elevation* of the wing. The posterior set of muscles are the lateral dorsal muscles (labelled lA in Fig. 8.4). In most insects the lateral dorsal muscles are small and function in the same way as the tergo-sternal muscles -- to depress the notum. However, in cicadas and Diptera the lateral dorsals are greatly enlarged and supplement the tergo-sternal muscles as wing elevators. Note that the ventral margin of 2Ph is connected to the sternum by a small set of muscles (labelled P_3 in Fig. 8.4). What role do you think these muscles perform?

Carefully remove the tergo-sternal muscles and the lateral dorsal muscles. Below the large indirect flight muscles that you have just seen are a series of smaller muscles primarily associated with wing folding, coxal movements and change in the angle of the wing during the stroke cycle. One set of muscles connects the sternal apophyseal arms with the pleural apohyseal arms. These are called the pleuro-sternal muscles. Find the long, thin muscle extending from the posterior margin of the coxa upward to the lateral margin of the mesonotum. This is the tergal remotor of the coxa. It is connected to the coxa by a thin tendon-like apodeme. Anterior to this muscle is a muscle connecting the pleural apophyseal arm with the third axillary sclerite. This muscle (the posterior flexor of the wing) is responsible for folding the wing at rest. Beneath the pleural apophyseal arm is the large subalar muscle, which originates on the outer margin of the coxa and inserts on the subalare. If you feel ambitious, try to identify the muscles of the hind wing. These will primarily be the muscles of wing folding and the subalar and basalar muscles.

2.

Examine the demonstration of the sagittal section of the dragonfly thorax. Note that the pterothorax in dragonflies has a far more complex arrangement of muscles than the simple arrangement that you observed in the cicada. This is because, unlike the cicada in which the wings are powered primarily by indirect flight muscles, the flight of dragonflies is mostly powered numerous direct flight muscles, which have their attachments (via "ligaments") directly to the wing bases.

Hatch (1966, Ann. Entomol. Soc. Am. 59:702-714) presents a very clear and detailed description of the dragonfly flight mechanism (Figs. 8.5 A-F). The muscles that power the downstroke are all direct muscles (meaning they attach directly to the wing base):

1st subalare (pm1 in Fig. 8.5) - depresses wing on the pleural fulcrum
2nd subalare (pm2 in Fig. 8.5) - depresses wing and causes supination on the downstroke
1st basalare (dvm3 in Fig. 8.5) - depresses wing and causes pronation on the downstroke

Muscles that power the upstroke include a mix of direct and indirect muscles:

1st tergo-sternal (dvm1 in Fig. 8.5) - depresses the tergum thus raising the wings
anterior coxoalar (dvm6 in Fig. 8.5) - applies force to humeral plate
posterior coxoalar (dvm7 in Fig. 8.5) - pronates wing on upstroke

Both coxoalar muscles are direct muscles because they have their origins on the coxa and their insertions directly on the wing base. Therefore, only one of the six major muscles of the dragonfly flight mechanism is an indirect muscle.

Note also that in dragonflies both the meso- and metathoracic segments are tilted backwards slightly so that the stroke plane angle is not vertical (as in most insects). Can you illustrate the likely stroke plane angle in a dragonfly by flapping your arms?

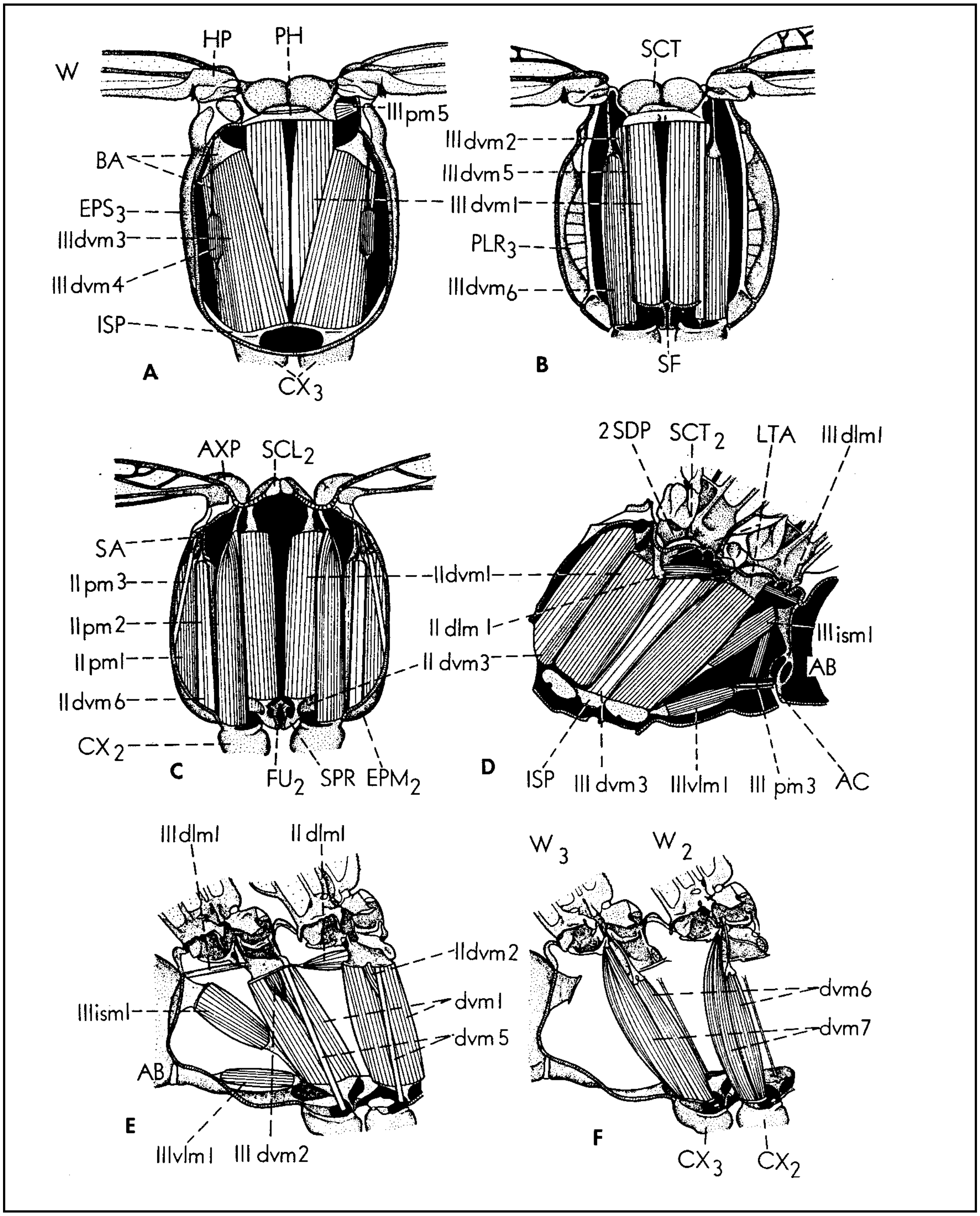


Figure 8.5 Musculature of the dragonfly pterothorax (Hatch 1966)

3.

Examine the demonstration of the sagittal section of the scorpionfly thorax (Mecoptera: Panorpidae *Panorpa*), an example of a generalized indirect flight mechanism with both pterothoracic segments well developed. Notice the large dorsal longitudinal muscle (dlm) running between the phragmata in each segment and the four dorsoventral muscles (dvm) in each segment that are "behind" (lateral to) the longitudinal muscles and run from the scutum to the episternum, trochantin, coxa and trochanter. It is easy to see that these are modified extrinsic leg muscles as some are still bifunctional, depressing the scutum and moving the leg.

4.

Examine the demonstration of the indirect flight muscles of the honey bee (Hymenoptera: Apidae, *Apis mellifera*). In this insect only the mesothoracic muscles are used to power flight. Identify the dorsal longitudinal muscles (labelled 71 in Fig. 8.6) and the tergo-sternal (=dorso-ventral) muscles (labelled 72 in Fig. 8.6) in this segment. Note also the simplified musculature in comparison to *Panorpa* above. This insect has asynchronous flight muscles.

Notice the placement of the mesothoracic phragma (2Ph; refer to Fig. 8.6). The meso-postnotum in most Hymenoptera (except some sawflies) has been greatly reduced in size and is no longer visible externally. In contrast, the mesothoracic phragma (2Ph), associated with the meso-postnotum, has been greatly enlarged and retains its connection to the mesonotum (mesoscutellum, to be exact) laterally. Identify this connection and note the position of 2Ph in relation to the first abdominal segment, called the propodeum in Hymenoptera (labelled IT [first tergum] in Fig. 8.6). Do you see any functional advantage for the propodeum to be fused to the thorax? Hint: What effect does the fusion of the propodeum with the thorax have on the length of the dorsal longitudinal indirect flight muscles?

Where are the meta-postnotum and associated phragma (Ph3) in the honey bee? (see Fig. 8.7 for a hint).

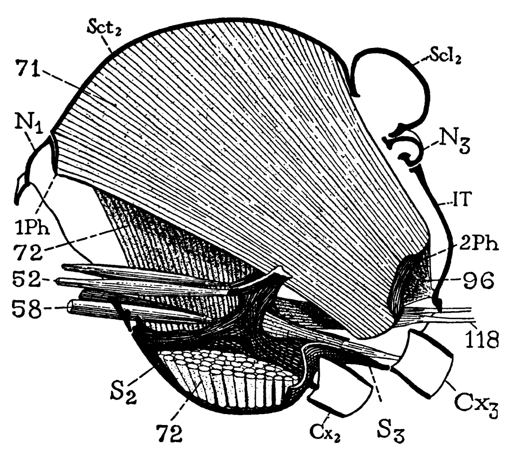


Fig. 48. The indirect muscles of flight and ventral thoracic muscles as seen in a median section of a drone's thorax.

52, 58, 118, ventral intersegmental muscles; *71,* indirect wing depressor muscle; *72,* indirect wing elevator muscle; *96,* retractor muscle of postphragma. For explanation of abbreviations see page 133.

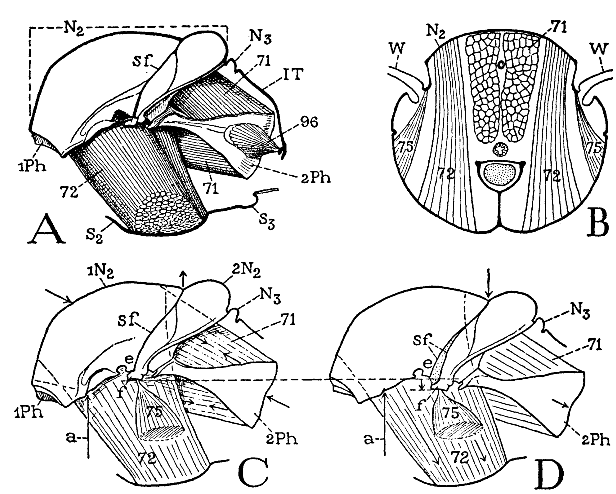


Fig. 49. Mechanism of wing movements by indirect muscles of flight.
A, indirect flight muscles in left side of pterothorax. B, diagrammatic cross section of mesothorax showing position of muscles. C, diagram of dorsal muscles (*71*) in contraction, wing articulations at *e* and *f* lifted, wings depressed. D, same with vertical muscles (*72*) in contraction, notum depressed at arrow, scutal fissure (*sf*) opened, wing articulations lowered, wings elevated.
71, indirect wing depressor muscle; *72,* indirect wing elevator muscle; *75,* pleuronotal wing elevator muscle. For explanation of abbreviations see page 133.

Figure 8.6 (Snodgrass, 1956)

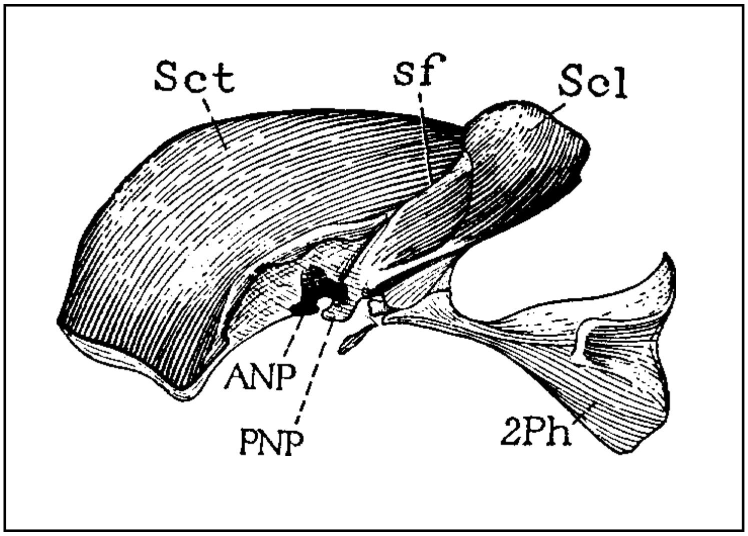


Figure 8.7 (Snodgrass, 1956)

5.

Examine the demonstration of the thoracic musculature in a whirligig beetle (Coleoptera: Gyrinidae; Fig. 8.8). This insect represents the extreme in reduction of flight muscles in a flying insect. Only one muscle in the metathorax (the nototrochanteralis or extra-coxal depressor of the trochanter, noto-troch. in Fig. 8.8) is responsible for powering flight. This muscle powers the upstroke while tergal elasticity is responsible for the downstroke. The muscle is also used in swimming and is thus bifunctional. Identify the origin and insertion of this muscle. Would you say that this muscle is homologous to the indirect flight muscles in other insects. If not, to what muscle is this homologous? What advantages might this reduction in the number of indirect flight muscles give the beetle? (For more information, see Larsen, O. (1966). Opuscula Entomologica Supplementum 30: 1-47).

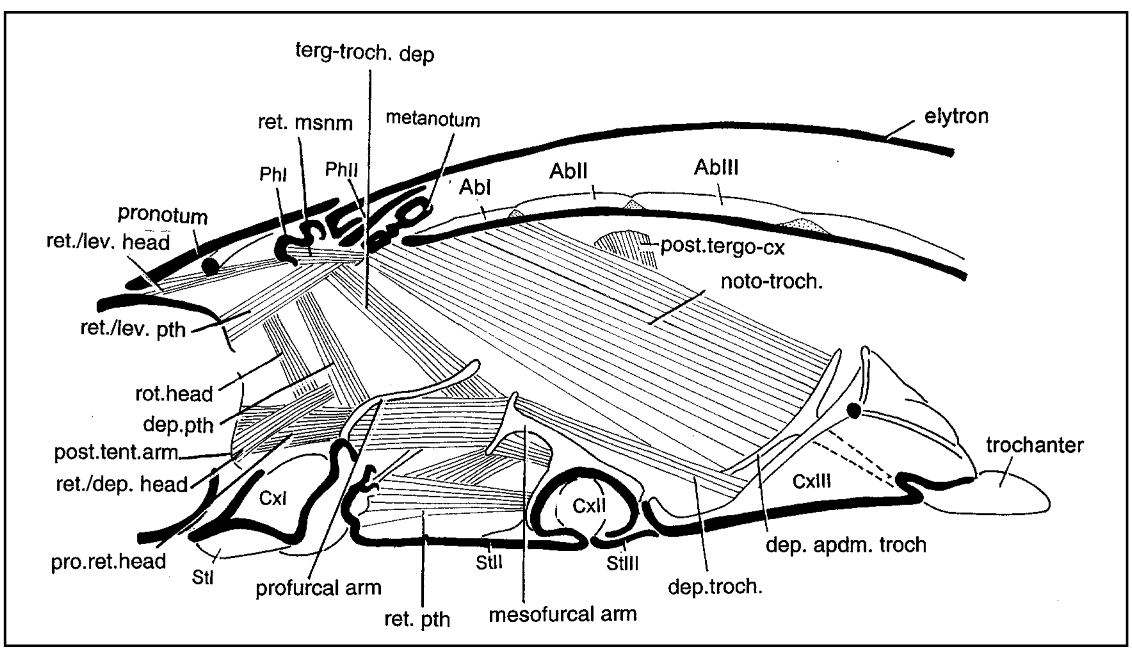
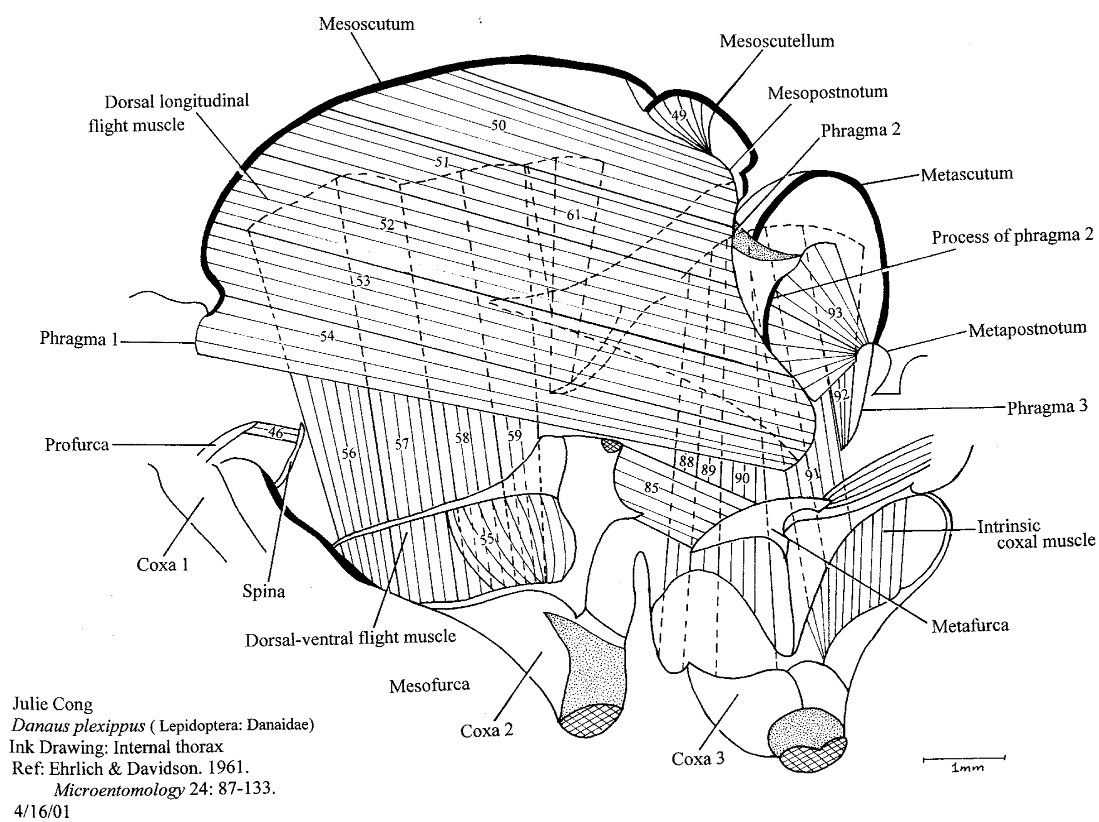


Figure 8.8 Gyrinidae, lateral view of thoracic musculature (Ainsley Seago, 2001)

6.

Select a preserved specimen of your insect, and slit the body longitudinally, *just to the left of the midline*, into 2 parts. Secure the right half internal-side-up in a dissecting pan with pins through the abdomen and head, and legs if necessary. Remove the digestive tract and ovaries, if they obscure thoracic muscles.

From this view, you should be able to observe the cut edges of the terga and sterna of the thorax, the phragmata, portions of the pleural and sternal apodemes or furca, and the dorsal longitudinal flight muscles. With the aid of sketch 2 you should be able to identify the principal sclerites of the terga and sterna as seen in the parasagittal section. Your cleared and stained thoraces will also be of help here.



Julie Cong (Spring 2001)

Sketch #3: Parasagittal section of indirect flight musculature

Sketch the parasagittal view of the thorax. Indicate the cut edges of the terga and sterna in section, labeling the important sclerites. Also draw and label the following:

In principal flight segment

- **coxa (only right side)**
- **pleural apophyseal arms (where visible)**
- **phragmata**
- **furcal arm (where visible)**
- **sternal apodeme or cryptosternum (where visible)**
- **dorsal lontitudinal indirect flight muscles**
- **dorso-ventral indirect flight muscles**

Now carefully remove only the dorsal longitudinal flight muscles from your insect, being careful not to disrupt its position in the dissecting pan. Locate the dorso-ventral flight muscles and trace them to their ventral origins, removing ventral longitudinal muscles if necessary. Draw in your sketch the rest of the dorso-ventral flight muscles of the principal flight section, showing the portion behind the dorsal longitudinal muscles or inside the coxa and trochanter with dashed lines.

Remove the remainder of the indirect flight muscles. Locate the direct flight muscles that insert on the basalare, subalar, and third axillary sclerite, and their origins (these muscles do not need to be drawn). Note the internal structure of the sternal apodemes (or furca) and the pleural apopyseal arms (indicated externally by the pleural suture). If the pleural and sternal apophyseal arms are not united, note the pleuro-sternal muscles that extend between them. Examine also the articulations of the coxae, and the pleural wing process, which serves as a fulcrum for the wing. Cleared and stained preparations prepared previously should be of aid in examining endoskeletal features. (A sample illustration is provided on the opposite page.)