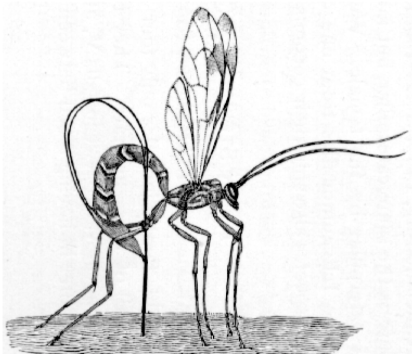

ENTOMOLOGY 322 LAB21
Ovipositor

The insect ovipositor is a complex structure consisting of up to seven interlocking sclerites associated with the 8th and 9th abdominal segments in female insects (termed the genital segments). Female insects use the ovipositor to deposit eggs in specific locations, such as deep within the soil, in plant tissues, under the bark of trees, and even within the bodies of other insects (e.g., parasitoid wasps)!

The sclerites that make up the ovipositor are homologous to parts of the legs primitively associated with the 8th and 9th abdominal segments. However, the morphology of these leg appendages in most insects has become so modified that it is difficult to recognize their true homologies. In fact the true homologies of the parts of the pterygote ovipositor have been the source of much confusion in the morphological literature.

The most widely used system is that of Snodgrass (1935). Snodgrass chose the Archaeognatha as the groundplan for the pterygote ovipositor. In the Archaeognatha the ovipositor consists of a gonocoxite, a gonapophysis, and a gonostylus associated with each of the genital segments in females (the 8th and 9th segments; Table 21.1 and Fig. 21.1D, E). Snodgrass identified structures in the pterygote ovipositor that corresponded to this basic pattern in the Archaeognatha, and developed a system for the pterygotes that corresponds to that of the Archaeognatha: gonocoxites are called valvifers, gonapophyses are called valvulae (1st and 2nd), and the gonostylus of the 9th segment is called the 3rd valvula (the 1st gonostylus is lost in pterygotes; Table 21.1).

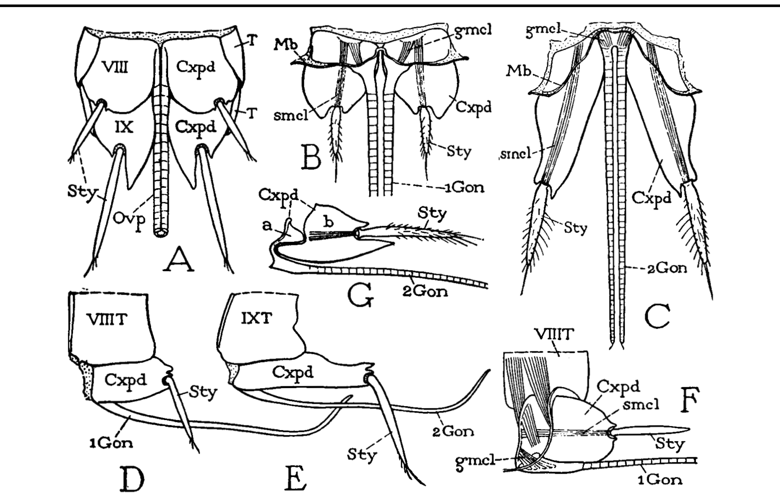

FIG. 313.—The ovipositor of Thysanura. A, *Thermobia*, eighth and ninth abdominal segments, ventral view. B, *Nesomachilis maoricus*, dorsal view of first gonopods. C, same, second gonopods. D, E, *Machilis*, lateral view of right gonopods and supporting tergal plates. F, *Thermobia*, muscles of first gonopod, diagrammatic. G, same, second gonopod, showing subdivision of coxopodite.

Figure 21.1 (Snodgrass, 1935)

While Snodgrass's system is widely used, it is now believed that Snodgrass's system fails to accurately reflect the true homologies across the pterygote orders. This is primarily because Snodgrass neglected to account for a small sclerite that is present in both Thysanura and all pterygotes, the gonangulum (Fig. 21.2, Ga).

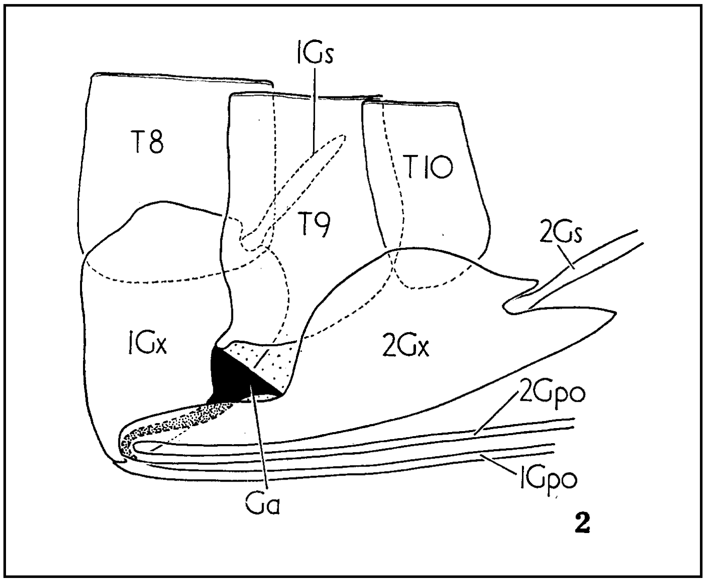

Figure 21.2 Ovipositor of the Thysanura, showing gonangulum (in black) (Scudder, 1961)

While Snodgrass was aware of the gonangulum (and even illustrated it [Fig. 21.1G; labelled a]!), he did not attempt to find its homologue in the pterygote ovipositor. G.G.E. Scudder, in a series of extremely detailed studies (1957, 1961, 1971), reanalyzed the homologies of the pterygote ovipositor and discovered that the gonangulum is present in pterygotes, but has undergone a number of evolutionary modifications that have obscured its identify. For example, in the Orthoptera the gonangulum has become fused with the first gonocoxa (Fig. 21.3 [5]), in Hemipteroid orders the gonangulum has become fused to the lateral margin of the ninth tergum (Fig. 21.3 [8]), and in the Hymenoptera the first gonocoxa is lost, and the gonangulum is greatly enlarged and serves as the base of the first gonapophysis (Fig. 21.3 [9 & 10]). Scudder's system is therefore preferable to Snodgrass' because it correctly accounts for the confusing homologies among the sclerites of the pterygote ovipositor. Consider, for a moment, why this might be the case. In Snodgrass' day, the apterygote insects were thought to form a monophyletic group, the Apterygota. It is now widely believed that the Thysanura are more closely related to the Pterygota than to the Archaeognatha (Microcoryphia). Had Snodgrass known that, he might have paid closer attention to the gonangulum!

Snodgrass' terminology, however, remains useful in a descriptive sense (you can't always identify the gonangulum, even when you know it is there), and most of the literature still uses Snodgrass' terms. We shall hold you responsible for knowing Snodgrass's terminology in the lab, but you should become acquainted with the appendicular names and understand the basis for the homology assessments proposed by Scudder (Table 21.1).

Table 21.1

Archaeognatha	Thysanura	Pterygota (Scudder's system)	Pterygota (Snodgrass's system)
8th segment	**8th segment**	**8th segment**	**8th segment**
1st gonocoxite	1st gonocoxite	1st gonocoxite	1st valvifer
1st gonapophysis	1st gonapophysis	1st gonapophysis	1st valvula
gonostylus	gonostylus	[absent]	[absent]
9th segment	**9th segment**	**9th segment**	**9th segment**
2nd gonocoxite	2nd gonocoxite	2nd gonocoxite	2nd valvifer
[absent]	gonangulum	gonangulum	[no term]
2nd gonapophysis	2nd gonapophysis	2nd gonapophysis	2nd valvula
gonostylus	gonostylus	gonoplac	3rd valvula

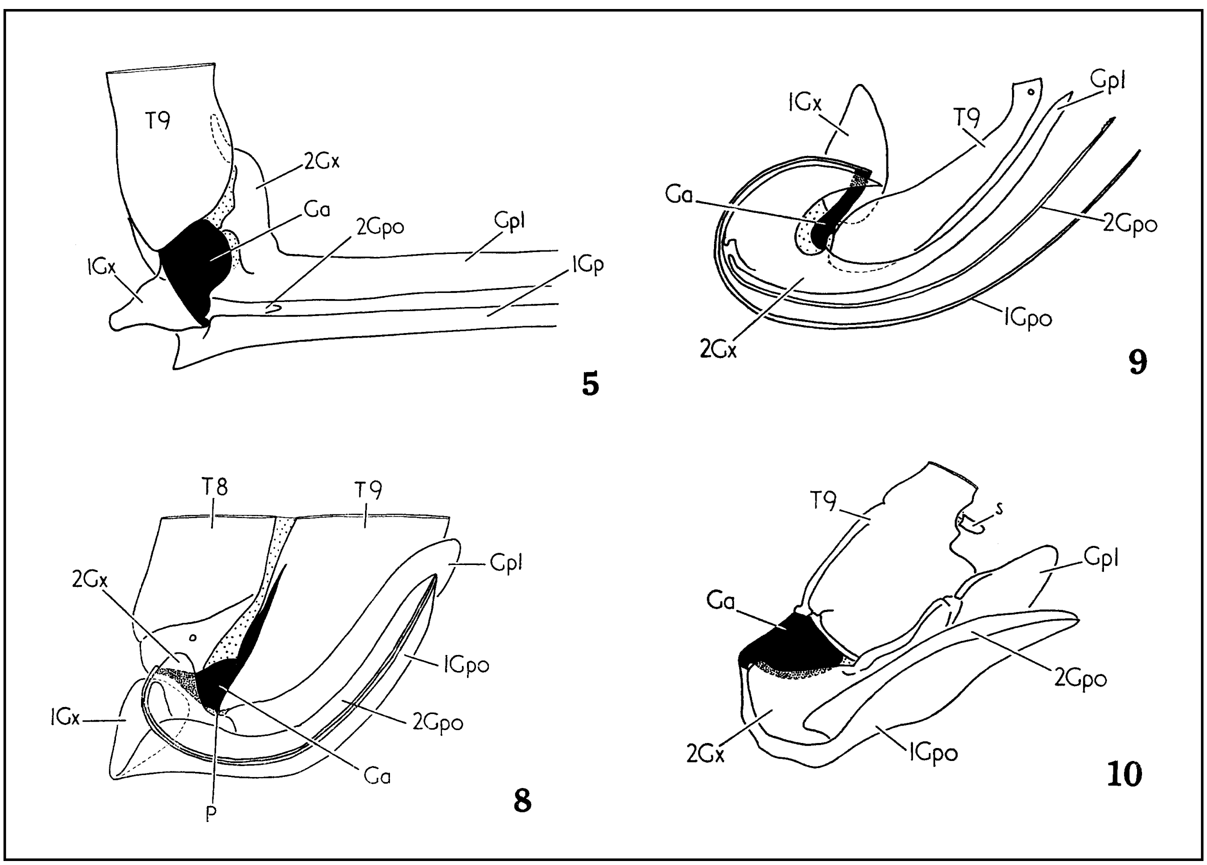

Figure 21.3 Pterygote ovipositors, showing gonangulum (in black). 5 -- *Acheta domestica* (Orthoptera); 8 -- *Tettigella viridis* (Hemiptera); 9 -- *Tetramesa calamagrostidis* (Hymenoptera); 10 -- *Tenthredo maculata* (Hymenoptera) (Scudder, 1961)

1.

Examine the demonstration of the ovipositor of a silverfish (Thysanura) (Fig. 21.2). Its structure, with basal coxa-like plates (gonocoxite) and distal telopodite-like appendages (gonapophyses and styli), is thought to reflect homology with the thoracic legs. The morphology of the Thysanuran ovipositor is the groundplan for the pterygotes. Locate the following:

- 8th segment
  - 1st gonocoxite (1Gx)
  - 1st gonapophysis (1Gpo)
  - 1st gonostylus (1Gs)
  - gonangulum (Ga)
- 9th segment
  - 2nd gonocoxite (2Gx)
  - 2nd gonapophysis (2Gpo)
  - 2nd gonostylus (2Gs)

2.

Obtain a female specimen of a cicada (Cicadidae: Hemiptera), which bears a relatively generalized pterygote ovipositor (Fig. 21.4). Examine the <u>ovipositor</u>, using the following directions (modified from DuPorte, 1977). Do not destroy or take apart the specimen.

Examine the vental side of the posterior (caudal) region. Note that the last visible sternum is the seventh, which forms a <u>subgenital plate</u>. The eighth and ninth terga are well developed; the large ninth extends ventrally until its lateral edges almost meet and partially cover the ovipositor. The two heavily sclerotized <u>1st valvulae</u> (=1st gonapophyses, 1Vl) lie in the middle line, their mesal edges joined by a tongue-and-groove joint.

If the base of the ovipositor is not exposed, grasp the first valvulae with forceps and the body of the cicada with your other hand, and pull the ovipositor until its bases are exposed. Do not separate the ovipositor from the rest of the body.

Trace a first valvula (1st gonapophysis) anteriorly and note the enlarged base which is attached laterally to a curved sclerite extending backward to the anterior edge of the ninth tergum. This is the <u>1st valvifer</u> (=1st gonocoxa, 1Vlf). Observe its articulation with <u>tergum nine</u>.

The soft <u>2nd valvifers</u> (=2nd gonocoxae, 2Vlf) lie alongside the first valvulae basally. From the apices of the second valvifers, the <u>3rd valvulae</u> (=gonoplac, 3Vl) laterally ensheath the tip of the shaft of the ovipositor. The second valvifers and third valvulae are partially overlapped by T9. Note the articulations of the second valvifers with tergum 9 and the base of the ovipositor shaft.

The <u>shaft</u> of the ovipositor is formed from the first and second valvulae only. The second valvifers and the third valvulae form a sheath for this shaft. The third valvulae is provided with sensory setae and is probably used to test the twigs in which the eggs are laid.

Observe the demonstrations of the internal structure of the ovipositor, prepared by slitting tergum 9 longitudinally and spreading the two halves of the basal apparatus of the ovipositor. In top view, note the <u>2nd valvulae</u> (=2nd gonapophyses, 2Vl), which are completely fused dorsally except at their proximal ends, which are connected by a membrane. They thus form the roof of the egg passage. The two sets of valvulae forming the shaft slide back and forth on each other by means of a <u>sliding interlock</u> (Fig.

21.4E) formed from opposing apodemes. Note that the apodemes of the first valvifers also articulate with T9. This region of tergum 9 is thus important as a base for articulation with both sets of valvifers as well as the first valvulae, and is considered by Scudder to be the gonangulum (n in Fig. 21.4F), secondarily fused to tergum 9. (If available, observe a cleared cicada ovipositor.)

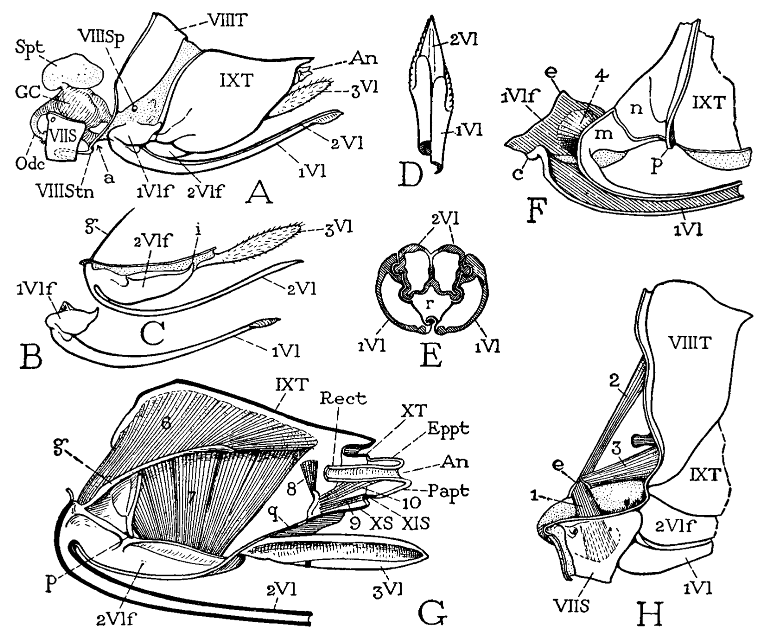

FIG. 316.—The ovipositor of a cicada, *Magicicada septendecim*. A, end of abdomen, with ovipositor, genital chamber (*GC*) and spermatheca (*Spt*) exposed. B, C, parts of ovipositor dissociated. D, tip of ovipositor, ventral view. E, cross section of shaft of ovipositor. F, first valvifer and associated parts, inner view of right side. G, muscles of second valvifer and terminal segments, inner view of right side. H, base of ovipositor, showing muscles of concealed first valvifer.

Figure 21.4 (Snodgrass 1935. p 616)

3.

Obtain a female lubber grasshopper (*Romalea*, Orthoptera: Acrididae) and examine its ovipositor (Figs. 21.5 and 21.6). This ovipositor is highly modified for digging. Refer to Chapman (pp. 333-335) for a complete description and illustration.

Locate the large 3rd valvula (=dorsal valve, =gonoplac) and 1st valvula (=ventral valve, =1st gonapophysis) which enclose medially a small pair of 2nd valvulae (=inner valves, =2nd gonapophyses). The orthopteroid ovipositor is unique in including the third valvulae as part of the ovipositor shaft. (If available, observe a cleared *Romalea* ovipositor.)

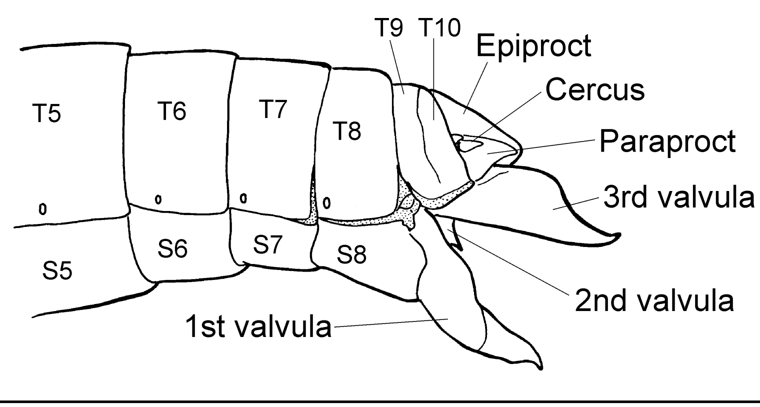

Figure 21.5 *Romalea* abdomen, lateral view; showing ovipositor (A. Burke)

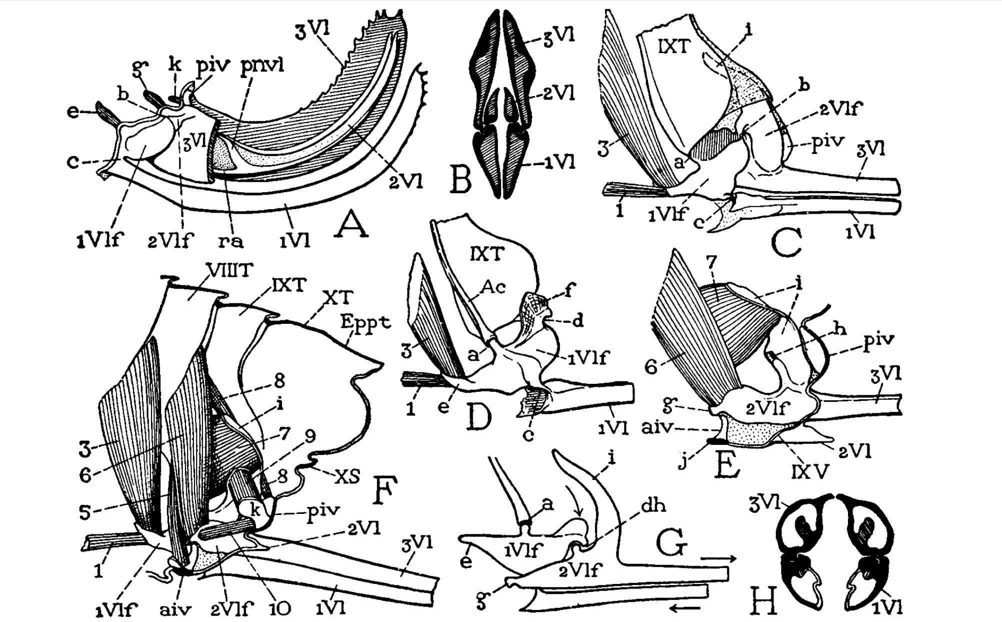

FIG. 315.—The ovipositor of Orthoptera. A, *Scudderia* (third valvula cut off near base). B, *Locusta viridissima*, cross section of shaft of ovipositor. (*From Weber*, 1933.) C, *Gryllus assimilis*, base of ovipositor. D, E, same, first and second valvifers with muscles, inner view of right side. F, same, base of ovipositor with muscles, inner view of right side. G, same, diagram of mechanism of ovipositor. H, same, cross section of shaft of ovipositor.

Figure 21.6 (Snodgrass, 1935. p 613)

4.

Observe the demonstration of the female scorpionfly (Mecoptera: Panorpidae) (Fig. 21.7). Note that a true appendicular ovipositor is lacking. The terminal abdominal segments are modified to form a telescopic tube which is used as an ovipositor. This is a Type II ovipositor of Scudder.

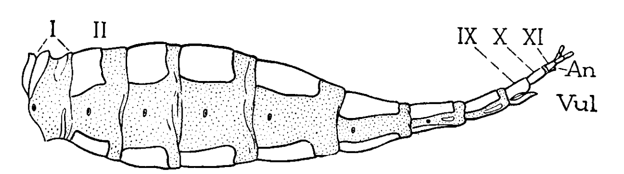

FIG. 312.—Examples of an "ovipositor" formed of the terminal segments of the abdomen. *Panorpa consuetudinis*

Figure 21.7 (Snodgrass, 1935. p. 609)

5.

We shall now trace the evolution of the bee sting -- truly one of the most amazing evolutionary innovations in the animal kingdom. The most primitive members (families) of the order Hymenoptera are phytophagous, feeding on plants as larvae. Adult females have ovipositors modified for sawing into plant tissues, where they lay their eggs. In the course of hymenopteran evolution some ancestral species of sawflies began parasitizing other insects by using the ovipositor to inject eggs into the hemocoel of their hosts. This event marked the dawn of the parasitoid wasps! The ghoulish lifestyle of the parasitoid wasps (the inspiration for such movies as Aliens I, II, III...) has been highly successful and parasitoid wasps are now a common feature of all terrestrial habitats with over 200,000 species worldwide. The parasitoid wasps have in turn given rise to the aculeate, or stinging, wasps (and bees) through (once again) a major evolutionary innovation in the ovipositor -- the evolution of the sting.

Examine the demonstration dissections of a sawfly, ichneumonid, and bee. First, note the short, stout, serrated 1st and 2nd valvulae (1Vl, 2Vl) of the sawfly (Fig. 21.8). These form the shaft of the ovipositor and are used by the female sawfly to cut into plant tissues. Follow the thin, gently curving apodemes upward to where they connect to the valvifers (1Vlf, 2Vlf). The 1st valvifer (1Vlf) is a small, quadrate plate articulating with T9 (IXT in Fig. 21.8) and the second valvifer (2Vlf). (Unlike the configuration seen in the cicada, in the Hymenoptera the second valvifer does not articulate directly with T9.) Note that T9 is visible externally in sawflies and parasitoid wasps but (as you will see below) T9 in bees is reduced to two, weakly sclerotized lateral plates of the sting apparatus. Note that the 3rd valvulae (3Vl) are soft and have padlike apices bearing sensillae used by the wasp to select sites for oviposition.

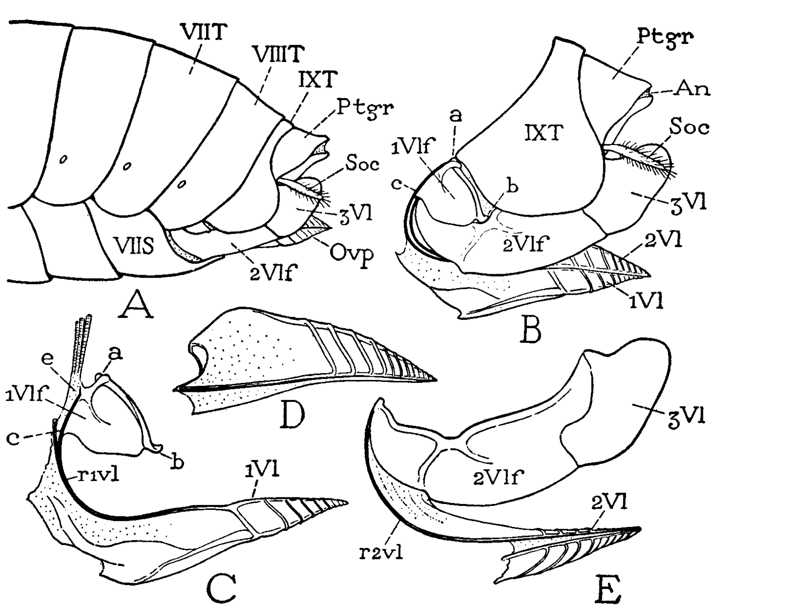

FIG. 317.—The ovipositor of a tenthredinid, *Pteronidea ribesii*. A, end of abdomen. B, showing relation of basal parts of ovipositor to each other and to ninth tergum. C, first valvifer and valvula. D, second valvula. E, second valvifer with second and third valvulae.

Figure 21.8 (Snodgrass, 1935. p. 617)

Now turn your attention to the Ichneumonid wasp (Fig. 21.9). Note that as in the sawfly, T9 (IXT in Fig. 21.9) is exposed and well-sclerotized. The first valvifer is small and articulates with the lateral margins of T9 and the second valvifer is elongate. In contrast to the sawfly, however, in the ichneumonids the first and second valvulae are thin and elongate -- well suited for laying eggs in their caterpillar hosts. The third valulae are also elongate and (in life) enclose the first and second valvulae. Some ichneumonids (e.g., *Megarhyssa*) have ovipositors several inches long that are used to reach insect larvae deep within logs.

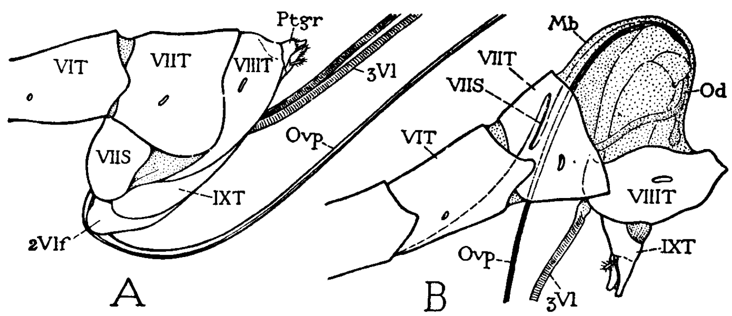

FIG. 318.—The ovipositor of *Megarhyssa*. A, *M. atrata*, end of abdomen and base of ovipositor with parts in usual position. B, *M. lunator*, showing position of abdominal segments and base of ovipositor during oviposition.

Figure 21.9 (Snodgrass 1935. p. 618)

Next examine the bee (Fig. 21.10). Note that the morphology of the bee's sting is essentially similar to the morphology of the ovipositors of the sawfly and the ichneumonid. Because the sting (as well as the 8th and 9th terga) are withdrawn within the abdomen (the 7th tergum is the last visible tergum in bees) most of the components of the sting are relatively weakly sclerotized. The first and second valulae form the sting shaft. The 1st valvulae (also called the lancets [Lct]) lies between the 2nd valvulae (also called the stylets [stl]). Note that the stylets bear barbs laterally, which hold the sting in the skin of vertebrates (like ourselves) long after the worker bee has flown off. Identify the 1st and 2nd valvifers. How do they compare to the morphology of the sawfly and the ichneumonid? Finally, identify the soft, membranous 3rd valvulae which encase the sting when it is retracted into the body. Because of the alterations in the ovipositor as a sting the egg no longer passes down the sting shaft but instead issues from the base.

The sting apparatus is not complete without the venom sac, the large, yellowish gland attached to the sting base. When a worker bee altruistically stings an animal threatening her hive, the barbed stylets anchor the sting apparatus in the skin of the intruder and when the bee flies off her sting apparatus remains, including the entire the venom sac and the muscles which pump venom into the victim. Refer to pp. 325 and 333 of Chapman (1982) for figures and descriptions of the mechanism of the sting.

If live honey bees are available allow a worker to sting a squash ball or similarly rubbery surface and observe the mechanism of the sting in action.

6.

Examine the ovipositor of your own insect and identify its parts. Is it a type I or type II ovipositor? If Type I, identify the parts, including 1st and 2nd valvifers, 1st, 2nd, and 3rd valvulae and the articulations of these parts with the 8th and the 9th terga. If Type II, try to determine what parts of the abdomen have been modified for oviposition and identify the genital opening.

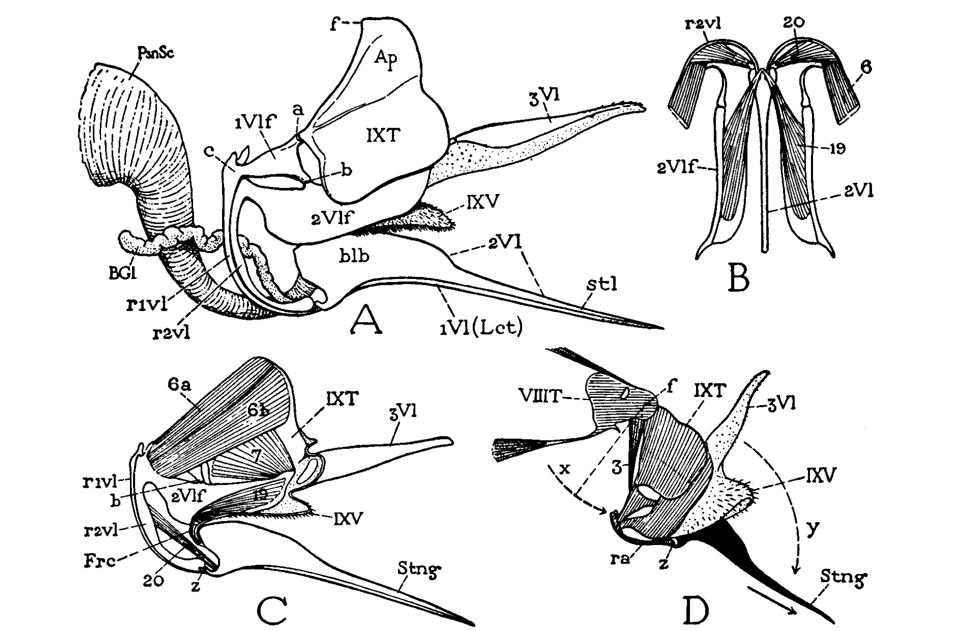

Fig. 319.—The ovipositor (sting) of Hymenoptera. A, *Apis mellifica*, shaft and basal apparatus of sting, showing relation of valvifers to ninth tergal plate. B, *Atanycolus rugosiventris* (Braconidae), basal part of ovipositor and muscles, dorsal view. C, *Apis mellifica*, muscles of sting, inner view of right side. D, same, position of parts of sting when shaft is extruded, diagrammatic.

Figure 21.10 (Snodgrass, 1935. p. 619)