INSECT MORPHOLOGY - THE THORAX

The thorax is truly an amazing and very interesting part of the insect body. It has evolved complicated, yet very efficient mechanisms to accomodate both walking and flight. We are going to discuss the evolution of the thoracic tagma, discussing the specializations that have come about due to the influence of the legs and the wings.

EVOLUTION OF THE THORAX

* If you remember our earlier discussions of the evolution of the insect body, we envisioned the early insect ancestor as a 20-segmented worm-like organism with a functional head and body. Articulation of the body segments was probably enhanced by the development of a longitudinal suture that divided each segment into a dorsal **tergum** and a ventral **sternum.** Eventually, nearly all of the body segments bore a pair of appendages employed at first only for locomotion. Later, some of these appendages became modified for other functions such as feeding and reproduction.

* The primitive legs arising from the lateral aspects of the metamere probably were simple evaginations of the body wall, and its integument was confluent with the body of the organism. Even when a point of articulation developed between the metamere and the appendage, it was probably some distance from the actual point of evagination, forming a fixed protruding base or **coxopodite** and a freely articulating distal appendage or **telopodite.** Then the coxopodite probably migrated into the membranous area of an expanded longitudinal suture. This development then gave the leg base or coxopodite a membranous field for free articulation.

* In the actual evolution of the insect body the 6th, 7th, and 8th (or the 3 segments posterior to the head) segments became the center for locomotion. These 3 segments became so specialized to accomodate this function that they became one of the 3 distinct regions of the insect body called the **thorax**. The anterior segment is called the **prothorax**, the middle segment is called the **mesothorax**, and the posterior segment is called the **metathorax**.

* The thorax must have evolved very early in the phylogenetic history of the insects. It is easily differentiated from the abdomen in both the apterygota and the pterygota. This means that the development of the thorax must have come before the development of wings.

* The typical thoracic metamere is a boxlike structure with a dorsal **tergum**, a ventral **sternum,** and additional side regions called **pleura.** The development of the pleural regions was probably intimately associated with the development of the legs. The efficiency of the walking mechanism is surely enhanced when its basal structure can operate with a socket or between sclerotized areas which provide support for the leg and attachment for muscles. Such a basal structure probably developed in the membranous longitudinal suture by a flattening of the walls of the coxopodite and a subsequent fractionation and detachment of these flattened areas into distinct plates or **pleurites.**

* These detached sclerites, also called **coxites,** formed sclerotized arches both above and below the original coxopodite. A dorsal arch in close proximity to the basal segment of the leg is called the **coxopleurite.** Another arch directly above the coxopleurite is the **anapleurite.** There may also be a ventral arch called the **sternopleurite.**

* These arches are still present in many of the primitive insects. In more advanced insects, however, it appears that these sclerites have further expanded into the broad plates of the typical pleurum. It is believed that the anapleurite has migrated anteriorly and laterally to form the anterior sclerotization of the pleurum called the **episternum** (if the episternum is divided into two parts, the more dorsal part is the **anepisternum** and the more ventral part is the **katepisternum**. The coxopleurite appear to have further subdivided into a small anterior portion or **trochantin** which remained in direct articulation with the leg, and a posterior portion which migrated posteriorly and laterally to form the posterior sclerotization called the **epimeron.** It also appears that the sternopleurite has fused with the sternum, thus bringing the base of the leg closer to the ventral plate of the metamere.

INSECT MORPHOLOGY - THE THORAX

* So far, we have only discussed the evolution of the thorax as it was influenced by the development of the legs. These specializations, however, have given us the typical or generalized insect thorax. The development of the wings also had a large influence on the evolution of the thorax, most of which we will discuss later. But the mesothorax and metathorax have become so intimately associated with the wings that they have almost become a subunit separate from the prothorax, and as such the two segments combined are often referred to as the **pterothorax.** So, now we can recognize three distinct areas of the typical pterygote insect: the **neck region** or **cervix**, the **prothorax,** and the **pterothorax.**

THE NECK OR CERVIX

* The **neck** or **cervix** is the narrow passageway between the head and the thorax. It may be quite constricted in some insects, but it must still allow for the passage of all the important internal organ systems such as the oesophagous of the digestive system, the salivary gland ducts, the ventral nerve chord, the dorsal blood vessel, the tracheal trunks of the respiratory system, and the dorsal and ventral longitudinal muscles articulating the head with the thorax. Also, there must still be enough open cavity for the return of the blood from the head back to the thorax.

* The neck is largely membranous and is usually covered by overlapping parts of the prothorax. There has been some debate as to just what did the neck evolve from. Did it evolve from the postocciput of the head or from the prothorax? A few authors also believe that it may be a reduced segment of its own, but there is no real evidence to support this. So which of the other two possibilities is true? Well, it is actually believed that it has developed from both to some extent. The main evidence for this comes from a study of the musculature involved in the movement of the head. The primary longitudinal muscles that move the head are attached anteriorly to either the postocciput or the tentorium, and posteriorly to the antecosta or phragma of the mesothorax. There are no attachments of the longitudinal muscles in the prothorax. So, it appears that the neck region developed at the expense of the prothorax at least in part. There are no longer places for attachment of the muscles on the anterior part of the prothorax. The longitudinal muscles have either migrated their insertion to the head region or they have longitudinally fused with the muscles of the labial head segment.

* At any rate the neck is largely membranous and allows for a multitude of different movements of the head. Most insects are capable of manipulating their heads through such motions as projection and retraction, elevation and depression, and rotation. In order to facilitate these movements, specialized sclerites and musculature located in the cervical region are required. These sclerites are situated in the cervical membrane. There is a set of **lateral cervical plates** on each side. Each set of plates often is composed of 2 distinct sclerites: the **anterior lateral cervical plate** and the **posterior lateral cervical plate**. The ALCP articulates with the postocciput and PLCP articulates with the episternum of the prothorax. Each of these plates has a nob-like projection or **cervical condyle** which fits into a corresponding notch on the margin of the postocciput or the episternum. The 2 plates form a hinge at their median juncture. When the longitudinal muscles contract the hinge bends outward allowing the head to be retracted into the thorax. There is also a specialized set of muscles running from the tentorium to the ALCP and another set running from the PLCP to the mesothorax. When these 2 sets of muscles contract the hinge is straightened out and the head is protracted away from the thorax.

* There are also 2 **dorsal plates** located on the dorsal aspect of the cervix. Anteriorly, they are attached to the the postocciput at the base of the epicranial suture. Posteriorly, the dorsal plates are extended into a membranous pocket identified in the drawing as the **membranous pocket of cervix** and are attached to a projection, identified as the **protergal apodeme** on the anterior margin of the overhanging protergum. This posteriorly reflexed apodeme forms with the dorsal plates a V-shaped joint. Muscles attached to the apex of the joint effect a posterior pull on the head and appear to be the mechanism for tilting the head upward. A downward tilt may be accomplished by a contraction of the ventral longitudinal muscles. The mechanisms for rotation of the head are not completely understood, but is probably brought about by a combination of the above 2 mechanisms.

INSECT MORPHOLOGY - THE THORAX

* In some insects there are additional ventral sclerites called **gular sclerites.** The function of these sclerites is not known.

* In some insects the neck membrane is very reduced. Look at overhead of Hemiptera neck region. In this insect the prothorax is produced forward and forms a collar that overlaps the base of the head. The neck membrane actually attaches to the posterior part of the collar and is quite reduced. All cervical sclerites are absent.

THORACIC REGIONS

<u>General Comments</u>:

The pterothoracic segments are similar to the prothorax in many respects, but quite different in a number of other respects. Most of these differences have come about due the accomodation of the flight mechanism.

* We will discuss flight in more detail later, but briefly flight in insects is achieved by an **indirect flight mechanism.** This means that the muscles which initiate the stroke of the wing are not applied directly to the base of the wing. Flight in these insects is accomplished by altering the shape of the dorsal surface of the tergum to which the wings are attached. When the tergal surface is buckled or arched, the wings are forced downward; when the tergum is depressed, the wings rise upward. The **dorsal longitudinal muscles**, extending lengthwise from one phragma to the next, arch the tergum upon contraction and therefore indirectly cause the downstroke. Since this is the power stroke of the wing, the dorsal longitudinal muscles are very well developed and may occupy most of the thoracic cavity.

* An antagonistic set of muscles operate from the tergum to the sternum. These are the **dorso-ventral muscles**, and their contraction depresses the tergum and indirectly causes the upstroke of the wing.

* Such a flight mechanism requires considerable modification of the wing-bearing metameres or **pterothorax**. There must be strong apodemes or **phragma** for the attachment of the dorsal longitudinal muscles. Since flight is accomplished by altering the curvature of the tergum, the shape of the sclerotized areas of the tergum must be such that the most efficient alternating curvature is accomplished by the antagonistic muscles. The entire thorax must be effectively braced so that contraction of the flight muscles will only effect the shape of the tergum. Where two pair of flight wings must respond in unison, articulation or movement between the wing-bearing metameres must be reduced. And of course, flight is not a matter of simply flapping two wings up and down. The wings must be rotated, so that the tilt or pitch of the wing can be regulated. This means that a pivotal structure must be provided beneath the base of the wing along with structures for accomplishing this tilt.

* The prothorax differs from other body segments in that its tergum and sternum always lack the antecostal and precostal elements of typical segments. These have been lost by membranization of the neck region. The prothorax never bears a phragma as the first phragma is always associated with the mesothorax. Also, the acrotergite of the mesothorax is never sufficiently enlarged to form a postnotum of the prothorax.

<u>Pleura</u>:

* As discussed above, the pleural region is derived from 3 basic sclerites, one ventral, and two more dorsal. The ventral **sternopleurite** as become fused with the sternal sclerites, and articulates with the coxa. The dorsal sclerites, **anapleurite** and **coxopleurite** are present as separate sclerites in the Apterygota and in the prothorax of larval stoneflies. In other insects they form the main pleurites, the coxopleurite has divided in some insects to form the **trochantin** near the base of the coxa.

* The prothoracic pleura is well developed for the support of an effective walking mechanism, and may have evolved in its early phylogenetic history for the support of paranotal lobes. Lying dorsal of the coxa of the prothoracic leg are the 2 principal pleural sclerites: anteriorly, and articulating with the lateral cervical plates is the **episternum;** posteriorly is the **epimeron.** The episternum also articulates with the anterior sternal sclerite, and both the episternum and the epimeron are closely united to the lateral aspect of the protergum.

INSECT MORPHOLOGY - THE THORAX

The episternum may also be divided by a longitudinal suture into a dorsal **supraepisternum** (or **anepisternum**) and a ventral **infraepisternum** (or **katepisternum**). The two sclerites are united mesally by means of a deeply invaginated suture, the **pleural sulcus**, which continues dorsally to form the **pleural wing processes**. In front of the pleural wing process may be one or two **basalar sclerites**, these may not be distinctly separated from the episternum. Also posterior to the pleural wing process may be a small **subalar sclerite**. The basalare and subalare are sometimes collectively called **epipleurites**.

* The **mesothoracic spiracle** is situated in the intermetameric membrane between the prothorax and mesothorax; the **metathoracic spiracle** is located between the mesothorax and the metathorax.

* Internally, the pleural suture produces a flanged apodeme, the **pleural ridge.** The distal aspect of the pleural ridge becomes an armlike apodeme called the **pleural apophysis**. This ridge serves as a site for muscle attachment, and also it unites with the sternal apodeme to form a transverse brace for mechanical support for the entire prothoracic metamere.

<u>Tergum</u>:

* The tergum of the prothorax in many primitive insects (Orthoptera, Blattaria, etc.) is often a single plate that may be greatly expanded on its margins to form a shield-like sclerite, often referred to as a **pronotal** or **protergal shield.** In some insects this plate may also be expanded anteriorly over the head and posteriorly over the pterothorax. These expansions are sometimes strengthened by a series of sclerotized ridges called **tergal carinae**. In some insects, such as the grasshopper, these ridges may appear to divide the tergum into distinct sclerites. These should not be confused with intersegmental divisions though.

* The notal areas of the pterothorax are relatively small in wingless insects and larvae, but they are greatly modified to accomodate the above described flight mechanism in winged insects. The acrotergites of the metathorax and the first abdominal segment extend forward to join the tergum of the segment in front, and in many cases become secondarily separated from its own segment by a narrow membranous region. Each acrotergite and the associated antecostal sulcus is now known as a **postnotum**. There may be a mesopostnotum and a metapostnotum if both wings are used equally in flight, but in those insects where the hind wings are responsible for the flight (Coleoptera, Orthoptera), only the metapostnotum is well developed. Conversely, the Diptera have a well developed mesopostnotum, but no metapostnotum. The antecostal ridges at the anterior and posterior of the mesothorax and the posterior of the metathorax are often greatly expanded forming **phragmata**, again the number and position of these relate to which wings are used for flight.

* The meso- and metanotum will often have other sulci (or internal ridges) to help strengthen the sclerites. Often a transverse sulcus will divide the notum into an anterior **prescutum** and a posterior **scutum**. Generally, the scutum is the broader, arched sclerite of the tergum, and it is often divided longitudinally by a single **median sulcus**. Also, a more posterior V-shaped sulcus (the **scutoscutellar sulcus**) separates off the **scutellum**. If the intermetameric suture is sclerotized, the resulting tergite is called the **postscutellum**. Usually the prescutum connects with the pleuron by a narrow extension in front of the wing, called the **prealar arm**; behind the wing, a similar extension, the **postalar arm**, connects the postnotum with the epimeron. The scutum laterally has two processes which articulate with the **axillary sclerites** around the base of the wing - these are called the **anterior** and **posterior notal processes**. The posterior fold of the scutellum continues laterally behind the wing as the **axillary cord**.

* One can readily determine the capability of the flight mechanism of a particular insect by observing the following tergal development: 1) sclerotization of the secondary intermetameric sutures so that the entire tergal area of the pterothorax can be arched or depressed in unison, 2) an incorporation of the third phragma into the pterothorax rather than its remaining as an anterior margin of the first abdominal metamere, and 3) the width and degree of sclerotization of the phragmata.

INSECT MORPHOLOGY - THE THORAX

* There are quite a few smaller sclerites around the base of the wing which help accomodate the fine tuning of flight in insects. Some of these are **intertergal sclerites** (lie in the intermetameric membrane between the mesothorax and metathorax), **axillary 1** (articulates with the anterior tergal [notal] wing process, the lateral margin of the tergum, the subcostal vein, and axillary 2), **axillary 2** (probably most important in the manipulation of the wing, articulates with the pleural wing process, two small pleural sclerites [basalare, subalare], axillarys 1 & 3, and the radial vein), **axillary 3** (roughly Y-shaped, articulates with posterior tergal [notal] wing process, axillary 2, and median plate 1), **median plate 1** (articulates with axillary 3), **median plate 2** (articulates with axillary 2), **humeral plate** (in membranous area at base of wing near the costal vein). The median plates have a deep sulcus called the **plica basalis**. A roughly triangular area that encloses the axillarys is called the **axillary angle**. There may also be several other sclerites of uncertain function: **tegula** (anterior base of the wing), **subcostal sclerite**, and the **vannal sclerite**.

* I will leave the discussion of how these small sclerites function to direct the wings during flight, and the wing folding mechanism until later when we discuss the wings and flight in insects.

Sternum:

* The ventral surface of the prothorax is usually composed of 2 distinct sclerites: the **eusternum** (which is sometimes just called the **sternum**, and is the combined **basisternum** and **sternellum**) and the **acrosternite** (from the mesothorax). The acrosternite is sometimes called the **spinasternum** or **intersternum**. In the thorax, the acrosternite may be an independent sclerite or it may migrate anteriorly to become a part of the ventral complex of the metamere preceding the primary suture (there is no prothoracic acrosternite). The acrosternite may bear a median spine-like apodeme, the **intersternal apodeme** (or sometimes called the **spina**).

* Chapman indicates that there are differing degrees of fusion between sternal plates in the thorax such that 4 different conditions may occur: 1) all elements separate - prothoracic eusternum, first spinasternum, mesothoracic eusternum, second spinasternum, metathoracic eusternum (fig. a on overhead); 2) eusternum of mesothorax and second spinasternum fuse, the rest remaining separate; 3) eusternum of prothorax and first spinasternum also fuse so that there are now 3 main elements - compound prosternum, compound mesosternum, and metathoracic sternum; and 4) complete fusion of meso- and meta-thoracic elements to form a pterothoracic plate (fig. b on overhead).

* Arising from the eusternum are a pair of apophyses, called **sternal apophyses**. You can see these externally by a pair of pits connected by a sulcus. This divides the eusternum into an anterior **basisternum** and a posterior **sternellum**. In more advanced insects, these two internal apophyses have become united along the midline, and only separate internally, forming a Y-shaped **furca**. Distally the arms of the sternal apophyses are associated with the pleural apophyses (see fig. 7.4).

* The basisternum tends to be larger in the pterothoracic region than in the prothoracic region to allow for more muscle attachment.

* There is no evidence that true wings were ever present on the prothorax, but in many early fossil insects small lateral lobes project from the lateral margins of the prothoracic tergum. This suggests that all 3 segments of the thorax may have had these **paranotal lobes** which may be the precursor of wings. The immediate ancestor of winged insects then probably had 3 pairs of paranotal lobes, one pair on each segment. The insects then probably used these lobes to glide on. They then developed into wings. There are other theories on the origin of the wings; we will discuss them later.