EVOLUTION OF THE INSECT HEAD

- We have theorized that the tagmata of the insect body were evolved as composites of cylindrical metameres, each of which in the primitive form bore a pair of ambulatory appendages. While this theory seems plausible for the abdomen and in most forms for the thorax, it appears at first examination to be a rather remote assumption for the head tagma.

- There are many theories about the number of segments of the insect head. Most are based on differences in the number of pregnathal segments, which in turn depends on just what is the definition of a segment.

- In the past a segment has been variously defined as posessing one or all of the following (remember that the acron and periproct are not considered to be true segments):
  1. a pair of appendages
  2. a neuromere
  3. a pair of mesodermal coelomeres
  4. a pair of apodemes

  The Canadian morphologist Rempel says that all are necessary, while Snodgrass says that the only parts necessary are the appendages and the neuromere.

- Snodgrass defines a segment as:
  1. a primary embryonic metamere - a complete ring of an arthropod.
  2. bears a pair of appendages (at some time)
  3. contains a ganglion and motor nerve supply of its own.
  4. ganglion is double with commissures between each side.

- Muscle insertion and sensory innervation are not reliable due to migration. Sensory neurons do not necessarily lead to the ganglion of their own segment.

- As I mentioned earlier there are a number of different theories on the actual number of segments that comprise the head.

- As you can see from this overhead, some authors do not even recognize the presence of a acron, and the number of segments they recognize range from 3 to 7.

- There has been very little dispute about the number of gnathal (gnathocephalon) segments. These are the **mandibular, maxillary,** and **labial** segments.

- There is a great deal of dispute on the remaining segments (protocephalon). As many as 5 more have been named:
  1. **intercalary = pre-mandibular = first pre-oral.** Most authors accept this as a segment. Evidence for it: first legs in the Trilobites, 2nd antennae in the Crustacea, and chelicerae in the arachnids and xiphosurans
  2. **antennal.**
  3. **preantennal = ocular.**
  4. **labral.** This segment is disputed by many.
  5. **superlingual.**

- For those people who do not believe the first segment is a true metamere, they call this anterior-most area the **acron**. Several others do recognize it as a true metamere, but they do not always refer to it the same way - some call it the labral segment while others refer to it as the pre-antennal segment.

- Your text book (Chapman) indicates that recent molecular studies on *Drosophila* seem to indicate that there are 7 post-oral segments: labral, ocular, antennal, intercalary, mandibular, maxillary, and labial. At any rate the

head capsule has become a highly evolved or specialized structure involving at least five primitive or generalized metameres.

- The 1st metamere or prostomium probably bore the mouth opening at its posterior margin in addition to a pair of appendages that evolved into the sensory antennae.

- By studying the brain of present day insects and the head tagma of the crustacea has led morphologist to theorize that the prostomium and the next following metamere both developed sensory antennae.

- With later evolution, the principal sensory structures were then situated on the first two metameres. These metameres may have fused early in the evolution of the head to form a theoretical protocephalon.

- The development of the photoreceptors or eyes is not clear, although these sensory structures must certainly have developed on the prostomium.

- From a comparative study of the morphology of present-day insect mouth parts and the nerve centers associated with them, we may conclude that these organs of ingestion probably evolved from ambulatory appendages. Since 3 pairs of structures make up the generalized feeding mechanism, we may assume that 3 metameres were involved in the formation of a second primitive head complex or gnathocephalon.

- In the present-day insect, the sensory protocephalon and the ingestive gnathocephalon have coalesced and have become completely fused into a composite structure.

- Unlike the thorax and abdomen, segmentation of the head is obscure and the sutures as we know them today have little correlation with the metameres that were involved in its formation.

POSITIONS OF THE HEAD OR MOUTHPARTS RELATIVE TO THE BODY

1. Hypognathous - this is the primitive condition. This is where the head is more or less vertical and the mouthparts are directed ventrally. Example: the grasshopper.
2. Prognathous - This is where the mouthparts are directed anteriorly. This is common in insects that burrow and in predatory insects.
3. Opisthognathous (opisthorhynchus in sucking insects) - This is where the mouthparts are directed posteriorly. This is common in the Hemiptera and Homoptera. This type is sometimes divided into 2 distinct types:
   a. Auchenorrhynchous - The beak arises from the back of the head or near the "neck". This is found in the cicadas.
   b. Sternorrhynchous - The beak arises from the front of the head. Example: aphid

GENERAL EXTERNAL STRUCTURES OF THE INSECT HEAD

- The head can be viewed as an ovoid envelope of sclerotized integument enclosing the brain centers, certain glands, and muscle systems for the operation of the head appendages.

- **Note:** Most previous authors refer to the inflexions of the head as sutures. Your text book (Chapman) distinguishes between true sutures (inflexions marking the juncture of two sclerites) vs. sulci (singular = sulcus; an inflexion of the sclerite to give rigidity to the structure). The position of the sulci may be somewhat variable. Consequently, the areas of the head bounded by these sulci are given names so we can refer to the various areas, but they do not represent primitive sclerites. Since the position of the sulci may be variable, the exact boundaries of the regions of the head may not be clearly delimited.

- The head capsule is open at its posterior junction with the thorax to permit a passageway for certain connectives such as the ingestive tube which connects the mouth with the digestive system. This opening is referred to as the **occipital foramen.** The thin, flexible cylinder of integument connecting the margins of the occipital foramen with the thorax is the **neck** or **cervix.**

- A mouth opening is situated on the ventral aspect of the capsule which is also depressed to form a pocket or **oral cavity** to accommodate the operation of the mouth parts.

- The conspicuous **photoreceptors** or **compound eyes** occupy the dorso-lateral aspects of the head, and the **antennal sockets** are situated on the frontal surface between the eyes. A suture outlines and separates the compound eye and antennal socket from the adjoining sclerotized areas. These sutures may also enclose a sclerotized area forming a ring about the sensory structure. The **ocular suture** (CH: **circumocular sulcus**) encloses the **ocular sclerite**, and the **antennal suture** (CH: **circumantennal sulcus**) encloses the **antennal sclerite.** There may also be a vertical sulcus from the eye to the subgenus sulcus called the **subocular sulcus**. The subocular sulcus acts as a brace against the pull of the muscles associated with feeding.

- The anterior surface of the head lying between the compound eyes is called the **frons.** Although the frons is usually easily identified as the broad frontal area between the eyes, an accurate identification of facial areas is best made with reference to the sutures lining the integument of the head.

- Ventrad of the frons is a short suture bearing at its lateral ends the **anterior tentorial pits.** This is the **frontoclypeal** or **epistomal suture** (CH: **epistomal sulcus**). In most insects, the epistomal suture is continuous across the face and is probably the most constant frontal suture to use for the identification of facial areas. When anterior tentorial pits are present they will always be on the epistomal suture.

- The facial area above the epistomal suture is the frons; the area below the suture is the **clypeus.** Sometimes the distal portion of the clypeus is membranous. In this case, the proximal sclerotized portion of the clypeus is called the **postclypeus** and the distal, membranous portion as the **anteclypeus.**

- Muscles attaching to the inner surface of the frons lead to the pharynx, labrum, and the hypopharynx; those attaching to the inner surface of the clypeus lead to the cibarium, and the frontal ganglion is always situated between these two sets of muscles.

- An oblong sclerite freely articulating at its proximal margin with the clypeus, is the **labrum.** This sclerite serves as an upper lip for the mouth cavity. Although the labrum is generally considered as a part of the organs of ingestion, it is a true sclerite of the head and was not evolved from an appendicular structure.

- The **gena** or **cheek** is a poorly defined area in most insects, but usually lies below and immediately behind the compound eyes. Sometimes this area may be set off by a **subocular groove.**

- An area immediately above the articulations of the mandibles may be heavily sclerotized to support the powerful jaws. This area, margined by a **subgenal suture** (CH: **subgenal sulcus**), is called the **subgena**. Actually, the subgenal sulcus above the mandibles is often called the **pleurostomal sulcus** and the portion more posterior, behind the mandibles is often referred to as the **hypostomal sulcus**. The subgenal suture is usually continuous with the epistomal suture. The subgenal area above the mandibles is called the **pleurostoma** and the area above and posterior to the mandibles is the **hypostoma.**

- A **frontal suture** in the form of an inverted Y is common in immature insects and sometimes faintly visible in adult insects. It is often called the **epicranial suture.** The stem of the Y is referred to as the **coronal suture** and the arms as the **frontal sutures.** This is actually an ecdysial suture or a point of rupture in the integument during the molting process. When this suture is developed the area enclosed by it is called the frons.

- The top of the head is another poorly defined area called the **vertex.** When the epicranial suture is developed the vertex is the area directly on either side of the coronal suture.

- Identification of the posterior areas of the head is best accomplished by locating the **posterior tentorial pits.** These are always located on the **postoccipital suture.** This suture is the most constant suture of the posterior

region. The sclerite enclosed by the postoccipital suture is the **postocciput** which serves as a sclerotized ring about the occipital foramen. The neck membrane or cervix is attached to this sclerite, and a mesal projection or **occipital condyl** serves as a point of articulation for the sclerites of the cervix.

- An additional suture may occur anterior to the postocciput and margins the posterior aspect of the head. It is referred to as the **occipital suture** (CH: **occipital sulcus**) and the area it encloses as the **occiput.** Generally, the term occiput is used only to describe the posterior area immediately behind the vertex. The lateral, ventral portion of this sclerite is then referred to as the **postgena.**

THE INTERNAL STRUCTURES OF THE HEAD

- The main internal structure of the head is the **tentorium.** It supports the cranial wall, it supports the stomadeum, and it serves as the origin of many muscles of the mouthparts and the antennae. It basically is made up of two pairs of apodemal arms (sometimes 3) and a body.

- The **anterior tentorial arms** have their origin in the epistomal sulcus (frontoclypeal sulcus). The external evidence is the **anterior tentorial pits.**

- The **posterior tentorial arms** take their origin in the postoccipital suture and have as their external evidence the **posterior tentorial pits.**

- **Dorsal tentorial arms** are sometimes present. If they are, they are considered outgrowths of the anterior arms. Pits on the frons called the **tentorial maculae,** are not true envaginations and are not homologous with the anterior tentorial pits.

- The anterior and posterior arms are often united in a tent-like manner, hence the name tentorium.

- The tentorium may be strengthened by a central plate called the **corpotentorium.**

SPECIALIZED HEAD STRUCTURES

- Once again I want to emphasize that what I have presented here so far is the generalized head structure (similar to what is found in the Orthoptera). Most other families and orders of insects will be different in some or many ways. Sutures will sometimes be reduced, or in a different position, or even be absent. When the sutures are in different places or absent then it becomes difficult to identify the sclerites of the head. **[Fig. 63 in text, p. 120]** One rule of thumb to serve as a starting point is that the anterior tentorial arms (externally the pits) will always have their origins on the episternal ridge (externally the suture) and the posterior tentorial arms will have their origins on the postoccipital ridge. Most of the modifications of the head have occurred in the posterior areas of the head near where the head joins with the thorax.

- In hypognathous insects that have a thick neck, the posteroventral part of the head is membranous with the **postmentum** of the labium connecting to this membrane area (see Fig. A on overhead), and it articulates with the subgena on either side. The hypostomal sulci bend upwards posteriorly and are continuous with the postoccipital suture.

- In insects with a narrow neck, and in prognathous insects, the area of the head below the occipital foramen has become sclerotized, but this sclerotization may have different origins. In Diptera (see overhead, Fig. B), the hypostoma on each side meet along the midline below the occipital foramen to form the **hypostomal bridge**; this bridge is continuous with the postocciput.

- In some Hymenoptera, and some Hemiptera (Notonectidae and Naucoridae) (see overhead, Fig. C), a similar bridge is formed by the postgena on each side, but the bridge is separated from the postocciput by the postoccipital suture; this is called the **postgenal bridge**. The postgenal bridge can be differentiated from the hypostomal bridge in that the postgenal bridge has no connection with the postocciput and is continuous only with the postgenae.

- In many prognathous insects (see overhead, Fig. D), the lower ends of the postocciput fuse and extend forward to form a median ventral plate; this is called the **gula**. The gula may form a continuous sclerotization with the labium (called the **gulamentum**). Sometimes the postgenae are expanded medially, making the gula very narrow, and in some cases may even obliterate the gula, thus forming a suture along the midline - this suture would be called the **gular suture**.

- The position of the posterior tentorial pits (PTP) is important - marks where the post occipital suture ends and where the hypostomal sulcus (part of the subgenal sulcus) begins. PTP's more dorsal (Fig. B) - hypostomal bridge; PTP's more ventral (or forward) (Fig. D) - gula.