

MORPHOLOGY OF THE BRACING ELEMENTS IN  
THE HYMENOPTERAN HEAD

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## ABSTRACT

### MORPHOLOGY OF THE BRACING ELEMENTS IN THE HYMENOPTERAN HEAD

by Jeffrey J. Jackson

The internal head bracing elements of 56 species representing fourteen superfamilies of Hymenoptera were studied and described. Strength and support of the head capsule are contributed to primarily by the tentorium and associated inflections.

Some structures appear to have phylogenetic relationships. Dorsal tentorial arms are best developed in primitive groups and are either absent or vestigial in advanced superfamilies including the Vespoidea, Scolioidea, and Apoidea. These advanced groups generally have much more elaborately developed tentoria which include a tentorial bridge, a feature lacking in the Symphyta.

Similar structures are found occasionally in species widely separated taxonomically. Such similarities may be due to convergent evolution.

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IN THE HYMENOPTERAN HEAD

By

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## INTRODUCTION

The tentorium is an internal head structure found only in the insects and is the most important of the bracing elements within the head capsule. It consists of strengthening struts which are formed by two pairs of cuticular invaginations that unite within the head.

Major general works on the insect tentorium include Snodgrass (1935 and 1956) and Matsuda (1965). These references, where discussing the tentorium, are primarily concerned with theories of origin, evolution, and general statements of function.

Hudson (1945, 1947 and 1948) has described the tentorium as found in the Orthoptera, Dermaptera, Isoptera, Odonata, and Plecoptera. There has been no general study on the tentorium of the Hymenoptera, but a few limited primarily to descriptions of single species. The honeybee (Snodgrass, 1956) is an outstanding example and Michener (1944) described the tentorium of Anthophora.

Some valuable information closely related to the hymenopteran tentorium can be gleaned from work done on sutures and the external facial morphology of the face of Hymenoptera (Bigelow, 1954) and the clypeus and the epistomal suture in Hymenoptera (DuPorte and Bigelow, 1953). The relationship of the tentorium to the epistomal suture and strengthening inflections that are associated with it are well described.

This paucity of published information has lead the author to investigate the morphology of the internal supporting mechanisms of the hymenopteran head.

No one appreciates better than the author the incomplete nature of this work; for representatives of only 56 species and fourteen superfamilies have been studied intensively. The tentorium and associated inflections which illustrate the various ways in which strength and support of the head capsule may be achieved are described for each of the taxa.



## TERMINOLOGY

Descriptions presented herein pertain to the location of the anterior tentorial pits, the shape of the anterior arms, the rear insertion of the anterior arms, dorsal arms, tentorial bridge, spine, and internal inflections. This terminology is used consistently in the discussion of the morphology of the bracing elements of the hymenopteran head.

The number and complexity of facial sutures may vary considerably from group to group and from species to species. The sutures, when invaginated internally, form inflections which add to the bracing of the head. The Clypeogenal Inflection extends from the anterior mandibular articulation to a pit demarking the anterior external invagination of the anterior arm of the tentorium, known as the Anterior Tentorial Pit (abbreviated herein as ATP). In Fig. 1A only the clypeogenal sutures are present. In Fig. 1B the ATP are connected by the Epistomal Suture, a suture extending between the two anterior pits. Other sutures that may be present and inflected include the Frontogenal, (Fig. 1C), which extends from the anterior pits dorsally to the base of the antennae, and the Malar which extends from the base of the compound eye to the region of the posterior mandibular articulation.

Compound eyes (Fig. 5E) are nearly always ringed with an Ocular Inflection but in some cases it is nearly absent (Fig. 1D).

The postgenae, the lateral and ventral parts of the occipital arch, may be inflected (Fig. 4C).

Union of the inflected postgenae with the face is seen in some specimens.

When most hymenopteran head capsules are viewed from the ventral side with the mouth parts removed a single large opening is seen, Fig. 1E. Usually the rim of the opening is thicker than the remainder of the exoskeleton.

There may be slight indentations which tend to isolate the mandibular sockets (Fig. 1F). Some species, however, have the mandibular sockets completely isolated so that there are three openings in the ventral head capsule (Fig. 1G).

Separate mandibular sockets as in Fig. 1G probably provide the greatest mandibular support.

#### Anterior Arms

The Anterior Arms in their simplest form are approximately cylindrical and extend from either side or below the occipital foramen to the anterior tentorial pits which are commonly found not far above the anterior mandibular articulations (Fig. 4B). Frequently, however, the arms bear extended flattened areas termed, wings, which may be lateral (Fig. 3A) or vertical in position (Fig. 5C). The wings may be so greatly expanded that the anterior arms may have the appearance of elaborately twisted ribbons (Fig. 5E). If the anterior arms are flat the ATP will be slits and may occupy nearly the entire clypeogenal and/or epistomal sutures. (Fig. 1C, 5E).

**Fig. 1, terminology of facial sutures and ventral aspect of head capsules.**

### Dorsal Arms

Dorsally, and usually about at their mid point, the anterior arms give rise to Dorsal Arms. These may be strong and attach solidly to the face (Fig. 3C & D) or absent (Figs. 4A, 5C). Intermediate degrees of development of the dorsal arms are common. In such instances dorsal arms may not extend all the way to the face. They may be mere vestiges which are difficult to see and are easily broken off while preparing the specimen (Fig. 5E).

### Posterior Arms

Immediately anterior to the occipital foramen Posterior Arms may extend upward and mesally from the anterior arms and join to form the tentorial bridge. Commonly a slender projection, the Spine, extends forward and/or downward from the center of the bridge. In rare cases the posterior arms are not joined (Fig. 4B). Posterior arms are absent in many Hymenoptera (Fig. 3B) but the occasional presence of a spine at the juncture of the anterior arms suggests that in these cases it may be fused with the anterior arms (Fig. 2F).

## MEGALODONTOIDEA

### Figure 2A and B

Megalodontes cephalotes Fabricius has a fairly simple tentorium. The dorsal and anterior arms are smooth rods of about the same size. The dorsal arms are solidly attached to the face just above the antennae. The anterior arms meet the face midway between the antennal sockets and anterior mandibular articulation. On the ventral side, at the point of attachment to the face, is a short inflected area of the clypeogenal suture. There is no visible reinforcing ridge connecting the anterior arm and the anterior mandibular articulation. The relatively weak appearing sickle shaped mandibles of this species apparently obtain little support from the anterior arms. Perhaps a well differentiated supportive mechanism is not necessary for the adults are believed to feed mainly on pollen.

The posterior arms are very prominent. The tentorial bridge appears as a flat ribbon in the shape of a squared off horse shoe. A small spine extends toward the lower face from the bridge. The bridge is situated low on the anterior arms and cannot be seen through the occipital foramen.

## CEPHOIDEA

### Figure 2C and D

The anterior arms of the tentorium are arc shaped, laterally compressed posteriorly, and fused at the base. They meet the face at the anterior mandibular articulations and at this point the arms are dorsoventrally flattened. The dorsal arms are fairly stout rods and meet the face just laterally and slightly above the antennal insertions. There is a median spine at the angle where the anterior arms meet.

TABLE 1.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE MEGALODONTOIDEA AND CEPHOIDEA

|                                 | Megalodontidae                                                                                              |                          |                                                                                                                                       |
|---------------------------------|-------------------------------------------------------------------------------------------------------------|--------------------------|---------------------------------------------------------------------------------------------------------------------------------------|
|                                 | Megalodontes cephalotes Fabricius                                                                           | Cephus tabidus Fabricius | Cephidae                                                                                                                              |
| LOCATION OF THE ATP             | Below bases of antennae                                                                                     |                          | At the anterior mandibular articulation                                                                                               |
| SHAPE OF THE ANTERIOR ARMS      | Smooth cylindrical rods                                                                                     |                          | Downward curving and expanded laterally at the anterior ends                                                                          |
| REAR INSERTION OF ANTERIOR ARMS | Anterior most part of hypostomal bridge                                                                     |                          | Fused near bases, inserting just below the occipital                                                                                  |
| DORSAL ARMS                     | Smooth cylindrical rods 1/2 the diameter of the anterior arms, they meet the face just above the antennae   |                          | Strong--inserting just above antennal bases                                                                                           |
| TENTORIAL BRIDGE                | Broad, flat, ribbon like in cross section                                                                   |                          | Absent                                                                                                                                |
| SPINE                           | Present                                                                                                     |                          | Very weak, but with obvious base. Inserts at junction of anterior arms                                                                |
| INFLECTIONS                     | Ocular well developed, epistomal absent, clypeogenal inflected just below ATP but not extending to mandible |                          | Ocular--medium, clypeogenal--absent due to low position of ATP, epistomal--appears to be fused with ridge around base of head capsule |
| OTHER COMMENTS                  | Weak appearing, sickle shaped mandibles                                                                     |                          |                                                                                                                                       |

## TENTHREDINOIDEA

### Figure 2E and F

The anterior tentorial arms may be flattened, twisted, or with mesal wings as in Tenthredo. Clypeogenal inflections may be present if the insertion of the anterior tentorial arms is remote from the anterior mandibular articulation. In Cimbex, the insertion of the anterior tentorial arms is remote but the clypeogenal inflection is not developed. A small apodeme is present on the ventral side of the anterior arms near the near insertion in Cimbex and Tenthredo. The rear insertion of the anterior arms is often at the inflected post-genae. Dorsal arms are strong and join the face near the antennal bases. Posterior arms are not present, but a spine projects anteriorly from the fork of the anterior arms of Tenthredo.

Inflections are in general fairly well developed with the exception of Cimbex in which internal supporting inflections are lacking, including the usually conspicuous ocular inflections of other forms. This may be compensated for by the thick exoskeleton of Cimbex.



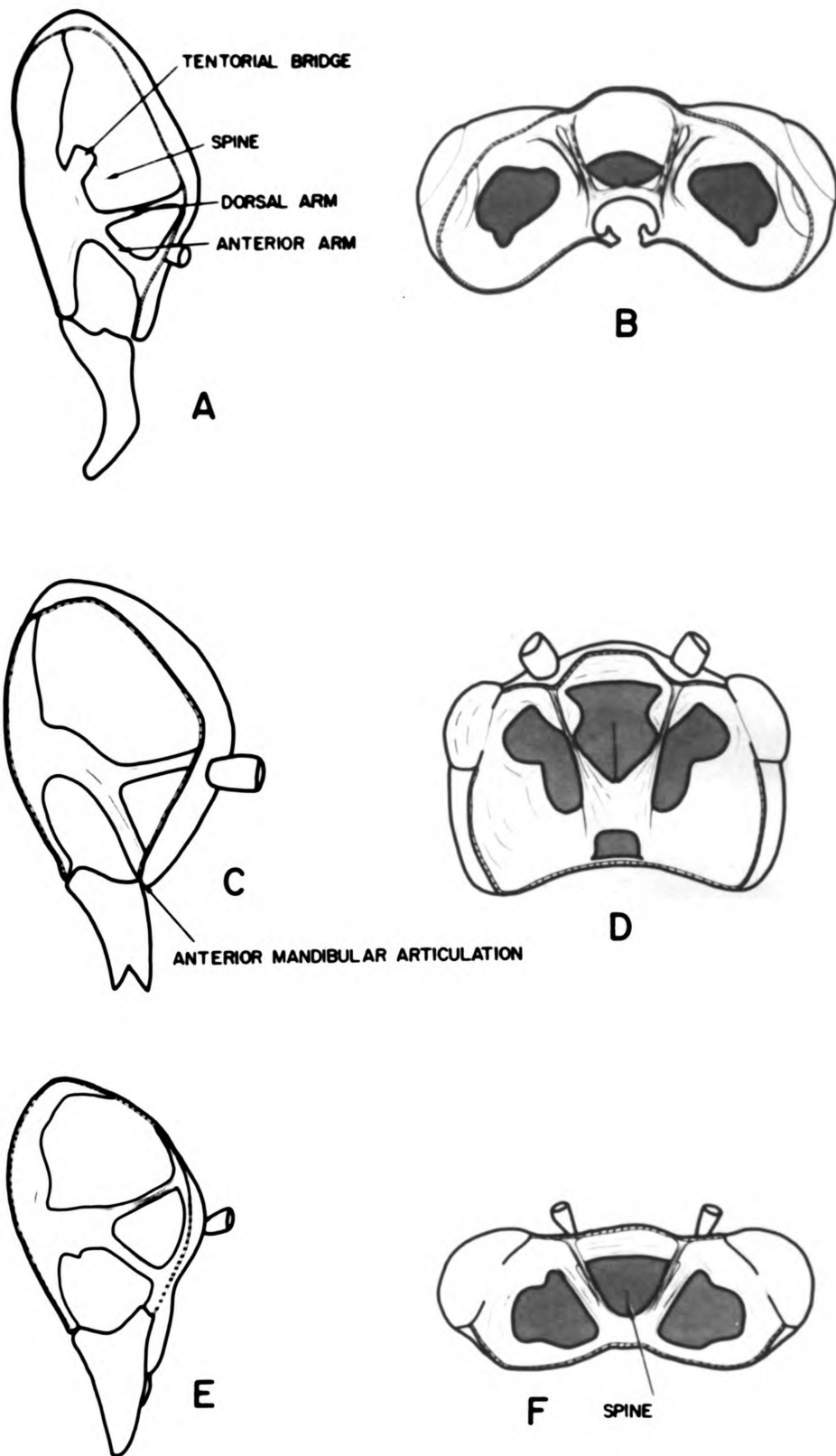
TABLE 2.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE TENTHREDINOIDEA

|                                    | Cimbicidae                                                        |                                                                                                                                 |  |
|------------------------------------|-------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------|--|
|                                    | <u>Cimbex americana</u> Leach                                     | Diprionidae<br><u>Neodiprion lecontei</u> (Fitch)                                                                               |  |
| LOCATION OF THE<br>ATP             | Midway between anterior mandibular articulation and antennal base | Slits--including part of the epistomal and clypeogenal sutures above and slightly mesad of the anterior mandibular articulation |  |
| SHAPE OF THE<br>ANTERIOR ARMS      | Short, thick, with small downward projecting apodeme              | Flattened dorsoventrally and somewhat twisted                                                                                   |  |
| REAR INSERTION<br>OF ANTERIOR ARMS | Inflected postgenae                                               | Just below occipital foramen                                                                                                    |  |
| DORSAL ARMS                        | Stout, attaching immediately above antennal bases                 | Fairly stout, attaching above lateral of the antennal bases                                                                     |  |
| TENTORIAL BRIDGE                   | Absent                                                            | Absent                                                                                                                          |  |
| SPINE                              | Absent                                                            | Absent                                                                                                                          |  |
| INFLECTIONS                        | Epistomal and clypeogenal not present                             | Ocular, epistomal, clypeogenal                                                                                                  |  |
| OTHER COMMENTS                     | Thick exoskeleton                                                 |                                                                                                                                 |  |

TABLE 3.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE TENTHREDINOIDEA

| LOCATION OF THE<br>ATP             | Tenthredinidae                                                                                     |                                      | Argidae                                                 |
|------------------------------------|----------------------------------------------------------------------------------------------------|--------------------------------------|---------------------------------------------------------|
|                                    | <u>Tenthredo basilaris</u> Say                                                                     | <u>Sphacophilus cellularis</u> (Say) |                                                         |
|                                    | Just below antennal bases                                                                          |                                      | Above and mesad of anterior mandibular articulations    |
| SHAPE OF THE<br>ANTERIOR ARMS      | Vertically flattened lateral projections on the mesal edges with small downward projecting apodeme |                                      | Laterally compressed and twisted                        |
| REAR INSERTION<br>OF ANTERIOR ARMS | Connected to small postgenal inflection                                                            |                                      | Inflected postgenae                                     |
| DORSAL ARMS                        | Stout, attaching above antennal bases                                                              |                                      | Medium and inserting at lateral edge of antennal socket |
| TENTORIAL BRIDGE                   | Absent                                                                                             |                                      | Absent                                                  |
| SPINE                              | Absent                                                                                             |                                      | Absent                                                  |
| INFLECTIONS                        | Ocular, epistomal--fairly strong, clypeogenal--strong                                              |                                      | Ocular, epistomal--very strong, clypeogenal--strong     |
| OTHER COMMENTS                     |                                                                                                    |                                      | Large eyes                                              |

**Fig. 2, A,B, Megalodontes cephalotes, Megalodontoida;  
C,D, Cephus tabidus, Cephoidea; E,F, Tenthredo  
basilaris, Tenthredinoidea.**



**FIG. 2**

## SIRICOIDEA

Figure 3A and B

The thick walled head of Tremex is supported by a relatively simple tentorium. The anterior arms are fused into a single rod posteriorly, and adorned with small, flattened lateral wings anteriorly on each side--the mesal wings being larger. Where the anterior arms meet the face they join a moderately thickened clypeogenal inflection that connects them to the anterior mandibular articulations. Strong dorsal arms are attached solidly to the face above the antennal bases.

The tentorium of Xiphidria maculata is very similar except the anterior arms lack the flattened wings and the tentorium is bent sharply downward posterior to the origin of the dorsal arms. For this reason the dorsal and anterior arms join the face slightly lower than in Tremex.

The ventral edges of the head capsule are strengthened in both species.

TABLE 4.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE SIRICOIDEA

|                                    | Siricidae                                                                                        |  | Xiphidriidae                                                                                                               |  |
|------------------------------------|--------------------------------------------------------------------------------------------------|--|----------------------------------------------------------------------------------------------------------------------------|--|
|                                    | <u>Tremex columba</u> (Linnaeus)                                                                 |  | <u>Xiphidria maculata</u>                                                                                                  |  |
| LOCATION OF THE<br>ATP             | Above anterior mandibular articulation                                                           |  | As in <u>Tremex</u>                                                                                                        |  |
| SHAPE OF THE<br>ANTERIOR ARMS      | With flattened lateral wings on both sides. Fused posteriorly into a single rod                  |  | Posterior half fused into solid rod. At the point of separation arms are bent downward. No lateral wings                   |  |
| REAR INSERTION<br>OF ANTERIOR ARMS | The single rod meets the back of the head below the occipital foramen                            |  | As in <u>Tremex</u>                                                                                                        |  |
| DORSAL ARMS                        | Strong, joining the face above the antennal bases                                                |  | As in <u>Tremex</u>                                                                                                        |  |
| TENTORIAL BRIDGE                   | Absent                                                                                           |  | As in <u>Tremex</u>                                                                                                        |  |
| SPINE                              | Absent                                                                                           |  | As in <u>Tremex</u>                                                                                                        |  |
| INFLECTIONS                        | Epistomal weak, clypeogenal broad and thick, ventral edges of head capsule strong, ocular strong |  | Epistomal weak, area between ATP and anterior mandibular articulations very thick, ocular, ventral edges of capsule strong |  |
| OTHER COMMENTS                     | Eyes small, exoskeleton thick                                                                    |  |                                                                                                                            |  |

## ICHNEUMONOIDEA

### Figure 3C and D

The tentorium and other aspects of the internal head skeleton in this group are structurally quite consistent. The anterior tentorial pits are found immediately above the anterior mandibular articulations or in some instances at the anterior mandibular articulation. Where they meet at the face the anterior arms are often dorsoventrally flattened. The wings extend laterally for at least half the length of the anterior arms. The anterior arms may either fuse posteriorly into a single median rod which connects below the occipital foramen or, if the postgena is inflected they may join it instead. Dorsal arms are usually well developed and connect to the face in the vicinity of the antennal sockets. The tentorial bridge bears a spine. The inflections joining the ATP and also connecting to the mandibular articulations are not especially well developed.

Agathis appears to be an exception in some of its morphological features for it differs from other members of the group in several respects. In this species the deeply inflected postgenae connect with the short, relatively unmodified anterior arms. Dorsal arms, the tentorial bridge, and spine are lacking.

TABLE 5.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE ICHNEUMONOIDEA

|                                    | Braconidae                                          |                                                                                                        | Braconidae                                                                   |  |
|------------------------------------|-----------------------------------------------------|--------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------|--|
|                                    | <u>Agathis tibiator</u><br>Provancher               | <u>Atanycolus ulmicola</u><br>(Viereck)                                                                | <u>Macrocentrus ancylivorus</u><br>Rohwer                                    |  |
| LOCATION OF THE<br>ATP             | Above anterior mandibular<br>articulations          | Epistomal suture, mesad<br>of anterior mandibular<br>articulations                                     | Above anterior mandibular<br>articulations                                   |  |
| SHAPE OF THE<br>ANTERIOR ARMS      | Very short rods                                     | Fused posteriorly,<br>flattened anteriorly so<br>that combined cross sec-<br>tion is shaped like a "U" | With flattened lateral<br>wings                                              |  |
| REAR INSERTION<br>OF ANTERIOR ARMS | Hypostomal bridge--bridge<br>extends nearly to face | Single rod connects below<br>occipital foramen                                                         | Inflected postgenal                                                          |  |
| DORSAL ARMS                        | Absent                                              | Slender & delicate, in-<br>serting just below & lat-<br>erad of antennal sockets                       | Long, slender, delicate<br>inserting at lateral edges<br>of antennal sockets |  |
| TENTORIAL BRIDGE                   | Absent                                              | Small & stout                                                                                          | Present, spans occipital<br>foramen                                          |  |
| SPINE                              | Absent                                              | Present                                                                                                | Present                                                                      |  |
| INFLECTIONS                        | Epistomal, ocular, strong<br>clypeogenal            | Ocular, epistomal weak                                                                                 | Ocular strong, epistomal,<br>clypeogenal                                     |  |



TABLE 6.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE ICHNEUMONOIDEA

|                                    | <u>Ichneumonidae</u><br><u>Cratichneumon annulatipes</u><br><u>quintilus (Viereck)</u>         | <u>Ichneumonidae</u><br><u>Netelia sayi</u><br>(Cushman) | <u>Ichneumonidae</u><br><u>Megarhyssa m. macrurus</u><br>Linnaeus |
|------------------------------------|------------------------------------------------------------------------------------------------|----------------------------------------------------------|-------------------------------------------------------------------|
| LOCATION OF THE<br>ATP             | Above anterior mandibular articulations                                                        | Above mandibular articulations                           | At anterior mandibular articulations                              |
| SHAPE OF THE<br>ANTERIOR ARMS      | Dorsoventrally flattened becoming wider anteriorly                                             | Dorsoventrally flattened with wide wings                 | Dorsoventrally flattened becoming wider anteriorly                |
| REAR INSERTION<br>OF ANTERIOR ARMS | At hypostomal bridge                                                                           | At hypostomal bridge                                     | Fused arms insert below occipital foramen                         |
| DORSAL ARMS                        | Weak, attaching above antennal sockets                                                         | Weak, attaching above antennal sockets                   | Strong, inserting laterad of antennal sockets                     |
| TENTORIAL BRIDGE                   | Present                                                                                        | Present                                                  | Present                                                           |
| SPINE                              | Present with a stiff basal part extending forward and a delicate distal part pointing downward | Present, extending forward and then curving downward     | Present                                                           |
| INFLECTIONS                        | Ocular                                                                                         | Ocular, clypeogenal--very weak                           | Ocular, epistomal                                                 |

## CHALCIDOIDEA

### Figure 3E and F

The ATP of the Chalcidoidea are usually located just above the anterior mandibular articulations and may be either a spot or slit-like in form depending on the cross sectional shape of the anterior arms. The anterior arms may continue as separate rods to join the back of the head on either side of the occipital foramen or they may fuse into a single structure which bounds the occipital foramen on three sides. If this is the case, the tentorium is fused to some degree with the inflected postgenae.

Great variation is exhibited in this group in the form of the tentorial bridge. In some cases it is fairly typical and bears a spine. Of the specimens examined the spine is present in two species, absent in one species, and in Chalcis microgaster the posterior arms do not meet in the center--an unusual condition. The tips of the posterior arms are pointed forward. Supporting inflections in the face and mouth area are in general not as well developed as in the more advanced Hymenoptera.

TABLE 7.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE CHALCIDOIDEA

|                                    | Eurytomidae                                        |              | Chalcididae                                                                                                    |                                             | Leucospidae                                                                                                      |                                           |
|------------------------------------|----------------------------------------------------|--------------|----------------------------------------------------------------------------------------------------------------|---------------------------------------------|------------------------------------------------------------------------------------------------------------------|-------------------------------------------|
|                                    | <u>Eurytoma</u><br><u>bvetera</u><br>Phillips      | <u>parva</u> | <u>Chalcis</u><br><u>microgaster</u><br>Say                                                                    | <u>Chalcis</u><br><u>microgaster</u><br>Say | <u>Leucospis</u><br><u>affinis</u><br>Say                                                                        | <u>Leucospis</u><br><u>affinis</u><br>Say |
| LOCATION OF THE<br>ATP             | Above the anterior mandib-<br>ular articulations   |              | Above & connecting to<br>anterior mandibular<br>articulations                                                  |                                             | Nearly vertically oriented<br>in clypeogenal suture<br>above anterior mandibular<br>articulations                |                                           |
| SHAPE OF THE                       |                                                    |              |                                                                                                                |                                             |                                                                                                                  |                                           |
|                                    | Slender, smooth, down<br>curving rods              |              | Flattened at 45° angle<br>from the perpendicular,<br>lower edge laterad                                        |                                             | Flattened laterally with<br>mesal lobe at anterior<br>end. United into flat-<br>tened plate posteriorly          |                                           |
| REAR INSERTION<br>OF ANTERIOR ARMS | Below & on either side<br>of the occipital foramen |              | Inflected postgenae, but<br>continuing as a ridge to<br>either side of the occip-<br>ital foramen              |                                             | Inflected postgenae as<br>in <u>Chalcis</u>                                                                      |                                           |
| DORSAL ARMS                        | Absent                                             |              | Slender rods meeting the<br>face laterad of antennal<br>sockets                                                |                                             | Well developed & con-<br>necting to face at either<br>side of antennal sockets                                   |                                           |
| TENTORIAL BRIDGE                   | Present                                            |              | Posterior arms are present<br>but they do not meet. They<br>are directed forward to<br>appear as a split spine |                                             | Present--spans occipital                                                                                         |                                           |
| SPINE                              | Present                                            |              | See Tentorial Bridge                                                                                           |                                             | Absent                                                                                                           |                                           |
| INFLECTIONS                        | Ocular, clypeogenal<br>epistomal absent            |              | Ocular, epistomal                                                                                              |                                             | Epistomal--none, clypeo-<br>genal--occupied largely by<br>ATP but connecting to both<br>mandibular articulations |                                           |

Fig. 3, A,B, Tremex columba, Siricoidea;  
C,D, Megarhyssa m macrurus, Ichneumonidea;  
E,F, Chalcis microgaster, Chalcidoidea.

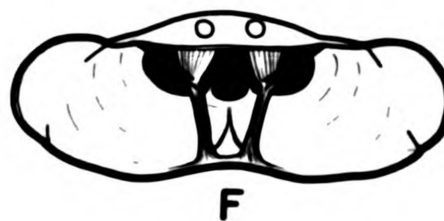
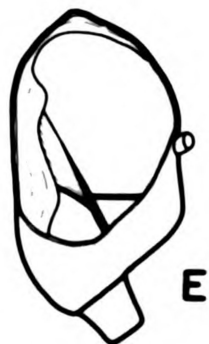
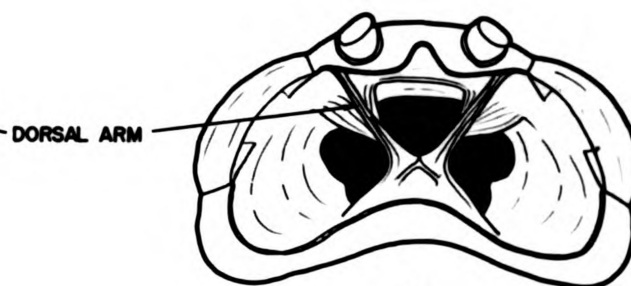
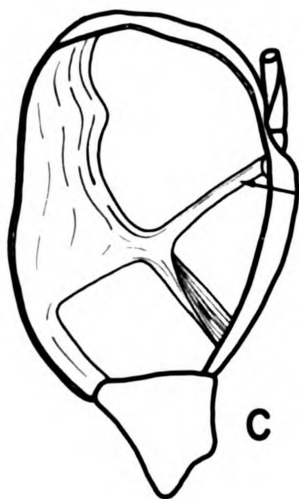
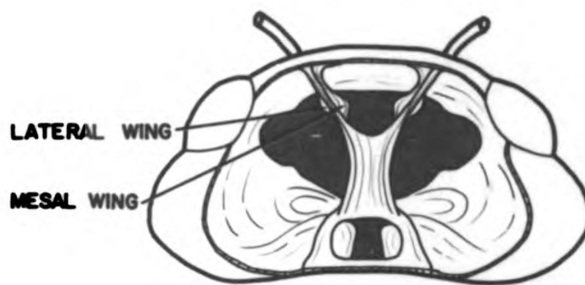
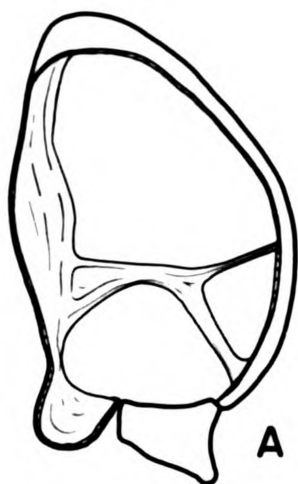


FIG. 3

## CYNIPOIDEA

### Figure 4A and B

The ATP are located near the anterior mandibular articulations. The anterior arms vary from straight, smooth, parallel rods to flattened and twisted structures. They connect posteriorly at either side and/or below the occipital foramen but may also be partly fused with inflected postgenae (Xyalophora). Dorsal arms may be well developed or absent. Posterior arms may be joined to form a tentorial bridge or they may be unjoined as in Diplolepis. If the bridge is complete there is a spine. Inflections are generally weak.

TABLE 8.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE CYNIPOIDEA

|                                 | Cynipidae                                                                       |                                     |                                                                      |
|---------------------------------|---------------------------------------------------------------------------------|-------------------------------------|----------------------------------------------------------------------|
|                                 | <u>Diplolepis rosae</u> (Linnaeus)                                              | <u>Ibalia maculipennis</u> Haldeman | Ibalidae                                                             |
| LOCATION OF THE ATP             | Above anterior mandibular articulation                                          |                                     | Close together and above the anterior mandibular articulations       |
| SHAPE OF THE ANTERIOR ARMS      | Straight, parallel, smooth rods                                                 |                                     | Straight rods flaring laterally in the anterior third                |
| REAR INSERTION OF ANTERIOR ARMS | At base of and at either side of occipital foramen                              |                                     | Below occipital foramen                                              |
| DORSAL ARMS                     | Absent                                                                          |                                     | Insertion lateral of antennal sockets                                |
| TENTORIAL BRIDGE                | Posterior arms present but not joined and projecting forward like a split spine |                                     | Present                                                              |
| SPINE                           | See tentorial bridge                                                            |                                     | Present                                                              |
| INFLECTIONS                     | Ocular, epistomal & clypeogenal short due to low position of ATP                |                                     | Ocular, epistomal weak, clypeogenal short due to low position of ATP |
| OTHER COMMENTS                  | Postgenae inflected                                                             |                                     |                                                                      |

| Figitidae                              |                                                                       | Cynipidae                                               |  |
|----------------------------------------|-----------------------------------------------------------------------|---------------------------------------------------------|--|
| <u>Xyalophora quinquelineata (Say)</u> |                                                                       | <u>Callirhytis seminator (Harris)</u>                   |  |
| LOCATION OF THE<br>ATP                 | Above anterior mandibular articulations<br>--slitlike                 | Above and mesad of anterior mandibular<br>articulations |  |
| SHAPE OF THE<br>ANTERIOR ARMS          | Twisted and flattened dorsoventrally<br>for anterior half             | Straight, smooth, rods                                  |  |
| REAR INSERTION<br>OF ANTERIOR ARMS     | Either side of occipital foramen and<br>partly to inflected postgenal | Laterad of occipital foramen                            |  |
| DORSAL ARMS                            | Strong--connecting to face laterad<br>of antennal sockets             | Absent                                                  |  |
| TENTORIAL BRIDGE                       | Present                                                               | Present                                                 |  |
| SPINE                                  | Present                                                               | Present                                                 |  |
| INFLECTIONS                            | Postgenae inflected                                                   | Ocular, epistomal, clypeogenal--short                   |  |





## PROCTOTRUPOIDEA

### Figure 4C and D

The ATP are found very near the anterior mandibular articulations. The anterior arms are usually not greatly modified and may be united into a single rod posteriorly. Their connection to the back of the head is at either side and/or below the occipital foramen or to inflected postgenae. Pelecinus is exceptional in having the anterior arms nearly entirely fused with deeply inflected postgenae.

The tentorial bridge, if present, bears a spine.

Inflections are generally weak but this deficit is probably compensated for by a relatively thick exoskeleton.

TABLE 9.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE PROCTOTRUPOIDEA

|                                    | Proctotrupidae<br><u>Proctotrupes terminalis</u><br>Ashmead       | Gasteruptionidae<br><u>Rhydinofoenus barnstoni</u><br><u>perplexa</u> (Cresson) | Pelecinidae<br><u>Pelecinus polyturator</u><br>(Drury)               |
|------------------------------------|-------------------------------------------------------------------|---------------------------------------------------------------------------------|----------------------------------------------------------------------|
| LOCATION OF THE<br>ATP             | Immediately above & joining the anterior mandibular articulations | Immediately above anterior mandibular articulations                             | Immediately above anterior mandibular articulations                  |
| SHAPE OF THE<br>ANTERIOR ARMS      | Fused at base and flattened                                       | Long very slender delicate rods                                                 | Short bars                                                           |
| REAR INSERTION<br>OF ANTERIOR ARMS | Below & on either side of occipital foramen                       | Either side of occipital foramen                                                | Inflected postgenae                                                  |
| DORSAL ARMS                        | Strong--inserting laterad of antennal bases                       | Thin & delicate, attaching at antennal bases                                    | Originating from hypostomal bridge, inserting above antennal sockets |
| TENTORIAL BRIDGE                   | Present                                                           | Present                                                                         | Absent                                                               |
| SPINE                              | Short & broad                                                     | Present                                                                         | Absent                                                               |
| INFLECTIONS                        | Ocular--strong, epistomal --weak                                  | Epistomal weak but clearly defined, clypeogenalar ocular                        | Ocular, clypeogenalar epistomal weak                                 |
| OTHER COMMENTS                     | Thick exoskeleton                                                 | Fairly thick exoskeleton                                                        | Exoskeleton thick                                                    |

## BETHYLOIDEA

### Figure 4E and F

The ATP may be at or above the anterior mandibular articulations. The anterior arms are laterally compressed with dorsal wings or somewhat twisted and insert on either side and/or below the occipital foramen. Dorsal arms may be vestigial (Trichrysis) or strong and connecting to the face (Lycogaster). A tentorial bridge is present and bears a spine.

The exceptional feature observed in this group is a ventral arm branching off just below the dorsal arm on the tentorium of Pristocera. The arm extends downward only a short distance. The distal end is free. Pristocera has the most well developed example of this type of ventral structure that has been observed.

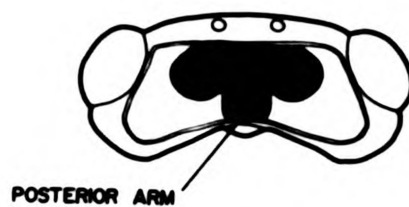
TABLE 10.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE BETHYLOIDEA

|                                    | Chrysididae<br><u>Trichrysis tridens</u><br>(Lepeletier)                 | Bethylidae<br><u>Pristocera armifera</u><br>Say                                            | Trigonalidae<br><u>Lycogaster pullata</u><br>Schuckard             |
|------------------------------------|--------------------------------------------------------------------------|--------------------------------------------------------------------------------------------|--------------------------------------------------------------------|
| LOCATION OF THE<br>ATP             | Dorsal & laterad of antennal sockets (antennae very low in this species) | At antennal sockets-- antennae originate at the anterior mandibular articulations          | Between antennal sockets and the anterior mandibular articulations |
| SHAPE OF THE<br>ANTERIOR ARMS      | Somewhat twisted rods                                                    | Slender rods with large dorsal wings running the entire length                             | Laterally compressed rods                                          |
| REAR INSERTION<br>OF ANTERIOR ARMS | Below & on either side of the occipital foramen                          | Lower lateral edges of occipital foramen                                                   | Either side of occipital foramen                                   |
| DORSAL ARMS                        | Vestigial                                                                | Fused with and barely projecting above the dorsal wings                                    | Laterally compressed rods --nearly as large as anterior arms       |
| TENTORIAL BRIDGE                   | Present                                                                  | Present & partly fused with dorsal wings                                                   | Flattened dorsoventrally                                           |
| SPINE                              | Present                                                                  | Not observed                                                                               | Present                                                            |
| INFLECTIONS                        | Epistomal--absent<br>clypeogenal, ocular                                 | Epistomal--thick,<br>ocular                                                                | Epistomal, clypeogenal--absent, ocular                             |
| OTHER COMMENTS                     |                                                                          | A ventral arm projects downward just below the origin of the dorsal arm, exoskeleton thick |                                                                    |

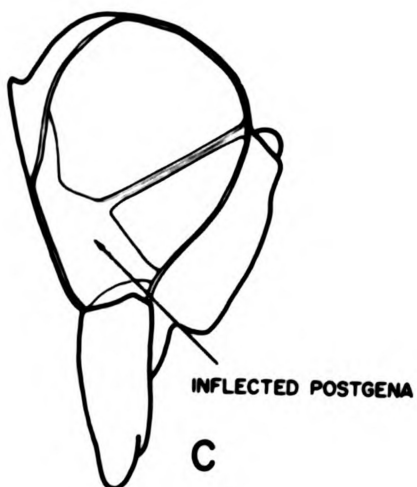
**Fig. 4, A,B, Diplolepis rosae, Cynipoidea;**  
**C,D, Pelecinus polyturator, Proctotrupeidea;**  
**E,F, Trichrysis tridens, Bethyloidea.**



A



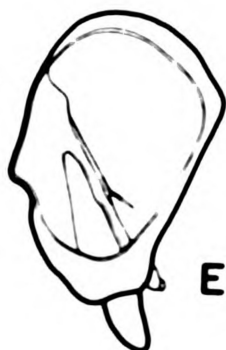
B



C



D



E



F

FIG. 4

## SCOLIOIDEA

### Figure 5A and B

The anterior arms may be a stout rod with mesal wings (Campsomeris) or laterally or dorsoventrally compressed. The ATP are either at or above the anterior mandibular articulations. If the latter is the case the clypeogenal suture is inflected. Posterior arms meet the back of the head at either side of the occipital foramen. Dorsal arms are often absent and if present they do not reach the face.

The tentorial bridge differs from most other Hymenoptera in that it is usually a broad plate rather than a thin rod. A spine is present. Inflections are generally well developed and the lower face is additionally reinforced as the mandibles are set in separate sockets.



TABLE 11.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE SCOLIOIDEA

|                                    | Mutillidae<br><u>Dasymutilla</u> <u>O.</u><br><u>occidentalis</u><br>(Linnaeus)            | Tiphiidae<br><u>Myzinum</u> <u>quinquecinctum</u><br>(Fabricius)            | Scoliidae<br><u>Campsomeris</u> <u>quadrinaculata</u><br>(Fabricius) |
|------------------------------------|--------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------|----------------------------------------------------------------------|
| LOCATION OF THE<br>ATP             | Laterad of the antennal<br>sockets & mesad of the<br>anterior mandibular<br>articulations  | Laterad of antennal<br>sockets & above anterior<br>mandibular articulations | Below antennal base &<br>above anterior mandibular<br>articulation   |
| SHAPE OF THE<br>ANTERIOR ARMS      | Dorsoventrally flattened,<br>stout                                                         | Laterally compressed but<br>with median rod                                 | Stout rods with large<br>mesal wing on ventral<br>margin             |
| REAR INSERTION<br>OF ANTERIOR ARMS | Either side of the<br>occipital foramen                                                    | Either side of occipital<br>foramen                                         | Either side of occipital<br>foramen                                  |
| DORSAL ARMS                        | Degenerate                                                                                 | Absent                                                                      | Absent                                                               |
| TENTORIAL BRIDGE                   | Present as a triangular<br>plate with apex anterior                                        | Present                                                                     | Broad, pointed anteriorly                                            |
| SPINE                              | Present at apex of<br>tentorial bridge                                                     | Present                                                                     | Downward pointing                                                    |
| INFLECTIONS                        | Clypeogenal, ocular, epi-<br>stomal absent as antennae<br>insert between ATP &<br>antennae | Epistomal clypeogenal &<br>ocular                                           | Ocular, epistomal, &<br>clypeogenal inflections<br>largely lacking   |
| OTHER COMMENTS                     | Thick exoskeleton,<br>mandibular sockets<br>separate                                       | Mandibular sockets<br>separate                                              | Very thick exoskeleton,<br>mandibular sockets<br>separate            |

## FORMICOIDEA

### Figure 5C and D

More structural uniformity was observed in the ants than in any other superfamily. Five species in addition to Camponotus (see Table 12) were dissected and their internal head structure was found to be remarkably similar. The species examined were Lasius neoniger En., Formica fusca L., Atta cephalotes (L.), Monomoron pharaonis (Linnaeus) and Ponera coarctata pennsylvanica (Buckl.).

Relatively slender anterior arms bearing narrow wings dorsally span the length of the head from either side of the occipital foramen to the anterior mandibular articulations. The anterior arms are joined near the occipital foramen by the tentorial bridge which bears a spine. Dorsal arms were not observed in any of the specimens examined.

The outstanding feature of the internal head skeleton of the ants, not observed in the other Hymenoptera, is a deeply inflected gular suture. This longitudinal support probably adds much to the overall strength of the head capsule.

TABLE 12.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE FORMICOIDEA

| <div>Formicidae</div> <div><u>Camponotus pennsylvanicus</u> DeGeer</div> |                                                               |
|--------------------------------------------------------------------------|---------------------------------------------------------------|
| LOCATION OF THE ATP                                                      | Immediately above the anterior mandibular articulations       |
| SHAPE OF THE ANTERIOR ARMS                                               | Slender rods with narrow long wings                           |
| REAR INSERTION OF ANTERIOR ARMS                                          | Either side of the occipital foramen                          |
| DORSAL ARMS                                                              | Absent                                                        |
| TENTORIAL BRIDGE                                                         | Short as arms are close together at that point                |
| SPINE                                                                    | Long and very slender                                         |
| INFLECTIONS                                                              | Eyes small but with strong inflections, gular deep, epistomal |

## VESPOIDEA

### Figure 5E and F

The internal supporting structures in the head of the Vespoidea are more numerous and more elaborately developed than most Hymenoptera.

The anterior arms are roughly the shape of a broad, flat ribbon which has been twisted 180 degrees. They meet the face at the anterior tentorial pits which are long and slitlike and occupy most of the clypeogenal suture and part of the epistomal suture. The anterior arms extend diagonally upward from the ATP to meet the back of the head on either side of the occipital foramen.

Extending mesally and laterally along much of the length of the anterior arms are flattened wings which serve as enlarged areas for muscle attachment.

Dorsally, and near the occipital foramen, the anterior arms give rise to dorsal arms. In Vespula and Arachnophroctonus these arms are very weak and delicate and do not reach the region of the antennal sockets. Dorsal arms are absent in Hypodynerus.

The posterior arms extend upward and mesally and cross the occipital foramen to form the tentorial bridge. A spine extends anteriorly and downwardly from the center of the bridge.

The epistomal suture, where it is congruent with the anterior arms, is inflected. The clypeogenal suture is strongly inflected and

connects the tentorium to the anterior mandibular articulation. In Vespula, a unique sclerotized bar, the strengthening inflection to the posterior mandibular articulation, originates at the lower end of the facial insertion of the anterior arms and connects to the tentorium at the posterior mandibular articulation. Strengthening inflections are also found along the malar suture as well as the lower, lateral edges of the head capsule. The eyes are surrounded with a deep ocular inflection as they are in most Hymenoptera.

TABLE 13.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE VESPOIDEA

|                                    | Vespidae                                                                                                        |  | Vespidae                                                                                                             |  | Pompilidae                                                                   |  |
|------------------------------------|-----------------------------------------------------------------------------------------------------------------|--|----------------------------------------------------------------------------------------------------------------------|--|------------------------------------------------------------------------------|--|
|                                    | <u>Hypodynerus lachesis</u><br>(Lepeletier)                                                                     |  | <u>Vespula maculata</u><br>Linnaeus                                                                                  |  | <u>Arachnophroctonus</u><br><u>marginalis</u> (Banks)                        |  |
| LOCATION OF THE<br>ATP             | Entire length of clypeo-<br>genal suture                                                                        |  | Entire length of clypeo-<br>genal suture                                                                             |  | Horizontal slits above &<br>mesad of the anterior<br>mandibular articulation |  |
| SHAPE OF THE<br>ANTERIOR ARMS      | Broad & laterally com-<br>pressed at the ATP nar-<br>rowing to the middle &<br>expanding again poste-<br>riorly |  | Like <u>H. lachesis</u> except<br>that posterior half has<br>expanded wings mesally                                  |  | Flattened and twisted<br>with small mesal wings in<br>the middle             |  |
| REAR INSERTION OF<br>ANTERIOR ARMS | Fused at base, attaching<br>on lower and lateral mar-<br>gins of occipital foramen                              |  | Very like <u>H. lachesis</u>                                                                                         |  | Either side of occipital<br>foramen                                          |  |
| DORSAL ARMS                        | Absent                                                                                                          |  | Very delicate--threadlike                                                                                            |  | Vestigial                                                                    |  |
| TENTORIAL BRIDGE                   | Highly arched and deli-<br>cate                                                                                 |  | Highly arched--thin                                                                                                  |  | Present                                                                      |  |
| SPINE                              | Very delicate                                                                                                   |  | Present                                                                                                              |  | Very delicate                                                                |  |
| INFLECTIONS                        | Ocular, epistomal, clypeo-<br>genal short                                                                       |  | Ocular, epistomal weak,<br>clypeogenal short,<br>slender bar connects ATP<br>to posterior mandibular<br>articulation |  | Epistomal                                                                    |  |
| OTHER COMMENTS                     | Large eyes & clypeus                                                                                            |  | Large eyes & clypeus                                                                                                 |  |                                                                              |  |

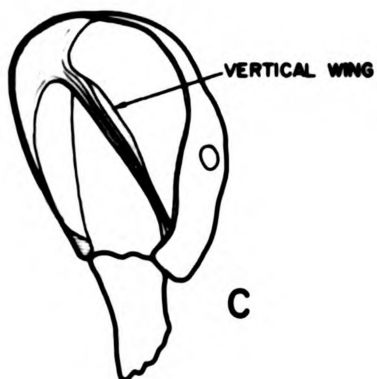
**Fig. 5, A,B, Campsomeris quadrimaculata, Scolioidea;**  
**C,D, Camponotus pennsylvanicus, Formicoidea;**  
**E,F, Vespula maculata, Vespoida.**



A



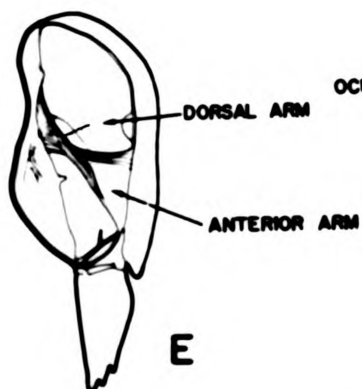
B



C



D



E

OCULAR INFLECTION



F

FIG. 5



## SPHECOIDEA

Figure 6A and B

The tentorium of the Sphecoidea is similar in many respects to the Vespoidea. The anterior arms are variously flattened and twisted. The rear insertion is on either side of and/or below the occipital foramen. Dorsal arms if present appear as vestiges and never extend as far as the face. In every specimen examined the tentorial bridge was present and bore a spine. Facial inflections are usually well developed.

A major difference was noted in the head capsule of Cercerus and Ectemnius. In these species the mandibular sockets were separate from the main mouth opening. Ectemnius is also unusual in that the anterior arms are fused with the mesal ocular inflection. The eyes of Ectemnius occupy much of the face and are very close together. The very deep mesal ocular inflection doubtless adds a great deal of strength to the head capsule.

TABLE 14.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE SPHECOIDEA

|                                    | Sphecidae                                                                                                                                           |                                                                                                  |                                                                                                                 |
|------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------|
|                                    | <u>Chlorion i. ichneumon</u><br>Linnaeus                                                                                                            | <u>Bicyrtes ventralis</u><br>(Say)                                                               | <u>Ectemnius (Lophrocrabro)</u><br><u>singularis</u> (Smith)                                                    |
| LOCATION OF THE<br>ATP             | Long slits running from<br>antennal base to anterior<br>mandibular articulation                                                                     | Similar to <u>Chlorion</u>                                                                       | At lower mesal corner of<br>eye                                                                                 |
| SHAPE OF THE<br>ANTERIOR ARMS      | Laterally compressed and<br>widening anteriorly, thin<br>horizontal sheet connect-<br>ing arms posteriorly &<br>extending forward as mesal<br>wings | Similar to <u>Chlorion</u> ex-<br>cept mesal wings are<br>wider and horizontal<br>sheet narrower | Laterally compressed, con-<br>nected to ocular inflec-<br>tion anteriorly                                       |
| REAR INSERTION<br>OF ANTERIOR ARMS | Below occipital foramen                                                                                                                             | Lower corners of occip-<br>ital foramen                                                          | Either side of occipital<br>foramen                                                                             |
| DORSAL ARMS                        | Vestigial                                                                                                                                           | Absent except for in-<br>dication of bases                                                       | Conspicuously protruding<br>from anterior arms but<br>very short & not reaching<br>face                         |
| TENTORIAL BRIDGE                   | Present                                                                                                                                             | Present                                                                                          | A broad ribbon with a<br>strengthening rod like<br>support extending mesally<br>& anteriorly from both<br>sides |
| SPINE                              | Present                                                                                                                                             | Present                                                                                          | Downward pointing                                                                                               |

## INFLECTIONS

Epistomal--high on face,  
ocular

Epistomal, ocular

Ocular inflection very large on mesal border, epistomal & clypeogenal suture almost lost as ATP & antennae are crowded to the bottom of the face by the eyes

## OTHER COMMENTS

Mandibular sockets separate

---

TABLE 15.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE SPHECOIDEA

|                                 | Sphecidae                                                                                                |                                                                                                                                             |
|---------------------------------|----------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
|                                 | <u>Philanthus politus</u> Say                                                                            | <u>Oxybelus emarginatus</u> Say                                                                                                             |
| LOCATION OF THE ATP             | Mesad and above anterior mandibular articulation slitlike & at $45^{\circ}$ < .<br>Outer ends lower most | Above anterior mandibular articulations                                                                                                     |
| SHAPE OF THE ANTERIOR ARMS      | Laterally compressed & with dorsal lobe anteriorly, more rod like posteriorly                            | Twisted, laterally compressed posteriorly, dorsoventrally compressed anteriorly                                                             |
| REAR INSERTION OF ANTERIOR ARMS | Either side of occipital foramen                                                                         | Either side of occipital foramen                                                                                                            |
| DORSAL ARMS                     | Barely perceptible vestiges extending from bases on dorsal side of anterior arms                         | Vestigial--extending as weak rods 1/3 of way to face                                                                                        |
| TENTORIAL BRIDGE                | Present                                                                                                  | Present                                                                                                                                     |
| SPINE                           | Very delicate--downward pointing                                                                         | Small                                                                                                                                       |
| INFLECTIONS                     | Ocular & epistomal                                                                                       | Ocular--very large on mesal side, epistomal connects ATP & antennae in a straight line, exoskeleton thickened in area of clypeogenal suture |

|                                    | Sphecidae                                                                                                                            |                                                                    |
|------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------|
|                                    | <u>Cercerus nigrescens</u> Smith                                                                                                     | <u>Tachytes distans</u> Smith                                      |
| LOCATION OF THE<br>ATP             | A horizontal line which extends mesally from the anterior mandibular articulation                                                    | At 45° < between antennal base & anterior mandibular articulations |
| SHAPE OF THE<br>ANTERIOR ARMS      | Complex--large mesal wings--dorsoventrally flattened anteriorly, vertically compressed posteriorly, connected to inflected postgenae | Variously twisted & flattened                                      |
| REAR INSERTION<br>OF ANTERIOR ARMS | Either side of occipital foramen & also to hypostomal bridge                                                                         | Either side & below occipital foramen                              |
| DORSAL ARMS                        | Absent                                                                                                                               | Absent                                                             |
| TENTORIAL BRIDGE                   | Present                                                                                                                              | Present                                                            |
| SPINE                              | Delicate--downward pointing                                                                                                          | Present                                                            |
| INFLECTIONS                        | Epistomal--fairly strong, ocular                                                                                                     | Epistomal, ocular                                                  |
| OTHER COMMENTS                     | 3 openings at bottom of head capsule                                                                                                 |                                                                    |

## APOIDEA

### Figure 6C and D

In all the bees examined the anterior tentorial pits are connected to the anterior mandibular articulations by inflected clypeo-genal sutures. The anterior arms vary from relatively unmodified rods to flattened or twisted bands. Often they are fused for a large part of their length with inflected postgenae. The anterior arms meet the back of the head on either side and below the occipital foramen.

Dorsal arms are often present but only as vestiges that do not meet the face. The posterior arms join to form a bridge and a spine is always present. Most inflections are well developed and the mandibular sockets may be nearly separate due to deeply inflected postgenae.

TABLE 16.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE APOIDEA

|                                 | Andrenidae                                 | Halictidae                                          | Halictidae                                                            |
|---------------------------------|--------------------------------------------|-----------------------------------------------------|-----------------------------------------------------------------------|
|                                 | <u>Calliopsis andreniformis</u>            | <u>Dialictus admirandum</u>                         | <u>Nomia heteropoda</u>                                               |
|                                 | Smith                                      | Sandhouse                                           | (Say)                                                                 |
| LOCATION OF THE ATP             | Laterad and slightly below antennal socket | Between antennal bases & mandibular opening         | Junction of clypeogenal epistomal & frontogenal sutures               |
| SHAPE OF THE ANTERIOR ARMS      | Laterally compressed rods                  | Variouly flattened & fused with inflected postgenae | Fused with postgenal inflection                                       |
| REAR INSERTION OF ANTERIOR ARMS | Either side & below occipital foramen      | Either side of occipital foramen                    | Either side of occipital foramen                                      |
| DORSAL ARMS                     | Absent                                     | Absent                                              | Vestigial                                                             |
| TENTORIAL BRIDGE                | Present                                    | Thin & delicate                                     | Present--thin                                                         |
| SPINE                           | Present                                    | Thin & delicate                                     | Present                                                               |
| INFLECTIONS                     | Ocular, postgenal, clypeogenal & epistomal | Postgenal, clypeogenal                              | Epistomal, clypeogenal, ocular frontogenal met by inflected postgenae |
| OTHER COMMENTS                  | Mandibular sockets separate                | Mandibular sockets separate                         | Mandibular sockets nearly enclosed                                    |

TABLE 17.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE APOIDEA

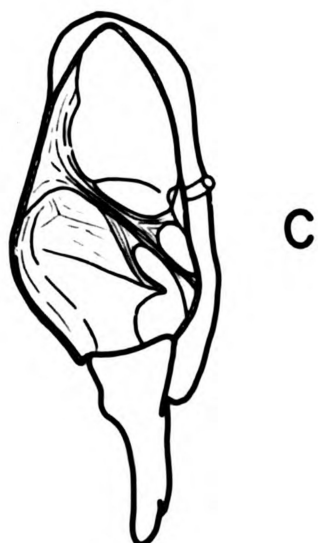
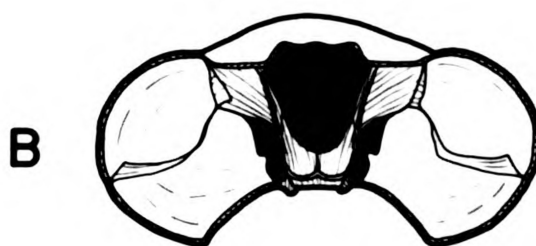
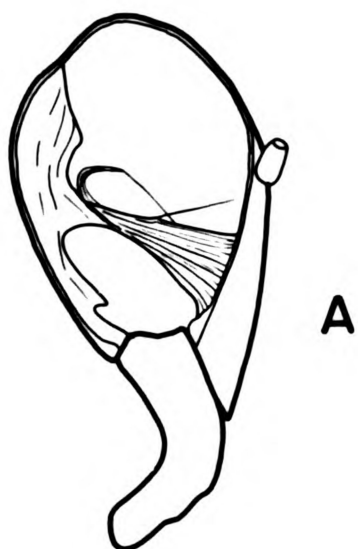
|                                    | Colletidae                                                                           |                | Colletidae                                                        |                       | Andrenidae                            |                                                                           |
|------------------------------------|--------------------------------------------------------------------------------------|----------------|-------------------------------------------------------------------|-----------------------|---------------------------------------|---------------------------------------------------------------------------|
|                                    | <u>Colletes simulans</u><br>Patton                                                   | <u>armatus</u> | <u>Hylaeus modestus</u><br>Say                                    | <u>As in Colletes</u> | <u>Andrena helianthi</u><br>Robertson | <u>As in Colletes</u>                                                     |
| LOCATION OF THE<br>ATP             | Between antennal sockets<br>& anterior mandibular<br>articulations. ATP are<br>slits |                |                                                                   |                       |                                       |                                                                           |
| SHAPE OF THE<br>ANTERIOR ARMS      | Variouly twisted &<br>flattened                                                      |                | Flattened rods, laterally<br>compressed near ATP                  |                       |                                       | Where free of postgenal<br>inflections they are later-<br>ally compressed |
| REAR INSERTION<br>OF ANTERIOR ARMS | Either side & below<br>occipital foramen                                             |                | Either side of occipital<br>foramen                               |                       |                                       | Fused for posterior 2/3<br>with postgenal inflections                     |
| DORSAL ARMS                        | Vestigial                                                                            |                | Vestigial                                                         |                       |                                       | Vestigial                                                                 |
| TENTORIAL BRIDGE                   | Slender & delicate                                                                   |                | Present                                                           |                       |                                       | Present                                                                   |
| SPINE                              | Present                                                                              |                | Present                                                           |                       |                                       | Present                                                                   |
| INFLECTIONS                        | Epistomal, clypeogenal<br>& ocular                                                   |                | Ocular, epistomal &<br>clypeogenal, postgenae<br>deeply inflected |                       |                                       | Ocular--epistomal &<br>clypeogenal                                        |
| OTHER COMMENTS                     | Mandibular sockets nearly<br>separate                                                |                |                                                                   |                       |                                       | Mandibular sockets nearly<br>separate                                     |



TABLE 18.--STRUCTURES OF THE INTERNAL HEAD SKELETON OF THE APOIDEA

|                                 | Megachilidae                                                                        |                    | Megachilidae                                          |         | Apidae                                                |          |
|---------------------------------|-------------------------------------------------------------------------------------|--------------------|-------------------------------------------------------|---------|-------------------------------------------------------|----------|
|                                 | <u>Megachile (xanthosarus)</u>                                                      | <u>latinus</u> Say | <u>Heriades carinata</u>                              | Cresson | <u>Apis mellifera</u>                                 | Linnaeus |
| LOCATION OF THE ATP             | Below antennal socket at juncture of clypeogenal epistomal, and frontogenal sutures |                    | As in <u>Megachile</u>                                |         | Above anterior mandibular articulations               |          |
| SHAPE OF THE ANTERIOR ARMS      | Variously flattened                                                                 |                    | Fused for basal half-- variously flattened            |         | Rods                                                  |          |
| REAR INSERTION OF ANTERIOR ARMS | Either side and below occipital foramen. Arms are fused below foramen               |                    | Below & on either side of occipital foramen           |         | Either side of occipital foramen                      |          |
| DORSAL ARMS                     | Very thin, extending to antennal sockets but not attaching                          |                    | As in <u>Megachile</u> but not extending quite as far |         | Very weak--nearly reaching but not connecting to face |          |
| TENTORIAL BRIDGE                | Present                                                                             |                    | Present                                               |         | Present                                               |          |
| SPINE                           | Long & thin                                                                         |                    | Present                                               |         | Present                                               |          |
| INFLECTIONS                     | Ocular, epistomal, clypeogenal, frontogenal, postgenal                              |                    | As in <u>Megachile</u>                                |         | Clypeogenal, epistomal, postgenal                     |          |
| OTHER COMMENTS                  |                                                                                     |                    | Mandibular sockets nearly enclosed                    |         |                                                       |          |

**Fig. 6, A,B, Chlorion 1 ichneumon, Sphecoidea;**  
**C,D, Andrena helianthi, Apoidea.**



**FIG. 6**

## SUMMARY

Structural support of the hymenopteran head capsule may be contributed to by inflected postgenae, separate mandibular sockets, various inflected sutures, and in every case a tentorium. The tentorium is of greatest interest in this regard and is commonly composed of anterior and posterior arms. The anterior arms often bear dorsal arms.

Some interesting differences in the tentorium appear to be associated with phylogenetic relationships. The tentorial bridge is generally better developed in the more advanced Hymenoptera while dorsal arms are best developed in the more primitive groups. The symphyta have in most cases lost the posterior arms which usually form the tentorial bridge in the higher superfamilies. The presence of a spine, protruding from the juncture of the anterior arms suggests that the posterior arms are lacking; they may be fused with the anterior arms. The tentorial bridge does not appear to have great reinforcing value but it is interesting to notice that the protruding spine is especially well developed in those Hymenoptera that have mouth parts well adapted for sucking. The extent of variation of the tentorial bridge is considerable. It is best developed in the Sphecoidea, Vespoidea and Apoidea.

The primitive Hymenoptera while often lacking a tentorial bridge usually have dorsal arms well developed and connected to the

face. All the Symphyta and the four of the more primitive superfamilies of the Apocrita show this feature. None of the scolioids, vespoids, sphecoids, apoidea, and formicoids examined was found to have the dorsal arms attached to the face and in many cases dorsal arms were vestigial or absent. However, elaborate compensatory development is observed in these groups in the anterior arms which are often widely expanded for muscular attachment, fused with inflected postgenae, and attached over considerable distances at the epistomal and/or clypeogenal sutures.

Less complex anterior arms are usually the case in the more primitive Hymenoptera. Their anterior tentorial pits however are often located at or very near the anterior mandibular articulations (Fig. 2C). The separation of the anterior tentorial pits and mandibular articulations common in the higher Hymenoptera creates the need for an auxiliary structure to retain the rigidity against mandibular action that was originally provided more or less directly by the anterior tentorial arms. The author concurs with Bigelow (1954) that this has been accomplished by the development of clypeogenale inflections. These form braces between the tentorial arms and the mandibular articulations. Further bracing is sometimes provided by an inflected epistomal suture and/or by a ridge around the lower rim of the head capsule.

These thickened sclerotized areas combined with the tentorium serve to brace the lower part of the head and allow stresses caused by biting to be transmitted more evenly to other parts of the head. Inflections of this kind are usually most pronounced in Hymenoptera

that have powerful mandibles. Mandibular support is sometimes achieved in other ways. The postgenae may be inflected so deeply that they connect with the face below the tentorium. In some groups--notably the Scolioidea the mandibles are enclosed in separate sockets rather than occupying a large single opening with the other mouthparts.

Enlarged eyes also present a bracing problem especially in the Scolioidea, Vespoidea, and Apoidea. Since the eyes are covered with thinner exoskeletal material they are in a sense a hole in the head capsule. This weakness in the head capsule is compensated for by a circular inflection that supports both the eye and the capsule. Those species that have very large eyes often have very large ocular inflections and in a few cases (Ectemnius for example) the mesal eye inflections are united with the flattened anterior arms of the tentorium for still greater rigidity.

There are many exceptions to the previously described relationships. Similarities in structure often exist between groups that are widely separated by taxonomists. This perhaps is a result of convergent evolution and the functional necessity for rendering support and rigidity and support of the head capsule.

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