

MORPHOLOGY OF THE FACE IN THE HYMENOPTERA

by

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INTRODUCTION

This is a study in comparative animal morphology. The method used is entirely descriptive, and most of the conclusions cannot be tested experimentally. The validity of these conclusions for any particular reader must, therefore, depend upon the degree to which the evidence and reasoning impress him as adequate and logical. To assist the reader in thus assessing the conclusions and suggestions that are presented, I will attempt to outline, as briefly as possible, the point of view from which the study was carried out.

Many insect morphologists have ignored the role of function in evolutionary change, and some have implied that the consideration of function is actually detrimental to morphological work. This study, however, was made on the assumption that most structural changes cannot be adequately understood unless they are considered simultaneously with function.

Very little fossil evidence is available to students of insect morphology, and consequently there is a great gap in our knowledge of the ancestral beginnings of insects. Admirable attempts have been made to fill this gap through studies of existing forms, and some progress has been

achieved. Nevertheless, our knowledge of early ancestral conditions has remained, of necessity, hypothetical and obscure. Most morphological studies have been based on the assumption that primitive conditions are known, or at least on the assumption that, if such and such a condition can be considered primitive, then such and such a series of changes may have taken place. This is understandable, since we must begin somewhere, and the logical point at which to begin is the beginning. This is often a dangerous starting point in insect morphology, however, for the beginnings are usually unknown. The point of view adopted here is that science must proceed from the known toward the unknown, not from the unknown to the known. We know, or can know, the structural conditions in many thousands of insect species, and from these conditions it should be possible, through a comparison of differences within well defined groups, to attain an understanding of the more recent evolutionary changes. When these more recent changes are sufficiently well understood, it may be possible to deduce less recent changes, through which the well defined existing groups originally diverged from a common ancestral stock. Until existing differences are more fully understood, however, it is held that "phylogenetic trees" involving many distantly related groups cannot be inferred on a sound, scientific basis.

For these reasons, the facial structure in the Hymenoptera was studied as it exists today and an attempt was made to draw conclusions from the existing differences. Only two assumptions were made as to conditions probably present in ancestral Hymenoptera. It was assumed that the structure in sawflies has retained more of the ancestral features than has that in most other groups of the order; and that the orthopteroid facial structure, in which the clypeus projects as a free lobe below the ventral edges of the genae, was present in ancestral Hymenoptera. These assumptions are considered valid by virtually all entomologists, and are supported by a large body of evidence, including the scanty fossil evidence that is available. Apart from these assumptions, conclusions were drawn from the structural differences studied.

The possibility that integumental grooves of the insect face may be remnants of primitive intersegmental lines, and the possibility that the facial regions known as the clypeus and frons may each have been derived from a distinct plate, or sclerite, were rejected as valid working hypotheses.

Attention was focussed on differences in the interrelationships between the anterior mandibular articulations, the anterior tentorial pits, and the system of strengthening integumental inflections usually associated with these

structures. The possible adaptive significance of these differences was taken into consideration before conclusions were drawn as to their evolutionary background. The basic principles of that body of modern evolutionary theory known as the mutation-selection theory were assumed to be valid, and an attempt was made to draw conclusions consonant with these principles. An attempt was made to draw conclusions from definite differences rather than from possibly convergent similarities.

It is believed that this study is original in that it is the only comparative study of hymenopteran facial structure, including the entire order, that has so far been carried out from the point of view outlined above. Evidence is presented and discussed to support the conclusion that the currently accepted explanation of the facial structure in bees, wasps, etc., as proposed by Snodgrass (1935), is probably incorrect, and another explanation is presented. Evidence of the appearance of additional cuticular material apparently at a late stage of pupal development, which may be one of the ways in which evolutionary integumental changes are effected in insects, is described and discussed. Similarities in facial structure between groups that are widely separated by taxonomists, and which either represent convergent evolution or unnatural classification, are pointed out. Comparison of the results of this study with those of a similar survey of a

different character complex should be of assistance in improving the existing classification of the higher categories in the Hymenoptera. One hundred and ninety-eight original figures of hymenopterous facial structure are included, and various minor suggestions are made throughout the text, which may prove to be of assistance in further research.

Beyond such claims of originality, however, this study is little more than an application of ideas obtained from the literature, from many fellow entomologists, and particularly from my director of research, Dr. E.M. DuPorte.

REVIEW OF LITERATURE

BACKGROUNDS

In the early days of the nineteenth century, before the publication of Darwin's "Origin of Species", there were two schools of thought in the science of animal morphology. In one of these schools, function was considered to be of primary importance in the study of animal structure; in the other it was relegated to secondary importance. This difference in point of view was paramount in the great controversy between Cuvier and E.Geoffroy St.Hilaire, Cuvier favouring the functional, and Geoffroy the structural points of view.

Our acceptance of the theory of evolution has not transported us into an altogether new realm of morphological thought. Basic pre-Darwinian morphological concepts and attitudes of mind can be traced directly from the days of Cuvier and Geoffroy St.Hilaire to our own contemporaries, as clearly and continuously as the ancestry of the horse can be traced from eohippus to Equus through a series of fossil bones. Like the skeleton of the horse, these morphological

concepts have undergone an evolutionary change; but, also like the horse, they have changed very slowly. No sudden of catastrophic "saltation" can be detected during the early post-Darwinian days. Acceptance of the theory of evolution did not, for example, resolve the old controversy over the relative importance of structure and function. Darwin's almost, but not entirely, new idea of evolution brought, if anything, an added pertinence to the question. As animals evolve, which comes first, structure or function? This question can arouse controversy even today.

The continuity from pre-Darwinian to post-Darwinian students of insect morphology is clear in the following statement of Comstock and Kochi (1902):

"The early entomologists, among whom were Fabricius (1775), Illiger (1800, 1806), Kirby (1802, 1826), Savigny (1816), Straus-Durckheim (1828), Burmeister (1832), Newman (1834), and Newport (1839), laid the foundation of our knowledge of the structure of this skeleton; and it is remarkable, considering the extent of entomological literature, how little has been added in this particular field since the publication of the article 'Insecta' by the last-named writer."

This review must be confined to literature that

bears directly on the morphology of the insect face. However, insofar as the philosophical grounds for certain assumptions are not made sufficiently clear in this literature, a very condensed summary of those pre-Darwinian principles which may possibly be related to the assumptions in question, will be included.

Cuvier insisted that structure and function should be studied simultaneously. Snodgrass (1935) has recommended this approach, but although function has occasionally been considered, it has been considered in a secondary sense, if at all, in the bulk of the literature on the morphology of the insect head.

E.Geoffroy St.Hilaire recognized in the presence of arms, legs, wings, fins, teeth, eyes, lungs, etc., an interrelationship between structure and function. Despite this, however, he studied structure per se, and considered function only in a secondary sense. The extent to which he did this is clear in the following quotation from Russell (1916):

"The best example of Geoffroy's insistence upon the priority of structure to function, and so of his purely morphological attitude, is perhaps his interpretation, already alluded to, of the appendages of the Articulates. The segments of the Articulates are, he says, the equivalents

of the bodies of the vertebrae of higher forms. Now 'from the circumstance that the vertebra is external, it results that the ribs must be so too; and, as it is impossible that organs of such a size can remain passive and absolutely functionless, these great arms, hanging there continually at the disposition of the animal, are pressed into the service of progression, and become its efficient instruments.' The ribs become locomotory appendages."

Geoffroy not only recognized a unity of structural plan in certain large groups of animals, as had Aristotle before him, but he insisted that the same unity of plan was present in all animals. He sought "generalized abstract types" in the hope of discovering the "divine idea" of structural plan in one all-embracing abstract type which would express in itself all existing variations. From his all-embracing concept of unity of plan, he derived a "principle of connections":

"Geoffroy, a synthesist, contended, in accordance with his theory of unity of plan in organic composition, that all animals are formed of the same elements, in the same number, and with the same connections: homologous parts, however they differ in form and size, must remain associated in the same invariable order." (Encyclopedia Britannica, 14th edition, vol. 10, p. 137, 1937).

These principles of Geoffroy's are no longer defended by insect morphologists. They were, however, widely taught and vigorously defended during the first half of the nineteenth century. Their application can be detected in early works in the field of insect morphology, and they were modified, but not discarded, during the rise of the theory of evolution. The generalized abstract type became the ancestral prototype. Something at least similar to the "principle of connections" is involved in the assumption that sclerites presumably present typically on locomotory segments can be traced through the profound changes involved in the fusion of those segments into the solid head capsule of insects.

However this may be, it is certain that the philosophical point of view from which structure is studied in itself, divorced from function, has been handed down, undiluted, from E.Geoffroy St.Hilaire in the early nineteenth century to Ferris (1942), who said:

"Morphology, as a study, has nothing whatsoever to do with function."

This statement may be valid, but since it is not convincingly justified by Ferris, and since it is considered as invalid by the majority of the foremost biological thinkers of our day, it cannot be accepted without question.

MORPHOLOGY OF THE FACE

The early studies which have perhaps had the greatest effect on subsequent morphological work on the insect head were Savigny's (1916, cited in Newport, 1839, Comstock, 1902) comparative study of the insect mouthparts, and Audouin's (1824, cited in Newport, 1839, Comstock, 1902) comparative study of the thorax.

Savigny first suggested that the insect head was a composite structure, and that the mandibles, maxillae and labium were homologous with walking legs. Russell (1916) mentions that Savigny, using the principles of "pure morphology", selected the Orthoptera as most nearly approaching a generalized abstract type in the mouthparts. This is accepted today, except that the type to which modern workers refer is the theoretical ancestor of insects.

Audouin proposed that each thoracic segment in insects is composed of four sub-segments, and that each of these is itself composed of a ring of plates, or sclerites. Many of Audouin's terms are still in use today, and a tendency to think in terms of individual sclerites has persisted from 1824 to Comstock (latest revision, 1948).

The terminology of the regions of the insect head began with the taxonomists of the eighteenth century. Most of these men were not concerned with either developmental or evolutionary morphology, but in their descriptions of species they required terms for head parts. There was considerable lack of uniformity in this terminology during the eighteenth century. Burmeister (1836) was among the first to insist on the importance of establishing a uniform terminology. He chose the term clypeus, first used by Fabricius in 1775, from other terms previously used for that part of the face he described as:

"... that portion which lies above the organs of the mouth; it is bordered laterally by the sides of the head, and extends as far as the eyes."

He defined the frons as "that portion which intervenes between the posterior margin of the clypeus between the eyes, to where the head commences to be flattened above."

The vertex he defined as "the upper flattened portion of the head upon which very generally the simple eyes or ocelli are found."

He defined the genae as "the sides of the head, from the eyes downwards to the mouth."

He included all these structures under the term face, or facies, "the anterior portion of the head above the mouth, and includes the clypeus, the front, and the parts bordering upon the eyes."

These terms have been used since 1836 for the same general regions. The structure of the insect face varies widely in different insects, however, and since Burmeister's terms were arbitrary and topographical, it is often difficult to determine the limits of the various regions. For example, he placed the dorsal limits of the clypeus "as far as the eyes". This unsatisfactory state of affairs has from time to time inspired attempts to define the head regions in a more fundamental, less arbitrary way.

Burmeister thought topographically, in terms of spatial relations of the head regions. He did not associate any of the internal parts of the head with the external parts, and was apparently concerned primarily with the introduction of a uniform terminology that could be used more effectively by taxonomists.

Most later workers continued to think of the facial structures in a topographical sense, but attempts were made, by Burmeister's contemporaries, to find a more fundamental method for distinguishing the head regions.

Savigny, as mentioned above, drew attention to the fact that the head was a composite structure, containing several originally separate body segments. This brought new hope to the perplexing problem of the head regions, since if the originally separate head segments could be traced from their beginnings in the immature stages (not to their beginnings in the ancestral sense, in those pre-Darwinian days), the regions of the head could thus be determined from a sounder scientific basis.

Newport (1839) summarized the point of view, and the state of knowledge, in his time as follows:

"According to the investigations of the most careful observers, Savigny, Audouin, Macleay, Kirby, Carus, Straus-Durckheim, Newman, and others, every segment of the perfect insect is made up of distinct parts, not always separable from each other or developed to the same extent, but existing primarily in all. It is also believed that the head itself is formed of two or more segments, but the exact number which enters into its composition is yet a question. So uncertain are the opinions held upon this subject, that while Burmeister recognizes only two segments, Carus and Audouin believe there are three, Macleay and Newman four, and Straus-Durckheim, even so many as seven. These different conclusions of the most able investigators

appear to have arisen chiefly from too exclusive examinations of the head in perfect insects, without reference to the corresponding parts in the larvae. It is only by comparing the distinctly indicated parts of the head in the perfect insect with similar ones in the larva that we can hope to ascertain the exact number of segments of which it is composed. In the head of the perfect insect there ought to be found some traces of all the segments which exist in the larvae of the same species, and in that of the more perfectly developed larvae that undergo a true metamorphosis, there ought in like manner to be found the rudiments of all the segments in the least perfectly developed."

Thus, by 1839, a considerable amount of work had been done on the insect head. The similarity in point of view between these early workers and the post-Darwinian embryologists and comparative anatomists, is very clear. Both groups thought of the head as a composite structure, composed of originally separate segments. Both groups assumed that these originally separate segments could be found in the immature stages. The only essential difference in point of view is that the evolutionists interpreted the word "original" in an ancestral sense, whereas the Creationists interpreted it in a developmental sense.

Newport (1839) applied the term clypeus to "that broad cover of the anterior surface of the head, bounded posteriorly by the epicranium and anteriorly by the labrum, with which it is freely articulated ... It appears originally to be formed of two portions, which we have called clypeus anterior and posterior, and which are completely united in some families."

This definition is, in some insects, less vague than that of Burmeister. Newport placed the dorsal limits of the clypeus at the epicranium, rather than "as far as the eyes". He defined the epicranium as follows:

"The epicranium is the whole of the posterior and upper surface of the head, bounded posteriorly by the occiput, laterally by the corneae and sides of the gula, and anteriorly by a triangular suture which extends along the median line to the occiput. This triangular suture **is** a marked character in the head of many insects, both in the larva and perfect state, and is of great importance in determining the number of sub-segments." (This triangular suture of Newport's, under the name epicranial suture, was destined to be regarded as a fundamental feature of the insect head for over a century). The clypeus thus found a definite dorsal limitation, in some insects, at a definite integumental suture.

As defined by Newport, the clypeus extends dorsally

from the labrum, over what is now considered as the frons. His clypeus anterior and posterior do not correspond to the anterior and posterior clypeus of some later workers, which are sub-divisions of Newport's clypeus anterior.

Burmeister (1836) and Newport (1839) were apparently the only works of their time that were used widely as texts. Kirby and Spence published, in 1815, an "Introduction to Entomology" which was widely used as an entomology text, as testified by its seventh edition in 1856. This work, however, was concerned primarily with behaviour, and with economic aspects of entomology. The structure of the head was apparently not treated in detail.

In 1869 the first edition of Packard's "Guide to the Study of Insects" was published. This excellent textbook of general entomology was the first in a long series of similar texts, culminating in Comstock (latest revision, 1948), perhaps the most widely used entomology textbook of today. In the ninth edition of Packard's "Guide" (1888) he adopted Audouin's assumption that the "typical" insect body segment is composed of discrete "pieces":

"A segment of a winged six-footed insect (Hexapod) consists typically of eight pieces which we will now examine more leisurely. Figure 12 represents a side-view of the

thorax of the Telea Polyphemus, or Silkworm moth, with the legs and wings removed. Each ring consists primarily of the tergum, the two side-pieces (epimerum and episternum) and the sternum, or breast-plate. But one of these pieces (sternum) remains simple, as in the lower orders. The tergum is divided into four pieces. They were named by Audouin going from before backwards, the praescutum, scutum, scutellum, and postscutellum."

In the section entitled "The Structure of the Head", Packard said:

"After studying the composition of the thorax and abdomen, where the constituent parts of the elemental ring occur in their greatest simplicity, we may attempt to unravel the intricate structure of the head. We are to determine whether it is composed of one, or more, segments, and if several, to ascertain how many, and then to learn what parts of the typical arthromere are most largely developed as compared with the development of similar parts in the thorax and abdomen. In this, perhaps the most difficult problem the entomologist has to deal with, the study of the head of the adult insect alone is only guesswork. We must trace its growth in the embryo."

This is not very different from Newport's statement, published in 1839, and quoted above. Audouin's "elemental

ring" was still present; a lack of faith was expressed in the study of adults; and the typical "arthromere" was assumed to be recognizable in the embryo.

Packard concluded that the "typical" segment is modified in the three body regions as follows:

"In the abdomen the upper (tergal) and under (sternal) surfaces are most equally developed, while the pleural line is reduced to a minimum. In the thorax the pleural region is much more developed, either quite as much, or often more than the upper, or tergal portion, while the sternal is reduced to a minimum. In the head the pleurites form the main bulk of the region, and the sternites are reduced to a minimum."

Unfortunately, these conclusions could not be used to define more fundamentally the arbitrary head regions, and the latter are not mentioned in the ninth edition of Packard's "Guide" (1888).

In a later text, Packard (1898) reviewed contemporary work on the segmentation of the head, and concluded that the head is composed of six primitive segments rather than five, as he had proposed in 1888. In this work he remarked on a correlation between the structure of the head capsule and its function of providing a rigid base for the action of mandibular and other muscles. He also defined the clypeus, as follows:

"The clypeus - This is that part of the head situated in front of the epicranium, and anterior to the eyes, forming the roof of the posterior part of the mouth, and is, as embryology shows, probably a tergal sclerite. It varies greatly in shape and size in the different orders of insects. It is often divided into two parts, the clypeus posterior and clypeus anterior, or which may be designated as the post- and ante-clypeus."

It is clear from Packard's figure of the head of a grasshopper, that his conception of the clypeus in the Orthoptera was exactly the same as the universally accepted conception of today. He called the region above the groove now known as the frontoclypeal suture the epicranium, however, and made no mention of the frons.

In this text, Packard showed a distinct interest in possible correlations between the structure of the head and the functions it performs. This interest in a possible structure-function interaction is particularly evident in his discussion of the "mechanical origin of the limbs". Packard's views on this subject were definitely Lamarckian; he assumed that characters acquired by the individual are inherited by its offspring. This is not surprising, considering that he studied the problem before the re-discovery of Mendel's Laws of Heredity. Darwin before him

had entertained such possibilities, and Lamarck's original theory was essentially reasonable in view of the evidence at his disposal. We now know that experimental evidence for the inheritance of acquired characters is extremely slight, and that function does not actually mould structures, but this knowledge does not entitle us to avoid the problem of explaining the obvious structure-function interrelationship. The early attempts to do so of Lamarck, Darwin, Packard, and others, should be commended.

Comstock and Kochi (1902) made an attempt to solve the problem of the insect head. On the assumption that the "typical" body segment in the primitive ancestors of insects was composed of separate and individual sclerites, as Audouin had proposed from a non-evolutionary point of view, and that these sclerites preserve their individuality despite the profound changes involved in the fusion of the originally separate segments into the solid head capsule, Comstock and Kochi proceeded, without the aid of fossil evidence, to trace these theoretically primitive sclerites through the changes that had taken place during hundreds of millions of years of evolutionary development.

They reviewed the literature on the subject from the earliest days, including the extensive embryological literature on the segmentation of the head that had recently

been published. Their conclusions were apparently drawn primarily from evidence in the literature. Their assumption that the sclerites were originally present was clearly drawn from Audouin, for they say:

"The parts of a thoracic segment that are commonly recognized are those described by Audouin ('24): a ventral part, sternite; two lateral parts, pleurites; and a dorsal part, tergite."

Comstock and Kochi drew many conclusions about the head sclerites. They concluded that the compound eyes are homologous with walking legs, that the clypeus is "the sternite of the intermediate of the three preoral segments, the deutocerebral," etc. Many of their conclusions have been rejected by morphologists and, unfortunately, they did little to make the taxonomic conceptions of the facial regions less arbitrary. As Comstock and Kochi (1902) themselves pointed out:

"In descriptions of insects it is necessary to refer to the different regions of the surface of the head. This has resulted in the establishment of a nomenclature, which, although based on the work of the early insect anatomists, is really of comparatively little morphological value; for but few of the primitive sclerites of the head have remained distinct, and some of them greatly overshadow others in

their development. The result is that in some cases a named area includes several sclerites, while in other cases only a portion of a sclerite is included.

"This nomenclature, however, is sufficient for the needs of describers of species, and will doubtless continue in use."

This statement, very slightly modified, appeared in Comstock (1924), and in the 1940 and the 1948 revisions of this text. Since the latter revision is perhaps the most widely used entomology text of our day, the statement will be quoted as it appears in this revision, in order to show its similarity to the original:

"This terminology is really of comparatively little morphological value; for in some cases a named area includes several sclerites, while in others only a portion of a sclerite is included. This is due to the fact that but few of the primitive sclerites of the head have remained distinct, and some of them greatly overshadow others in their development. The terms used, however, are sufficiently accurate to meet the needs of describers of species, and will doubtless continue in use. It is necessary, therefore, that students of entomology become familiar with them."

It is thus still assumed that sclerites retain their individuality through most profound functional changes, for

although the sclerites of the head cannot be distinguished, they are still assumed to be present, as sclerites. This is somewhat reminiscent of E.Geoffroy St.Hilaire's "principle of connections".

Comstock and Kochi (1902) discussed the terminology of the facial regions at some length. They attempted to make this terminology more definite, as follows:

"The best landmark from which to start for this purpose is the epicranial suture, the inverted Y-shaped suture on the dorsal part of the head, in the more generalized insects. Behind the arms of this Y there is a series of paired sclerites, which meet on the middle line of the dorsal wall of the head, the line of union being the stem of the Y; and between the arms of the Y and the mouth there are typically three single sclerites. It is with these unpaired sclerites that we will begin our definitions of the areas of the head.

"The front (frons, Kirby; clypeus posterior, Newport). - The unpaired sclerite between the arms of the epicranial suture.

"The Clypeus (clypeus, Fabricius; chaperon, Straus-Durckheim; clypeus anterior, Newport). - The intermediate of the three unpaired sclerites between the epicranial suture and the mouth. To this part one condyle (the ventral) of the mandible articulates.

"Although the clypeus almost always appears to be a single sclerite, except when divided transversely as indicated below, it really consists of a transverse row of three sclerites, - one on the median line and one on each side articulating with the mandible. The median sclerite may be designated the clypeus proper, and each lateral sclerite, the antecoxal piece of the mandible. Usually there are no indications of the sutures separating the clypeus proper from the antecoxal pieces; but in some insects they are distinct. In the larva of *Corydalis* the antecoxal pieces are not only distinct but are quite large.

"In some insects the clypeus is completely or partly divided by a transverse suture into two parts. These may be designated as the first clypeus and the second clypeus, respectively; the first clypeus being the part next the front and the second clypeus being that next the labrum.

"There is a great lack of uniformity in the application of the term clypeus, arising from the fact that many writers apply it to the entire area between the epicranial suture and the labrum; either overlooking the fact that the part here designated as the front is a distinct sclerite, or, following Newport, terming it the clypeus posterior. But as the front and the clypeus (in the more restricted sense) pertain to different segments of the head, it is desirable to use

distinct names for them; and as the names proposed by Newport are morphologically incorrect, the so-called clypeus posterior being in front of the so-called clypeus anterior, as will be shown later, it is doubtless better to use the older term frons, or front, for the sclerite next the epicranial suture, and to restrict the term clypeus to the part termed clypeus anterior by Newport."

Comstock and Kochi restricted the term epicranium to "all the paired sclerites of the skull, and sometimes also the front." Although the frons may apparently be included in the epicranium, the latter was restricted to the regions dorsal to the Y-shaped epicranial suture, in those insects that possess such a suture, and the term epicranium was used in a more restricted sense than it was by Packard (1898).

The vertex was defined as "the dorsal portion of the epicranium, or, more specifically, that portion which is next the front and between the compound eyes."

The genae were defined as "the lateral portions of the epicranium." This, in effect, corresponds to Burmeister's (1836) definition of the genae as the portions of the face below the compound eyes, although it is somewhat more vague.

These definitions of the facial regions have been handed down, almost verbatim, to Comstock's well known

textbook (latest revision, 1948).

Perhaps the most recent general textbook of entomology is that of Borror and DeLong (1954). They define the head regions in much the same way as had Packard (1898) and Comstock (1902, 1948) before them:

"The head is divided by sutures into a number of more or less distinct sclerites; these vary somewhat in different insects, and the following account applies to a generalized insect. Typically, there is a suture shaped like an inverted Y extending along the dorsal and anterior part of the head; just above the median ocellus this suture forks to form two diverging sutures, which extend down the anterior side of the head. The dorsal part of this suture (the base of the Y) is called the coronal suture, and the two anterior branches are called the frontal sutures. At the lower end of the frontal sutures is a transverse suture which extends across the face just above the base of the mouthparts; the medial or anterior part of this suture is called the epistomal suture, and the lateral portions, above the mandibles and maxillae, the subgenal sutures. The anterior sclerite of the head, between the frontal and epistomal sutures and including the median ocellus, is the frons. The area above the frons on the dorsal part of the head between the compound eyes is the vertex. The area on each side of the head, laterad of the frontal sutures and between the compound eye and the

subgenal suture, is the gena. Below the epistomal suture is a flaplike structure composed of two sclerites; the upper sclerite is the clypeus, and the lower one is the labrum or upper lip.

"There is considerable variation in the development of the head sutures and the shape of the head sclerites. The frontal sutures are often short or poorly developed, and there may be sutures extending ventrally from the compound eyes or the antennae. There are usually sutures closely paralleling the compound eyes, and surrounding the bases of the antennae. The head sclerites posterior to the occipital suture are often on the posterior surface of the head."

Borrer and DeLong speak of the head sclerites as they appear in existing insects, and do not imply, with Comstock and Kochi (1902) and Comstock (latest revision, 1948) that the existing head sclerites are composed of more primitive component sclerites which can no longer be distinguished. They do speak of the head capsule, however, as being composed of "more or less distinct sclerites", rather than as a solid structure in which the "sutures", and the resulting sclerites between them, appear secondarily. Borrer and DeLong may possibly regard the head in this light, but the student gets

the impression that the head sclerites in insects form the sutures, somewhat as the dermal bones of the vertebrate skull form the sutures in the vertebrate skull. The unqualified use of the term suture implies such a condition. The possibility that many of the "sutures" of the insect head are merely secondary grooves in an otherwise homogeneous sclerotized integument is not emphasized.

It has been mentioned that a considerable amount of embryological and comparative work had been done on the segmentation of the insect head during the latter part of the nineteenth century. This review is not directly concerned with either insect embryology, or with the segmental composition of the insect head. This study was done entirely from a comparative point of view, and the evolutionary history that is considered is relatively recent, beginning long after the insect head had become a solid, composite structure. However, some mention must be made of the extent and the net results of the work done on the segmentation of the head.

As already mentioned, a considerable amount of work had been done on this problem in pre-Darwinian days. The Creationists had seriously studied the problem, from a developmental point of view, in the early nineteenth century. During the latter part of the nineteenth and the early

twentieth centuries T.H.Huxley, Butschli, Wheeler, Claypole, Uzel, Folsom, Comstock, Kochi, Riley, Janet, Philiptschenko, Heymons, Verhoeff, Berlese, Hanstrom, Hansen, Snodgrass, Ferris, and others, studied the problem. The number of segments proposed by these workers varied even more than those proposed by the Creationists. Janet, at one time, even proposed nine. At the turn of the present century, however, there was more or less widespread agreement that the number of original head segments was six. This number is cited in the Encyclopedia Americana (Canadian Edition, vol.15, p.161, 1952). Snodgrass (1928), however, threw grave doubts on this conclusion. He presented at least equally convincing evidence that the pregnathal region of the head was probably not metameric in origin. This view is expressed in his "Principles" (1935). Thus, the net result of all this work is that we are in almost as much doubt as ever as to the original number of head segments. It is certain that the insect mandibles, maxillae and labium represent the appendages of originally separate body segments. This much was implied by Savigny in 1816, and it is all we know today with any certainty, after more than a century of admirable work by capable scientists.

Although the essential features of the conclusions of Comstock and Kochi (1902) have been handed down to the

1948 revision of Comstock's "Introduction to Entomology", most of their conclusions have been discarded long ago. The first serious criticism of their work was published by Riley (1904), who had made an admirable embryological study of the head of the cockroach Blatta germanica. Like Comstock and Kochi, Riley also carefully reviewed the literature. With regard to the extreme individuality of primitive sclerites that was assumed by Comstock and Kochi, he concluded that:

"... so intimate a relation between primary segmentation and the sclerites cannot be shown."

Riley maintained that, since we cannot distinguish the original segments themselves in the existing head capsule, we are even less able to distinguish the individual sclerites of those segments. He made an attempt to determine the present limits of the original segments, but not of their component sclerites, in the head of Blatta, and drew several conclusions which have not been generally accepted.

The importance of Riley's work for the purposes of this review lies in the fact that he made slightly less sweeping assumptions than had Comstock and Kochi (1902), but also in the fact that he did assume that segmental sclerites could be traced from their ancient to their present locations on the insect body without the aid of fossil evidence. The

essential difference between his point of view and that of Comstock and Kochi is thus slight.

Yuasa (1920) defined the facial regions more or less as they had been defined previously. He introduced the term frontogenal suture, which he had apparently learned from his teacher, MacGillivray. He applied this term to certain integumental grooves present in some insects, and considered them to be extensions of the epicranial arms, i.e. the arms of the epicranial suture now known as frontal sutures. Yuasa proposed that the anterior tentorial pits (pretentorina) be used as "landmarks" to denote the dorsal (posterior) limits of the clypeus. His approach to the morphology of the face is purely topographical. He said, for example, that:

"The frontogenal sutures are considered as the cephalic portions of the epicranial arms which have been isolated from the caudal portions by the encroachment of the antacoriae and lateral ocelli." (The term antacoriae denotes the membranes connecting the antennae with the head). He did not attempt to correlate structural changes within the head with those of the exterior, and did not attempt to explain, for example, why the antacoriae and lateral ocelli may have encroached on the epicranial arms and thus created the frontogenal sutures.

MacGillivray (1923) defined the frontal, genal and clypeal regions of the face in much the same way as had his

predecessors. He defined the clypeus as follows:

"The area borne at the cephalic margin of the front is the clypeus. It consists typically of four sclerites, two that are unpaired, the postclypeus and preclypeus, and one that is paired, the clypealia. In the great majority of insects, adults at least, these four sclerites are fused into a single piece or the sutures are only in part indicated and the entire area in such cases is designated as the clypeus. This fused area is also known as the chaperon, clypeus anterior, epistoma, ansus, and prelabrum."

This definition, like those before it, does little to fix the dorsal limits of the clypeus in those insects in which the "cephalic margin of the front" is difficult to determine.

Crampton (1921) attempted to clarify the situation. Following Riley (1904) he concluded that "the definitive sclerites can afford us little or no evidence as to the primary segmentation of the insect". He made the not very original suggestion that the best way to study the insect head was by way of "landmarks". He recognized the fact that sutures or grooves present in lower insects may be obliterated and replaced in higher forms by new grooves or sutures that mask the original conditions. In such cases he said that "it is often impossible to do more than state that the secondarily formed region is equivalent to the original one only in a general way."

He then defined the clypeus as that region of the head between the labral suture (separating the clypeus and labrum) and the clypeal suture (separating the clypeus and frons). He went on to point out that the clypeal suture is not present in all insects, and that when it is not "the posterior limits of the clypeus are demarked by a line drawn across from the base of one mandible to the base of the other mandible, since the clypeal suture, when present, corresponds in general to such a line connecting the bases of the mandibles, which are therefore the chief 'landmarks' delimiting the posterior extent of the clypeus." He thus first selected the clypeal (frontoclypeal) suture as the posterior limit, then pointed out that this is an unreliable "landmark", and turned to the mandibular bases. But though he called these the chief landmarks, he did so because "the clypeal suture, when present, corresponds in general to such a line connecting the mandibles."

Crampton did not, at this time, associate the anterior tentorial pits with the clypeus. His approach to the problem was entirely topographical.

In a later paper, Crampton (1925) recognized the anterior tentorial pits (frontal pits) as the dorsal (posterior) limits of the clypeus, following Yuasa (1920).

Snodgrass (1928) brought out what is unquestionably the best morphological work ever published on the insect head. His review of the literature on the segmentation of the head is thorough and masterful. His conclusions on segmentation are drawn from many sources, and are made only after careful and logical consideration. His proposal that the pregnathal region, or at least most of this region, is probably not metameric in origin is logical and convincing.

Snodgrass not only attempted to explain what changes may have taken place, but also the possible reasons for these changes. He assumed that function has played an important role in the formation of the head:

"The functional differences at the two poles of the body, however, determine the course of the subsequent development of physical characters."

He did not merely assume that separate body segments existed, in a "typical" form, but attempted to explain the possible underlying causes for their appearance, and hence to understand them. He said:

"Since so many other essential features in the body structure of animals are connected with the mode of locomotion, the writer holds as most probable the idea that segmentation also had its beginning as an adaptation to a specific kind of movement. The creeping, worm-like

ancestors of the annelids and arthropods certainly at an early period must have developed a contractile tissue in their mesoderm bands - that they did so is attested by the early development of a central nervous system consisting of motor neurons, following the lines of the later established ventral longitudinal muscle bands. It is, then, clear that a breaking up of the contractile tissue into short lengths would give a greater efficiency of movement, with the possibility of more variety of action, and that, with the differentiation of true muscle fibers, the attachment of the ends of the fibers to the ectoderm would carry the metamerism into the body wall."

This possibility is so logical, and is so consistent with both the mass of evidence on evolutionary change, and with the most widely accepted evolutionary theories of the present day, that it cannot reasonably be rejected. Regarded in this light, the body segments of insects and their ancestors are more than topographical regions of the body. In the mind of the observer, they become definite organs that perform the vital function of providing the animal with a means of moving. The segments are thus no longer regarded as merely structures, but structures that move. Attention is drawn to the fact that they were present on living animals, and that they played an important role

in keeping those animals alive.

It is perhaps due to Snodgrass' awareness of the importance of motion to animals that he placed so much emphasis on the muscular system. He has painstakingly described the origin and insertion of virtually every muscle in the bodies of certain generalized insects, and this information should prove to be very useful to future morphologists.

Snodgrass may have carried the assumption that muscles retain their primitive connections somewhat too far, since DuPorte (1946) points out that:

"Discrete muscles, such as found in insects and other higher animals, are among the most inconstant structures in the body. They shift their positions, especially as to origins, to meet changed needs, new muscles arise to meet new needs and muscles no longer needed atrophy."

Snodgrass (1928) himself admits this possibility: "... it must be admitted that muscles can undergo extensive migrations."

However this may be, the clear recognition of an intimate interrelationship between structure and function that is implied in both Snodgrass' and DuPorte's points of view, is a distinct advance over the purely topographical

approach of Comstock, MacGillivray, Crampton, and others.

Snodgrass (1928) not only defined the facial regions in a generalized insect, as had many others before him, but went on to discuss modifications in this region, and attempted to explain them.

He defines the frontoclypeal or epistomal suture in the grasshopper Dissosteira carolina as "a deep groove forming internally a strong epistomal ridge, from the lateral parts of which arise the tentorial arms."

He defines the clypeus as follows:

"The clypeus is a distinct area of the prostomial region, and is to be identified by the origin of the dilator muscles of the mouth and buccal cavity on its inner wall. It is almost always in biting insects separated from the labrum by a flexible suture, and it is demarked from the frons whenever the epistomal suture is present."

Snodgrass points out that: "The principle departure from the typical structure in the prostomial sclerites arises from variations in the development or in the position of the epistomal suture, and from a partial or complete suppression of the frontal sutures.

"The epistomal suture is the external groove formed incidentally to the development of an internal transverse

ridge across the prostomial area. Since this ridge in generalized insects lies approximately between the anterior articulations of the mandibles, its primitive position suggests that it was developed to strengthen the lower edge of the face between the mandibular bases. The epistomal ridge itself is a continuation of the subgenal ridges, and the epistomal suture is, therefore, continuous with the subgenal sutures."

He goes on to say: "In some of the more generalized insects, the epistomal ridge and its suture are lacking, as in the roach, and there is then present only a single fronto-clypeal sclerite. In such cases, the tentorial pits lie in the anterior extremities of the subgenal sutures, above the anterior articulations of the mandibles. Where an epistomal ridge unites the subgenal ridges across the face, separating the clypeus from the frons, the tentorial pits may retain their positions above the mandibular articulations, but more commonly they move into the epistomal suture. In any case, the tentorial pits identify the epistomal suture, when this suture is present. The mandibular articulations are carried by the ventral margin of the epicranium and are not true landmarks of the epistomal suture, as has been pointed out by Yuasa (1920), and by Crampton (1925).

"As long as the epistomal suture maintains its direct course across the face, no complications arise; but the suture is frequently arched upward, and this shift in the position of the suture extends the clypeus into the facial region above the bases of the mandibles, and reduces the area of the frons. A modification of this kind has taken place in the Hymenoptera. ... In the adult of Apis ... the epistomal suture, identified by the tentorial pits, is arched upward almost to the bases of the antennae, and the frontal sutures are obsolete."

Snodgrass noted a close relationship between the anterior tentorial pits and the anterior mandibular articulations, but stressed the need for strength between the mandibular bases rather than between the tentorial pits. Although he considered certain functional aspects of the problem, Snodgrass still spoke in terms of "landmarks", and thus more or less fell back on the old topographical approach. He made no mention of the fact that, since a large number of the head muscles are attached to the anterior tentorial arms, a need for a strengthening ridge of the face should exist between the tentorial pits. He did not mention whether or not the orientation of the anterior tentorial arms within the head suggests that a dorsal shift of the tentorial pits has taken place.

This explanation of the facial modification present in many species of Hymenoptera was published in Snodgrass' "Principles of Morphology" (1935), and is still widely taught.

Ferris (1942) brought forth a daring theory on the segmentation of the insect head, based on a comparative study of integumental grooves. He rejected the tendency of Snodgrass and DuPorte to consider function while studying structure, and returned to the completely topographical approach. In this regard, he says:

"Morphology, as a study, has nothing whatever to do with function. It is not the business of the morphologist - as a morphologist - to enquire into the question of what the structure is used for. The comparative morphologist is enquiring into the changes in structure throughout a series of forms as those changes reflect the genetic capacities of the organisms concerned. This is in direct contradiction to the views of Snodgrass (1935), who has remarked that 'Morphology must be intimate with function, since it must see forms as plastic physical adaptations to the work to be performed.' The prevalent idea concerning the great 'plasticity' of insect structure, carrying the implication that structure responds readily to and changes with the demands of the environment and of functional need and that consequently any new appearance may be dismissed

as merely an 'adaptation' is from the point of view adopted by the present writer quite erroneous and misleading. It represents a but thinly veiled Lamarckianism that finds no support in the biological evidence that is now available to us."

It is difficult to understand how Ferris would explain the immense diversity in animal structure, and the adaptation of every animal to its environment.

Dobzhansky (1951), Simpson (1953), Mayr (1942), Huxley (1940, 1942), and many others among the foremost biologists of our day, recognize an intimate interrelationship between the effects of heredity and environment, structure and function, in evolutionary change. This viewpoint is clearly expressed by Simpson (1953):

"The preceding discussions have led to the conclusion that most evolution involves adaptation. Absolutely or relatively inadaptive phases occur and organisms develop nonadaptive and inadaptive characteristics, but over-all patterns of evolution are predominantly adaptive and adaptation has been seen to be the usual orienting relationship even in minor details of the pattern. Adaptation, itself, evolves. We do not simply have on one side a discrete something called 'environment' with a neatly fixed set of prospective functions packaged into niches and on the other

side discrete things called 'organisms' or 'populations' the evolution of which consists of progressive occupation of the niches. That is a process that happens in the course of evolution or, at least, it is one way of stating one of the aspects of what happens. For purposes of analysis of some phases of evolution it is a valid and useful manner of speaking. For fuller understanding, however, it is equally or more useful to focus neither on environment nor on organisms but on the complex interrelationship in which they are not really separable."

This point of view is neither "Lamarckian" nor "Vitalistic", but is based on principles of Mendelian genetics that have been amply proved experimentally.

Ferris' assumption that grooves on the insect head capsule are remnants of intersegmental lines may be correct. As he himself said: "Not until the evidence is conclusive should it be assumed that any structure could not have been derived from some preceding structure and consequently must represent an entirely new development." In reply to this statement, it could be said that not until evidence is conclusive should it be assumed that any structure has been derived from any preceding structure. In the case of integumental grooves on the insect head, it is at least

as reasonable to assume that they have been developed secondarily, since the original head segments became fused, than it is to assume that they have persisted since before the Carboniferous despite the profound changes that have taken place. Snodgrass (1928, 1935), DuPorte (1946) and others favour the view that most integumental grooves of the insect head are secondary structures.

DuPorte (1946) proposed a new interpretation of the morphology of the insect face. On the assumptions that, in the ancestral insect:

"(1) The anterior or facial region, bearing the ocelli, antennae and labrum, extended ventrally like a visor far beyond the ventral edges of the lateral regions which bear the eyes, and the posterior regions to which the mouthparts are articulated. (2) The mandible had a single articulation with the cranium, the posterior articulation of the pterygote mandible. The mouth appendages were suspended from the ventral margins of the posterior regions of the cranium, and the basal portion of the mandible was connected to the upper part of the lateral edge of the face by a membrane." DuPorte proposed that a second, anterior mandibular articulation, had been formed with the lateral edge of the face some distance ventral to the original, posterior, articulation, and that subsequently the lateral and posterior edges of the face had descended, bringing the posterior

mandibular articulations to the same level as the anterior articulation, and leaving the primitive edge of the face extending dorsally above the anterior mandibular articulation. Although fully incorporated into the face, this primitive edge of the face did not disappear, but persisted in the form of the frontogenal suture.

As it was assumed to be more likely that the tentorial pits should migrate along the edge of the face than along a merely secondary inflection, as Snodgrass had assumed had taken place along the epistomal suture, DuPorte thus explained the apparent dorsal shift of the pits in honey bees and similar forms by proposing that the anterior tentorial pits had migrated dorsally along the primitive edge of the face, the frontogenal suture.

In a later paper, DuPorte and Bigelow (1953) modified this theory, in view of the possibility that the pits had remained relatively stationary while the genae were extended ventrally on either side of the clypeus. The frontogenal suture thus became confined to that portion dorsal to the tentorial pits. This possibility will be discussed more fully in later sections.

The features of the literature on the morphology of the insect face most pertinent to this study are those

involving the basic, philosophical approach to the problem. The bulk of the work done on this subject has been based on the assumption that the evolutionary changes that have taken place in animal structures can be adequately understood without the simultaneous consideration of function. As mentioned previously, Snodgrass and DuPorte have taken functional factors into consideration in some instances, and Packard once entertained the possibility that evolution proceeds along Lamarckian lines. All other literature reviewed here has either ignored function altogether, or considered it as little more than an afterthought.

A tendency to regard structural features of the insect integument as very stable structures can also be seen, very clearly, in the literature. Ferris (1942) assumes that intersegmental lines have persisted since before the Carboniferous, despite profound functional changes. Comstock and Kochi (1902) and Comstock (latest revision, 1948) assume that sclerites of a hypothetically "typical" segment have persisted throughout the changes involved in their fusion into the head capsule.

Another tendency that is very apparent in the literature is the tendency to attempt to trace the evolutionary changes that have taken place in the insect integument to their very beginnings. Some studies have been confined to groups of

insects, but many have sought to trace the ancestry of all insects. None of these studies used fossil evidence.

This study was made on the assumption that evolutionary change in animal structures most often proceeds gradually, toward a closer adaptation to a changing environment. It is assumed that these changes appear first in the form of sudden, more or less random, mutations, but that the mutations most likely to be effective in evolutionary change are those that produce very slight phenotypic effects. Therefore, although the basic changes are sudden and more or less random, the overall effect is that of gradual change of one form into another. It is assumed that the majority of evolutionary change is adaptive, and hence that the validity of morphological explanations of the course followed during the evolutionary transformation of animal structures depends upon the degree to which these explanations show a gradual increase in adaptive value to the animal of the new structural form throughout the course of its development. Theories that assume the passage of structural change through stages of distinct adaptive disadvantage are considered as invalid unless reasons are clearly stated in scientific terms.

It is also assumed that the validity of conclusions drawn from comparative morphology depends upon the type of

morphological character being studied. Characters that differ distinctly in closely related species are considered to be valid only for the comparison of closely related groups. The use of such characters in studies that involve the comparison of orders and classes is regarded as illogical unless reasons for the assumption of stability are clearly stated. Similarly, studies that attempt to trace the course of evolutionary development from very remote ancestors are considered to be illogical if they are based on characters that differ distinctly in closely related species.

It is assumed that comparative studies of distantly related groups should be based on the comparison of fundamental characters common to the great majority of species in both groups. For example, similarities in the basic features of the nervous system, digestive system, etc. between the Arthropoda and Annelida are accepted as conclusive evidence that these two phyla are relatively closely related. Minor features of these fundamental characters, such as the finer nerve branches, which vary widely within the groups being compared, are not, however, regarded as valid characters.

It is held that a given character can be assumed to have been present in remote ancestral forms of a group if it is present in the vast majority of the extant

representatives of that group. For example, the sclerotized integument of insects is assumed to have been present in the remote ancestors of insects because it is present in nearly every species of existing insect. It is maintained, however, that minor features of the insect integument, such as grooves and sclerites, cannot logically be assumed to have persisted from remote ancestors, since these features are strikingly variable in existing insects, and are widely and effectively used in differentiating between closely related species.

It cannot be asserted that such minor characters have not persisted since remote ages, but it is held to be highly likely that they have been as variable in the past as they are in the present.

2 Since the anterior tentorial arms, anterior mandibular articulations and compound eyes were present in every specimen of Hymenoptera studied, it is logical to assume that these structures were present in the common ancestors of the entire order. Since the relative distance separating the anterior tentorial arm and the anterior mandibular articulation varies within the order from almost direct contact between the two structures to the extensive separation present in sphecoids, vespoids, apoids, etc., and since virtually all intermediate stages are present within the order, it is assumed that logical conclusions as

to the course of evolutionary development of this characteristic can be derived from a comparative study of existing Hymenoptera. These conclusions will not be applicable to insects other than Hymenoptera, except insofar as the same processes may have taken place independently in these other groups, because differences in this characteristic are apparently greater within the Hymenoptera than they are between Hymenoptera and other mandibulate forms, considered as groups rather than individuals.

Before proceeding with the survey of hymenopteran facial structure, it is necessary to discuss certain structural features of that part of the face called the clypeus, in the sense in which they will be considered here. This is necessary because the conception of clypeal structure that was developed in the course of this study differs somewhat from those so far published.

Where present, the hymenopteran clypeus is usually marked off from the remainder of the face by a system of integumental grooves, or sutures. These grooves are associated with a pair of anterior tentorial pits, which mark externally the points at which a pair of anterior tentorial arms are invaginated from the integument of the face. These tentorial arms form internally a pair of "struts" or "beams" which are continuous with a similar pair originating from invaginations of the integument called posterior tentorial pits on

the posterior region of the head. The entire structure is called the tentorium, and it forms an internal framework that provides strength and rigidity to the otherwise open, more or less unsupported, ventral region of the head. In many species a pair of dorsal tentorial arms project dorsally as continuations from the anterior arms and meet the integument of the face some distance above the tentorial pits.

The tentorium also provides attachment for muscles of the mandibles, maxillae, labium, hypopharynx, stomodaeum, and antennae. It therefore not only braces the ventral walls of the head capsule, but also provides a rigid base from which motion can be transmitted to the mouthparts, foregut and antennae.

The anterior mandibular articulations are almost always associated with the anterior tentorial arms, either directly, through the medium of short ventral protuberances from the latter, which are also continuous with the integument of the clypeus, or less directly, through the medium of distinct internal ridges extending from the mandibular articulations to the tentorial arms, and entirely continuous with the latter (See figures 190, 191, 197, 198, c.g.i.). These internal ridges are usually marked on the exterior surface of the integument by distinct grooves, or sutures, and these sutures mark the lateral or dorso-lateral limits

of the region of the face called the clypeus in most morphological and taxonomic literature. The anterior tentorial pits are often connected by an integumental groove called the frontoclypeal sulcus. This groove may extend directly from one tentorial pit to the other, or it may be arched dorsally above the level of the pits.

The system of grooves extending from one anterior mandibular articulation to the other, and passing through the anterior tentorial pits, is called the epistomal suture. This system of grooves is consistently associated with the tentorial pits.

One of the most consistent interrelationships among the facial structures in the Hymenoptera is that between the anterior tentorial arms and the anterior mandibular articulations. In the vast majority of species the mandibles and tentorial arms are distinctly united, either more or less directly, or through internal ridges as outlined above. This is explained on the assumption that the tentorial arms provide the most rigid fulcrum, or base for the fulcrum, against which the anterior mandibular articulations must get purchase, or support. It is likely that the consistency in the interrelationship between the tentorial pits and the frontoclypeal sulcus can be explained on the similar assumption that the groove provides additional rigidity,

and that this rigidity is required most between those points where the anterior tentorial arms meet the face. When the frontoclypeal sulcus is not visible externally, an internal ridge often connects the tentorial arms. Where both the sulcus and the internal ridge are absent, the integument usually appears to be thicker generally than it is in species that possess the sulcus.

A functional interrelationship between the anterior mandibular articulations and the tentorial arms is clear in the vast majority of the Hymenoptera studied. Even where the tentorial arms are relatively far removed from the mandibles, strong internal ridges always connect each pair of structures, wherever the mandibles are well developed. There is probably also a functional interrelationship between the tentorial arms and the frontoclypeal sulcus. Therefore, these internal inflections (or the external grooves marking the inflections, if present), can be thought of as a definite organ serving the vital function of providing necessary strength to the face along the lines of greatest stress.

The clypeus, then, is regarded as that part of the facial integument between these strengthening ridges and the labrum, and an attempt has been made to consider what possible selective advantages or disadvantages may have been

involved in changes in these strengthening ridges, before conclusions as to the course or direction of these changes were drawn.

As a final note, I would like to quote the following paragraph from Snodgrass (1928), since it applies to this study as well as it does to his own:

"It is regrettable that we must arrive at an understanding of things by way of the human mind. Lacking organs of visual retrospection, for example, we can only hold opinions or build theories as to the course of events that have preceded us upon the earth. Knowledge advances by what biologists call the method of trial and error, but the mind can not rest without conclusions. Most conclusions, therefore, are premature and consequently either wrong or partly wrong, and, once in every generation, or sometimes twice, reason back tracks and takes a new start at a different angle, which eventually leads to a new error. By a zigzag course, however, progress is slowly achieved. Error, then, is a byproduct of mental growth. It is not a misdemeanor in scientific research unless the erring one clings to his position when he should see its weakness. It is better to write beneath our most positive contentions that we reserve the right to change of opinion without notice. The reader, therefore, should not take it amiss if he finds certain conclusions drawn in this paper that do not fit with

former statements by the writer, for no apology will be offered."

MATERIALS AND METHODS

This study was conducted from a purely descriptive point of view. In view of the essential differences between the descriptive and the experimental methods, no attempt was made to present proofs in the neat, incisive manner characteristic of the experimental method.

Since some of the conclusions deduced from this study cannot be tested directly by experiment, their validity must depend upon the quantity of supporting evidence, the degree to which this evidence is drawn from different sources, and particularly on the soundness of the reasoning upon which they are based. The greatest achievement of the descriptive method of scientific research is undoubtedly the proof of the theory of organic evolution. Before the re-discovery of the Mendelian Laws of Heredity, and the consequent introduction of experimental methods into the study of evolutionary phenomena, the fact of evolution had been proved so thoroughly that the rational mind had no other choice than to accept it. It was not accepted, however, on the basis of a few well designed experiments, such as Newton's on the Laws of Motion, but only after a veritable mountain range of evidence, from many fields of biology, had been erected.

The specimens studied were confined to those present in the Canadian National Collection, Ottawa, and in the Macdonald College Collection. All specimens considered were determined by specialists.

Specimens were examined under a Zeiss-Option dissecting microscope and dissections were carried out under water after warming or boiling in caustic potash. All drawings were made with the aid of a squared eyepiece micrometer.

Since the facial characters could be seen without dissection in the majority of specimens, it was possible to examine a very large number. The integumental structure of the face was studied primarily, and internal structures were examined only as they were considered to affect the integumental structure. The system adopted during the survey of the order was to examine specimens of both sexes, and from widely separated localities, wherever possible in each group. Where variability appeared to be great, more specimens were examined; where structural features were constant throughout large groups, fewer specimens were examined. During the examinations, facial structure was sketched where it was considered necessary, and notes were made on all observations.

The classification followed throughout is that of Muesebeck et al. (1951). Scientific names are listed as they appear in this catalogue, even where such names have since been declared invalid (e.g. Pimpla irritator (F.) is used as listed in the catalogue despite the fact that the correct generic name, according to Opinion 159, is Ephialtes). This is done in order to facilitate reference to the catalogue.

A list of the genera and higher categories, in the order in which they appear in Muesebeck et al. (1951), is given in the Appendix. Genera from which specimens were seen are indicated by an asterisk in this Appendix, and the thoroughness with which any group was studied can thus be readily determined, and the possible validity of statements made concerning that group can be assessed.

The terms "tentorial arms" and "mandibular articulations" refer to the anterior tentorial arms and anterior mandibular articulations in all cases, unless otherwise specified. Other terms are either defined in the text as they appear, or are illustrated in figure 1, Plate I.

SURVEY OF FACIAL STRUCTURE IN THE HYMENOPTERA

MEGALODONTOIDEA

1. Xyelidae (fig.4)

The facial structure in all xyelid genera examined closely resembles that in Pleroneura aldrichi (fig.4). The clypeus projects ventrally as a free lobe beyond the ventral extremities of the genae, and the mandibular articulations lie very close to the tentorial pits. There is no direct contact between the clypeus and genae in these forms. In Macroxyela, and to a lesser extent in some Xyela species, the anterior mandibular articulations are somewhat displaced laterally from their position in Pleroneura. In such forms the clypeus lies in contact with the genae on each side, but the line of contact is very short, and the condition does not differ essentially from that in the Orthoptera, as can be seen by comparing figure four with figure two.

The facial structure in the Xyelidae supports the generally accepted view that this family includes some of the most generalized members of the Hymenoptera.

2. Pamphiliidae (fig.5)

All five nearctic genera are very similar to Cephalcia fascipennis (fig.5). The tendency for lateral displacement of the mandibular articulations noted in Xyela and Macroxyela has apparently been carried much farther in this family. In all forms studied the line of contact between the clypeus and genae is extensive. The displacement is more lateral than ventral, although in Pamphilius fletcheri MacGillivray the mandibular articulations are distinctly ventral as well as lateral to the tentorial pits. The clypeus and genae are closely united, and the clypeogenal suture has become very faint in some species, especially in the genus Pamphilius. C.fascipennis (fig.5) may represent a stage in this process, as the clypeogenal sutures are obscured under rugosity. The integument is thick and heavily sclerotized in the Pamphiliidae, and the head is apparently a very rigid structure.

TENTHREDINOIDEA

1. Pergidae

This family is represented in the nearctic region by the single genus Acordulecera. The facial structure in this genus is not essentially different from that in the family Argidae, to be described below.

2. Argidae (figs. 6,7)

The face in this family resembles the typical tenthredinid face (figs. 11-25), but the antennal foramen and the tentorial pit are more widely separated in most cases. In Arge clavicornis (fig.6) the frons bulges between the antennal foramina and the tentorial pits, and the sutures separating the frons, clypeus and genae are less distinct than is usual in the tenthredinid face. Sterictiphora species resemble Arge, but the frontogenal and clypeogenal sutures are distinct and deep. In Sphacophilus (fig. 7) and Sofus the tentorial pits lie very near the mandibular articulations, and the facial structure closely resembles that in the Xyelidae. Frontogenal sutures were present in all argid species examined.

3. Cimbicidae (figs. 8-10)

The face in Trichiosoma (fig.9) and Cimbex (fig.10) differs strikingly from that of all other tenthredinoids. The mandibular articulations are much more widely separated from the tentorial pits, the mandibles are larger, and the general configuration of the face differs noticeably. In Zaraea americana (fig.8), however, the facial structure is clearly intermediate, linking the more specialized cimbicids with the remainder of the Tenthredinoidea. The frontogenal suture is distinct in all these forms.

4. Diprionidae and Tenthredinidae (figs.11-25)

The facial structure in these two families is very similar. Variation is slight around the facial type represented by Tethida cordigera (fig.20).

The mandibular articulations are displaced laterally and ventrally from the tentorial pits, and lie at a horizontal level corresponding approximately to a line drawn through the clypeus midway between its distal and proximal extremities. This basic structure, and most of the variations present in the tenthredinid face, can be seen in figures eleven to twenty-five.

One of the most interesting features of this group is the manner of union between the clypeus and genae. In Blennogeneris spissipes (fig.22) the tentorial pits are widely opened, and the mandibles articulate with short, inflected bridges that are continuous with the clypeus, genae, and tentorial arms. The major part of the clypeus projects ventrally as a free lobe, but the mandibular articulations are somewhat more displaced ventrally than they are in Pleroneura (fig.4), and the region of contact between the clypeus and genae is distinctly increased. Similar conditions are present in Hemitaxonus albido-pictus (fig.12), Sphacophilus plumiger (fig.7) and others, except that the clypeus and gena have come together externally over the inflected

bridge to form a short, but distinct clypeogenal suture on each side. The mandibular articulations lie below their position at the tentorial pits in Pleroneura (fig.4). It is simpler to assume that the mandibles have been shifted ventrally in these species, rather than that the tentorial pits have migrated dorsally. A ventral shift of the mandibular articulations could be effected merely by the addition of cuticular material below the tentorial arms and between the clypeus and genae, whereas a dorsal shift of the tentorial pits would involve a dorsal shift of the tentorial arms and relatively complex rearrangements of the internal organs associated with them.

In most tenthredinids, the relative distance between the tentorial pits and the mandibular articulations is somewhat greater than it is in the three species mentioned above. Variation in the extent of this mandibular displacement is not great, and the most usual condition resembles that in Tethida cordigera (fig.20). Variation in the manner of union between the clypeus and genae, however, is considerable, as can be seen in figures 11-25. In some species the edges of the clypeus and genae have apparently closed over the clypeogenal inflections (e.g. figs. 12, 17, 19, 23). In other species the open clypeogenal inflections have been filled with a cuticular substance that differs distinctly in colour, texture and transparency from the surrounding

integument, and the edges of the clypeus and genae have not come together (e.g. figs. 11, 13, 16, 21, 24). In some of these species, the clypeogenal inflection can be seen clearly through this cuticular material; in others the cuticular material is opaque, but different in colour and texture from the surrounding integument; in others the cuticular material is very similar in colour to the surrounding integument, but differs in texture, being usually much more smooth. In some species the edges of the clypeus and genae have closed over part, but not all, of the clypeogenal inflection, the remainder of which is filled with the cuticular material discussed above. In some cases the clypeogenal closure is dorsal, just below the tentorial pits (e.g. fig.18); in others the clypeus and genae meet about midway between the tentorial pits and mandibular articulations. The variation in the colour and degree of transparency of the cuticular material, and in the extent and position of clypeogenal closure, is striking in tenthredinids, sometimes in different specimens of the same species. These variations strongly suggest that displacement of the mandibular articulations has taken place relatively recently in sawflies, and that structural adjustment to the new conditions has not become fully stabilized.

Where the edges of the clypeus and gena have not closed externally, the region between them, containing the

cuticular material mentioned above, is clearly not a true suture. The term clypeogenal bridge (B) is proposed here for such cases, and it will be seen that, in some hymenopterous groups, this bridge may take the form of a relatively extensive sclerite between the clypeus and gena.

Although variation in the length of the clypeogenal inflection is not great, as mentioned above, comparison of the extremes clearly shows that a marked displacement of the mandibular articulations from the more generalized conditions in figures 4, 7, 12 and 22 has taken place in some species (e.g. figs. 23, 25). Series can be selected which suggest stages in a gradual change from one condition to the other. One of these series is illustrated in DuPorte and Bigelow (1953).

Traces of the frontogenal suture can be detected in some tenthredinids (e.g. figs. 12, 16, 17, 18, 22, 24, 25), but in most species the antennal foramina lie very near the tentorial pits, and the frontogenal suture has been lost.

SIRICOIDEA

1. Syntexidae

This family is represented in the nearctic region by the single species Syntexis libocedrii Rohwer. As mentioned

by Ross (1937), this species is one of the more primitive siricoid forms, and this is apparently reflected in the facial structure. The striking modifications that have taken place in the facial structure of certain siricoid insects (to be discussed below) have scarcely begun in S.libocedrii. Specimens of this species were not seen in the course of this study, and therefore the face was not figured. A figure by Ross (1937, p.131), however, shows that the tentorial pits are situated near the ventral margin of the face, and that the frontal and genal areas are extensive below the eyes and tentorial pits. The facial structure shown in Ross' figure resembles that of Cephus cinctus (fig.34), except that, in the latter, the eyes are considerably lower.

2. Siricidae and Xiphidriidae (figs. 26-31)

The larvae of these forms burrow in wood, and pupation takes place within the larval burrow. Consequently the adult, upon emergence, must cut a path through the wood in order to reach the exterior. While thus boring through the wood, the freedom of movement of the insect is greatly restricted, as can be seen clearly in the photographs in Hanson (1939). The head in these insects is correspondingly robust, well braced with ridges and inflections, and the postgenae and genae have been extended and modified so that

the mandibular action takes place in a horizontal rather than a vertical plane. The mandibles thus open toward the anterior rather than beneath the head. Extensive pleurostomal sclerotizations have been formed between the genae and mandibles, and the genal edges have been flared outward, as shown in figures 27 and 29, G. In the genus Xiphydria (figs. 30, 31) this modification is less advanced than it is in Tremex (figs. 26, 27) and Urocerus (figs. 28, 29). In Xiphydria, although the postgenae have descended and moved forward to a certain extent, the posterior mandibular articulations are still distinctly posterior to the anterior articulations, and consequently the mandibular action takes place in a plane intermediate between the vertical and horizontal. In Tremex and Urocerus the postgenae have grown ventrally and anteriorly until the posterior mandibular articulations lie below the anterior articulations in approximately the same vertical plane. In these forms the mandibular orientation has been altered so that the insect is able to tunnel forward through wood without shifting the normal, hypognathous, orientation of the head. Whereas in many Coleoptera this horizontal action of the mandibles is achieved by a shift in the orientation of the entire head from the hypognathous to the prognathous, in the Siricidae the orientation of the mandibles alone has been altered. A similar functional requirement has thus been met by two very

different structural modifications.

The antennal foramina in these two families lie very near the tentorial pits, and frontogenal sutures cannot be distinguished.

As in tenthredinids, the cuticular material between the clypeus and genae (and also that in the pleurostomal region between the genae and mandibles) differs in colour and texture from the rest of the integument. The degree of this difference varies in different species, and in some the cuticular material has become almost homogeneous with the surrounding integument. In many tenthredinids and siricids this cuticular material is much more similar in appearance to that in the other superfamily than it is to the integument adjacent to it.

3. Orussidae (figs. 32,33)

In this family the clypeus and that part of the frons bearing the antennal foramina have been shifted ventrally and folded posteriorly beneath the frons to such an extent that they cannot be seen in the anterior aspect of the face. The mandibular action is not in a horizontal plane, as it is in the Siricidae, but the structure surrounding the mandibles, when seen from the ventral aspect, is strikingly similar to that in the Siricidae. Distinct pleurostomal sclerotizations

separate the mandibles from the genae along their entire length. In the Siricidae, the functional significance of these structures is obvious, since they support the mandibles in a position that is unusual in the Hymenoptera. In the Orussidae, however, the mandibular orientation is, in effect, normal, and the functional significance of these structures is less obvious, unless it can be assumed that the orussid structure was preceded by a siricoid structure in which the mandibles were directed forward. It is therefore reasonable to suggest that the evolutionary changes, whose end result was the orussid structure shown in figures 32 and 33, passed through a siricoid stage in which the mandibles were directed forward, and then returned to the normal downward orientation of the mandibles. This return to the normal orientation may have necessitated the ventral shift of the antennae and clypeus, and may explain this striking difference between orussids and other Hymenoptera.

CEPHOIDEA (figs. 34,35)

The facial structure in all five nearctic genera resembles that of Cephus cinctus (figs. 34, 35). The tentorial pits lie very close to the mandibular articulations. In the female specimen figured, a distinct clypeogenal bridge lies between the tentorial pit and the mandibular articulation.

The antennal foramina are situated relatively high in the face, and are connected with the tentorial pits by grooves which may represent frontogenal sutures.

ICHNEUMONOIDEA

1. Stephanidae (fig. 36)

Only six nearctic species are listed by Muesebeck et al. (1951). In Schlettererius cinctipes (fig. 36), the tentorial pits lie at the ventral edge of the face and the clypeus is reduced both dorso-ventrally and laterally. The antennal foramina also lie near the ventral edge of the face. Figure 36 shows the anterior condyles leaving the body of the mandibles and apparently terminating before they reach the anterior tentorial arms. This is illusive, since the mandibular condyles pass beneath the pleurostomal membrane at this point, and are probably continued dorsally to meet the tentorial arms. This could not be definitely determined, since it was not advisable to dissect the only available specimen, but it is reasonable to assume that this species does not differ from all other Hymenoptera in this respect. S. cinctipes differs distinctly from other nearctic ichneumonoids in the position of the antennal foramina, and in other facial features.

2. Braconidae (figs. 37-61)

The facial structure in this large and variable family

can be discussed from the basis of four "types", which may be termed:

(i) The meteorine, represented by Meteorus trachynotus (fig.40), and including all the modifications shown in figures 37-54).

(ii) The dacnusine, characteristic of the subfamilies Dacnusine and Alysiinae, and represented here in figures 55 and 56.

(iii) The braconine, characteristic of the Braconinae, Spathinae, Doryctinae and Rogadinae, and represented here in figures 57, 58 and 59.

(iv) The cosmophorine, characteristic of the small subfamily Cosmophorinae, and represented here in figures 60 and 61.

(i) The meteorine type (figs.37-54)

The facial structure in most Braconidae, and in many of the Ichneumonidae, resembles that in Meteorus trachynotus (fig.40). In this species the eyes are large; the tentorial pits are distinctly separated from the mandibular articulations; the mandibular action is normal; the antennal foramina are distinctly removed from the tentorial pits; and distinct frontogenal sutures are absent. In M.trachynotus traces of malar sutures intersect the genae from the

ventral extremities of the eyes to the pleurostomal region. These malar sutures are distinct in Macrocentrus cerasivoranae (fig.43), and in Diospilus (fig.46). They are present, though less distinct, in Myiocephalus boops (fig.41), Helcon (fig.45) and in Proterops (fig.54). In M.boops faint grooves extend dorsally from the tentorial pits to the antennal foramina. These may or may not be remnants of frontogenal sutures.

A typically meteorine facial structure prevails in the braconid subfamilies Aphidiinae, Euphorinae, Macrocentrinae, Helconinae, Blacinae, Agathidinae, Cardiochilinae, Ichneutinae and Cheloninae. In the latter three subfamilies the clypeus is broader, and more nearly rectangular in shape, than it is in the other subfamilies. Modifications occur in the Aphidiinae, Helconinae and Agathidinae, but the basic meteorine type prevails throughout all nine of these subfamilies, which include more than half the nearctic Braconidae.

Perhaps the most common modification of the meteorine structure is represented by Ephedrus nitidus (fig.38). Here the distal portion of the clypeus is folded posteriorly and is no longer visible in the anterior aspect. Possible precursors of this underfolding are present in the Ichneumonidae (e.g. figs. 62, 65, 91, etc.) and in some tenthredinids, in which the distal portion of the clypeus

is concave. In the Aphidiinae, the genus Ephedrus alone shows this modification; the other genera examined resemble Praon simulans (fig.39). In the Microgasterinae, however, including the large genus Apanteles, the E.nitidus type prevails.

Another modification of the meteorine structure is represented by Helcon (fig.45). Here the clypeus is greatly reduced, both dorsoventrally and laterally, and seems to have been crowded toward the ventral mid-line by additions to the frons and genae above and beside it. In Cenocoelius (fig.44) the clypeal structure does not differ greatly from that in Meteorus (fig.40). In Helconidea the structure is intermediate between that of Cenocoelius and Helcon. Species of these genera apparently represent different stages of the transition to the helconine modification.

A similar modification exists in the single nearctic genus of the subfamily Neoneurinae (i.e. Elasmosoma, fig.52). The clypeus is reduced here also, but has remained relatively wider than in Helcon, and the eyes are much larger than in the Helconinae.

A very interesting modification of the meteorine structure occurs in the Agathidinae. In the single genus Agathis the frons, clypeus and genae have been elongated ventrally from the typically meteorine condition in

A.texanus (fig.48) through A.buttricki (fig.49) to A.atripes (fig.50), in which the ventral elongation is most striking. In the genus Cremnops (fig.51) this condition is even more extreme, whereas in Earinus (fig.47) the facial structure is closer to that of Meteorus than it is in Agathis texanus. These forms show beyond all doubt that ventral extensions of the genal regions occur in the Hymenoptera. This modification is distinctly paralleled in the braconid genus Crassomicrodus; in the ichneumonid genera Coccygomimus, Hoplismenus, Pristomerus and Cremastus; in the apoïd genus Bombus; and to a lesser extent in many other hymenopterous forms.

In the genus Diospilus of the Helconinae (fig.46), yet another modification of the meteorine structure has taken place. Here the mandibular articulations have migrated laterally rather than ventrally, with the result that the clypeus still projects ventrally as a free lobe, although the mandibular articulations and tentorial pits are distinctly separated. An apparently intermediate condition can be seen in Syntretus vigilax (fig.42). Forms resembling S.vigilax occur also in the genus Opius of the Opiinae.

In the Paxylommatainae, represented in the nearctic region only by the rare genus Eupachylomma, the frontal and clypeal areas protrude along the midline and all trace of facial sutures has disappeared (fig.37). As this structure

does not differ fundamentally from that of Meteorus, it has been included under the meteorine type here.

(ii) The dacnusine type (figs. 55,56)

In the Dacnusinae and the Alysiinae the facial structure is very different from that in other braconids, or, for that matter, in most other Hymenoptera. The most striking feature of these forms is the orientation of the mandibles, which are apparently used for spreading material apart rather than for pressing it together. The mandibles in these forms cannot be brought together on the midline, and are reminiscent of the forelegs of a mole, which are used for digging. The general shape of the mandibles also suggests some function similar to digging. The dentations project outward rather than inward, and the convex and concave sides are exactly opposite to the usual condition. When fully extended laterally, the mandibles in these insects even more closely resemble the spread forelegs of a mole. The head in most of these forms tends toward an opisthognathous orientation, and consequently the mandibles open ventrally rather than anteriorly. If they are used for digging, the insect must dig directly downward. Whatever the actual function may be, it must certainly be similar to digging, at least in its mechanics.

The tentorial pits in these insects lie at the most ventral level of the genae, and the clypeus projects ventrally

as a free lobe, as it does in Pleroneura (fig.4), but the mandibular articulations are widely separated from the pits laterally, and are connected to the clypeus by narrow arms of the latter, as can be seen in figure 56. The opisthognathous orientation of the head has brought the clypeus to the ventral region, and has produced the effect of an underfolding of the clypeal region, as can be seen in figure 55. The frontogenal suture has been lost in these forms.

These two subfamilies include a considerable number of nearctic species, and apparently this modification is efficient in the exploitation of some widespread ecological niche.

(iii) The braconine type (figs.57-59)

In the Braconinae, Spathinae, Rogadinae and Doryctinae, which comprise a large part of the family Braconidae, the clypeus has been underfolded in a manner similar to that in Ephedrus nitidus (fig.38), mentioned above. In these subfamilies, however, the clypeus, labrum and mandibles are so shaped that, when the mandibles are opposed, a cup-like cavity is present in the face. The concavities in these three structures are so intimately correlated with one another that the cup-like shape of the interior of the cavity is virtually perfect in some forms. The maxillae also are modified, and form a trough beneath the cavity when brought together.

The entire complex gives the impression that the insects feed first by filling the cavity with liquid or other food, and then by allowing this food to fall into the maxillary trough (possibly with the assistance of movements of the labrum), from which it is brought upward in some way to the mouth. As so little is known of the feeding habits of these insects, this can be no more than conjecture, but the structural coordination of these three more or less independent organs must certainly be an adaptation to some particular functional need. The perfection with which the mandibular, clypeal and labral edges meet in these forms can be seen much more clearly in specimens than in figures 57-59.

(iv) The cosmophorine type (figs.60,61)

The subfamily Cosmophorinae is represented in the nearctic region by the single genus Cosmophorinus (figs. 60,61). In the specimens studied the frons is greatly enlarged and its ventral portion is bent posteriorly, so that the clypeus lies on the ventral side of the head and is not visible from the anterior view. The resulting condition is reminiscent of that in the Orussidae, except that the antennal foramina are still visible from the anterior aspect in Cosmophorinus. Sutures connecting the mandibular articulations and the ventral extremities of the eyes (see figs.60,61) are probably malar sutures.

3. Ichneumonidae (figs. 62-97)

This family includes more than twice the number of nearctic species present in any other family of the order Hymenoptera. The profusion of closely related species in this family affords an excellent opportunity to study the possible mode of transition of one form into another in facial type, by consideration of intermediate forms. Due to the unusual size of the family, the facial structure will be discussed from a subfamily basis.

(i) Pimplinae (figs. 62-74)

The predominant facial structure in this subfamily resembles that shown in figures 62-67. The most characteristic feature of this type of face is the ventral projection of a considerable portion of the clypeus as a free lobe below the ventral level of the mesal portions of the genae. The frontoclypeal sulcus is often arched, as in figures 62, 65-67; malar sutures are often present, as in figures 62 and 63; and the mandibular articulations are distinctly, but not widely, separated from the tentorial pits. This type of face is predominant in the tribes Pimplini, Polysphinctini, Theroniini, Xoridini and Acaenitini.

In the Rhyssini the face is modified, as shown in figures 69 and 70. The clypeus as a whole is much reduced

in relative size, the frontoclypeal sulcus is horizontal rather than arched, and the clypeus and genae are continuous below the tentorial pits and malar sutures. That this modification was probably derived from the typical pimpline facial type can be seen clearly by consideration of Pseudorhyssa sternata (fig.68) of the Pimplini. In this species the clypeogenal region, though relatively larger, is essentially identical in structure with that in the genus Rhyssa (figs. 69, 70). The malar sutures are more nearly horizontal than is the case in Pimpla (fig.67) or Arotes (fig.63), and the genae have been extended beneath them by the formation of clypeogenal bridges. In some P.sternata specimens (fig.68,P) these bridges are semitranslucent, and though the cuticular material is present without interruption over both the clypeus and genae, the typical pimpline clypeus can be clearly seen beneath it (as shown by dotted lines in figure 68). In other P.sternata specimens, however, the cuticular material has become opaque and the clypeus and genae appear to be completely continuous, as in Rhyssa. In Rhyssa also the cuticulin in this region has remained transparent in some specimens. The degree of opacity of this clypeogenal bridge varies in different specimens of the single species, P.sternata, in a manner that is entirely parallel with the conditions in the Tenthredinidae and Siricoidea mentioned previously. Intermediates are also common in the genera Delomerista and

Perithous of the Pimplini, and in Clistopyga and Zatypota of the Polysphinctini.

Neoxorides vittifrons (fig.71) of the Poememiini is an obvious modification of the rhyssine type, in which the clypeus and genae have remained separate.

A marked variation in the extent of the genal area below the eyes can be seen in figures 62-67. A gradual increase in the relative size of the eyes can be seen, from the condition in figure 62, where the entire clypeal area lies below the ventral extremities of the eyes, to that in figure 67, where the entire clypeal area lies above the ventral extremities of the eyes. Practically every conceivable intermediate stage between these two conditions occurs in the Pimplinae. This variation may be interpreted in several ways. Coccygomimus aequalis (fig. 62) may be the most primitive and the others may be modifications through increase in size of the eyes or decrease in the ventral extent of the frons and genae, or both. On the other hand, Pimpla irritator (fig. 67) may be the most primitive, and the others may be stages in a ventral extension of the frons and genae, reduction in the size of the eyes, or both. A third possibility is that both extremes may have been derived from a more primitive intermediate type. A fourth possibility is that no one of these types is more primitive than any other, all having been derived directly from a type, say, like Pleroneura (fig.4). These questions

will be discussed more fully in a later section.

In Grotea anguina (fig.72) and in Schizopyga frigida (fig.73) the tentorial pits are somewhat more widely separated, and the clypeus is correspondingly broader, than in most other pimpline species. The shape of the clypeus in G.anguina suggests that an underfolding of the distal portion may have taken place, as in Ephedrus nitidus (fig.38) of the Braconidae. It is also possible, however, that sclerites may have been added by the deposition of cuticular material at the lateral edges of the clypeus, as in rhyssine braconids. This is highly probable in the case of S.frigida, since in the genus Zatypota of the same tribe, Polysphinctini, there are forms that resemble both S.frigida and Pseudorhyssa sternata (fig. 68) of the Braconidae. Zatypota dictynae (Howard) resembles S.frigida closely in facial structure, and Z.nigriceps (Walsh) definitely resembles P.sternata. There can be little doubt that in Z.nigriceps such sclerites have been added to the clypeal region.

In Diacritus muliebris (fig.74), and in the genus Poemenia of the tribe Poemeniini, the tentorial pits are widely opened externally and are relatively widely separated. The clypeus projects ventrally, somewhat as in Schizopyga frigida (fig.73), and it is possible that similar modifications have taken place in both forms.

(ii) Tryphoninae (figs. 75-79)

The facial structure in the tribes Adelognathini, Phrudini and Phytodietini of this subfamily is distinctly pimpline. Most species are very close to Arotes amoenus (fig.63) in facial type, and in this respect form a more or less distinct group within the Tryphoninae.

The tribes Boëthini, Tryphonini and Cteniscini are uniformly like Tryphon communis (fig.75), with only very minor variations. The similarity between T.communis and Diacritus muliebris (fig.74) suggests that the latter may be more closely related to the typical tryphonine species than to many of those included with it in the Pimplinae. On the other hand, the similarity may be convergent rather than parallel.

Two striking, and very different, modifications occur in the Tryphoninae, one in the tribe Eclytini, and one in the Gryptocentrini. In the Eclytini the clypeus is large, more or less fully incorporated into the face, and tends to protrude. An extreme condition can be seen in Hybophanes nasutus (figs. 78, 79). A similar condition is present in the genus Campothreptus. In H.nasutus males (fig.77), though the clypeus is as completely incorporated into the face as it is in the females, there is only a slight bulge in the region which, in the females, protrudes to form the unusual snout-like structure shown in figures 78 and 79. The species is

clearly sexually dimorphic in this respect. Other genera of the Eclytini (e.g. Eclytus, Neliopisthus and Thymaris) resemble the normal tryphonines (i.e. fig.75), which suggests that the H.nasutus modification is derived directly from the normal facial type. There is, in fact, a distinct tendency for the frons to bulge outward above the clypeal area in a number of species of the tribe Tryphonini. It is thus possible that the dorsal portion of the "snout" in H.nasutus females (which is distinctly separated from the ventral portion) is derived from the frons, and is not a part of the clypeus in the morphological sense. However, since the entire "snout" probably functions as a unit in providing rigidity against the pull of the mandibular muscles, it can be considered as the functional clypeus.

In the Gryptocentrini, the genus Gryptocentrus is very close to the normal in facial type, but the genus Idiogramma is modified as shown in figure 76. The condition here is almost exactly opposite to that in Hybophanes nasutus. The clypeus is greatly reduced dorsoventrally, and the mandibular articulations are displaced laterally from the tentorial pits, rather than dorso-ventrally. It is possible that those portions of the clypeus laterad of the tentorial pits (fig. 76, C) are formed by the addition of cuticular material as in the tribe Rhyssini of the Pimplinae.

These two strikingly different modifications of the

same facial type (as they most likely are if Hybophanes and Idiogramma are correctly placed in the Tryphoninae) are an interesting example of divergence in structural evolution. Since structural differences of this magnitude can appear at the subfamily level, it is obviously risky to draw conclusions from a comparison of isolated specimens from different Classes, such as the Insecta, Myriapoda and Crustacea.

(iii) Gelinae (=Cryptinae) (figs.80-85)

The face in the majority of this large subfamily varies relatively little around the structure shown in Trachysphyrus altonii (fig.82) or Mastrus argeae (fig.83). The tentorial pits lie very near the mandibular articulations in most species, and the frontoclypeal sulcus is usually arched upward as in figures 82 and 83. The only modifications from the typical structure involve a more marked dorsal arching of the frontoclypeal sulcus, and a shift in the relative position of the tentorial pits. In Acroricnus aequatus (fig.80) the clypeus is larger than is usual in the Gelinae, and a relatively greater distance separates the tentorial pits and mandibular articulations. Grooves in the position of frontogenal sutures extend dorsally from the tentorial pits, and the pits themselves are elongated dorso-ventrally. In Listrognathus albomaculatus (fig.81) the tentorial pits are relatively lower than in A.aequatus,

the frontogenal grooves (i.e. the grooves just dorsal to the tentorial pits) are more distinct, and the pits are elongated dorsoventrally as in A.aequatus. The distal portion of the clypeus is sharply underfolded below the row of vertical lines in figure 81. In Trachysphyrus altonii (fig.82) the frontogenal grooves are also present, but lie mesad and dorsad of the tentorial pits. It can be seen from a comparison of these three figures that there has been a gradual increase in the genal areas beneath the eyes from A.aequatus to T.altonii. In the genus Lyneon, and in related genera, the positions of the frontogenal grooves are marked by lines of darker pigmentation. In many species, faint grooves are present in these positions.

It could be surmised that figures 80-82 represent stages in a ventral shift of the tentorial pits. If so, it could be further surmised that the typical geline face of figures 82 and 83 was derived from a facial type in which the clypeus was more or less extensively incorporated in the face. Without further study, however, this can be no more than a suggestion.

(iv) Ichneumoninae (figs. 86, 87)

The most prevalent facial type in this subfamily resembles Centeterus tuberculifrons (fig. 86). The clypeus

is extended laterally from the condition normal in the subfamilies described above, the tentorial pits are widely separated and are displaced mesally rather than dorso-ventrally from the mandibular articulations. In C.tuberculifrons two distinctly different regions are present in the clypeus. The boundary between these regions is indicated by the dotted line in figure 86. The dorsal and central region (fig.86,C) protrudes above the lateral and ventral regions (fig.86,B), and the line of separation between the two is sharp and distinct. The integument of the central region is indistinguishable in texture, colour, etc., from the frons above it, while the lateral regions are much more smooth, and very closely resemble in colour and texture the cuticular material previously described in the Tenthredinidae, Siricoidea, and in the rhyssine types of the Pimplinae. The central region of the clypeus is similar in shape and position to the clypeus in the majority of the previously described ichneumonid subfamilies, and the lateral portions have clearly been added by cuticular secretions in the same way as the clypeogenal bridge in tenthredinids and rhyssine ichneumonids. In most of the Ichneumoninae these two regions of the clypeus cannot be distinguished, but varying degrees of blending between them can be seen in some species.

In a number of ichneumonine genera the mandibular

articulations are displaced ventrally as well as laterally, so that the clypeogenal sutures extend diagonally, in a ventro-lateral direction, from the tentorial pits. In these forms the most dorsal portion of the clypeus is incorporated into the face to a greater extent than in C.tuberculifrons. The most extreme example of this modification was found in Hoplismenus morulus (fig.87), in which the greater part of the clypeal region is incorporated into the face. In all these forms a relative increase in the ventral extent of the genal regions seems to be correlated with the degree of ventral displacement of the mandibular articulations, and the trend is more or less exactly parallel to that described in Agathis and Cremnops (figs. 48-51) of the Braconidae.

(v) Banchinae (fig.88)

The banchine genera Glypta, Toxophoroides, Amersibia and Arenetra are typically ichneumonine in facial type. Toxophoroides tends somewhat toward Hoplismenus morulus (fig.87), the others resemble Centeterus tuberculifrons (fig.86), except that the lateral portions of the clypeus cannot be distinguished from the central portion. Most other genera resemble typical gelines such as Trachysphyrus (fig.82) or Mastrus (fig.83).

In the tribe Banchini, Exetastes suaveolens (fig.88)

resembles Hoplismenus morulus in the dorsal part of the clypeus, while the concave free distal portion is reminiscent of pimpline forms such as Coccygomimus aequalis (fig.62). In Ceratogastra and Banchus the mandibular articulations lie more lateral than ventral from the tentorial pits, and the median distal edge of the clypeus is often sharply emarginate. Some species of these two genera tend toward the typical geline face.

(vi) Scolobatinae (figs. 89-93)

In the majority of this subfamily the clypeus is reduced dorso-ventrally and the tentorial pits are relatively widely separated. A facial type similar to Mesoleius nigropictus (fig.93) is common, and is apparently more or less closely related to the ichneumonine type represented by figure 86.

In Scolobates auriculatus (fig.89) the tentorial pits are elongated and are possibly undergoing a shift in position. In Euceros thoracicus (fig.90) the tentorial pits lie at the ventral edge of the face in contact with the mandibular articulations. The clypeus in this species tends to be somewhat lens shaped, and thus to resemble typical gelines such as Mastrus (fig.83). This type of face is not uncommon in the Scolobatinae. In other Euceros species the

frontoclypeal sulcus has disappeared and the ventral edge of the clypeus is more evenly continuous with the ventral edges of the genae. In these species the facial structure approaches that of Orthocentrus (figs. 94, 95) and Exochus (fig.96), of the Orthocentrinae and Metopinae respectively, to be described below.

In Ctenopelma nigricorne (Provancher) the distal edge of the clypeus is emarginate as in Hymenoepimecis wiltii (fig.66) of the Pimplinae, and the clypeal structure resembles a pimpline type in which the frontoclypeal sulcus is horizontal rather than arched. In some species a considerable portion of the clypeus projects ventrally as a free lobe, very much as in the typical pimpline facial type (e.g. fig. 62, etc.). Protarchus longipes (Cushman) and Mesoleius tenthredinis (fig.92) show this condition. The concavity of the distal portion of the clypeus in M.tenthredinis, and the apparent absence of this portion in M.nigropictus (fig.93) suggest that in some cases reduction in the distal extent of the clypeus may have been accomplished by underfolding. In Himerta flavida (fig.91) the distal portion of the clypeus is markedly underfolded and could well be an intermediate stage between the Mesoleius tenthredinis and Euceros types. The step from Euceros to Mesoleius nigropicta types has almost certainly included the addition of cuticular material to the lateral edges of the clypeus, as in

Centeterus tuberculifrons (fig.86).

(vii) Collyrinae

This subfamily is represented in the nearctic region by the single species, Collyria calcitrator (Gravenhorst). Specimens of this species were not seen, but it appears from a figure by Salt (1931) that the facial structure resembles that of Scolobates auriculatus (fig.89).

(viii) Orthopelmatinae

A single genus, Orthopelma, is present in the nearctic region. The clypeus in the only specimen seen is underfolded distally somewhat as in Himerta flavida (fig.91).

(ix) Plectiscinae

The facial structure in this subfamily parallels that described in the Ichneumoninae, except that the predominant type resembles Hoplismenus morulus (fig.87) more closely than Centeterus (fig.86). The tentorial pits are relatively widely separated from the mandibular articulations (somewhat as in figure 87) in all genera seen except Cylloceria, in which the displacement is closer to that normal to the Ichneumonidae (e.g. as in figures 64, 75, 82, etc.).

(x) Orthocentrinae, Metopiinae (figs. 94-97)

These two subfamilies resemble the Scolobatinae, in that the clypeal area tends to be strongly reduced dorso-ventrally, and the tentorial pits are relatively widely separated. In Orthocentrus (figs. 94, 95) this condition is very marked. The tentorial pits lie at the extreme ventral edge of the face, the clypeal area is reduced to a very narrow strip along the ventral rim, and the frons protrudes, as shown in lateral aspect in figure 94. This facial type is very similar to that in many chalcidoids, to be discussed below. In the genus Stenomacrus of the Orthocentrinae the facial structure is essentially identical with that of Orthocentrus, but an indistinct groove arches upward from the tentorial pits and marks off an area similar in extent and shape to that of the clypeus in Hoplismenus morulus (fig. 87). Considered with other evidence for ventral shifts of the tentorial pits, this suggests that the orthocentrine facial type has been derived from a type in which the pits were situated some distance above the mandibular articulations, as in H. morulus, in many plectiscine, and in some ichneumonine species. That there has been a ventral shift of the tentorial pits in Orthocentrus (and in most chalcidoids) is suggested by the fact that the anterior tentorial arms extend downward from the level of the occipital foramen to the anterior ventral edge of the

face, as shown in figure 94, and also by the presence of many related species in which the pits lie some distance dorsal to the ventral edge of the face. There can be little doubt that chalcidoids, in which this type of face is almost universal, are derived from a more normal hymenopteran type in which the tentorial pits were situated dorsal to the mandibular articulations, and a glance at the tentorial structure in Dahlbominus fuscipennis (fig.194) strongly suggests that a ventral shift of the anterior arms has taken place.

In the Metopiinae (figs.96, 97) the tentorial pits do not actually meet the ventral edge of the face, but the clypeus is very strongly reduced dorso-ventrally and a distinct resemblance between the two types is obvious. In the Metopius specimen illustrated in figure 97 the frons is modified into a peculiar shield-shaped plate, the morphological significance of which is unknown.

(xi) Diplazoninae

The face in all diplazonine genera seen varies only slightly around the typical pimpline types of figures 62-67.

(xii) Ophionine, Mesochorinae

The facial type in these two subfamilies parallels

that in the Plectiscinae. Various intermediate stages between a condition resembling that of Hoplismenus morulus (fig.87) and that of Orthocentrus (fig.95) are present. Of the genera seen, Casinaria most closely approaches the orthocentrine type, Pristomerus, Cremastus and Cidaphus the Hoplismenus type.

Some species show a distinct tendency toward ventral extension of the frontal, genal and clypeal areas, as in the braconid genera Agathis and Cremnops (figs. 48-51). Probably most forms in which the tentorial pits are widely separated from the mandibular articulations arrived at this condition through such ventral extensions. On the other hand, definite orthocentrine types have probably been formed by ventral shifts of the tentorial pits. It would appear that in some cases the process may have taken place in a series of alternate stages, with ventral extension of the genae being followed by ventral shifts of the pits.

CHALCIDOIDEA (figs. 98-111)

As mentioned above, the typical chalcidoid face closely resembles that of Orthocentrus (fig.95). In most chalcidoids the clypeus is even more reduced than in Orthocentrus, since the tentorial pits are less widely separated. This extreme reduction in the clypeal area is

apparent in Dahlbominus fuscipennis (fig.98), where it will be noted that the ventral edge of the face is also underfolded (fig.99). With superficial variations, this facial type is uniformly present in the families Mymaridae, Trichogrammatidae, Eulophidae, Elasmidae, Thysanidae, Eutrichosomatidae, Tanaostigmatidae, Encyrtidae, Eupelmidae, Torymidae and Ormyridae. The extent of the variation in these families can be seen in figures 98-103, 105-106. Malar sutures are often present, and it is possible that these, combined with the underfolding of the ventral part of the face, and perhaps also with the minute size generally, have taken over the function of the normal hymenopteran clypeus (i.e. the provision of rigidity against the pull of the mandibular muscles).

In the Eupelmidae (fig.103), and in some torymid species (figs. 105, 106), the clypeus is usually somewhat more extensive than in the other families mentioned, since the tentorial pits extend dorsally from the ventral rim of the face, as shown in figure 103. This may represent a final stage in a ventral shift of the pits.

In the Eucharitidae and Perilampidae the clypeal area is distinctly larger than the normal chalcidoid type, and is uniformly similar in shape and size to the condition shown in Perilampus haylinus (fig.104).

The Agaontidae are a specialized group in which the normal chalcidoid modification is extreme. Both the tentorial pits and the antennal foramina have shifted ventrally, so that the clypeus is reduced to an almost indistinguishable sclerite between the antennae and mandibles.

In the large family Pteromalidae, and in the Eurytomidae, the facial structure is typically as in Amblymerus verditer (fig.107). In some species the clypeus is overlaid with transparent to semi-transparent cuticular material, which is usually thrown up into striae that converge on the median ventral point of the face, as shown in Psychophagus omnivorus (fig.108). In other species this cuticular substance is opaque, and the tentorial pits and the clypeal region cannot be seen beneath it. That the tentorial pits have not shifted from the normal pteromalid position can be seen by dissection and treatment of the head. The black spots in figure 109 represent the points at which the anterior tentorial arms meet the face. Their position was determined by dissection in this species, since they are not visible externally.

In some pteromalid genera (e.g. Trigonoderus) the meso-ventral edges of the genae approach one another along the ventral edge of the face, and in certain species they have come together on the mid-line, obscuring the ventral portion of the clypeus beneath them. An incipient stage in

this modification can be seen in the cynipoid Ibalia ensigera (fig.112). In the pteromalid genus Habrocytus the tentorial pits are deep and distinct. They are in the same relative position as in figure 108, but the clypeal area beneath them has become almost indistinguishable. This may be due to genal encroachment, as outlined above, to cuticular overlaying as in figures 108 and 109, or to a combination of both processes. Genal encroachments of this type are particularly marked and widespread in the Eurytomidae.

It can be seen from the foregoing statement that a facial type in which the tentorial pits cannot be distinguished in untreated specimens can be formed in two ways: (1) by ventral migration of the pits, or (2) by an overlaying of the pits, either with cuticular material, or by genal encroachment. It is often necessary to determine the position at which the anterior tentorial arms meet the face, by dissection and treatment, before a decision can be reached as to which of these modifications has taken place in a given specimen. More or less distantly related forms may thus be very similar superficially in facial structure, and it is important to bear this in mind in morphological and taxonomic studies of these groups.

In the genus Podagrion of the Podagrionidae, the face is very similar to that of Torymus chrysochlorus (fig.105).

In the Chalcididae the tentorial pits are typically near the ventral edge of the face, but a distinct clypeal area is discernible. The pits are often wider apart than is usual in chalcidoids, as they are in Brachymeria coloradensis (fig.110).

The family Leucospidae is represented in the nearctic region by the single genus, Leucospis. In L.affinis (fig.111) the clypeal region is extensive dorso-ventrally, and thus differs markedly from the normal chalcidoid type. Two deep pits, situated an unusual distance above the ventral edge of the face, appear to mark the points at which the anterior tentorial arms meet the face. These are indicated in figure 111 by the star-like, converging lines. Dissection, however, reveals that the actual points of contact between the anterior tentorial arms and the face lie distinctly ventral to these pits. The anterior tentorial arms are extended along the clypeogenal inflection internally as indicated by the arrows in figure 111, and this may indicate that they are undergoing a ventral shift along the inflection. Other evidence suggesting a ventral shift of the tentorial arms is their position ventral to the external pits. Although it is highly unlikely that this change was accomplished in a single "saltation", it is possible that the shift has taken place so recently that the pits have not yet disappeared.

The fact that the Leucospidae are represented by but a single genus in North America suggests that the family may be primitive, since rare and widely distributed families are usually survivors of very ancient similar types, which were at one time more common. This principle must be used with caution in particular cases, however, since in some cases such groups may be specialized rather than primitive.

CYNIPOIDEA (figs.112-115)

The facial structure in the Cynipoidea is relatively uniform. The normal range of variation can be seen in figures 112-115. Cynipoids are very similar in facial type to the chalcidoid family Pteromalidae; the clypeus occupies the same general region and is similar in size and shape in both groups. Genal encroachments (see figure 112), and a tendency for the clypeal area to be overlaid with striated cuticular material, are common in both groups. Where the clypeus is invisible the face superficially resembles that of chalcidoids. All intermediate stages between complete exposure and complete invisibility of the clypeus are present in the Cynipoidea.

PROCTOTRUPOIDEA (figs.116-126)

As listed in Muesebeck et al. (1951), the Procto-

trupoidea is a somewhat miscellaneous superfamily, containing very different facial types.

In the Evaniidae, Gasteruptiidae, Pelecinidae, Vanhorniidae, Roproniidae, Heloridae and Proctotrupidae, the tentorial pits are situated well up in the face and the clypeal area is extensive (figs. 116-119, 125-126).

In the majority of the Ceraphronidae, Diapriidae, Scelionidae and Platygasteridae, the tentorial pits are at or near the ventral rim of the face (figs. 120-124).

These two groups of families are so strikingly different in facial structure that it is doubtful whether or not they should be contained in the same superfamily. Most proctotrupoid families are poorly known, as mentioned in Muesebeck et al. (1951), and when they have been more thoroughly studied the group will doubtless be rearranged in a more natural classification.

The families Evaniidae, Gasteruptiidae, Pelecinidae and Proctotrupidae resemble one another in facial structure, as can be seen in figures 116-118. In all three families there is a strong tendency toward the formation of relatively extensive clypeogenal bridges (B) between the clypeus and genae near the mandibular articulations. These are clearly "cuticular" in origin, since they often differ distinctly

in colour and texture, varying from light brown to black, and are almost always distinctly set off from the clypeus and genae by grooves or sutures. The function of these sclerites in providing rigidity to the head capsule is obvious. Frontogenal sutures are present in the normal position in Gasteruption assectator (fig.117), and have apparently shifted laterally in Pelecinius polyturator (fig. 118), where they extend dorsally to the eyes rather than to the antennal foramina; it is possible, however, that these are malar rather than frontogenal sutures.

The single nearctic species of the family Heloridae, Helorus paradoxus (Provancher), resembles Disogmus canadensis (fig.119), except for the fact that, in Helorus, the clypeo-genal bridge, though present, is less extensive than it is in Disogmus.

In the Ceraphronidae the antennae tend to encroach upon the clypeus and the entire region is folded ventrally. The clypeus is reduced, but is more extensive than in Diapria conica (figs.120-121).

The Diapriidae somewhat resemble the Ceraphronidae, but the clypeus is less extensive and the antennae are situated well above the clypeus. The tentorial pits lie at the ventral edge of the face, and, in Diapria conica sutures

extend dorsally from the pits, become progressively more faint, and come together mesally, as shown in figure 120. The presence of these sutures suggests that a ventral shift of the pits may have taken place, and that the dorsal part of the original inflection has become almost obsolete.

In the Scelionidae and Platygasteridae the antennal foramina lie very near the ventral edge of the face. In other respects they are not essentially different from diapriids or typical chalcids.

Vanhornia eucnemidarum (fig.125) is the sole world representative of the family Vanhorniidae. The peculiar orientation of the mandibles in this species is paralleled only in the dacnusine braconids (figs.55-56) among the Hymenoptera examined. It would be interesting to compare the function of the mandibles in this species with that in dacnusine braconids.

The Roproniidae is also a rare family, represented in North America by the single genus Ropronia. The clypeus in R.garmani (fig.126) is extensive and probably contains cuticular additions beneath the tentorial pits.

CHRYSIDOIDEA (figs.127, 128)

With the single exception of Stilbum cyanurum (fig.128),

all chrysidoid species examined resemble Chrysis coerulans (fig.127). The antennal foramina encroach well into the clypeal area and the clypeus is extended laterally beyond the tentorial pits. In Stilbum the eyes, genae and frons have been elongated ventrally, leaving the antennal foramina dorsal to the clypeus, if it can be assumed to be a modification of the normal chrysidoid type, as its position in the group implies.

BETHYLOIDEA

In this group the antennal foramina and clypeus are uniformly ventral in position, and the face resembles those proctotrupoids shown in figures 122-124.

TRIGONALIDAE (fig.129)

The facial type in the trigonalids seen resembles that of Bareogonalos canadensis (fig.129).

SCOLIOIDEA (figs.130-137)

In this superfamily the antennal foramina lie very near the tentorial pits; in some species they encroach on the clypeal area, as in chrysidoids. The similarity between Chrysis coerulans and Tiphia inornata can be seen by comparing

figure 127 with figures 130-131. It would appear from the facial structure that the two groups are more closely related than is implied by the classification in Muesebeck et al. (1951).

The clypeal area is extensive in scolioids, although its dorsal extent is sometimes reduced, as in figure 131. In some species it occupies a large proportion of the facial area (e.g. figs. 133, 135-137).

There is a strong tendency toward sexual dimorphism in this group, as can be seen by comparing the males and females in figures 130 and 131; 133 and 134; 136 and 137. There is also a tendency for the tentorial pits and antennal foramina to be contained in concavities, and for the frons to project ventrally and laterally over these concavities, apparently as a protective shield. These conditions closely resemble those in the ants, to be discussed below. The female specimen of Dasymutilla fulvohirta (fig.134) is distinctly ant-like in facial structure.

FORMICIDAE (figs.138-149)

The facial structure of ants is copiously illustrated in Wheeler (1910). The conclusions drawn here on the morphology of the face in this group are based largely on Wheeler's illustrations, and on other illustrations in the

literature. Each facial type was also carefully studied from specimens, however, and figures 138-149 are all original.

In the subfamily Formicinae, the facial structure is strikingly similar to that in the proctotrupoid families Evaniidae, Gasteruptiidae and Pelecinidae, as can be seen by comparing figures 147-149 with figures 116-118. Clypeogenal bridges (B) are present in both groups. The position of the tentorial pits and the general conformation of the clypeus is closely parallel in both groups.

The extensive dorso-ventral extent of the clypeus in the Formicinae is unusual in ants. In other subfamilies the antennae and tentorial pits lie much nearer the ventral edge of the face, and many intermediate stages are present between the formicine condition and that represented by Eciton opacithorax (fig.145). In the latter, the clypeus is reduced to a very narrow sclerite extending along the ventral edge of the face between the mandibular articulations. Some of these intermediate stages can be seen by considering figures 148, 149, 147, 138, 139, 141, 144, 146 and 145, in the order given.

There is a strong tendency among the ants for the frons to project in the form of a shield (F.S.) over the antennal foramina. The outer edge of this shield is called the

frontal carina by myrmecologists, and is much used in the taxonomy of the group. Various stages of this modification are present. In the Formicinae only relatively low ridges are present, in a position corresponding to that of the frontogenal suture. In Camponotus abdominalis (fig.147) the ventral extremities of these ridges are uplifted over the antennal foramina. In Paraponera clavata (fig.138) the frontal shield is more fully developed, and in Cryptoceras atratus (fig.140) and in Ectatomma (fig.142) it projects laterally to such an extent that it completely covers the face, thus protecting the antennae, which lie in grooves beneath it. In Atta cephalotes (fig.139) part of the frontal shield is extended in the form of a spine over the antennal groove on each side. The frontal shield varies widely, and assumes many bizarre forms among the ants. It is the most striking feature of the face in many species, and its presence gives the impression of great complexity in formicid facial structure. This complexity is largely superficial, however, and clypeal structure is relatively uniform within the range of variation described above.

In association with the formation of the frontal shield and the antennal grooves, the antennal foramina and tentorial pits often lie in concavities. As previously mentioned, similar concavities, as well as similar tendencies toward the

formation of frontal shields, are present also in the Scolioidea (fig.132-134). The encroachment of the antennal foramina into the clypeal area in many ant species (figs. 141, 144, etc.) is also paralleled in the Scolioidea (figs.130-131), and in the Chrysidoidea (fig.127). It would be interesting to investigate whether these similarities are due to convergent or to parallel evolution.

The complexities of polymorphism in the facial structure of ants were not studied in detail. Males usually resemble the formicine type shown in figures 148 and 149, even where the workers are highly modified. Females often resemble workers more closely than males in facial structure. The widespread tendency for males to approach the formicine type suggests that this is the most primitive facial type, despite the fact that, in other respects (e.g. behaviour) the Formicinae are considered to be the most specialized group of the family. Highly specialized behaviour is not always accompanied by a corresponding specialization in structure, particularly in the case of a structure whose function has remained relatively constant. Human behaviour can be said to be more highly specialized than that of whales or bats in some respects, but human limbs are less specialized.

VESPOIDEA (figs.150-153)

Figures 150-153 show the normal range of variation in facial structure that occurs in this group. The clypeus is always extensive in area, and the tentorial pits are well separated from the mandibular articulations, the former being situated almost directly dorsad from the latter.

POMPILIDAE (fig.154)

The facial structure in this group varies very little around the type shown in figure 154. The median dorsal region of the clypeus tends to extend somewhat above the level of those portions laterad of the tentorial pits. This condition is marked in the sphecoid genus Philanthus (fig.171), in the apoid genus Ceratina (fig.180), and in some other related forms. It may be due to a ventral shift of the tentorial pits from positions resembling those shown in figures 181-185.

DRYINIDAE (figs.174,175)

This little known group was not studied closely. The faces of Dicondylus (fig.174) and Anteon (fig.175) were included for reference purposes, and it will be noted that they resemble sphecoids and apoids less closely than they do ichneumonoids.

SPHECOIDEA (figs.155-173)

The facial structure in this superfamily varies from the condition shown in Astata unicolor (fig.155), in which the dorso-ventral extent of the clypeus is reduced and the antennae are situated very low in the face, to that in Sphex ichneumoneus (fig.160), in which the tentorial pits and antennal foramina are situated well up in the face. Numerous specializations are present, such as the large and prominent labrum of Microbembex (fig.168), the protruding shelf over the median portion of the clypeus in Cerceris (fig.170) (which may be either frontal or clypeal in origin), and the ventral emarginations of the clypeus shown in Oxybelus (fig.172). The basic facial structure, however, is contained within the range outlined above. Many intermediates in dorso-ventral extent of the clypeus are present in the group, as can be seen in figures 155-173. It is very likely that the addition of cuticular sclerites has increased the lateral extent of the clypeus in some species (e.g. figs. 158, 161, 171, 172).

Sphex (fig.160), Sphecius (fig.165), Bicyrtes (fig. 167) and other sphecoid genera approach vespoids and apoids in facial type, while Astata (fig.155), Oxybelus (fig.177), and others approach conditions prevalent in the Formicidae,

Scolioidea and Chrysidoidea. The facial structure thus suggests a common ancestral background for all these groups. Such a relationship is suggested also by similarities in behaviour and other structural features.

APOIDEA (figs.176-185)

The facial structure in this group is relatively uniform, considering the number of species it contains. The basic types present are shown in figures 176-185. The position of the tentorial pits varies from that in Bombus and Apis (figs.182-185) to that in Colletes (fig.176) or Ceratina (fig.180). In none of the specimens seen were the pits noticeably lower than in Ceratina.

A distinct tendency toward ventral extension of the clypeal and genal areas is present in the genus Bombus (figs.182-184). The entire clypeal area appears to have been shifted ventrally in B.fervidus (fig.183) and B.borealis (fig.184).

DISCUSSION

Several facts emerge from the foregoing survey:

(1) The clypeus is "incorporated into the face" (i.e. it does not project ventrally as a free lobe, and the lateral margins are in contact with the genae), in many hymenopteran species.

(2) The clypeal area is greatly reduced in many species.

(3) Various stages in the formation of new sclerites, enlargement of existing sclerites, and the obliteration of sutures, by cuticular secretions, are present in many species.

(4) Similarities in facial structure exist between groups that are widely separated by taxonomists, as indicated by Muesebeck et al. (1951), which must either be due to convergent evolution or to unnatural arrangement in the catalogue.

These will be discussed in turn.

"INCORPORATION" OF THE CLYPEUS INTO THE FACE.

1. External Structure

Very many hymenopteran species fall somewhere between Pleroneura (fig.4) and Apis (fig.185) in facial structure. The Tenthredinoidea and Ichneumonoidea, which comprise about one fourth of the nearctic species of Hymenoptera, do not, on the whole, depart far from the generalized conditions in Pleroneura. In most species of both these groups the tentorial pits and mandibular articulations are not widely separated, the clypeus is distinct, and tends to project ventrally below the level of the remainder of the face. In most Sphecoidea, Vespoidea and Apoidea the tentorial pits and mandibular articulations are widely separated, the clypeus occupies a considerable portion of the facial area, and terminates ventrally at approximately the same level as the remainder of the face. Intermediates between these extremes are common in most superfamilies, and many series could be selected showing a gradual transition from one condition to the other.

It is generally assumed that the facial structure in Pleroneura (fig.4) is the most primitive type, and that all hymenopteran modifications have been derived from such a type. If this is correct, the most prevalent modification,

present in literally thousands of species, is that culminating in Apis, Bicyrtes, etc.

As discussed in the Review of Literature, there has not been complete agreement among morphologists as to the way in which this clypeal modification came into being. The explanation proposed by Snodgrass (1935) has apparently been accepted without question by the majority of teachers and students. As mentioned previously, Snodgrass proposed that the transition from the generalized (orthopteroid) to the Apis types began by an "arching upward" of the epistomal suture, and culminated in a dorsal migration of the tentorial pits to their position in bees and similar forms. That DuPorte and others have questioned this interpretation has already been mentioned.

On the average, in the Hymenoptera, the free distal portion of the clypeus decreases as the distance between the tentorial pit and the mandibular articulation increases. Thus either the clypeus as a whole has moved upward into the face, as implied by Snodgrass (1928, 1935); or the tentorial pits have migrated upward along the frontogenal suture while the distal portion of the clypeus was reduced, as suggested by DuPorte (1946); or else the genae have been extended ventrally on either side of the clypeus until the

clypeus became enclosed between them, as proposed by DuPorte and Bigelow (1953).

Any shift in the position of the tentorial pits would involve a shift in the orientation of the anterior tentorial arms, and would thus require a rather complex readjustment of the internal organs (e.g. muscles) associated with the tentorial arms. There is no doubt that such complex structural changes have taken place, but the hymenopteran modification in question can be explained in another way. It can be assumed that the tentorial pits and tentorial arms remained relatively stationary while the genae were extended ventrally on either side. Such a change would not disrupt the orientation of the internal organs of the head, and would involve only the development of an auxiliary structure to act as a brace between the tentorial arms and mandibular articulations.

Ventral extensions of the genae have certainly occurred in the Hymenoptera, as witnessed by the braconid genera Agathis and Cremnops (figs.48-51). Conditions in many sawfly species are apparently incipient stages in such a modification. It is at least as reasonable to assume that the genae have been extended ventrally in these sawfly species, as it is to assume that the tentorial pits have migrated upward.

Possible selective advantages of ventral extension of the genae would be increased space for ventral enlargement of the eyes, and increased space for the development of accessory pharyngeal organs. The unusually large eyes in the Hymenoptera in general suggests that in many cases enlargement of the eyes may have been the basic cause of a ventral extension of the genal areas.

In the ichneumonid subfamily Pimplinae (figs.62-67), there is a marked variation in the relative positions of the eyes and the clypeal area. As previously mentioned, these differences may be interpreted in several ways.

It could be assumed that there has been a decrease in the size of the eyes from the conditions in figure 67 to those in figure 62. It is obvious that the eyes have decreased in size in some Hymenoptera, notably in the Formicidae. On the other hand, an increase in the relative size of the eyes is equally obvious in many sphecoids, apoids and others. The adoption of more or less subterranean habits, and loss of the power of flight, has almost certainly been associated with ocular reduction in the ants. The highly developed power of flight has similarly been associated with increased size of the eyes in bees, sphecoids, etc. The pimpline ichneumonids in question resemble bees and sphecoids more closely than they do ants in these respects, and therefore

it is logical to conclude that any changes in relative eye size in this group would most likely be toward an increase rather than a decrease.

It could also be assumed that there has been a decrease in the extent of the genal areas from the conditions in figure 62 to those in figure 67. This would involve a dorsal migration of the clypeal area, and is held to be unlikely on the grounds already discussed.

It is possible that the genal areas have descended in figure 62 without a corresponding increase in eye size, and that the increase in eye size has not been accompanied by ventral extension of the genae in figure 67. It is maintained here that both these suggestions are valid. Ventral extension of the genae, far beyond the ventral extremities of the eyes, has certainly occurred in the Hymenoptera, notably in Cremnops (fig.51). Possible advantages of such an extension, apart from making ventral increases in eye size possible, may be the creation of internal space for the development of pharyngeal and other organs associated with feeding. On the other hand, increases in eye size are likely to precede ventral extension of genal and frontal areas in many cases. It is reasonable to assume that the tentorial pits and mandibular articulations will tend to retain their positions until such time

as changes in adjacent integumental structures confer a selective disadvantage on those positions. Enclosure of the mandibles between the eyes is obviously disadvantageous. There is, of course, no possibility that this could ever occur, since such forms would be unable to survive, and the ventral shifts of the genae and mandibles would take place more or less simultaneously. However, it is likely that the mandibles are forced to descend as a result of the descent of the eyes, and the latter change would most likely be the cause of the former. It is possible that in some cases ventral enlargements of the eyes may have initiated ventral extensions of the genae while in other cases they have not, and this appears to have been the case in the genus Pimpla.

Not every structural change confers an additional selective advantage, and some animal structures are known to be distinctly disadvantageous. Disadvantageous structural features may evolve through genetic association of these with the evolution of other, advantageous characters. Therefore, morphological explanations cannot be declared as invalid merely on the grounds that they involve apparently disadvantageous changes. However, there is a large body of evidence in support of the view that the overall pattern of evolution is adaptive. Even where altered

conditions of life have rendered formerly adaptive characters disadvantageous, subsequent changes in such characters are usually adaptive in the sense that the disadvantageous characters are usually reduced or transformed into neutral or advantageous characters.

In a choice between two possible explanations of a given structural change, one of which involves an apparent selective disadvantage and the other an apparent advantage, it is held here that the latter should be favoured as more likely until definite evidence to the contrary is available.

In any case, it is certain that ventral extensions of the genal regions have taken place in the Hymenoptera. As mentioned above, the conditions in the braconid genera Agathis and Cremnops (figs.48-51) can be interpreted in no other way, and such conditions recur in the ichneumonid genera Coccygomimus, Hoplismenus, Pristomerus, and Cremastus, as well as in the apoid genus Bombus. That a similar tendency toward ventral extension of the genae probably had very ancient beginnings in the Insecta was proposed by DuPorte (1946) in his discussion of the possible manner of origin of the frontogenal suture. It is therefore reasonable to conclude, with DuPorte and Bigelow (1953), that the clypeal structure in bees, sphecoids and vespoids has been the result of the genae enclosing the clypeus on either side,

and not the result of an upward arching of the epistomal suture, followed by a dorsal migration of the tentorial pits, as implied by Snodgrass (1928, 1935).

2. Internal Structure

(i) Clypeogenal inflections

Separation of the tentorial pits and mandibular articulations creates the need for an auxiliary structure to retain the original rigidity against mandibular action, as mentioned above. This has been accomplished in the Hymenoptera by the anatomical development of elongations from the ventral portions of the tentorial arms, at the point where the latter meet the face (see figures 190, 197, 198, c.g.i.). These extensions from the tentorial arms form braces between the latter and the mandibular articulations. Their development can be seen very clearly in sawflies, as described in the survey of the Tenthredinoidea, and illustrated in figures 21, 22, 24, 197. In some species they can be seen externally as well as internally, and are completely continuous with the tentorial arms. Their appearance can be readily understood on the assumption that the genae have been extended ventrally below the original level of the mandibular articulations, and that the mandibles were correspondingly shifted ventrally. It is also obvious that the

most direct way to achieve such a shift in the mandibular articulations is by ventral prolongation of the tentorial arms (in the form of the clypeogenal inflections). A ventral shift of the tentorial arms as a whole may have the same effect, but as this would involve a much more complex readjustment, affecting internal organs as well as the integument, it is more likely that the initial adjustment was accomplished by the formation of the clypeogenal inflections. This has apparently occurred in many Hymenoptera. These inflections are extensive in bees, sphecoids and vespoids, where the tentorial arms themselves are almost horizontal in orientation. The clypeogenal inflections are particularly marked in these forms, and apparently provide as efficient a brace against mandibular action as was perhaps originally provided directly by the tentorial arms. The selective disadvantage involved in the separation of the tentorial arms and mandibular articulations was apparently offset by the greater advantage of increased genal area, and the end result was the efficient structural design in bees, wasps, and sphecoids.

(ii) Anterior Tentorial Arms.

Snodgrass (1928) described the tentorium of orthopteroid insects as "a horizontal, X-shaped brace between the lower edges of the cranial walls." As orthopteroid insects are

considered to be generalized, i.e. primitive, in facial structure, this implies that the hymenopteran tentorium was also horizontal before the clypeus became incorporated into the face. A diagrammatic illustration of the generalized, horizontal, orientation of the tentorium is shown in figure 186. Assuming, then, with Snodgrass, that the hymenopteran tentorium was primitively horizontal, and, also with Snodgrass, that the tentorial pits have migrated dorsally from this position to that in the honey bee (fig.185), it is reasonable to expect the anterior tentorial arms in the honey bee to be tilted upward from the occipital foramen to the anterior edge of the face. It can be seen in figure 190, however, that this is not the case. The tentorial arms are tilted distinctly downward. If the pits have migrated dorsally in this case, then it follows that the occipital foramen must also have migrated dorsally, and that the dorsal portions of the cranium were similarly extended dorsally. By this reasoning, the entire head, except for the ventral rim, has migrated dorsally. This is like explaining a train journey from A to B by saying that the train remains stationary while the world moves past. It is simpler to assume that the ventral rim of the head has been extended ventrally.

Consideration of figures 186-196 shows that there is

considerable evidence in the Hymenoptera suggesting a ventral migration of the tentorial arms from an originally horizontal position, but no evidence of a similar dorsal migration, even where the tentorial pits lie well above the mandibles, as in figure 188-190. The tentoria in many species, including representatives from all superfamilies, were examined in the course of this study, and in every case the course of the anterior tentorial arms was anterior and ventral from the occipital foramen to the tentorial pits.

That the tentorial arms were probably more or less horizontal in the immediate ancestors of the Hymenoptera is attested by their horizontal orientation in generalized insects such as Orthoptera (fig. 187), and Snodgrass and others were not unreasonable in making this assumption. The tentorial arms may not, however, have been so nearly horizontal as is implied in figure 186. They may have been tilted somewhat downward, as in the sawflies (e.g. fig.191).

What the actual orientation of the tentorial arms may have been in the immediate ancestors of the Hymenoptera can only be surmised. It was probably also variable in those ancestors. In any case, a dorsal migration of the tentorial pits would involve a dorsal migration of the tentorial arms. If the condition in Diprion hercyniae (fig.191) is taken as the most primitive, and if the tentorium

alone is considered (ignoring the arguments against dorsal migration discussed above), it could be assumed that a dorsal migration has taken place from the condition in figure 191 to that in the honey bee (fig.190). It is equally likely, however, that a ventral migration of the arms and pits has taken place in the ancestors of Diprion hercyniae. Although dorsal migration of the pits would confer no apparent advantage, ventral migration would tend to regain the original close contact between the anterior arms and the mandibular articulations. Any shifts in the tentorial orientation would involve more complex internal adjustments, and would therefore require a longer time, than would changes involving the exterior integument alone. Therefore, the initial adjustments to the separation of the tentorial pits and mandibular articulations would most likely involve only external, integumental parts. Extensions of the clypeogenal inflections along the face would be more likely than shifts of the arms as a whole. Over longer periods of time, however, it is possible that the arms may shift ventrally, to increase their efficiency as a brace against mandibular action, or for other reasons. It is thus possible that, in the honeybee, the tentorial arms have retained an original horizontal, orientation, whereas in Diprion hercyniae they have shifted ventrally.

REDUCTION OF THE CLYPEUS

A tendency for the reduction of the clypeus is almost as widespread in the Hymenoptera as is the tendency for its "incorporation" into the face. In most species of the large subfamily Chalcidoidea, and in the proctotrupoid families Ceraphronidae, Diapriidae, Scelionidae and Platygasteridae, the tentorial pits lie at the extreme ventral edge of the face, and no clypeal lobe extends beyond this level. In these forms the clypeus has been excluded from the face, except insofar as the ventral rim of the face between the tentorial pits probably still functions as a strengthening mechanism.

This reduction of the clypeal region could be explained on the assumption that the free distal extremities of the clypeus have merely been lost. If this view is accepted, it must also be assumed that the occipital foramen has migrated dorsally to a great extent in order to explain the very marked antero-ventral orientation of the anterior tentorial arms (see fig.194). What appears to be dorsal migration of the occipital foramen has certainly occurred, not only in chalcidoids, but also in bees, wasps, sphecoids and other Hymenoptera. Here again, however, the

most likely explanation is to assume a ventral extension of the postgenal areas beneath the occipital foramen. There is no doubt that such extensions have taken place, and they have been discussed by Snodgrass (1935), Ross (1937) and others. The ventral closure of the occipital foramen by these postgenal extensions is called the hypostomal bridge by Snodgrass, and the genaponta by Ross. Where the postgenae have been extended ventrally to a greater extent than have the genae, the head may tend to be "tilted forward", and the clypeal region may appear to have migrated ventrally. This has undoubtedly taken place in many Hymenoptera, and is very likely one of the underlying causes of the tentorial orientation in chalcidoids. However, it is also very likely that the genae as well as the postgenae have been extended ventrally in chalcidoids and other Hymenoptera, and, if so, a ventral migration of the tentorial arms may be assumed in order to explain the position of the tentorial pits at the ventral rim of the face. The highly specialized orientation of the tentorium in chalcidoid types is probably the result of both ventral extensions of the postgenae and ventral migrations of the tentorial arms.

It would appear that, in chalcidoid types, the clypeus was reduced in size while the frons and genae were extended ventrally and mesally above and beside it. That such tendencies toward genal encroachment on the clypeal area

exist in chalcidoid types is evidenced by the marked genal encroachments present in the Pteromalidae and Cynipoidea. Frontal encroachments on the clypeal area are present in chrysidoids, ants, and sphecoids, and thus very likely occur also in chalcidoids. Ventral migration of the entire clypeal area is easily explained on the grounds that the integument is increased in extent above, rather than below, the tentorial pits.

If the clypeus has been reduced in the chalcidoid face by both frontal and genal encroachments, it must previously have been "incorporated" into the face.

This brings us to the consideration of the question: which of these two modifications is the most primitive? The chalcidoid condition probably did not arise directly, by mere loss of the clypeal area, as witnessed by (1) the extreme antero-ventral orientation of the tentorial arms, (2) the presence of an "incorporated" clypeus in Perilampus (fig.104), in pteromalids, and in Leucospis (fig.111), (3) the presence of an "incorporated" clypeus in the more generalized sawflies, and (4) the fact that the minute size and highly specialized parasitic way of life are obviously not primitive.

It is thus reasonable to conclude that the clypeus was "incorporated" into the face in ancestors of chalcidoids.

This sequence has probably been followed in other Hymenoptera as well. In ants, the clypeus of males (which are winged, and otherwise more similar to the less specialized Hymenoptera) is usually "incorporated" into the face, even in species in which the workers are highly specialized and the clypeus greatly reduced. In ants, chrysidoids, sphecoids, and proctotrupoids, the antennal foramina often encroach into the clypeal area. There can be little doubt that this is a specialized condition and thus that the clypeal area has been reduced from above.

In many sphecoids a ventral migration of the tentorial pits has also been common, if it can be assumed that such forms as oxybelines and crabronines are specialized in facial structure rather than primitive. In many sphecoids the tentorial arms are extended along the clypeogenal sutures, often some distance below the dorsal limits of the latter.

In the ichneumonid subfamily Gelinae, a trend either toward or away from the lens shaped clypeal structure of the typical geline face is probably taking place in Bathythrix and in the Acroricnus to Trachysphyrus trend (figs. 84-85; 80-82). If the trend is away from the typical gelines, then the pits are migrating dorsally; if it is toward the typical gelines, they are migrating ventrally. It is proposed here that the latter is more likely on the grounds discussed above,

including the undoubted presence of ventral shifts of the tentorial pits in closely related forms such as Cremnops.

The possibility that dorsal migration of the tentorial pits may have occurred in some hymenopteran lines is not denied here. Structural change will follow any course that offers selective advantage, and if dorsal migration of the pits confers such an advantage, directly or indirectly, it will probably take place. The tentorial pits have almost certainly shifted dorsally in certain non-hymenopterous lines, and may have done so in some Hymenoptera as well.

It is proposed that the evolution of facial structure in the Hymenoptera has, in most lines, proceeded first from conditions similar to those in Pleroneura (fig.4) toward an "incorporation" of the clypeus into the face as in sawflies, etc. From this condition it is proposed that two divergent modifications have occurred: (1) in some lines toward a continuation of the incorporation of the clypeus into the face and (2) in others toward a reduction of the clypeal area, involving a ventral shift of the anterior tentorial arms.

It has been mentioned in the Survey of Facial Structure that extension of the tentorial pits along the clypeogenal suture suggests that a migration of the pits is taking place. The grounds for this suggestion are as follows: When the

tentorial arms migrate, it is unlikely that they do so in a series of "saltations", or in a single "saltation". It is held to be more likely that complex structural changes occur gradually, while the genetic constitution of the animal makes the necessary adjustments. Therefore, as the tentorial pits gradually migrate along the clypeogenal suture, it is assumed that the pits are first extended in the direction of migration, and then closed behind. The tentorial arms are thus elongated along the clypeogenal inflections and readjustments of associated internal organs can be effected before the old limits of the arms have been altered. When these adjustments have been completed, those parts of the arms away from the direction of change will leave their old positions and the external pits will close behind them. Extension of the tentorial pits along the clypeogenal sutures is present in many hymenopterous groups. It is present in ichneumonoids such as Exetastes (fig.196), Acroricnus (fig.80), Listrognathus (fig.81), Trachysphyrus (fig. 82), Bathythrix (fig. 85), Agathis (figs. 48-50) and Cremnops (fig. 51); in chalcidoids such as Eupelmella (fig.103), Torymus (fig.105) and Leucospis (fig.111); in sphecoids such as Gorytes (fig.166) and Crossocerus (fig.173); and in many others.

In the Agathis to Cremnops trend (figs.48-51) there can be no doubt of a ventral shift, and the tentorial pits are consistently elongated.

In chalcidoids at least some ventral migration of the tentorial arms has almost certainly taken place, and where the pits lie dorsal to the ventral rim of the face they are often elongated dorso-ventrally, with the internal ventral extremities of the tentorial arms at or near the ventral rim of the face.

It is not maintained that a shift in the orientation of the tentorial arms is taking place in every instance where they are elongated along the face; it is merely suggested that such a shift is probably under way in some cases. The direction of the shift could, of course, be either dorsal or ventral. In the Hymenoptera, it is proposed that the direction of the shift is most often ventral.

FORMATION OF SCLERITES

The appearance of additional cuticular material was noted repeatedly in the course of the Survey of Facial Structure. This has certainly taken place in the Tenthredinidae, Siricidae, Ichneumonidae, Chalcidoidea, Cynipoidea, Proctotrupeoidea, Scolioidea and Formicidae, and probably also in many other Hymenoptera.

All intermediate stages between almost complete transparency and complete opacity of the cuticular material in question are present in different specimens of single

tenthredinid species (e.g. Ametastegia inornata (Say), Aphilodyctium fidum (Cresson), Allantus cinctus (L.), etc.) Differences were observed between opposite sides of the clypeus in single specimens (e.g. Eriocampa juglandis (Fitch), Hemichroa crocea (Fourcroy)). In one specimen of Hemichroa crocea the cuticular material between the clypeus and genae was semi-transparent. After boiling this specimen in caustic potash and leaving overnight in water, this same material became jet black and absolutely opaque. It was still clearly distinguishable, however, since it was more smooth and shiny than adjoining parts of the clypeus and genae. It had, in fact, become identical with conditions present in many pinned specimens. Similar conditions exist in rhyssine ichneumonids, chalcidoids, cynipoids and others, and there can be little doubt that the resulting sclerites were formed relatively rapidly, and at a late stage of pupal development. In the pimpline ichneumonid Pseudorhyssa sternata (fig.68), the limits of a typical pimpline clypeus can be distinctly seen beneath transparent cuticular material in some specimens, whereas in other specimens these limits are completely obscured beneath a hard, opaque clypeogenal bridge. Similar conditions are present in Centeterus tuberculifrons (fig.86). In the proctotrupoid families Evaniidae, Gasteruptiidae and Proctotrupidae extensive clypeogenal bridges (B) have been formed above the mandibular articulations between the clypeus

and genae. These clypeogenal bridges are superficially similar in shape and position to the "clypealia" of MacGillivray (1923), the "paraclypeal lobes" of Crampton (1921) and of Cook (1943). The latter terms, however, are based on conditions in the larvae of the neuropteran genus Corydalid and its near relatives, where they are lateral portions of the clypeus that have secondarily been cut off by the extension of the frontal sutures (ecdysial lines) across the clypeal area. They are therefore essentially different from the clypeogenal bridges described here.

It is clear from the results of this study that, in the Hymenoptera, these clypeogenal bridges serve to cement the edges of the clypeus and genae, when the genae have descended below the original position of the mandibular articulations. Prior to this descent of the genae, the sclerites almost certainly did not exist. Since virtually all stages of ventral descent of the genae are present within the order Hymenoptera, it is reasonable to conclude that both the genal descent and the resulting clypeogenal bridges have appeared relatively recently in some forms. The fact that the secretion of the cuticular material from which they are formed takes place at a late stage of pupal development further supports this view.

In the Pteromalidae and in the Cynipoidea, similar

cuticular additions have taken place, apparently at a late stage of development. In these groups the entire clypeal area has been overlaid. In species in which the cuticular material has become hard and opaque, the clypeus and tentorial pits are completely hidden beneath it.

Cuticular secretions of this kind are not difficult to understand. They are merely continuations of the normal process of cuticle formation. The entire integument, in fact, is formed in much the same way in all sclerotized insects. It is interesting that, before the genetic mechanisms underlying the formation of previous structures has been altered, this tendency for cuticular additions has appeared. This is in accord with the view that initial adjustments to new needs will be made in the simplest manner possible, and that more fundamental changes, involving greater readjustments of the genetic constitution, will tend to occur more slowly. When the genetic constitution has become fully adjusted to the new conditions, "pioneer" devices like the cuticular secretions in question will be indistinguishably blended into the normal process of development, i.e., traces of the old structural configuration in adults will tend to disappear.

The fact that new sclerites can be created and sutures completely hidden, through the very simple and rapid means

of additional cuticular secretions, has important implications for the science of insect morphology in general.

Since Ferris (1942), and others, assume that grooves and sclerites of the insect integument are extremely stable structures, it is advisable to discuss the possible validity of this assumption more fully.

The term sclerite is defined by Torre-Bueno (1937) as "any piece of the insect body wall bounded by sutures". By Snodgrass (1935), it is defined as: "any of the large or small sclerotized areas of the body wall," and also as "any sclerotized area of the body wall, or of internal parts derived from the body wall." Snodgrass (1935) also describes sclerites somewhat more fully as follows:

"The arthropod body wall is reinforced by a cuticula covering its outer surface. The cuticular substances are products of the body wall cells, but the protective layer formed by them becomes the most important part of the integument, and the matrix cells, after having generated the cuticula, take a subordinate place in the tegumentary structure. The cuticula may be entirely soft and flexible, but characteristically it becomes sclerotized, or hardened in certain areas, forming body-wall plates, or sclerites. The sclerites, which usually have definite shapes and interrelations, constitute the exoskeleton of the arthropod and play an important role in the motor mechanisms of the animal."

From this it can be seen that in every individual insect, the integument is at first a more or less homogeneous sheet of cells, and that these epidermal cells then secrete the cuticular substances which eventually make up the integument. In certain areas these cuticular substances become sclerotized. In most insects the sclerotization occurs over the greater part of the animal's exterior, with unsclerotized, membranous areas intervening between regions that are capable of moving relative to one another. The sclerotization process is now known to be the result of the successive secretion of certain chemical substances which interact to form the hard, sclerotized plates called sclerites. In the membranous regions, the epidermal cells do not secrete all the substances necessary for this process, and consequently the cuticle above them remains soft and pliable. The epidermal cells are therefore the primary structures, and the sclerites they produce through their secretions are clearly secondary. When it is assumed that a given sclerite has retained its individuality during many millions of years, it must therefore be assumed that the epidermal cells from which it has always been formed have also remained distinct and separate from the neighboring epidermal cells of neighboring sclerites. It must be assumed that, for some reason, the tendency to secrete the materials necessary for the sclerotization process has remained more or less

fixed and immutable in these cells, for if it is assumed that this tendency might be altered in any group of cells according to the demands of natural selection, then the concept of such extreme stability and individuality of sclerites becomes meaningless. I have been unable to find in the literature any explanation of why sclerites retain their individuality despite the fusion and loss of individuality of the original segments on which they presumably were borne. It is more reasonable to assume that structures are dynamic rather than static, that they tend to undergo profound changes rather than to retain, despite changes in adjoining structures, and in the environment as a whole, some hypothetical individuality or morphological identity.

Perhaps no contemporary insect morphologist will deny that, in some cases at least, secondary grooves and inflections have appeared in the insect integument in association with new or altered muscular action, or with new or altered needs for rigidity in certain places. Most morphologists will agree that such grooves and inflections have appeared separately in different insect lines, and that they are not necessarily homologous except within closely related groups. Some of these same morphologists, however, will then proceed directly to the comparative study of such grooves on the assumption that at least some of them were present in very remote ancestors of insects, without clarifying how they are able to differentiate between the primary and the

secondary grooves (e.g. Crampton, 1928; Ferris, 1942). It is of course possible that certain grooves, superficially similar in distantly related arthropods, and frequently present in many arthropods, were present also in the remote ancestors of all these arthropods. It is at least equally possible, however, that grooves have appeared and disappeared many times in the course of the evolutionary changes that must have taken place in the millions of years since these changes have followed their distinct and separate ways. There is no direct evidence that an "original quota" of sclerites, from which all others were derived, as implied by Audouin, Comstock and Kochi (1902) and Comstock (latest revision, 1948), ever existed. There is ample evidence that sclerites and integumental grooves have been formed in association with functional changes. It is thus logical to think of the ancestral integument of insects as a more or less homogeneous, unsclerotized, covering of the animal, as it is today in earthworms, and to assume that sclerotization took place differently in different evolving lines, according to differences in the forces of natural selection affecting those lines. If this can be assumed, integumental grooves cannot logically be considered as valid characters for the comparison of distantly related forms, as they are by Ferris (1942).

It is therefore maintained that the insect integument should be used in comparative morphological studies only

within its natural limits. Since many of the external configurations it assumes have developed, in all probability, independently in different evolving lines, these integumental configurations should be used as a criterion for comparative morphological studies only within those groups in which the configurations in question clearly have the same origin. The only evidence we have for assessing the probable stability of such structures in insects is the consistency of the presence of these structures in existing forms. If a given structure is present in the vast majority of species of a certain group it can validly be regarded as a stable structure, where that particular group is concerned, but superficially similar structural configurations, present in only a few specimens from each of several distantly related groups, cannot logically be assumed to be stable, or primitive, structures.

There is a great dearth of fossil evidence upon which evolutionary conclusions can be based in the case of the insects. On the other hand, there is a great wealth of evidence, in the form of many thousands of existing species, upon which comparative studies can be based. It would therefore seem reasonable to suggest that we should begin from today and work backward in our attempts to unravel the evolutionary story of insects, rather than to attempt first

to establish the unknown ancestral conditions. If fossil evidence were sufficiently complete, it would be preferable to begin with the past and work our way toward the present; but unfortunately this evidence is not sufficiently complete.

Most comparative morphological studies of insects have either assumed that certain hypothetical ancestral conditions preceded existing conditions, or have attempted to establish these very remote ancestral conditions. It is maintained here that remote ancestral conditions, especially in variable characters such as configurations of the insect integument, cannot be understood on a firm, scientific basis until more recent ancestral conditions have been firmly established by the comparison of existing forms. It is believed that ample evidence exists upon which conclusions can be based as to the probable course of evolutionary development of characters that are variable, but clearly related, within restricted groups; but it is held that we can only trace modifications within the groups in which they are known to have taken place. We cannot assume that the same modifications have taken place in all groups, or that all characters of the integument present in existing forms were present also in the common ancestors of all these existing forms, as Ferris (1942) claims. Therefore we must begin from the firm basis of existing insects and work our way backward as far as possible into the dimly seen past.

We will probably be able to trace certain characters only a relatively short distance backward through time. Others we will be able to trace farther. We should at any rate determine to the best of our ability how ancient a given character is before we assume that it was present in the remote ancestors of all insects.

The avowed object of morphology is to arrive at an understanding of structure as it appears in existing forms. This understanding is necessary from a taxonomic point of view; before we can classify animals in a natural, meaningful system, we must determine their relationships. The animals we should understand first are those alive today, and in the absence of fossil evidence, we must confine ourselves very largely to the study of these living forms. We have much to learn about the morphology of existing insects, and we have a great wealth of evidence from which to learn it. We have virtually everything to learn about the remote ancestors of existing insects, but almost the only evidence from which we can hope to learn it are the existing species themselves. We have no choice but to wait until we know more about extant forms before we can start from the past and work logically forward in insect morphology.

CONVERGENT OR PARALLEL EVOLUTION

Convergence, in the sense used here, means the independent development of superficially similar structures in different evolving lines. If the common ancestors of two species did not possess a structural feature that is now common to both, the similarity is the result of convergent evolution. If the common ancestors of two species did possess a character now present in both species, the similarity of the character in the two species is the result of parallel evolution. Convergent characters are thus analogous, and parallel characters homologous. Convergent similarities usually suggest a closer relationship than actually exists. Parallel similarities are usually more indicative of near relationship than are convergent similarities. It is thus important, both in taxonomy and morphology, to consider whether or not a given similarity is convergent or parallel before using it as a criterion of close relationship. Whales resemble fish more than they resemble mammals in certain features, but as these similarities are known to be convergent rather than parallel, they are given less taxonomic and morphological weight than certain other characters, which are known to be parallel.

In the course of this study, similarities in facial

structure have been noticed between hymenopteran species that are widely separated by taxonomists, as indicated by Muesebeck et al. (1951). In some instances these similarities may be parallel, and hence the species concerned should be placed nearer one another in the catalogue. In other instances, the similarities are certainly convergent, having developed independently in different lines.

No conclusions will be drawn here as to whether or not a given similarity is convergent or parallel, but some of the more noticeable similarities will be mentioned.

The braconid genus Ephedrus (fig.38), of the subfamily Aphidiinae, resembles the majority of the Microgasterinae more closely in facial structure than it does the majority of the Aphidiinae.

The mandibular orientation in the proctotrupoid Vanhornia (fig.125) is essentially like that in the dacnusine braconids (figs. 55, 56). As this is a very unusual modification, it would be interesting to compare the habits and structures of these two groups.

The pimpline facial type represented by figures 62-74 is consistently present in the subfamily Diplazoninae, which is widely separated from the Pimplinae in the catalogue. The pimpline structure is also consistently present in the

tribes Adelognathini, Phrudini, and Phytodietini, of the subfamily Tryphoninae, but not in other tryphonine tribes.

The rhyssine facial type is present in the genus Rhyssa (figs. 69, 70) of the Rhyssini, in Pseudorhyssa (fig. 68) of the Pimplini and in Clistopyga and Zatypota of the Polysphinctini. In the latter two tribes, not all genera show rhyssine facial characteristics.

Diacritus muliebris (fig. 74) of the Pimplinae is more similar to many tryphonine species in facial type than it is to other pimpline species.

Chrysidoids (fig. 127), scolioids (figs. 130-131), sphecoids (fig. 155), formicids (figs. 141, 144), gasteruptiids (fig. 117) and peleciniids (fig. 118) share similar facial characteristics, in that the antennal foramina encroach upon the clypeal area in some species from all these groups.

The ichneumonid subfamilies Orthocentrinae and Metopiinae, as well as a number of proctotrupoid families, resemble chalcidoids; pteromalids resemble cynipoids more closely than they do other chalcidoids.

The tendency toward ventral extension of the frontal, clypeal and genal areas that is so marked in the braconid genera Agathis and Cremnops is present also in the apoid

genus Bombus, and in a number of other widely separated hymenopteran genera. Some of these similarities are clearly convergent.

Facial structure is apparently a valid ordinal character in the Hymenoptera, and thus may be a valid criterion for the classification of categories above the genus. Surveys of similar character complexes, including the entire order, and the subsequent comparison of results with those derived from facial structure, might provide information that would be useful in the classification of these higher categories.

SUMMARY AND CONCLUSIONS

1. The clypeus, in the Hymenoptera, is that region of the face between the clypeolabral, frontoclypeal and clypeogenal sutures. The position of the clypeogenal sutures, when they are invisible externally, can usually be determined from the position of the clypeogenal inflections, which extend between the anterior mandibular articulations and the anterior tentorial arms along the interior surface of the face. The position of the frontoclypeal suture, when invisible externally, can often also be determined from the position of a corresponding internal inflection, connecting the anterior tentorial arms.

The anterior tentorial arms, and the related frontoclypeal and clypeogenal inflections, form a distinct supporting structure that provides rigidity to the anterior ventral region of the face between the anterior mandibular articulations. These structures determine the dorsal and lateral limits of the clypeus. Since the integument of the frons and clypeus has not been shown to be derived from two distinctly different sclerites, the boundary between these two regions may be defined by the positions of the anterior tentorial pits. If no

frontoclypeal sulcus or inflection is present, this boundary should be taken as a straight line between the anterior tentorial pits. The ventral limits of the clypeus can be determined in nearly every species of Hymenoptera from the position of the distinct clypeo-labral suture.

2. "Incorporation" of the clypeus into the face has been accomplished in the Hymenoptera by ventral extension of the genae below the level of the anterior tentorial pits, and by a corresponding ventral shift in the anterior mandibular articulations. It has not been accomplished by a dorsal arching of the epistomal suture and a dorsal migration of the tentorial pits, as proposed by Snodgrass (1928, 1935). "Incorporation" of the clypeus into the face has preceded its reduction in many hymenopteran forms.
3. Reduction of the clypeus has been accomplished by ventral migration of the anterior tentorial pits to the ventral rim of the face. This ventral shift of the clypeal region has been augmented, in many cases, by ventral extension of the frontal region above the level of the pits, and by mesal encroachments of the genae. Frontal encroachments on the clypeal area are common in the Hymenoptera.

4. Integumental grooves, and the sclerites formed between these grooves can be obliterated or lost relatively quickly, and are therefore not valid characters for the comparison of very distantly related groups.
5. Similarities in facial structure exist between groups that are widely separated by taxonomists, as indicated by Muesebeck et al. (1951), which must either be due to convergent evolution or to unnatural arrangement in this catalogue.
6. Surveys of other character complexes, based on ordinal rather than generic characters, should, when compared with the results obtained from the facial structures, provide useful evidence for the natural classification of the higher categories.

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TAXONOMIC LITERATURE

Hundreds of taxonomic papers were consulted in the course of this study, for anatomical details of facial structure. Of these, a few should be mentioned here. Ross (1937) on Symphyta, Weld (1952) on cynipoids, Wheeler (1910) on ants, and Michener (1944) on bees, were particularly helpful. Where specimens were not seen from certain groups, the facial structure was sometimes inferred from figures or descriptions in the literature. In these cases, the papers are indicated in the appendix and in the bibliography. In groups where specimens were seen, references to the corresponding literature that was consulted are omitted.

PLATES

Unless otherwise specified, all figures represent the anterior aspect of the face. Unlabelled structures may be inferred from the labels in figure 1.

ABBREVIATIONS

- A - integumental apophysis
- a.a.t. - anterior tentorial arm
- a.d. - antennal depression
- a.f. - antennal foramen
- a.m.a. - anterior mandibular articulation
- a.t.p. - anterior tentorial pit
- B - clypeogenal bridge
- C - clypeus
- c.g.i. - clypeogenal inflection
- d.a.t. - dorsal tentorial arm
- d.t.p. - dorsal tentorial depression
- F - frons
- f.c.i. - frontoclypeal inflection
- f.c.s. - frontoclypeal sulcus
- f.g.i. - frontogenal inflection
- F.S. - frontal shield
- G - gena
- L - labrum
- M - mandible
- Max. - maxilla
- Max. palp. - maxillary palpus
- m.i. - malar inflection
- o.f. - occipital foramen
- P - pleurostomal sclerotization
- PG - postgena
- p.m.a. - posterior mandibular articulation

PLATE I

PLATE I.

Fig. 1. Diagram of anterior aspect of hymenopterous face.

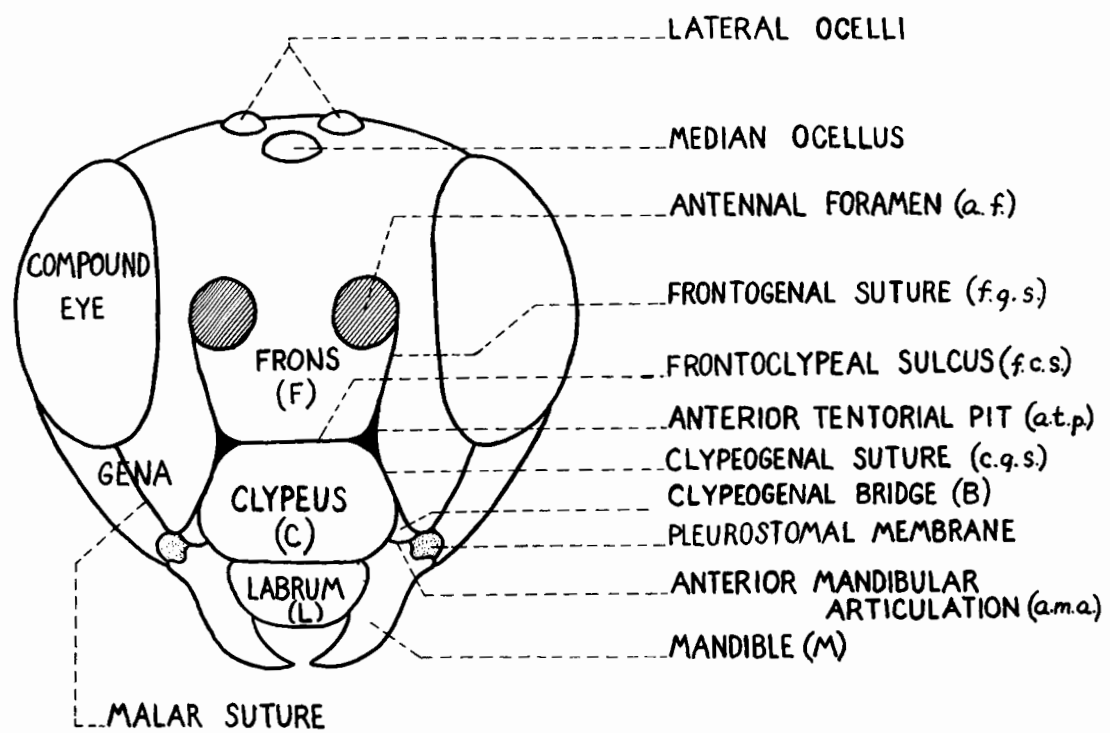


PLATE II

PLATE II.

Fig. 2. Rhomalea sp., Orthoptera.

Fig. 3. Rhomalea sp., anterior aspect of clypeus and
labrum, enlarged.

Megalodontoidea

Fig. 4. Pleroneura aldrichi Ross, Xyelidae.

Fig. 5. Cephalcia fascipennis (Cresson), Pamphiliidae.

Tenthredinoidea

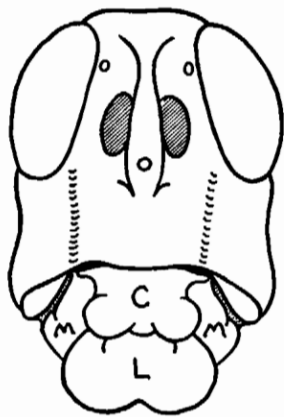
Fig. 6. Arge clavicornis (Fabricius), female, Argidae.

Fig. 7. Sphacophilus plumiger (Klug), Argidae.

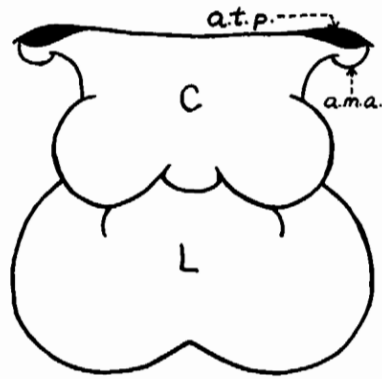
Fig. 8. Zaraea americana Cresson, female, Cimbicidae.

Fig. 9. Trichiosoma triangulum Kirby, Cimbicidae.

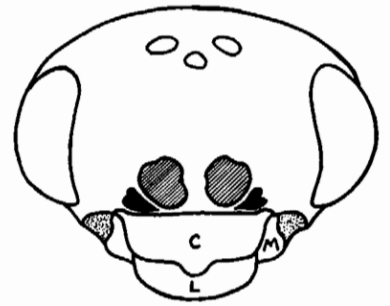
Fig. 10. Cimbex americana Leach, Cimbicidae.



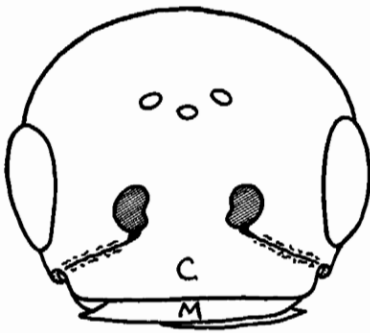
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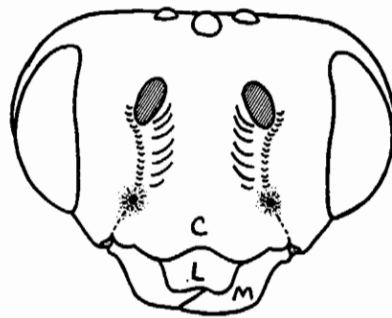
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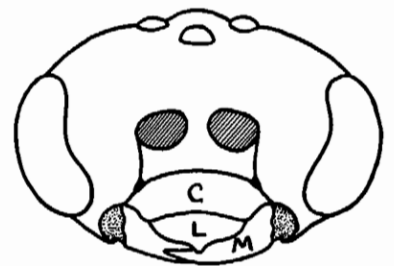
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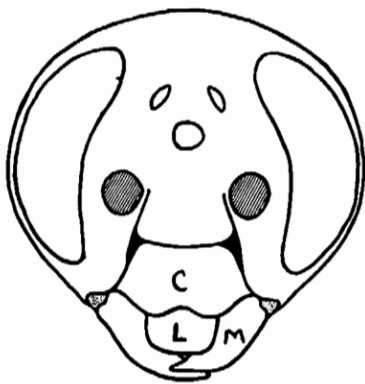
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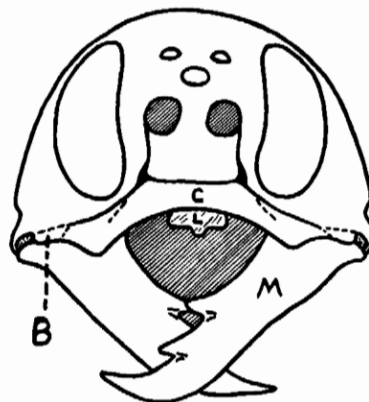
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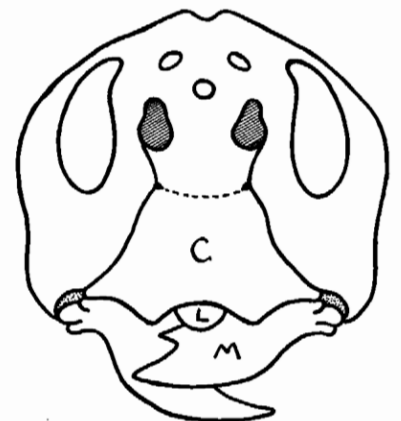
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9



10

PLATE III

PLATE III. Tenthredinoidea

Diprionidae

Fig. 11. Diprion (Gilpinnia) hercyniae (Hartig), female.

Tenthredinidae

Fig. 12. Hemitaxonus albido-pictus (Norton), male.

Fig. 13. Aneugmenus (Aneugmenus) flavipes (Norton).

Fig. 14. Dolerus (Dolerus) similis (Norton).

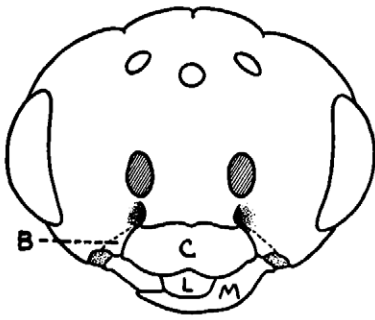
Fig. 15. Pikonema alaskensis (Rohwer), female.

Fig. 16. Ametastegia (Protemphytus) recens (Say), male.

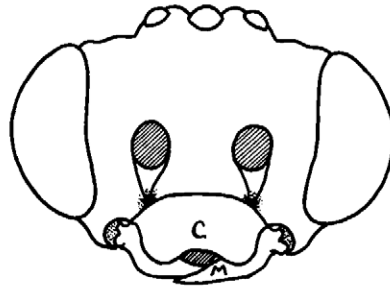
Fig. 17. Ametastegia (Ametastegia) equiseti (Fallén).

Fig. 18. Aphilodyctium fidum (Cresson), male.

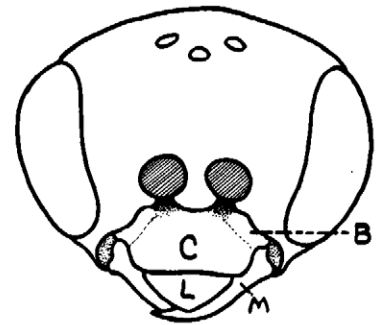
Fig. 19. Macremphytus semicornis (Say).



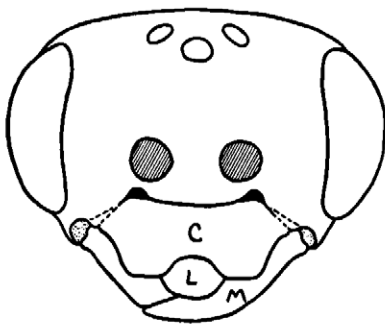
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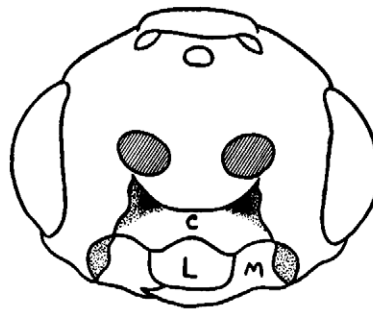
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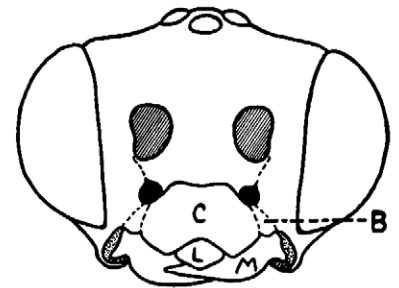
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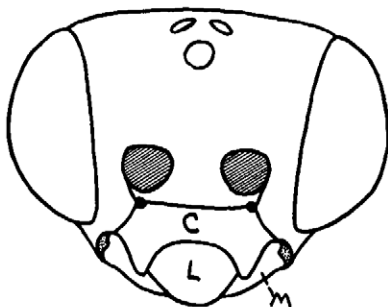
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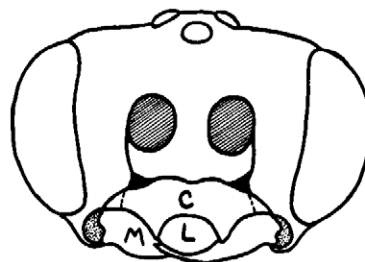
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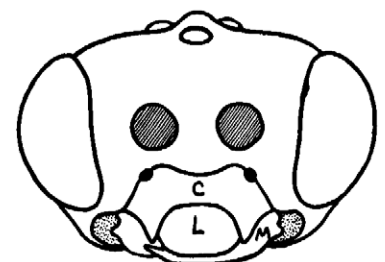
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PLATE IV

PLATE IV. Tenthredinoidea, Tenthredinidae

Fig. 20. Tethida cordigera (Beauvois).

Fig. 21. Dimorphopteryx abnormis Rohwer, male.

Fig. 22. Blennogeneris spissipes (Cresson).

Fig. 23. Taxonus terminalis (Say).

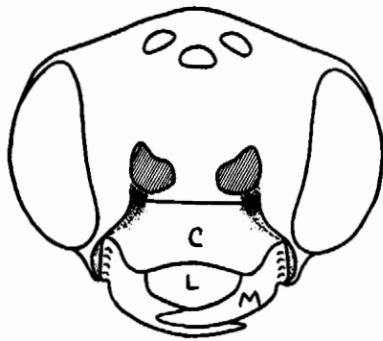
Fig. 24. Aglaostigma semiluteum (Norton), male.

Fig. 25. Tenthredo sp., male.

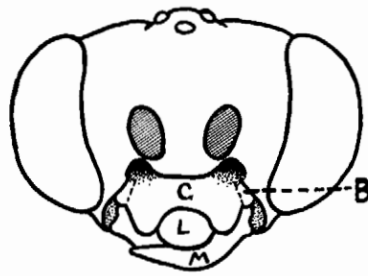
Siricoidea, Siricidae

Fig. 26. Tremex columba (L.), female.

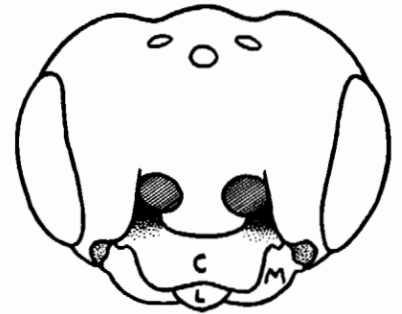
Fig. 27. Tremex columba (L.), female, lateral aspect.



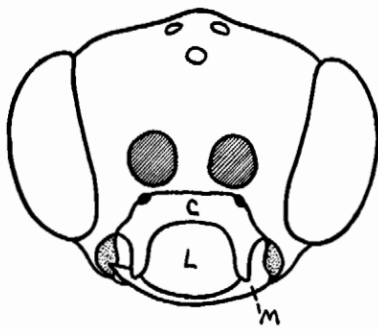
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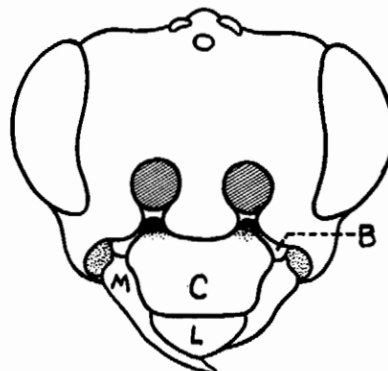
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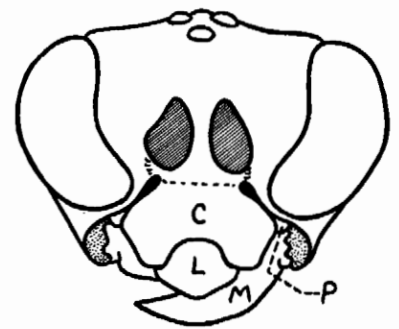
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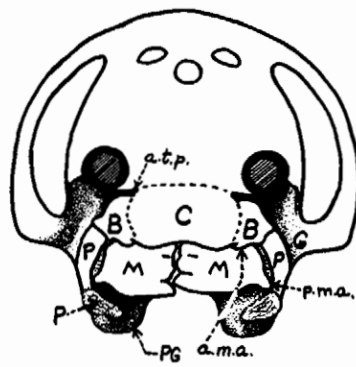
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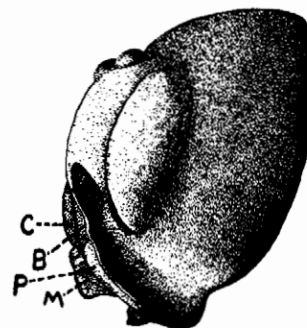
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PLATE V

PLATE V.

Siricoidea

Fig. 28. Urocerus sp., female, Siricidae.

Fig. 29. Urocerus sp., female, dorsal aspect.

Fig. 30. Xiphydria abdominalis Say, male, Xiphydriidae.

Fig. 31. Xiphydria mellipes Harris, female.

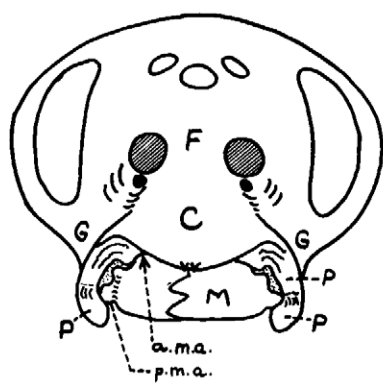
Fig. 32. Orussus terminalis Newman, female, Orussidae.

Fig. 33. Orusses terminalis Newman, female, ventral aspect.

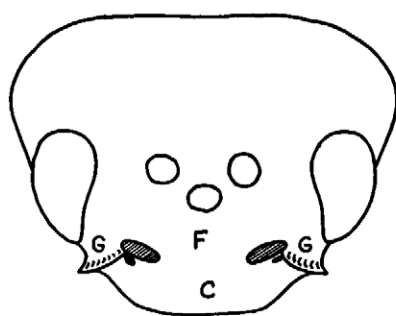
Cephoidea, Cephidae

Fig. 34. Cephus (Cephus) cinctus Norton, male.

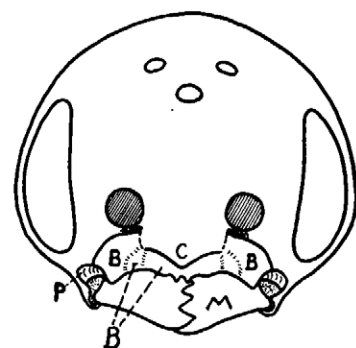
Fig. 35. Cephus (Cephus) cinctus Norton, female.



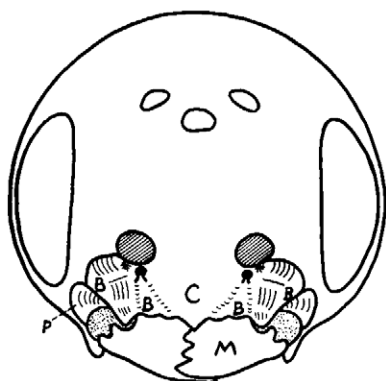
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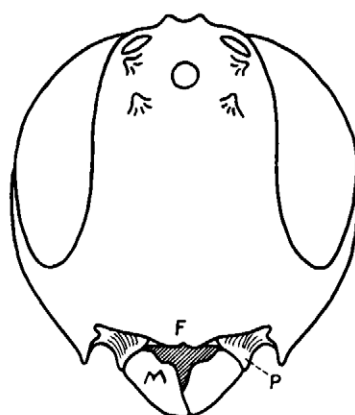
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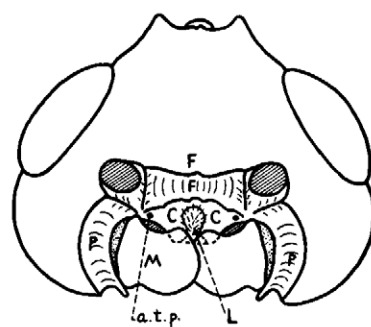
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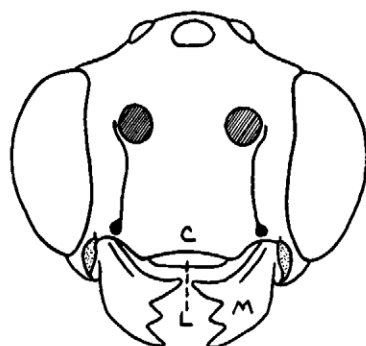
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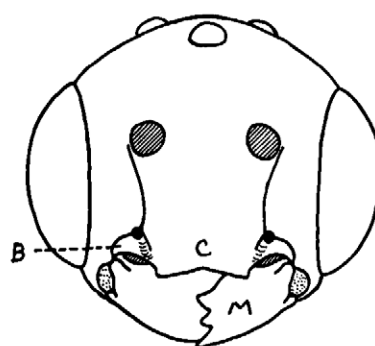
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PLATE VI

PLATE VI. Ichneumonoidea

Stephanidae

Fig. 36. Schlettererius cinctipes (Cresson), female.

Braconidae

Fig. 37. Eupachylomma sp., Paxylommatainae.

Fig. 38. Ephedrus nitidus Gahan, male, Aphidiinae.

Fig. 39. Praon simulans (Provancher), female, Aphidiinae.

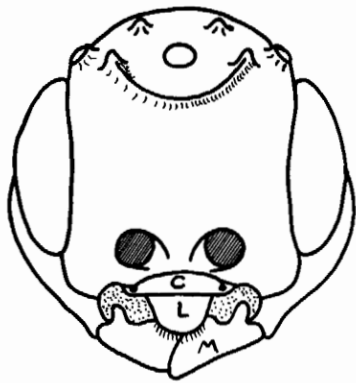
Fig. 40. Meteorus trachynotus Viereck, female, Euphorinae.

Fig. 41. Myiocephalus boops (Wesmael), male, Euphorinae.

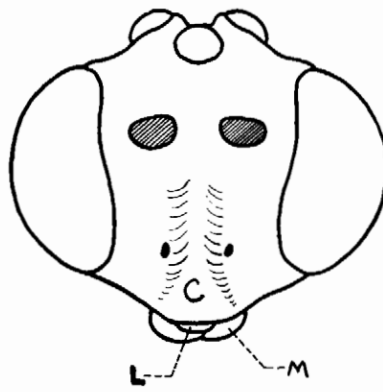
Fig. 42. Syntretus vigilax (Provancher), male, Euphorinae.

Fig. 43. Macrocentrus cerasivoranae Viereck, male,
Macrocentrinae.

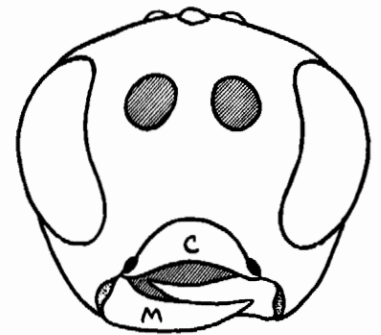
Fig. 44. Cenocoelius sp., female, Helconinae.



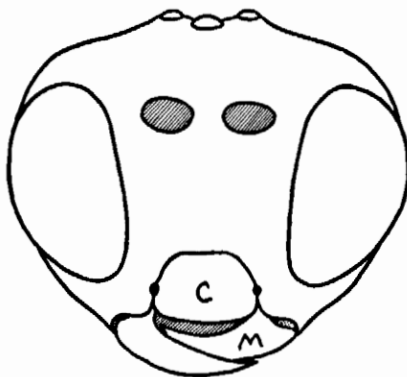
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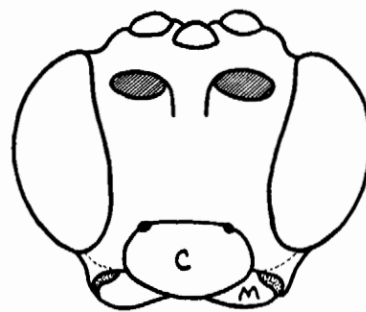
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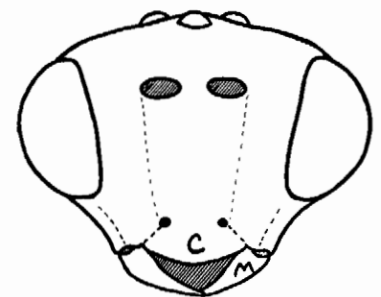
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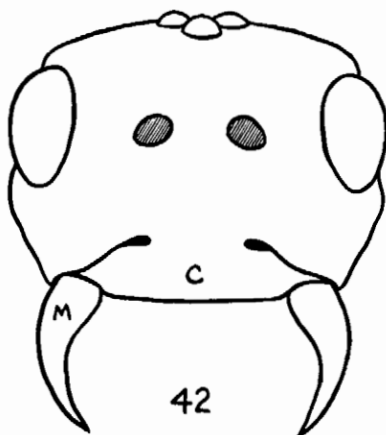
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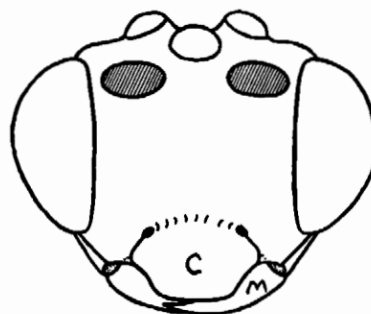
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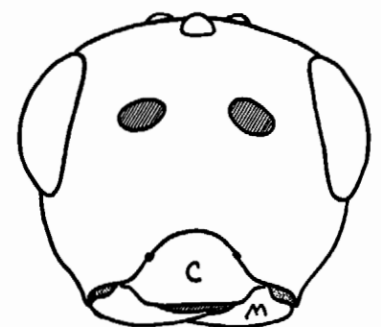
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PLATE VII

PLATE VII. Ichneumonoidea, Braconidae

Fig. 45. Helcon sp., female, Helconinae.

Fig. 46. Diospilus sp., male, Helconinae.

Fig. 47. Earinus limitaris (Say), male, Agathidinae.

Fig. 48. Agathis texanus (Cresson), male, Agathidinae.

Fig. 49. Agathis buttricki (Viereck), female, Agathidinae.

Fig. 50. Agathis atripes Cresson, male, Agathidinae.

Fig. 51. Cremnops vulgaris (Cresson), male, Agathidinae.

Fig. 52. Elasmosoma pergandei Ashmead, female, Neoneurinae.

Fig. 53. Cardiochiles magnus Mao, female, Cardiochilinae.

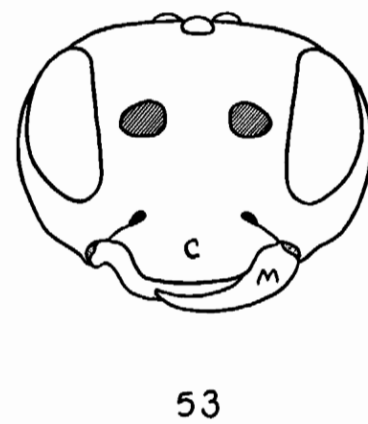
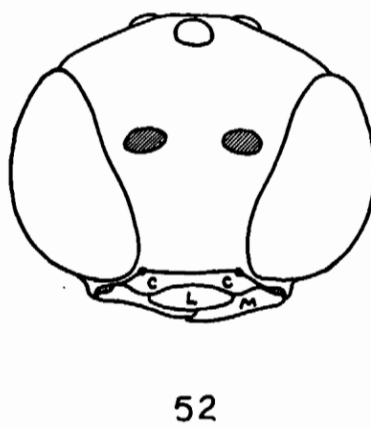
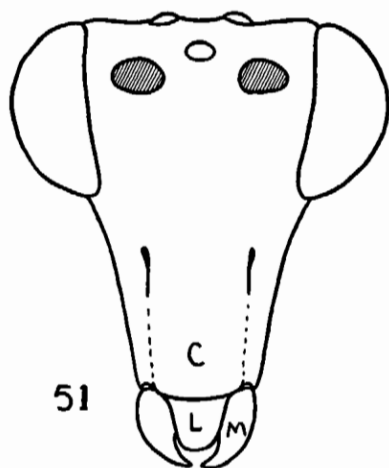
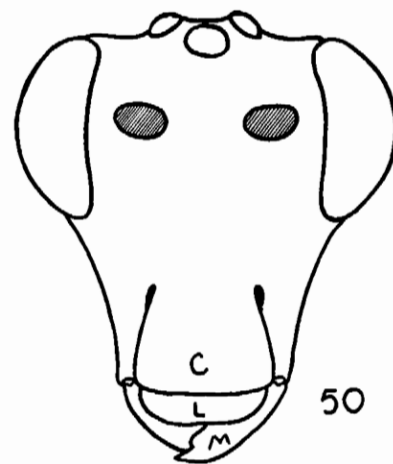
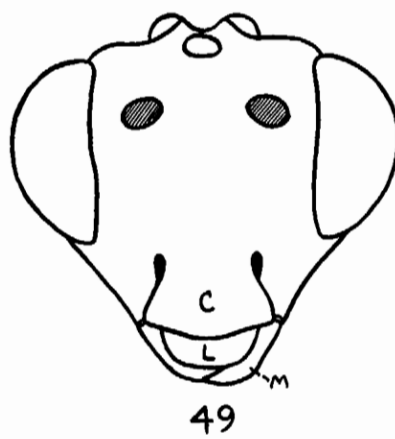
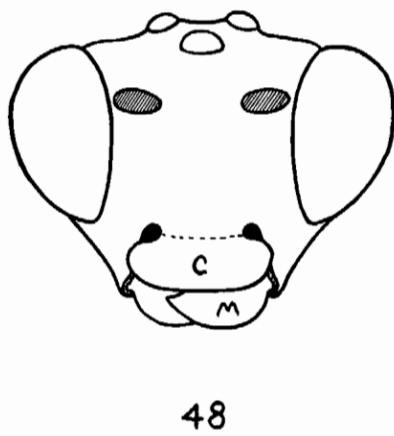
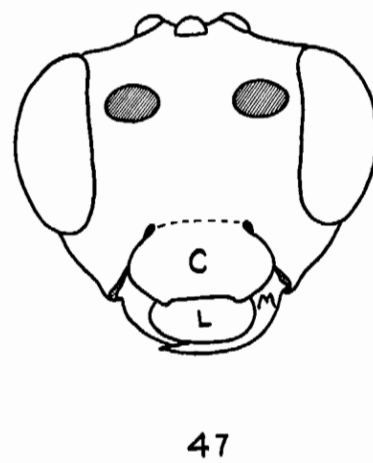
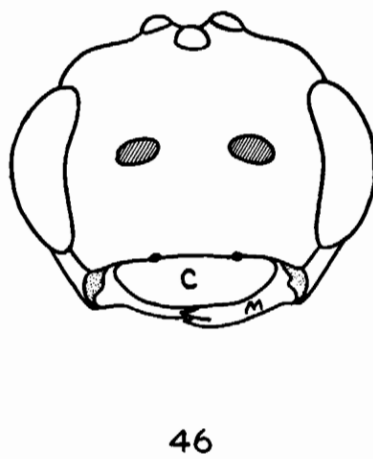
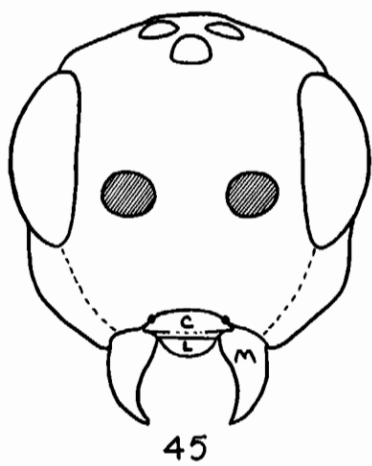


PLATE VIII.

PLATE VIII. Ichneumonoidea, Braconidae

Fig. 54. Proterops californicus Cresson, male, Ichneutinae.

Fig. 55. Dacnusa gracilis male,
Dacnusiinae (from England).

Fig. 56. Aphaereta sp., female, Alysiinae.

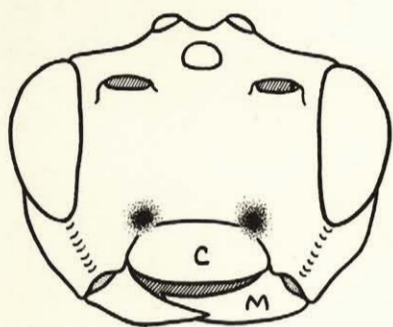
Fig. 57. Vipio croceus (Cresson), female, Braconinae.

Fig. 58. Cyanopterus sp., female, Braconinae, antero-
lateral aspect.

Fig. 59. Atanycolus sp., female, Braconinae.

Fig. 60. Cosmophorinus sp., female, Cosmophorinae.

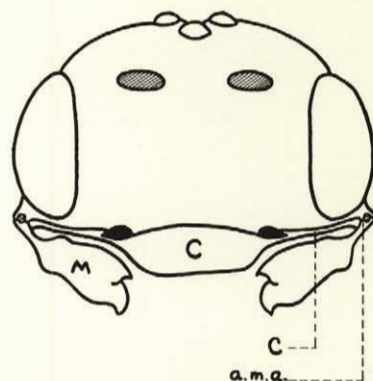
Fig. 61. Cosmophorinus sp., female, ventral aspect.



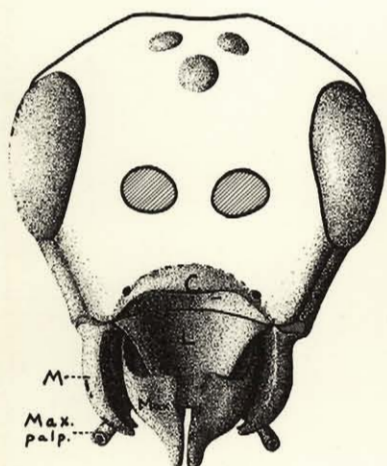
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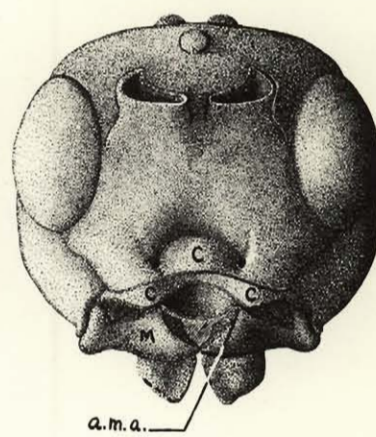
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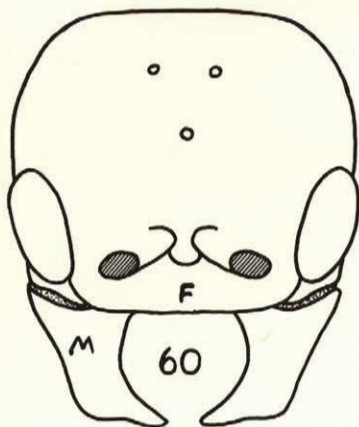
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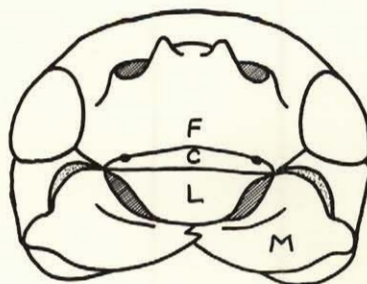
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PLATE IX

PLATE IX. Ichneumonoidea, Ichneumonidae, Pimplinae

Fig. 62. Coccygomimus aequalis (Provancher).

Fig. 63. Arotes amoenus Cresson, female.

Fig. 64. Coleocentrus rufus Provancher, male.

Fig. 65. Itoplectis conquisitor (Say), female.

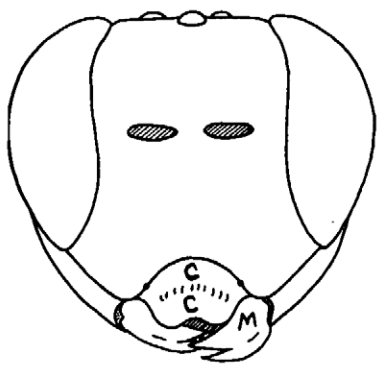
Fig. 66. Hymenoepimecis wiltii (Cresson), female.

Fig. 67. Pimpla irritator (Fabricius), female.

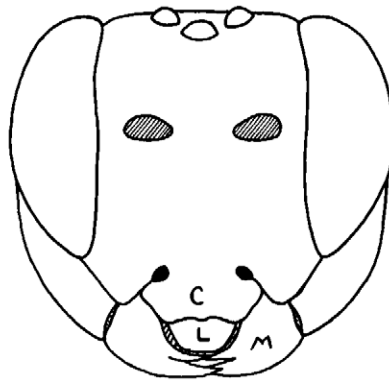
Fig. 68. Pseudorhyssa sternata Merrill.

Fig. 69. Rhyssa lineolata (Kirby), female.

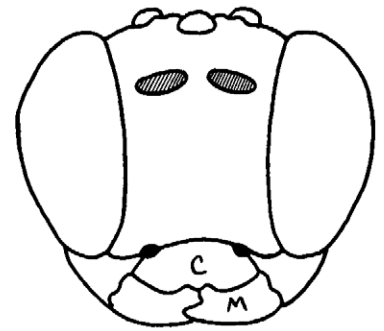
Fig. 70. Rhyssa lineolata (Kirby), male.



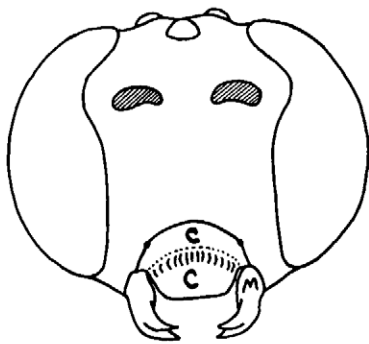
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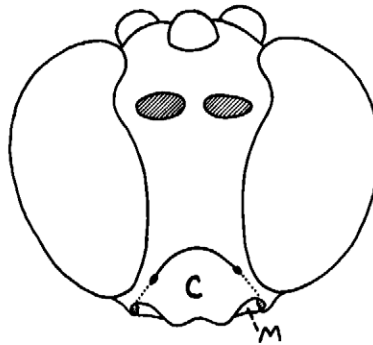
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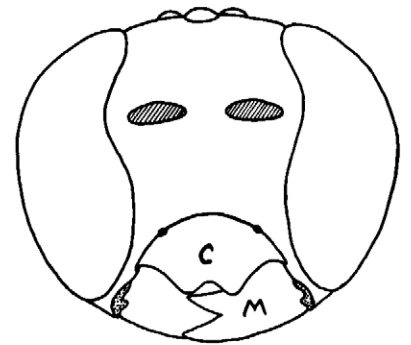
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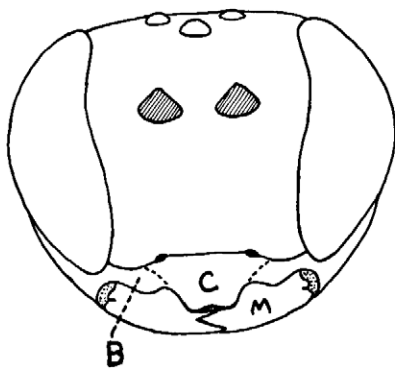
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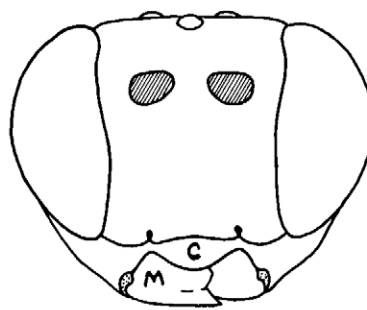
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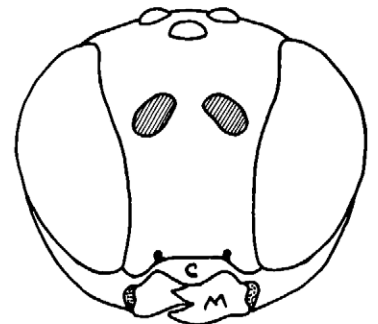
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PLATE X

PLATE X. Ichneumonidea, Ichneumonidae

Fig. 71. Neoxorides vittifrons (Cresson), Pimplinae.

Fig. 72. Grotea anguina Cresson, male, Pimplinae.

Fig. 73. Schizopyga frigida Cresson, Pimplinae.

Fig. 74. Diacritus muliebris (Cresson), male, Pimplinae.

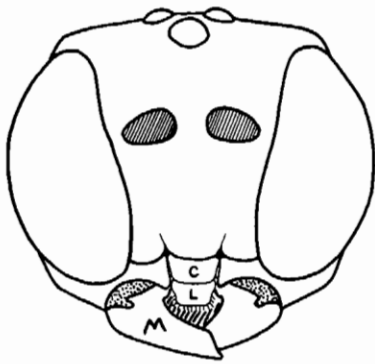
Fig. 75. Tryphon (Symboëthus) communis Cresson, Tryphoninae.

Fig. 76. Idiogamma longicauda (Cushman), female,
Tryphoninae.

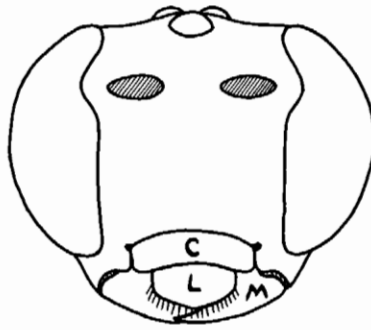
Fig. 77. Hybophanes nasutus (Cresson), male, Tryphoninae.

Fig. 78. Hybophanes nasutus (Cresson), female, lateral
aspect.

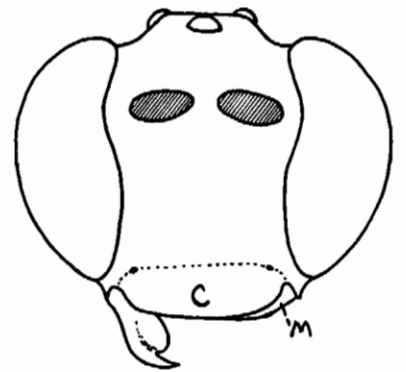
Fig. 79. Hybophanes nasutus (Cresson), female.



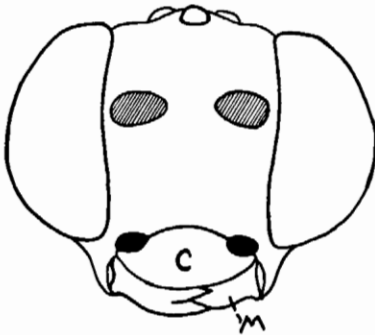
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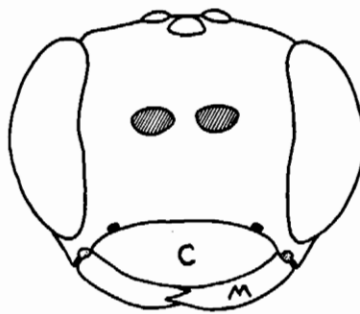
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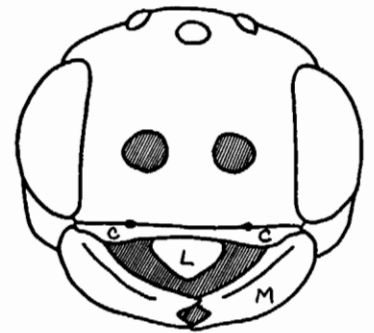
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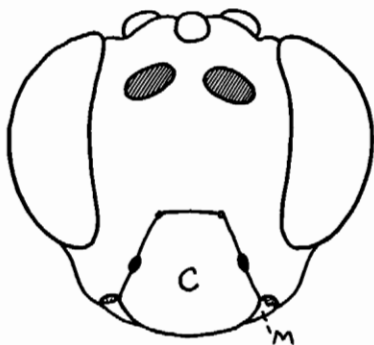
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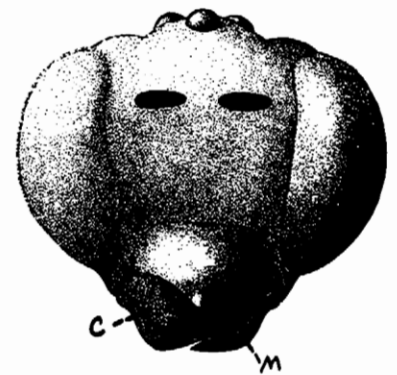
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PLATE XI

PLATE XI. Ichneumonoidea, Ichneumonidae

Fig. 80. Acroricnus aequatus (Say), male, Gelinae.

Fig. 81. Listrognathus albomaculatus (Cresson), female,
Gelinae.

Fig. 82. Trachysphyrus altonii (Dalla Torre), female,
Gelinae.

Fig. 83. Mastrus argeae (Viereck), male, Gelinae.

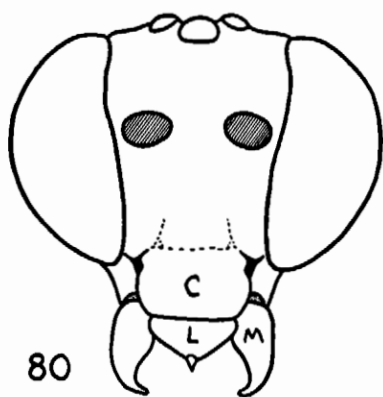
Fig. 84. Bathythrix triangularis (Cresson), male, Gelinae.

Fig. 85. Bathythrix peregrina (Cresson), female, Gelinae.

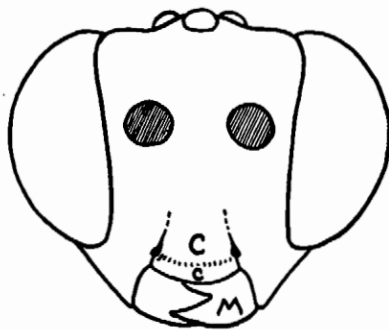
Fig. 86. Centeterus tuberculifrons (Provancher), female,
Ichneumoninae.

Fig. 87. Hoplismenus morulus (Say), female, Ichneumoninae.

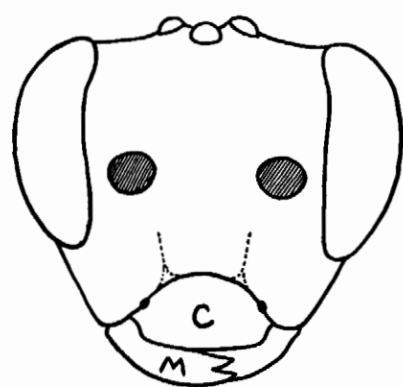
Fig. 88. Exetastes suaveolens Walsh, Banchinae.



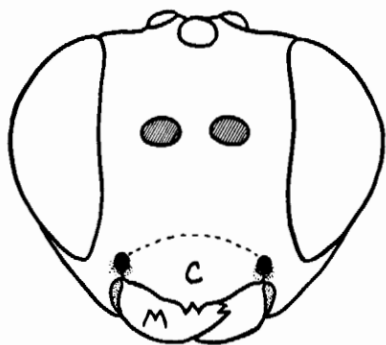
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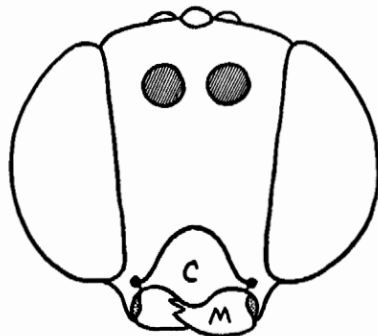
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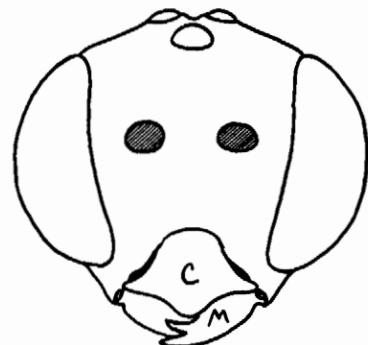
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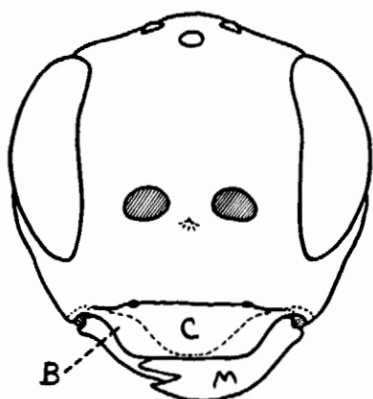
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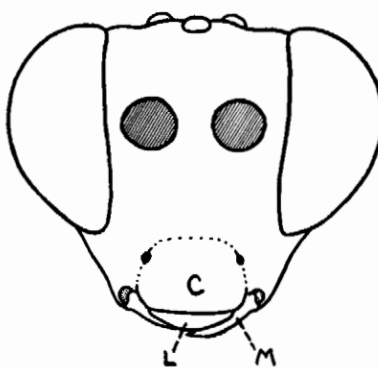
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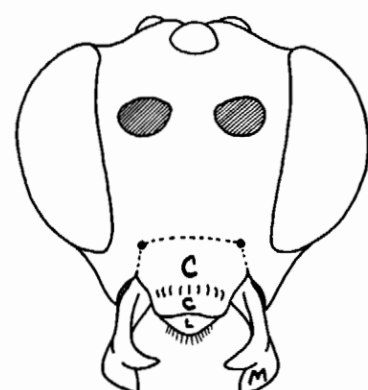
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PLATE XII

PLATE XII. Ichneumonoidea, Ichneumonidae

Fig. 89. Scolobates auriculatus (Fabricius), male,
Scolobatinae.

Fig. 90. Euceros thoracicus Cresson, male, Scolobatinae.

Fig. 91. Himerta flavida (Davis), Scolobatinae.

Fig. 92. Mesoleius tenthredinis Morley, Scolobatinae.

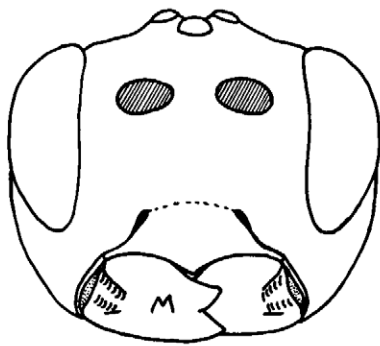
Fig. 93. Mesoleius nigropictus (Davis), Scolobatinae.

Fig. 94. Orthocentrus sp., female, Orthocentrinae,
lateral aspect.

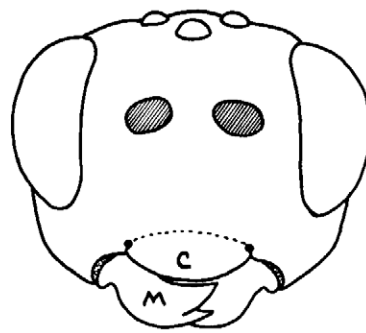
Fig. 95. Orthocentrus sp., female.

Fig. 96. Exochus sp., Metopiinae.

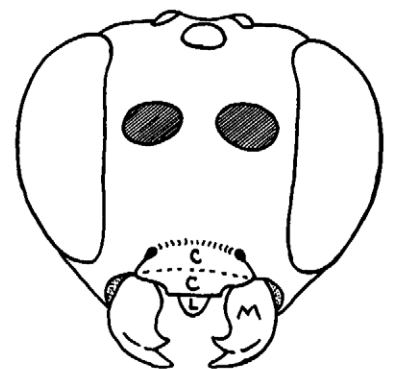
Fig. 97. Metopius sp., male, Metopiinae.



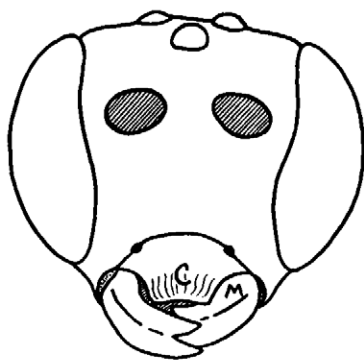
89



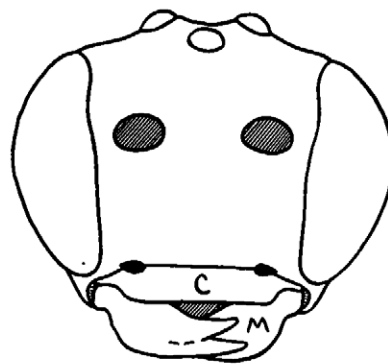
90



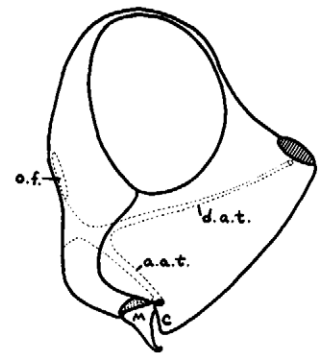
91



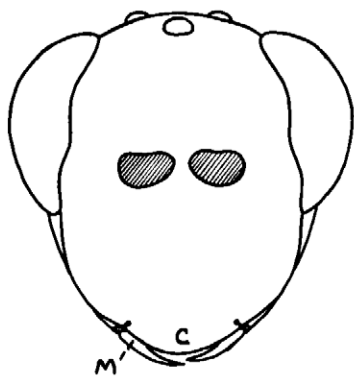
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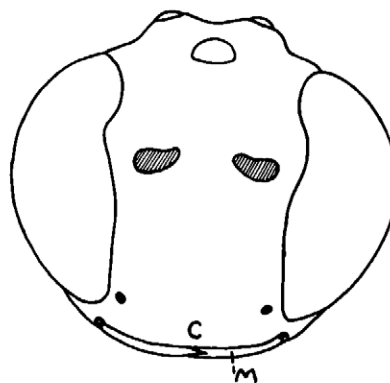
93



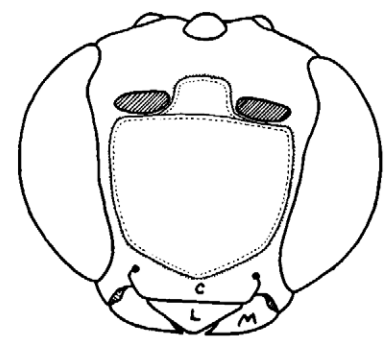
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95



96

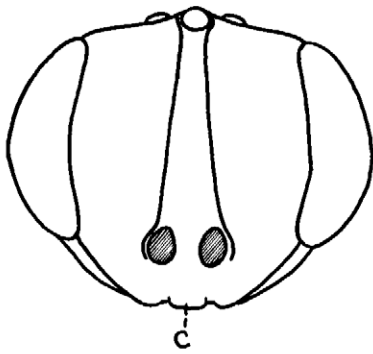


97

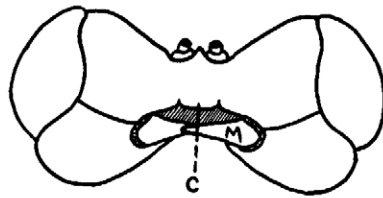
PLATE XIII

PLATE XIII. Chalcidoidea

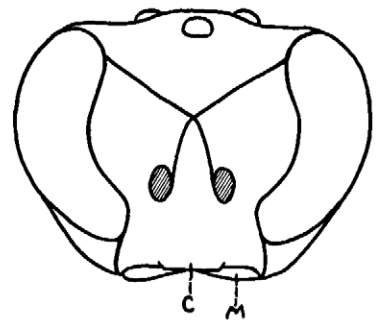
- Fig. 98. Dahlbominus fuscipennis (Zetterstedt), female,
Eulophidae.
- Fig. 99. Dahlbominus fuscipennis (Zetterstedt), female,
ventral aspect.
- Fig. 100. Pleurotropis benifica Gahan, female, Eulophidae.
- Fig. 101. Copidosoma sp., Encyrtidae.
- Fig. 102. Holcencyrtus piceae Girault, Encyrtidae.
- Fig. 103. Eupelmella vesicularis (Retzius), female,
Eupelmidae.
- Fig. 104. Perilampus hyalinus Say, Perilampidae.
- Fig. 105. Torymus chrysochlorus (Osten Sacken), female,
Torymidae.
- Fig. 106. Megastigmus physocarpi Crosby, male, Torymidae.



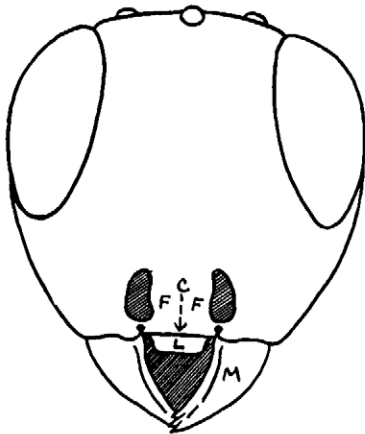
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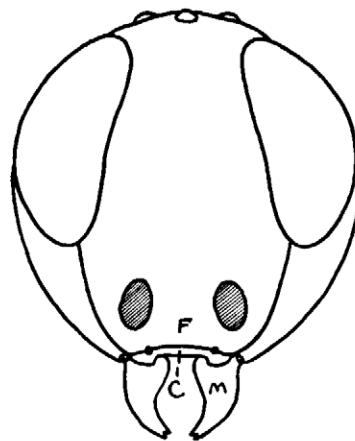
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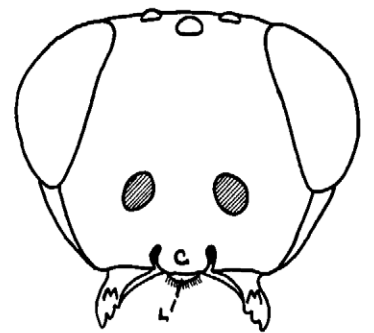
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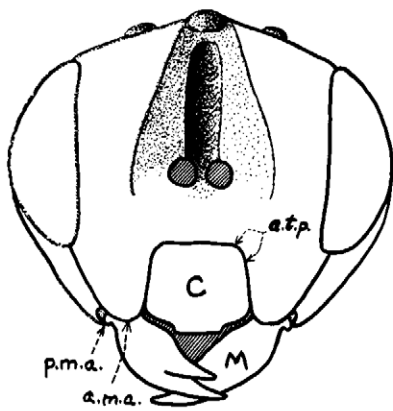
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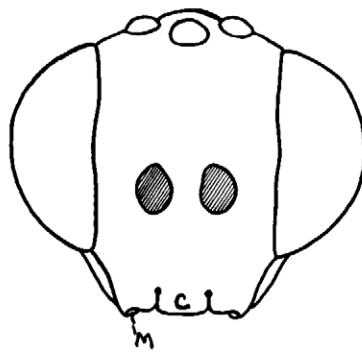
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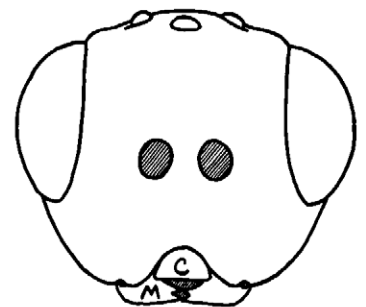
103



104



105



106

PLATE XIV

PLATE XIV.

Chalcidoidea

Fig. 107. Amblymerus verditer (Norton), female,
Pteromalidae.

Fig. 108. Psychophagus omnivorus (Walker) female,
Pteromalidae.

Fig. 109. Eurytoma pissodes Girault, female, Eurytomidae.
(The tentorial pits are not visible externally.
The black spots indicate the points, determined
by dissection, at which the tentorial arms meet
the face.)

Fig. 110. Brachymeria coloradensis (Cresson), female,
Chalcididae.

Fig. 111. Leucospis affinis Say, female, Leucospidae.

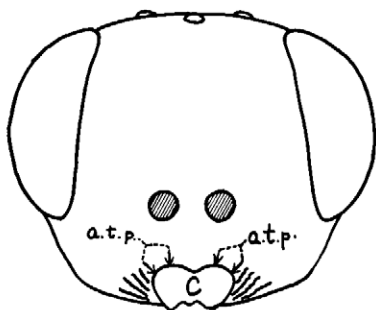
Cynipoidea

Fig. 112. Ibalia ensiger Norton, female, Ibaliidae.

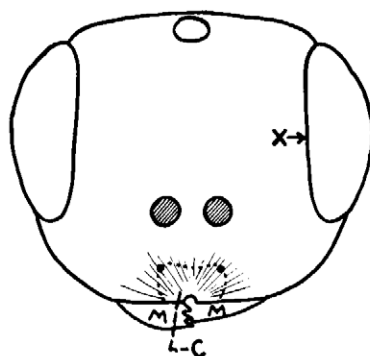
Fig. 113. Callaspidia provancheri Ashmead, Figitidae.

Fig. 114. Eucoilidea sp., female, Cynipidae.

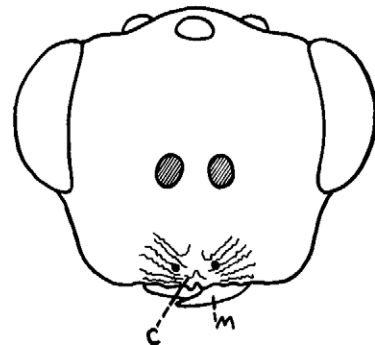
Fig. 115. Andricus singularis (Osten Sacken), Cynipidae.



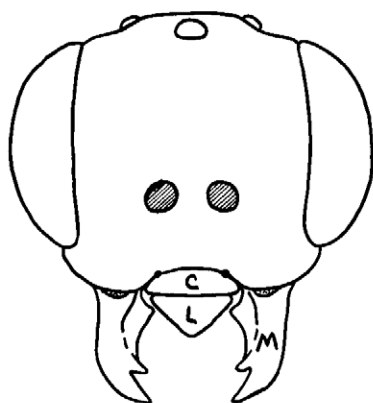
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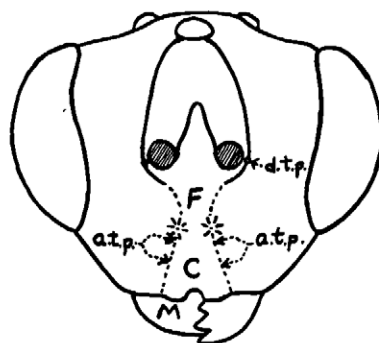
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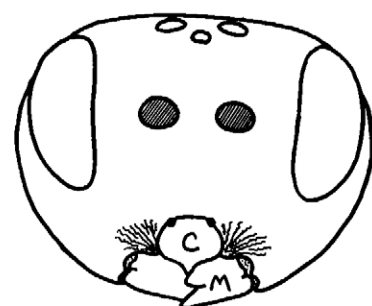
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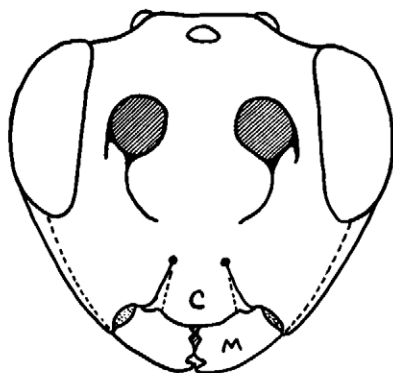
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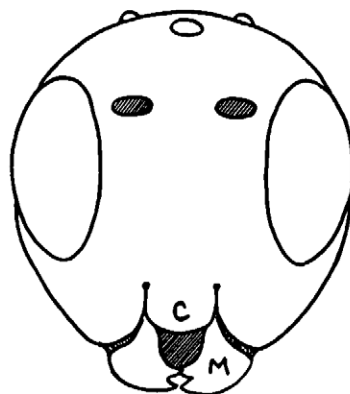
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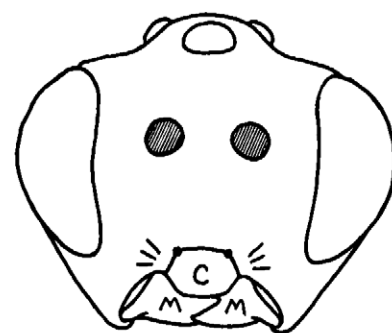
112



113



114



115

PLATE XV

PLATE XV. Proctotrupoidea

Fig. 116. Evania appendigaster (L), Evaniidae.

Fig. 117. Gasteruption assectator arca (Couper), female,
Gasteruptiidae.

Fig. 118. Pellicinus polyturator (Drury), female,
Pelecinidae.

Fig. 119. Disogmus canadensis Harrington, female,
Paratype 2526, Proctotrupidae.

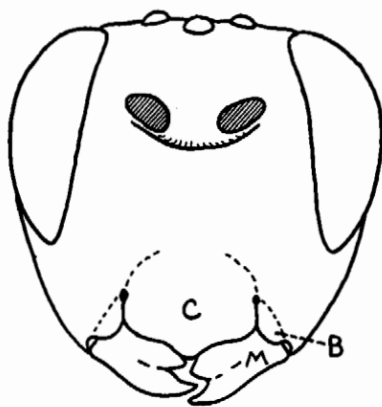
Fig. 120. Diapria conica (Fabricius), male, Diapriidae.

Fig. 121. Diapria conica (Fabricius), male, lateral
view.

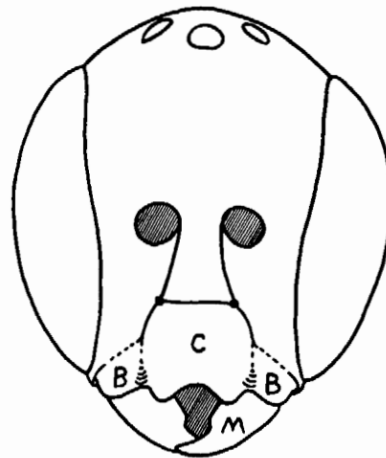
Fig. 122. Telenomus (Telenomus) clisiocampae Riley,
female, Scelionidae.

Fig. 123. Inostemma sp., Platygasteridae.

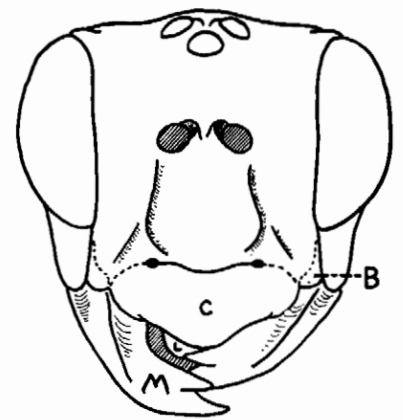
Fig. 124. Isocybus canadensis (Provancher), female,
Platygasteridae.



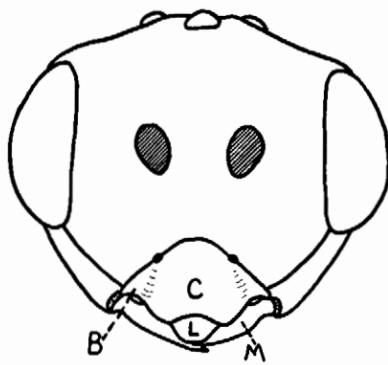
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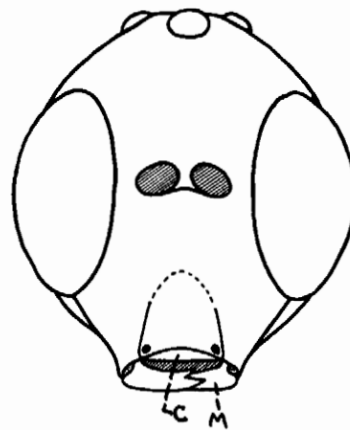
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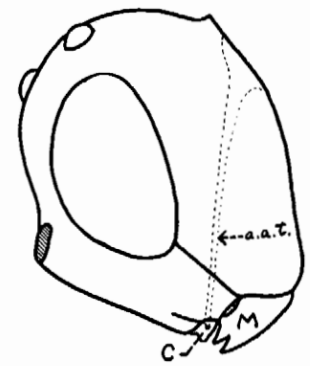
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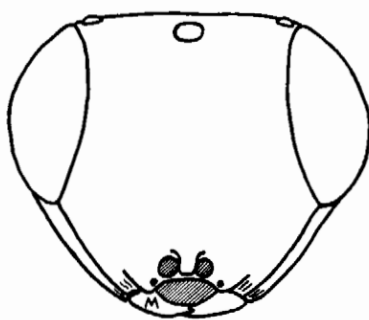
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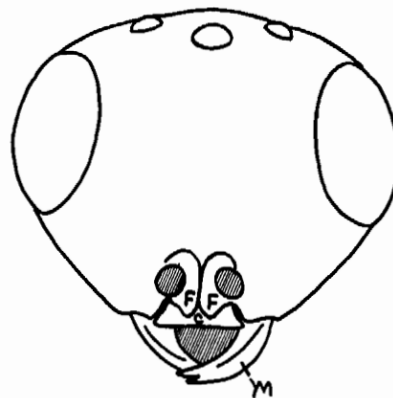
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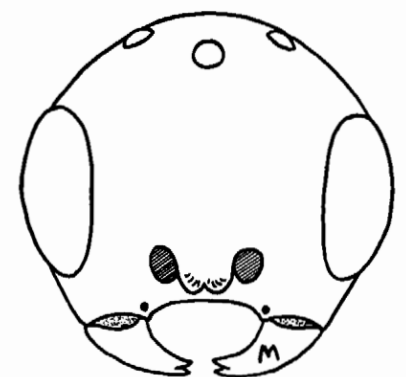
121



122



123



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PLATE XVI

PLATE XVI.

Proctotrupoidea

Fig. 125. Vanhornia eucnemidarum Crawford, Vanhorniidae.

Fig. 126. Ropronia garmani Ashmead, Roproniidae.

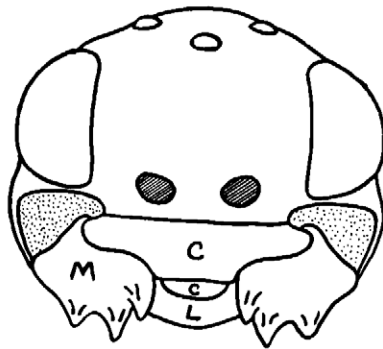
Chrysididae

Fig. 127. Chrysis (Chrysis) coerulans Fabricius,
Chrysididae.

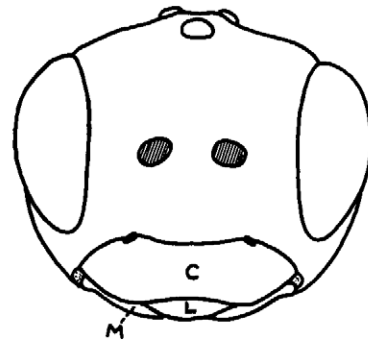
Fig. 128. Stilbum cyanurum (Fabricius), Chrysididae.

Trigonalidae

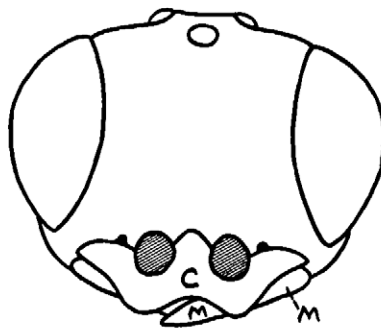
Fig. 129. Bareogonalos canadensis (Harrington).



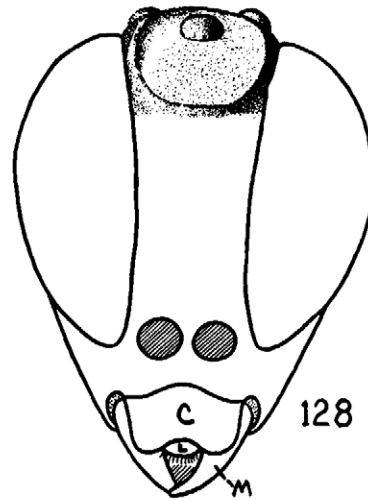
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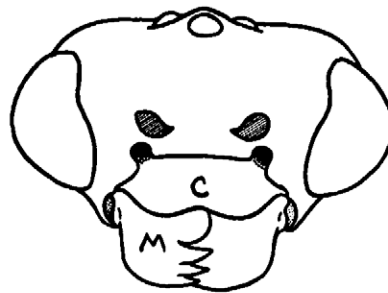
126



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128



129

PLATE XVII

PLATE XVII. Scolioidea

Fig. 130. Tiphia inornata Say, male, Tiphidae.

Fig. 131. Tiphia inornata Say, female.

Fig. 132. Myrmosa (Myrmosa) unicolor Say, female, Tiphidae.

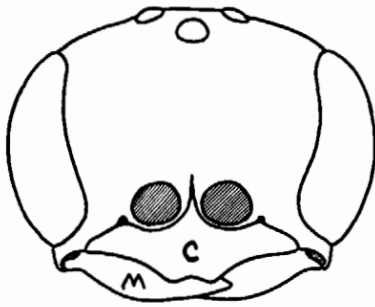
Fig. 133. Dasymutilla fulvohirta (Cresson), male,
Mutillidae.

Fig. 134. Dasymutilla fulvohirta (Cresson), female.

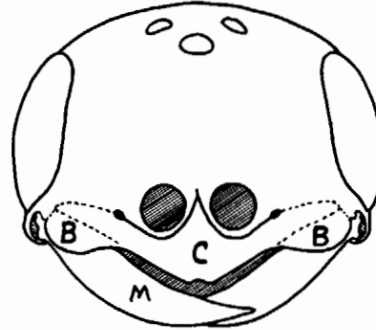
Fig. 135. Sapyga pumila Cresson, male, Sapygidae.

Fig. 136. Dielis dorsata Fabricius, male, Scoliidae.

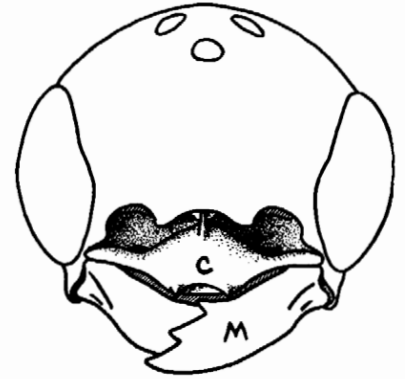
Fig. 137. Dielis dorsata Fabricius, female.



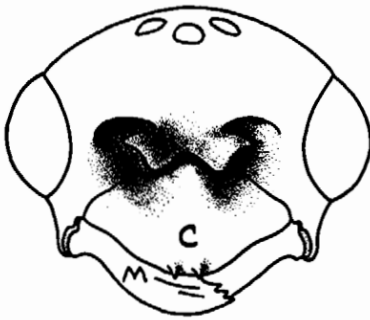
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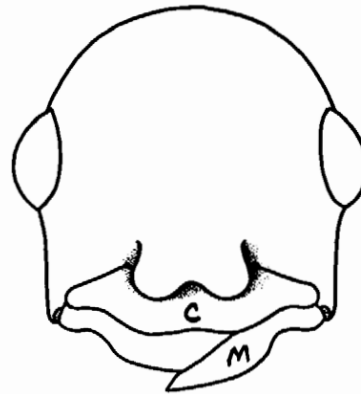
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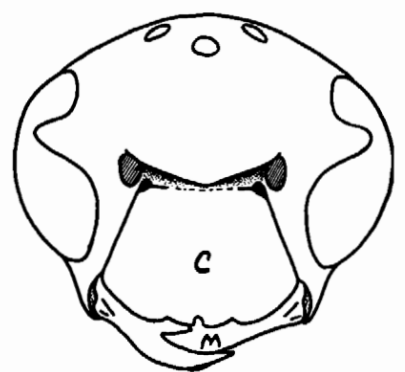
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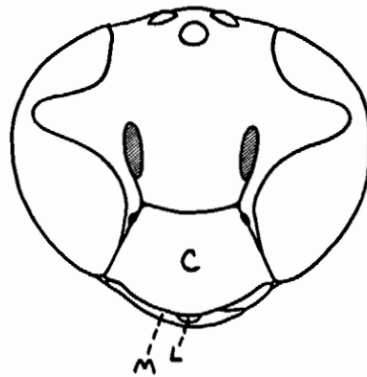
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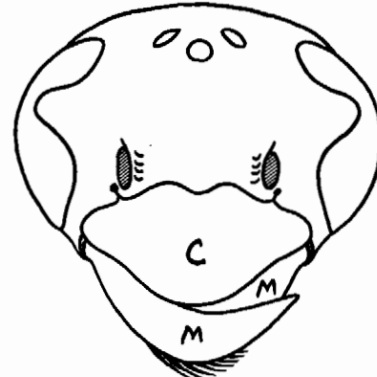
134



135



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137

PLATE XVIII

PLATE XVIII. Formicidae

Fig. 138. Paraponera clavata Fabricius, worker, Ponerinae.

Fig. 139. Atta cephalotes (L.), worker, Myrmicinae.

Fig. 140. Cryptoceras atratus L., soldier, Myrmicinae.

The frontal shield on one side (lateral to the heavy line) is not shown, in order that the antennal foramen and groove may be seen.

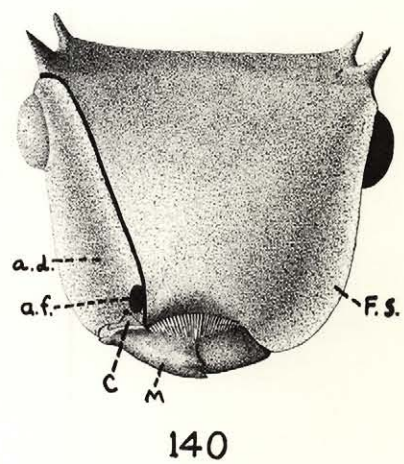
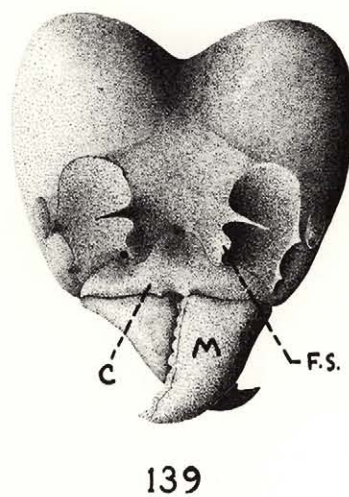
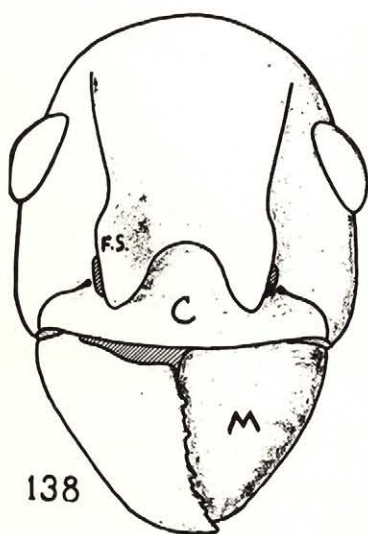
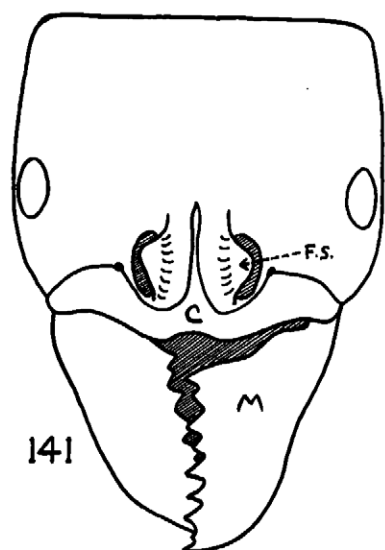


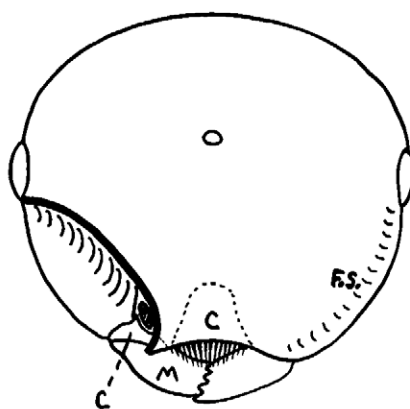
PLATE. XIX

PLATE XIX. Formicidae

- Fig. 141. Pachycondyla crassinoda (Latreille), worker,
Ponerinae.
- Fig. 142. Ectatomma sp., Ponerinae. (See explanation under
figure 140).
- Fig. 143. Eciton (Eciton) hamatum (Fabricius), probably
soldier, Dorylinae.
- Fig. 144. Eciton (Eciton) hamatum (Fabricius), probably
soldier, Dorylinae.
- Fig. 145. Eciton (Neivamyrmex) opacithorax Emery, worker,
Dorylinae.
- Fig. 146. Monomorium (Monomorium) pharaonis (L.), worker,
Myrmicinae.
- Fig. 147. Camponotus (Myrmothrix) abdominalis (Fabricius),
Formicinae.
- Fig. 148. Camponotus (Myrmothrix) abdominalis (Fabricius),
worker, Formicinae.
- Fig. 149. Camponotus (Camponotus) herculeanus pennsylvanicus
(DeGeer), worker, Formicinae.



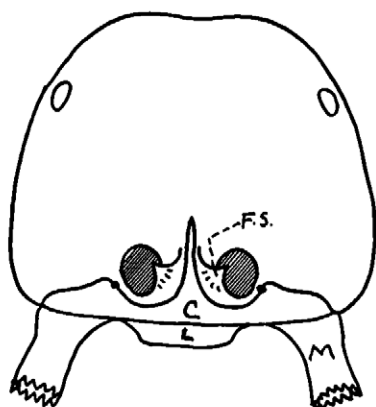
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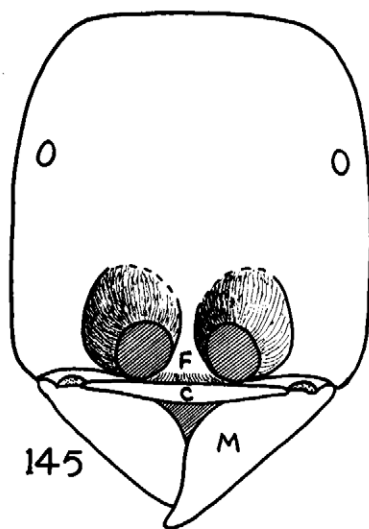
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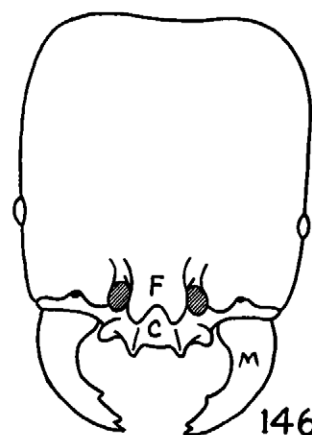
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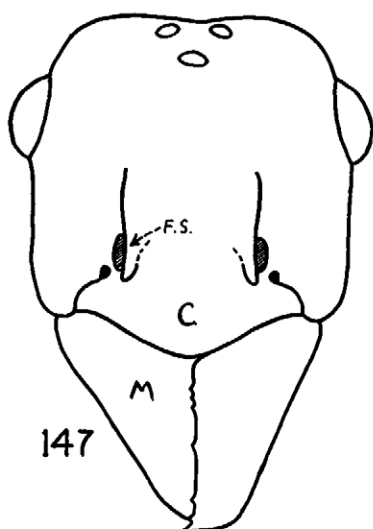
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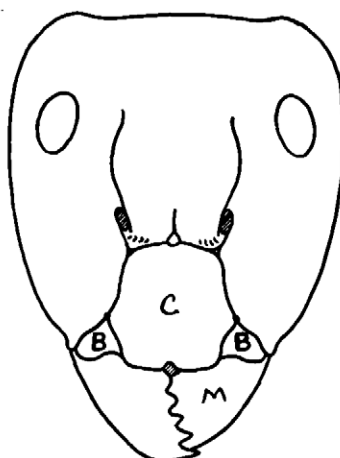
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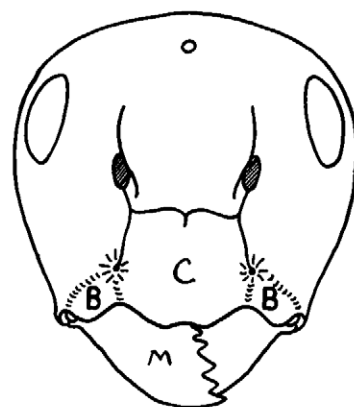
146



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149

PLATE XX

PLATE XX.

Vespoidea

Fig. 150. Vespula (Vespula) maculifrons (Buysson), female,
Vespidæ.

Fig. 151. Polistes fuscatus (Fabricius), female, Vespidæ.

Fig. 152. Zethus (Zethusculus) spinipes Say, Vespidæ.

Fig. 153. Eumenes crucifera nearcticus Bequaert, female,
Vespidæ.

Pompilidae

Fig. 154. Episyron quinquenotatus quinquenotatus (Say),
female.

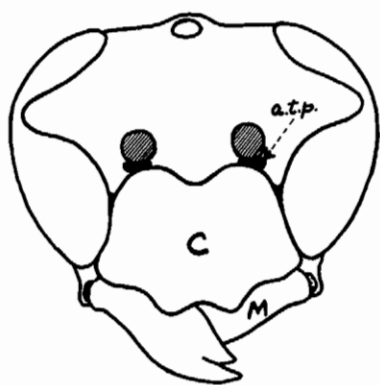
Sphecoidea, Sphecidae

Fig. 155. Astata (Astata) unicolor Say, male, Astatinae.

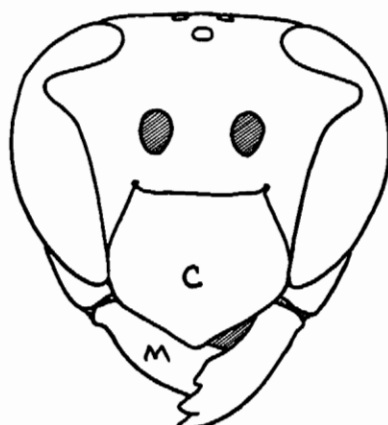
Fig. 156. Tachysphex (Tachysphex) tarsatus (Say), male,
Larrinae.

Fig. 157. Trypoxylon (Trypoxylon) figulum (L.), female,
Trypoxyloninae.

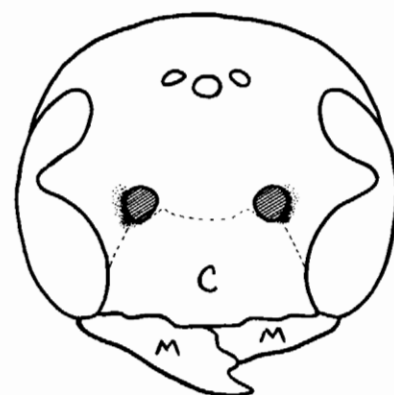
Fig. 158. Mimesa (Mimumesa) nigra (Packard), Pemphredoninae.



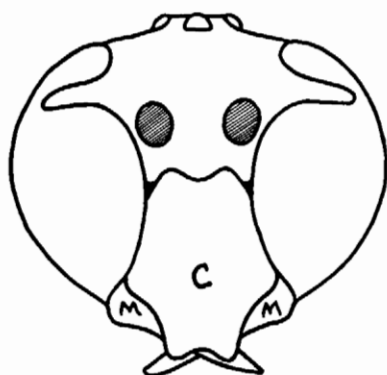
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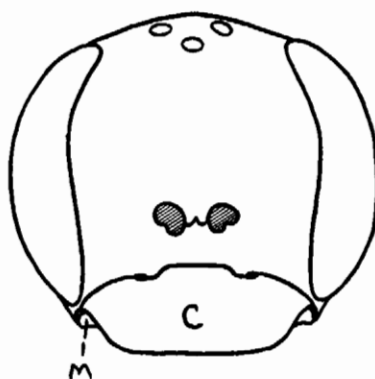
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152



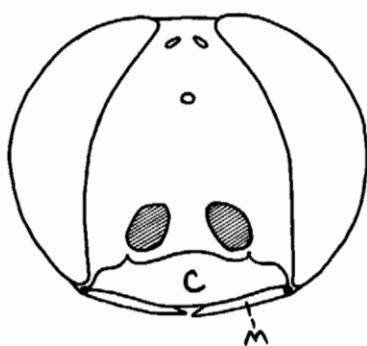
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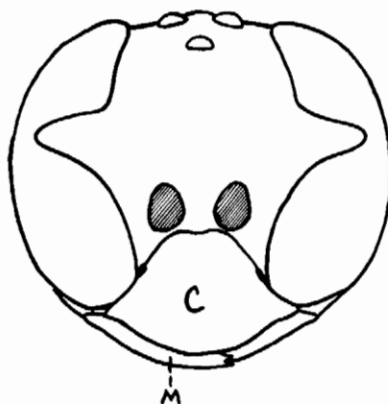
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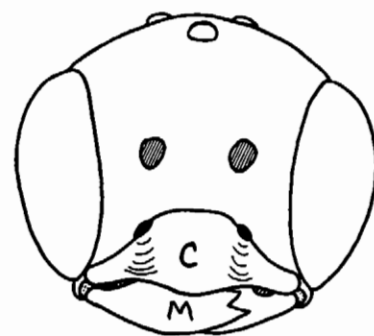
155



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PLATE XXI

PLATE XXI. Sphecoidea, Sphecidae

Fig. 159. Passaloecus ithicae Krombein, female,
Pemphredoninae.

Fig. 160. SpheX (SpheX) ichneumoneus ichneumoneus (L),
Sphecinae.

Fig. 161. Podalonia robusta (Cresson), female, Sphecinae.

Fig. 162. Chalybion californicum (Saussure), Sphecinae.

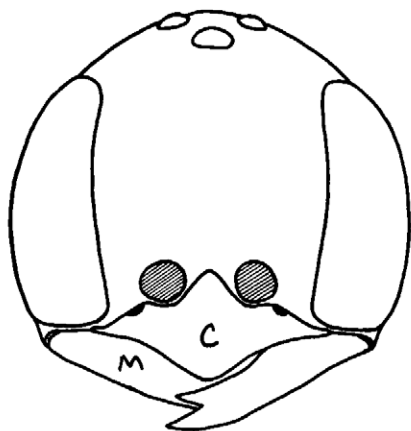
Fig. 163. Alysson oppositus Say, female, Nyssoninae.

Fig. 164. Nysson (Nysson) lateralis Packard, Nyssoninae.

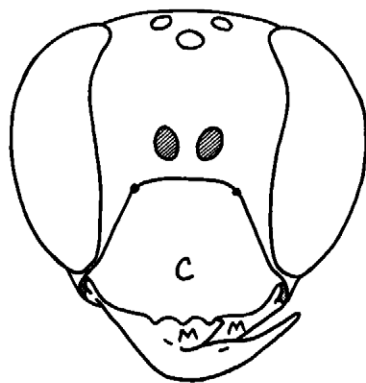
Fig. 165. Sphecius (Sphecius) speciosus (Drury), female,
Nyssoninae.

Fig. 166. Gorytes (Gorytes) atricornis Packard, female,
Nyssoninae.

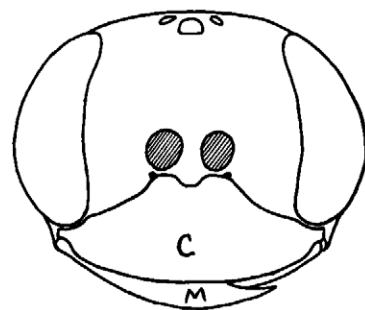
Fig. 167. Bicyrtes ventralis (Say), Nyssoninae.



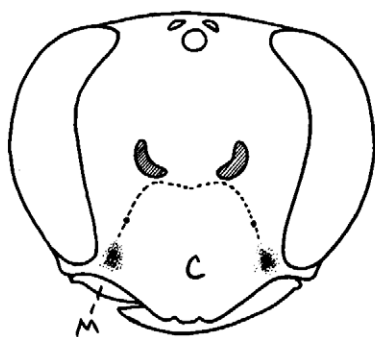
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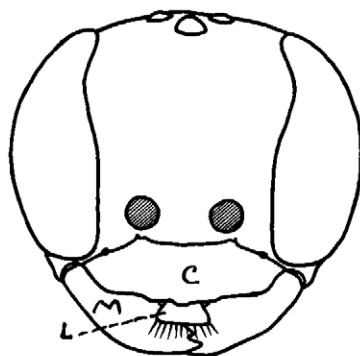
160



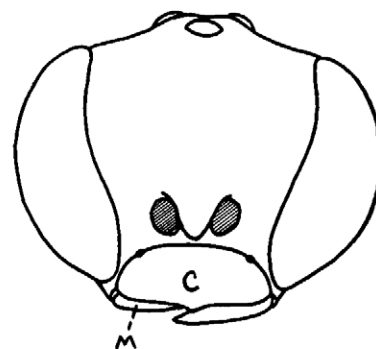
161



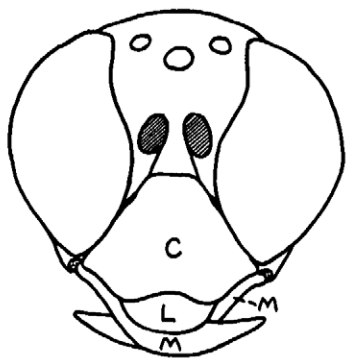
162



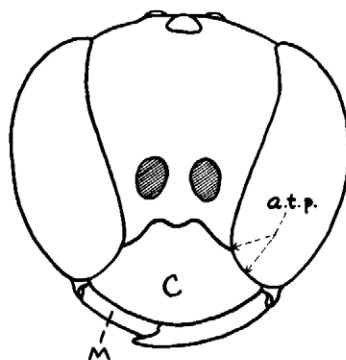
163



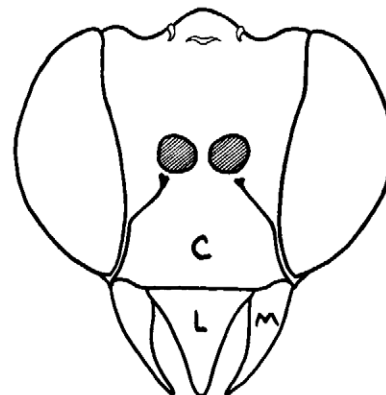
164



165



166



167

PLATE XXII

PLATE XXII

Sphecoidea, Sphecidae

Fig. 168. Microbembex monodonta (Say), Nyssoninae.

Fig. 169. Cerceris sp., Philanthinae, lateral aspect
of clypeal region.

Fig. 170. Cerceris sp.

Fig. 171. Philanthus politus politus Say, female,
Nyssoninae.

Fig. 172. Oxybelus sp., Crabroninae.

Fig. 173. Crossocerus sp., Crabroninae.

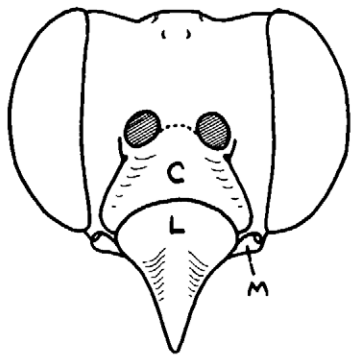
Dryinidae

Fig. 174. Dicondylus sp.

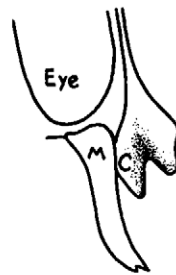
Fig. 175. Anteon sp.

Apoidea

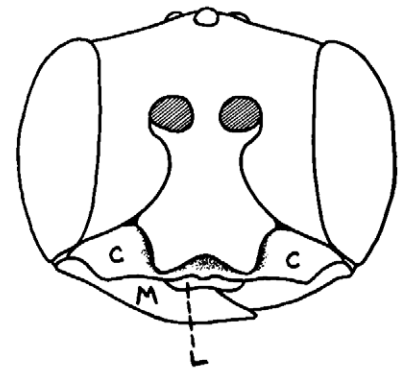
Fig. 176. Colletes sp., Colletidae.



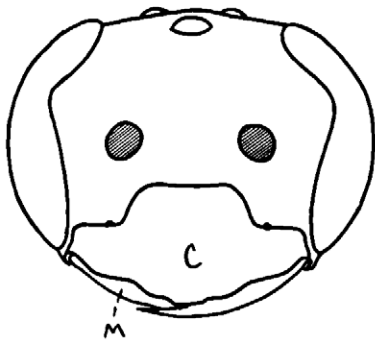
168



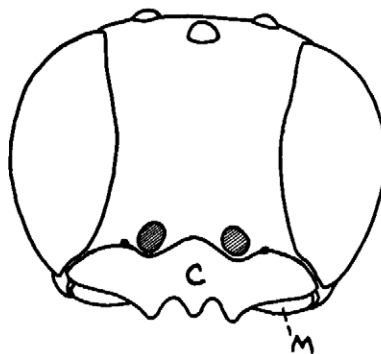
169



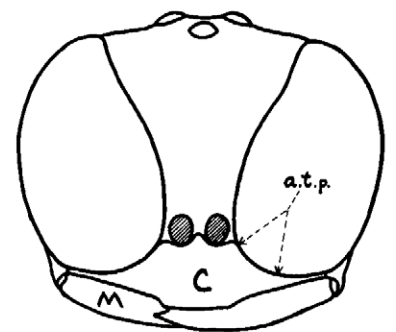
170



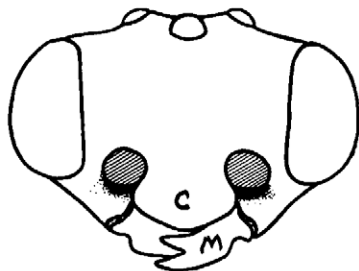
171



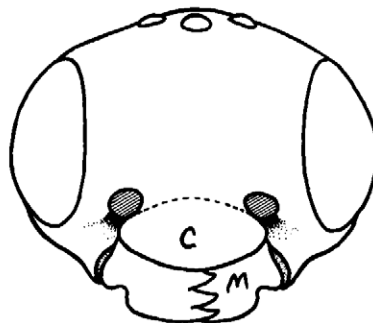
172



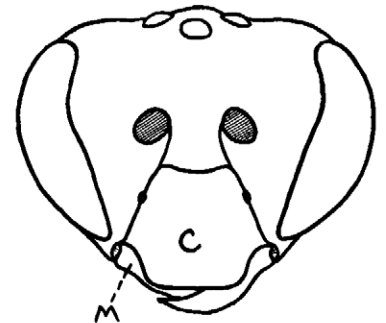
173



174



175



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PLATE XXIII

PLATE XXIII. Apoidea

Fig. 177. Andrena sp., Andrenidae.

Fig. 178. Lasioglossum sp., Halictidae.

Fig. 179. Megachile sp., Megachilidae.

Fig. 180. Ceratina sp., Apidae.

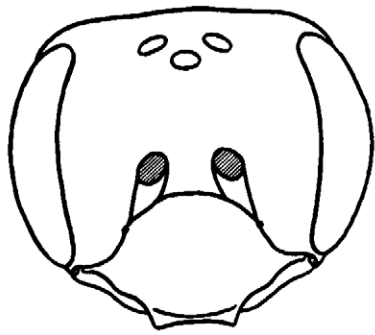
Fig. 181. Psithyrus ashtoni (Cresson), Apidae.

Fig. 182. Bombus (Separatobombus) griseocollis (DeGeer),
female, Apidae.

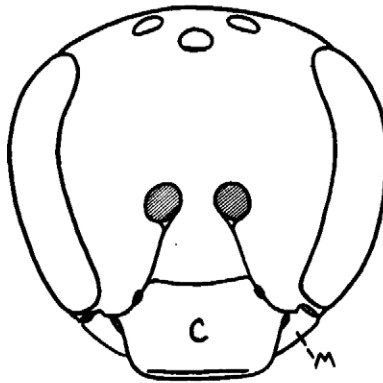
Fig. 183. Bombus (Fervidobombus) fervidus (Fabricius),
female, Apidae.

Fig. 184. Bombus (Subterraneobombus) borealis Kirby, female,
Apidae.

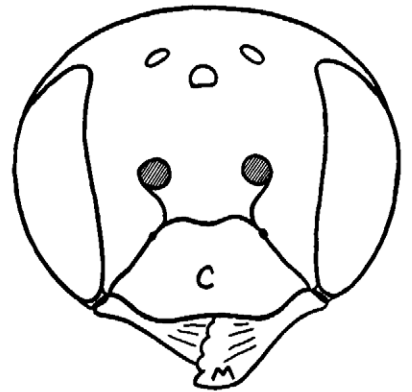
Fig. 185. Apis mellifera L., female, Apidae.



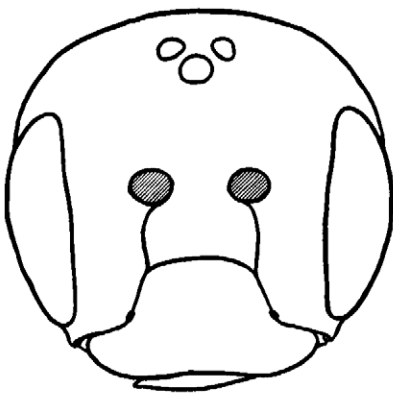
177



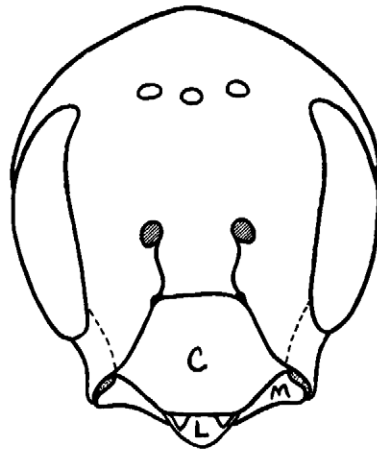
178



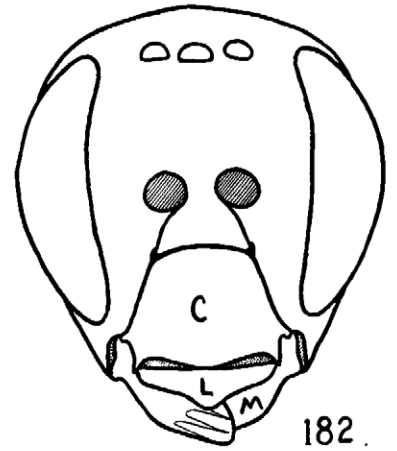
179



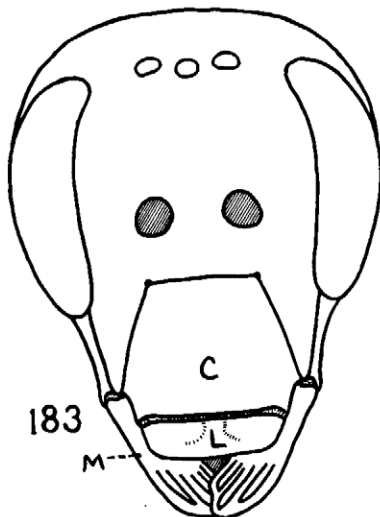
180



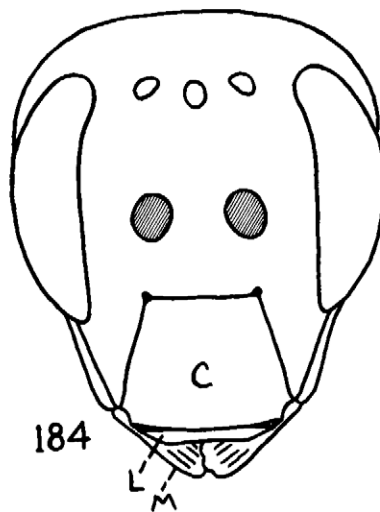
181



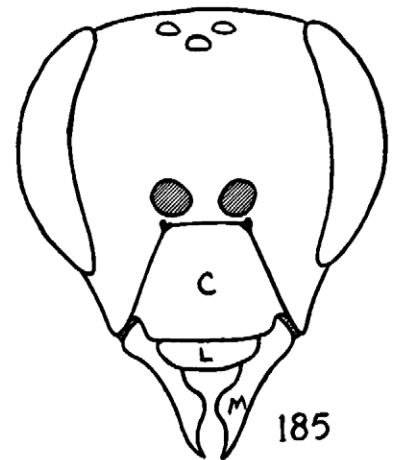
182



183



184



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PLATE XXIV

PLATE XXIV. Internal view of head, lateral aspect.

Fig. 186. Diagram of internal skeleton of head, showing horizontal orientation of tentorium characteristic of Orthoptera and other generalized insects.

Fig. 187. Rhomalea sp., Orthoptera.

Fig. 188. Perilampus hyalinus Say, Chalcidoidea, Perilampidae.

Fig. 189. Sphex (Sphex) ichneumoneus ichneumoneus (L.), Sphecoidea, Sphecidae.

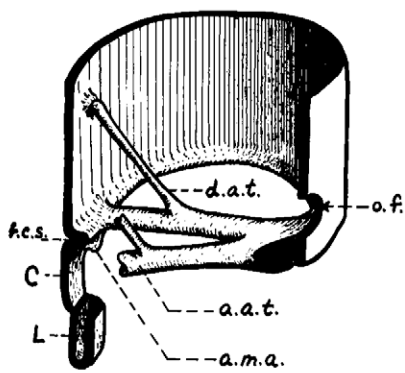
Fig. 190. Apis mellifera L., Apoidea, Apidae.

Fig. 191. Diprion (Gilpinnia) hercyniae (Hartig), Tenthredinoidea, Diprionidae.

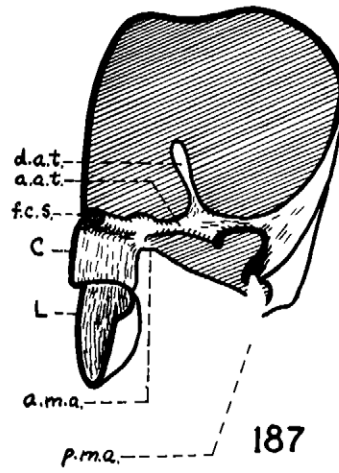
Fig. 192. Orthocentrus sp., Ichneumonoidea, Ichneumonidae.

Fig. 193. Diapria conica (Fabricius), Proctotrupoidea, Diapriidae.

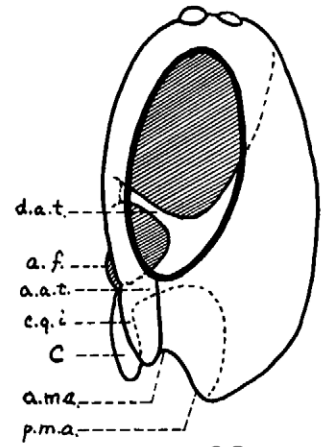
Fig. 194. Dahlbominus fuscipennis (Zetterstedt), Chalcidoidea, Eulophidae.



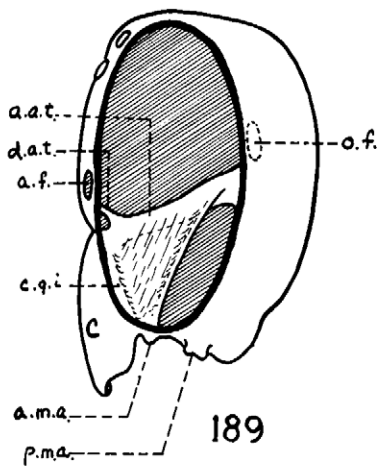
186



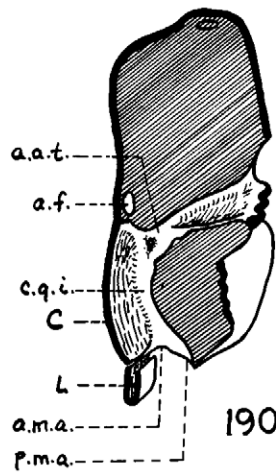
187



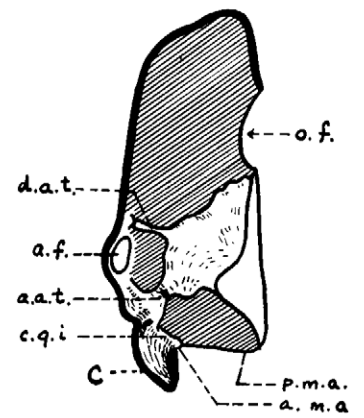
188



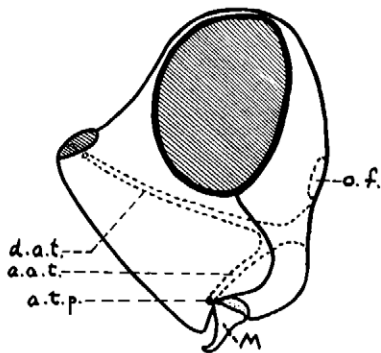
189



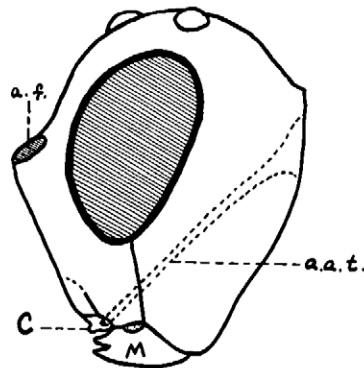
190



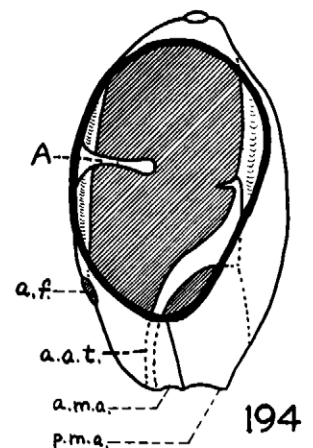
191



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PLATE XXV

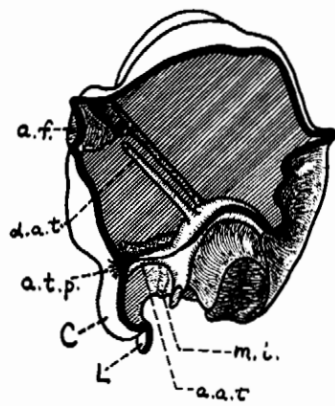
PLATE XXV.

Fig. 195. Pelecinus polyturator (Drury), Proctotrupoidea,
Pelecinidae, internal view of head, lateral view.

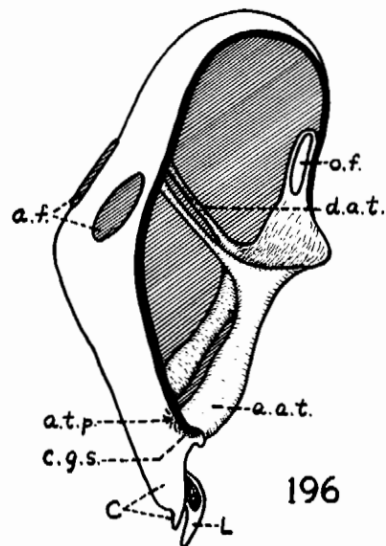
Fig. 196. Exetastes suaveolens Walsh, Ichneumonoidea,
Ichneumonidae, internal view of head, lateral view.

Fig. 197. Ametastegia (Ametastegia) equiseti (Fallén),
Tenthredinoidea, Tenthredinidae, internal view
of face.

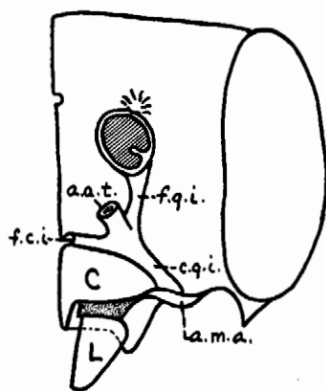
Fig. 198. Apis mellifera L., Apoidea, Apidae, internal view
of face.



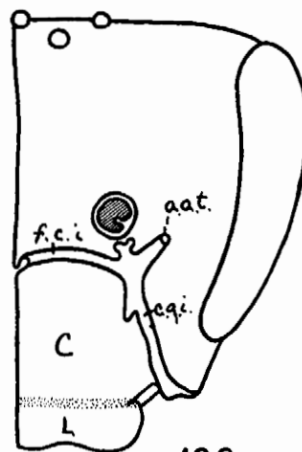
195



196



197



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APPENDIX

Generic and higher categories are listed as they appear in Muesebeck et al. (1951).

Genera from which specimens were examined are indicated by asterisks. Genera not listed in the catalogue (i.e. not present in the nearctic region) are underlined. Genera from which specimens were not seen, but in which the facial structure was inferred from the literature, are indicated by x, and the corresponding literature is cited.

SYMPHYTAMEGALODONTOIDEAI. XYELIDAE

*Xyela

*Pleroneura (fig.4)

*Xyelecia

Megaxyela

*Macroxyela

II. PAMPHILIIDAE

*Acantholyda

*Cephalcia (fig.5)

*Neurotoma

*Pamphilius

*MegalodontesTENTHREDINOIDEAI. PERGIDAE

*Acordulecera

II. ARGIDAE

1. ARGINAE

*Arge (fig.6)

2. ATOMACERINAE

Atomacera

3. STERICTIPHORINAE

*Sterictiphora

4. SERICOCERINAE

Aprosthemata

Neoptilia

Ptinus

*Sphacophilus (fig.7)

*Sofus

III. CIMBICIDAE

*Zaraea (fig.8)

*Trichiosoma (fig.9)

*Cimbex (fig.10)

IV. DIPRIONIDAE

1. MONOCTENINAE

*Monoctenus

Augomonoctenus

2. DIPRIONINAE

Zadiprion

*Neodiprion

*Diprion (Diprion)

* " (Gilpinnia)
(figs. 11,191)

*Macrodipteron

V. TENTHREDINIDAE

1. SELANDRIINAE

(1) Strongylogasterini

Eriocampidea

*Hemitaxonus (fig.12)

*Strongylogaster

*Aneugmenus (Aneugmenus) (fig.13)

* " (Stromboceridea)

* " (Eustromboceros)

(2) Selandriini

*Selandria

(3) Adelestini

*Adelesta

*Brachythops

*Melisandra

*Athalia

2. DOLERINAE

*Dolerus (Dolerus) (fig.14)

* " (Loderus)

3. SUSANINAE

*Susana

4. HETERARTHRIINAE

(1) Caliroini

*Endelomyia

*Caliroa

(2) Heterarthriini

*Heterarthrus

(3) Fenusini

*Metallus

*Messa

*Profenusa

Setabara

*Fenusa

(4) Nefusini

*Nefusa

5. NEMATINAE

(1) Cladiini

*Cladius

*Priophorus

*Trichiocampus

(2) Nematini

*Hoplocampa

Caulocampus

*Hemichroa (Hemichroa)

* " (Varna)

Craterocercus

*Platycampus

- *Anoplonyx
 - Adelomos
- *Neopareophora
- *Nematinus
- *Pristiphora
- *Pachynematus
- *Micronematus
- *Pikonema (fig.15)
- *Croesus
- *Nematus (Nematus)
- * " (Pteronidea)
- * " (Pontania)
- *Euura
- *Amauronematus
- (3) Pseudodineurini
 - Pseudodineura
 - Kerita
- (4) Pristolini
 - Pristola
- 6. ALLANTINAE
 - (1) Allantini
 - *Empria (Empria)
 - * " (Parataxonius)
 - *Monostegia
 - *Ametastegia (Ametastegia)
 - (figs. 17, 197)
 - * " (Protemphytus)
 - (fig. 16)
 - *Aphilodyctium (fig. 18)
 - *Allantus
 - *Macremphytus (fig.19)
 - *Taxonus (fig.23)
 - (2) Phrontosomatini
 - *Phrontosoma
 - (3) Eriocampini
 - *Eriocampa
 - *Dimorphopteryx (fig.21)
 - Pseudosiobla
- 7. BLENNOCAMPINAE
 - (1) Lycaotini
 - *Lycaota sodalis
 - *Blennogeneris (fig.22)
 - (2) Blennocampini
 - Tomostethus
 - *Tethida
 - *Eutomostethus
 - *Stethomostus
 - *Paracharactus
 - Ceratulus
 - Lagonis
 - *Pareophora
 - *Rhadinoceraea
 - *Phymatocera
 - *Periclista (Periclista)
 - " (Neocharactus)

*Ardis

Claremontia

*Monophadnus (fig.20)

*Blennocampa

*Monophadnoides

*Erythraspides

Halidamia

Waldheimia

8. TENTHREDININAE

*Leucopelmonus

*Lagium

*Aglaostigma (fig.24)

*Zaschisonyx

*Rhogogaster

*Tenthredo (fig.25)

*Macrophya

SIRICOIDEA

I. SYNTEXIDAE

xSyntexis (Ross, 1937)

II. SIRICIDAE

1. SIRICINAE

*Sirex

*Urocerus (figs.28,29)

*Xeris

2. TREMICINAE

*Tremex (figs. 26,27)

III. XIPHYDRIIDAE

*Xiphydria (figs. 30,31)

IV. ORUSSIDAE

*Orussus (figs. 32,33)

Ophrynella

Ophrynopus

Kulcania

CEPHOIDEA

I. CEPHIDAE

1. CEPHINAE

(1) Hartigiini

*Caenocephus

*Hartigia

*Janus

(2) Cephini

*Cephus (Cephus) figs. 34,35)

" (Trachelus)

APOCRITAICHNEUMONOIDEAI. STEPHANIDAE

*Schlettererius (fig.36)

Megischus

II. BRACONIDAE1. PAXYLOMMATINAE

*Eupachylomma (fig.37)

2. APHIDIINAE

*Ephedrus (fig. 38)

*Praon (fig.39)

*Monoctonus

Aphidius (Xenostigmus)

* " (Protaphidius)

* " (Aphidius)

" (Lysaphidus)

" (Lysiphlebus)

Trioxys (Trioxys)

* " (Acanthocaudus)

*Diaeretus

3. EUPHORINAE

Aridelus

*Meteorus (fig. 40)

Cryptoxilos

*Perilitus

*Microtonus

*Wesmaelia

*Myiocephalus (fig.41)

*Syntretus (fig.42)

*Euphoriella

Euphoriana

*Euphorus

4. MACROCENTRINAE

*Macrocentrus (fig.43)

5. HELCONINAE(1) Cenocoeliini

*Cenocoelius (fig.44)

(2) Helconini

*Helconidea

*Helcon (fig.45)

*Eumacrocentrus

(3) Diospilini

*Diospilus (fig.46)

Meteoridea

Taphaeus

(4) Zelini

*Zelee

6. BLACINAE

Neoblacus

*Blacus

Hysterobolus

*Centistes

Syrrhizus

*Orgilus

*Eubadizon

Stantonia

*Microtypus

Schizoprymnus

Urosigalphus

Triaspis

7. AGATHIDINAE

*Cremnops (fig.51)

*Earinus (fig.47)

*Aenigmostomus

Zelomorpha

Agathirsia

*Crassomicrodus

*Agathis (figs. 48-50)

8. NEONEURINAE

*Elasmosoma (fig.52)

9. MICROGASTERINAE

Dirrhope

Paroligoneurus

*Mirax

*Adelius

*Apanteles

*Microgaster

*Microplitis

10. CARDIOCHILINAE

*Cardiochiles (fig.53)

11. ICHNEUTINAE

*Ichneutes

*Proterops (fig.54)

Ichneutidea

12. CHELONINAE

*Sigalphus

*Phanerotoma

*Ascogaster

*Chelonus (Chelonus)
 " (Microchelonus)

13. DACNUSINAE

Symphya
 Chorebus
 Brachystropha

*Dacnusa (fig.55)

*Coelinidea

14. ALYSIINAE

*Aphaereta (fig.56)

Glyphogaster

*Pentapleura

Alysia

Idiasta

*Anarcha

*Orthostigma

Dinotrema

*Mesocrina

*Aspilota

*Synaldis

Oenonogastra

Hoplitalysia

Kahlia

Phaenocarpa

Asobara

15. OPIINAE

Ademon

Neopius

Gnaptodon

*Opus

16. BRACONINAE

*Vipio (fig.57)

*Iphiaulax

Atanycolimorpha

*Cyanopterus (fig.58)

Compsobracon

*Coeloides

*Atanycolus (fig.59)

*Bracon

17. SPATHIINAE

*Spathius

18. ROGADINAE

(1) Rogadini

*Rogas

Pelecystoma

*Petalodes

Tetrasphaeropyx

Yelicones

*Buccalatriplex

Polystenidea

*Oncophanes

*Clinocentrus

*Xenosternum

Amicoplidea

*Colastes

*Rhysipolis

*Phanomeris

Zamegaspilus

(2) Pambolini

Chremylus

Pambolus

(3) Hormini

*Hormius

Parahormius

Noserus

19. DORYCTINAE

(1) Doryctini

*Doryctes

Rhoptrocentrus

Doryctinus

Polystenoides

Glyptodoryctes

Glyptocolastes

Russellella

*Heterospilus

Pioscelus

Allorhogas

Callihormius

Dendrosoter

Rhaconotus

*Histeromerus

Odontobracon

(2) Hecabolini

Miocolus

*Monolexis

Acrisis

Pampolidea

*Ecphylus

Paraecphylus

20. COSMOPHORINAE

*Cosmophorus (figs.60,61)

Cosmophorinus

III. ICHNEUMONIDAE

1. PIMPLINAE

(1) Pimplini

*Scambus

*Alophosternum

*Calliephialtes

*Pimpla (fig.67)

*Iseropus

- *Tromatobia
- *Zaglyptus
- *Pseudorhyssa (fig.68)
- *Delomerista
- *Perithous
- (2) Polysphinctini
- *Clistopyga
 - Acrodactyla
 - Colpomeria
 - Laufeia
- *Schizopyga (fig.73)
- *Polysphincta
- *Hymenoepimecis (fig.66)
- *Oxyrrhexis
- *Zabrachypus
- *Zatypota
- (3) Ephialtini
- *Coccygomimus (fig.62)
- *Ephialtes
- *Itoplectis (fig.65)
- (4) Poememiini
- *Diacritus (fig.74)
- *Poemenia
- *Neoxorides (fig.71)
- (5) Rhyssini
- *Rhyssa (figs.69,70)
- *Rhyssella
- *Megarhyssa
- (6) Theroniini
- *Theronia
- (7) Brachycyrtini
- *Brachycyrtus
- (8) Labenini
- *Labena
- *Grotea (fig.72)
- (9) Xoridini
- *Xorides
- *Odontocolon
 - Aplomerus
- (10) Acaenitini
- *Coleocentrus (fig.64)
 - Mesoclistus
- *Arotes (fig.63)
- 2. TRYPHONINAE
- (1) Stilbopini
 - Stilbops
- (2) Adelognathini
- *Adelognathus
 - Cnemischys
 - Pammicra
- (3) Phrudini
 - Phrudus (Phrudus)

*Phrudus (Mengersenia)

(4) Phytodietini

*Phytodietus

Netelia (Paropheltes)

" (Parabates)

" (Toxochilus)

" (Prosthodocis)

* " (Netelia)

* " (Parabatus)

(5) Eclytini

*Eclytus

*Neliopisthus

*Campothreptus

*Hybophanes (figs.77,78,79)

*Thymaris

Atopotrophos

(6) Grypocentrini

*Grypocentrus

*Idiogramma (fig.76)

(7) Boëthini

*Boëthus

(8) Tryphonini

*Polyblastus (Polyblastus)

" (Cophenchus)

" (Labroctonus)

*Ctenochira

*Erromenus (Erromenus)

* " (Aderaeon)

*Monoblastus

Thibetoides

*Dyspetus

*Cosmoconus

Tryphon (Tryphon)

" (Noëmon)

* " (Symboëthus) (fig.75)

(9) Cteniscini

*Cteniscus

Acrotomus

*Diaborus

Exenterus

*Smicroplectrus

Exyston

3. GELINAE (= CRYPTINAE)

(1) Gelini

*Bathythrix (figs.84,85)

Amydraulax

*Mastrus (fig.83)

Apotemnus

*Otacustes

*Ethelurgus

Stiboscopus	*Atractodes
*Acrolyta	(2) <u>Aptesini</u>
*Isdromas	*Cubocephalus
Idemum	*Aptesis
*Alegina	Megaplectes
*Cyrtobasis	Opidnus
*Diaglyptidea	*Schenkia
*Phobetres	*Giraudia
*Haplaspis	*Polytribax
Anuroptropus	Rhembobius
*Gelis	*Demopheles
Arachnoleter	(3) <u>Sphecophagini</u>
*Myersia	*Sphecophaga
*Thaumatotypidea	(4) <u>Mesostenini</u>
*Hemiteles	*Christolia
*Gnypetomorpha	*Trachysphyrus (fig.82)
Hedylus	*Compsocryptus
*Sternocryptus	*Pycnocryptus
*Endasys (Endasys)	*Mesostenus
* " (Glyphicnemis)	*Polycyrtus (Polycyrtus)
*Eriplanus	*Cryptanura
*Phygadeuon	*Hidryta
Iselix	*Trychosis
Caenomeris	Idiolispa
*Stilpnus	*Apsilops
*Mesoleptus	*Gambrus

*Hoplocryptus
 *Agrothereutes
 *Joppidium
 *Ischnus
 *Chromocryptus
 *Listrognathus (fig.81)
 *Diapetimorpha
 *Mallochia
 Polistiphaga
 Nasutocryptus
 *Lymeon
 *Acerastes
 Polycyrtidea
 *Echthrus
 *Xylophrurus
 Agonocryptus
 Cryptohelcostizus
 *Helcostizus
 *Acroricnus (fig.80)
 *Messatoporus

4. ICHNEUMONINAE

(1) Alomyini
 *Phaeogenes
 *Diadromus
 *Rhexidermus

*Centeterus (fig. 86)
 *Colpognathus
 *Dicaelotus
 Stenodontus
 (2) Pristiceratini
 *Aphaeleticus
 Cyclolabus
 *Platylabus
 Pristoceros
 Thaumatoteles
 *Hypomecus
 *Ectopius
 (3) Listrodromini
 *Anisobas
 *Neotypus
 (4) Ischnojoppini
 *Trogomorpha
 (5) Acanthojoppini
 Pseudoplatylabus
 (6) Eurylabini
 *Probolus
 (7) Amblytelini
 *Hoplismenus (fig.87)
 Lobaegis
 Narthecura
 Plagiotrypes

Limonethe	Macrojoppa
*Melanichneumon	Trogus
*Cratichneumon	
*Aoplus	5. BANCHINAE
*Patroclus	(1) <u>Glyptini</u>
Anisopygus	*Glypta
*Exephanes	(2) <u>Lycorini</u>
*Ectopimorpha	*Toxophoroides
*Chasmias	(3) <u>Lyssonotini</u>
*Pseudamblyteles	*Amersibia
*Amblyteles	*Arenetra
Spilichneumon	*Lampronota
*Ctenichneumon	, Asymmictus
*Tricholabus	Mnioes
Pterocormus	*Lissonota (Lissonota)
(8) <u>Ichneumonini</u>	" (Anarthronota)
*Ichneumon	*Pimplopterus
Protichneumon	Trevoria
Amblyjoppa	*Cryptopimpla
(9) <u>Trogini</u>	*Asphragis
Catadelphus	*Syzeuctus
Gnamptopelta	*Diradops
Tricyphus	(4) <u>Neorhacodini</u>
Conocalama (Tmetogaster)	Neorhacodes
" (Conocalama)	

(5) Banchini

*Exetastes (figs.88, 196)

Agathilla

*Ceratogastra

*Banchus

6. SCOLOBATINAE

(1) Scolobatini

*Scolobates (fig.89)

(2) Euceratini

*Euceros (fig.90)

(3) Pionini

*Trematopygus

Oocenteter

*Rhorus (Rhorus)

" (Cyphanza)

Pion

(4) Ctenopelmatini

*Ctenopelma

Xenoschesis (Xenoschesis)

* " (Polycinetis)

*Homaspis

*Notopygus

(5) Mesoleiini

(a) Subtribe: Perilissina

*Opeltes

*Perilissus

*Absyrtus

Oetophorus

*Labrossyta

*Laphyroscopus

*Lathrolestes

*Synoecetes

Gnesia

(b) Subtribe: Mesoleiina

*Protarchus

*Himerta (fig.91)

*Mesoleius (figs.92,93)

*Lamachus

*Saotis

(6) Euryproctini

Synomelix

*Dialges

*Mesoleptidea

*Polyterus

*Syndipnus

*Hypamblys

*Ipoctoninus

Hyperallus

Anisotacrus

*Hadrodactylus

*Euryproctus

(7) Callidiotini

Callidiotes

7. COLLYRIINAE

xCollyria (Salt, 1931)

8. ORTHOPELMATINAE

*Orthopelma

9. PLECTISCINAE

Allomacrus

*Cylloceria

Blapticus

*Catastenus

*Dallatorrea

Symplecis

Eusterinx

*Megastylus

*Helictes

Aniseres

*Proclitus

Plectiscidea

Pantisarthrus

Aperileptus

Microleptes

Hyperacmus

10. ORTHOCENTRINAE

*Orthocentrus (figs. 94, 95, 192)

Picrostigeus

Neurateles

*Mnesidacus

*Stenomacrus

*Leipaulus

11. DIPLAZONINAE

*Diplazon

*Zootrephus

*Promethes

Syrphoctonus

*Phthorima

*Enizemum

12. METOPIINAE

*Metopius (Metopius) (fig. 97)

" (Clemontia)

" (Cultrarius)

Pseudometopius

Spudeaus

Chorinaeus

Triece

Periope

Leurus

Colpotrochia

*Triclistus

Hypsicera

*Exochus (fig.96)

13. OPHIONINAE

(1) Porizonini

*Pyracmon

Nemeritis

*Cymodusa

Cymodusopsis

*Campoplex

*Nythobia

*Idechthis

*Casinaria

*Charops

*Bathyplectes

Biolysia

*Campoletis

Ecphoropsis

*Spudastica

*Dusona

*Nepiera

*Phobocampe

*Horogenes

*Hyposoter

*Campoctonus

*Olesicampe

*Benjaminia

*Charopsimorpha

(2) Cremastini

*Dimorpha

*Pristomerus

Zaleptopygus

*Pseuderipternus

*Dolichopselephus

*Cremastus

Areolopristomeris

Eiphosoma

(3) Tersilochini

*Leptopygus

*Cratophion

*Barycnemis

Tersilochus

Heterocola

(4) Anomalini

(a) Subtribe: Anomalina

Anomalon

Neogreeneia

(b) Subtribe: Ophionellina

Ophionellus

(c) Subtribe: Ophiopterina

Ophiopterus

(d) Subtribe: Gravenhorstiina

Trichomma

Aphanistes

Barylypa

Gravenhorstia	Ooctonus
*Labrorychus	Cosmocomoidea
Atrometus	Camptoptera
(e) Subtribe: Therionina	Gonatocerus
*Therion	Alaptus
Heteropelma	Dicopus
(5) <u>Ophionini</u>	
*Threodon	2. MYMARINAE
Rhynchophion	Erythmelus
*Ophion	Parallelaptera
Simophion	Stethynium
Trophophion	Patasson
Clistorapha	Anagrus
Boethoneura	*Mymar
Genophion	Acmopolynema
Chilophion	Barypolynema
*Enicospilus	*Polynema
14. MESOCHORINAE	Caraphractus
*Cidaphus	Neomymar
*Astiphromma	Mymarilla
*Mesochorus	Arescon
<u>CHALCIDOIDEA</u>	x <u>Platypatasson</u> (Ogloblin, 1946)
I. <u>MYMARIDAE</u>	x <u>Platystethynium</u> (Ogloblin, 1946)
1. GONATOCERINAE	

(A number of miscellaneous trichogrammatids were examined)

II. TRICHOGRAMMATIDAE

Trichogramma

Aphelinoidea

Zaga

Trichogrammatomyia

Lathromeroides

Lathromeris

Megaphragma

Poropoea

Zagella

Xenufens

Tumidiclava

Oligosita

Brachista

Ufens

Hydrophylita

Uscana

Abbela

Neobrachistella

Centrobiopsis

III. EULOPHIDAE

1. EULOPHINAE

*Pnigalio

*Sympiesis

*Necremnus

*Hemiptarsenus

*Pardiaulomella

Diaulomorpha

*Solenotus

*Notanisomorpha

*Eulophus

*Dahlbominus (figs. 98, 99, 194)

*Dimmockia

*Dicladocerus

2. APHELININAE

Eretmocerus

Euderomphale

Archenomus

Centrodora

*Marietta

*Aphytis

*Aphelinus

Mesidea

*Ablerus

Azotus

Tumidiscapus

Physcus

*Prospaltella

*Encarsia

*Aspidiotiphagus

Aneristus

*Coccophagus

Tetracyclos

xEurymyiocnema (Compere, 1948)

3. TETRASTICHINAE

Ceratoneura

Paraspalangia

Winnemana

Thripoctenus

Thriposoma

Omphalomopsis

Galeopsomyia

Paragaleopsomyia

Prothmyus

Galeopsomopsis

Thymiscus

*Tetrastichus

*Aprostocetus

*Syntomosphyrum

Paromphaloidomyia

*Melittobia

*Crataepus

4. ELACHERTINAE

*Euplectrus

Euplectromorpha

Diaulinopsis

Ardalus

*Paraolinx

Stenomesius

*Miotropis

*Elachertus

*Hyssopus

Pseudolynx

Mirolinx

*Grotiusomyia

Apterolophus

Giraultia

Cirrospiloideus

*Cirrospilus

*Zagrammosoma

*Stenomesioideus

*Olynx

5. ENTEDONTINAE

Astichus

Euophthalmomyia

Omphale

Hubbardiella
 *Closterocerus
 Ephropalotus
 Emersonella
 *Euderus
 *Chrysocharis
 *Achrysocharoides
 Rhicnopeltomyia
 Rhicnopeltoidea
 Carlyleia
 Chrysocharomyia
 Parachrysocharis
 *Achrysocharis
 *Achrysocharella
 *Derostenus
 Lophocomus
 *Horismenus
 *Pleurotropis (fig.100)
 *Entedon
 Paracrias
 Emersonopsis
 Acrias
 Nesomyia

IV. ELASMIDAE

*Elasmus

V. THYSANIDAE

*Thysanus

VI. EUTRICHOSOMATIDAE

*Eutrichosoma

VII. TANAOSTIGMATIDAE

Tanaostigmodes

VIII. ENCYRTIDAE1. ENCYRTINAE

Tineophoctonus

*Leptomastix

*Anagyrus

*Comperia

xApoanagyrus (Compere, 1947)

xPseudleptomastix (Compere, 1947)

xEctromatopsis (Compere, 1947)

Henicopygus

Calocerinus

Tetralophidea

Anusia

Meromyzobia

Tetracnemus

Habrolepoidea

Tetralophiellus	Euryrhopalus
Tetracladia	Rhytidothorax
Tetracnemopsis	Homalotylus
*Pentacnemus	Anisotylus
*Leptomastidea	*Ageniaspis
*Habrolepteryx	Prionomitus
*Clausenia	Thysanomastix
*Encyrtus	Psyllaephagus
*Psilophrys	*Microterys
Parapsilophrys	Epiencyrtus
Psilophryoidea	*Isodromus
*Paralitomastix	Neococcidencyrtus
*Copidosoma (fig.101)	Coccidencyrtus
Sceptrophorus	Bothriocraera
*Cerchysius	*Pseudaphycus
Baeocharis	Acerophagus
Chestomorpha	Cirrhencyrtus
Aenasius	Aenasioidea
Chalcaspis	xAphycus (Compere, 1947)
Bothriencyrtus	Aphycoideus
*Bothriothorax	Blastothrix
Pentelicus	Ooencyrtus
Blepyrus	Aphidencyrtus
Hemaenasius	Syrphophagus
Trichomasthus	*Pseudencyrtus
Discodes	*Holcencyrtus (fig.102)

*Cheiloneurus	xHunterellus (Gahan, 1934)
x Achrysopophagus (Compere, 1938)	Paraleurocerus
*Chiloneurinus	Epanusia
Chrysopophagus	Formicencyrtus
*Cerapterocerus	Epicerchysus
Habrolepis	Zaommoencyrtus
*Anabrolepis	Nebaocharis
Adelencyrtus	Comperiella
Ceraproceroideus	Coccidoxenus
*Chrysoplatycerus	Quaylea
Anicetus	Parastenoterys
*Zarhopalus	Anarhopus
Stemmatosteres	Pseudorhopus
Helegonatopus	Hexacnemus
Coccobius	Tachardiobius
Pseudhomalopoda	Mayridia
Eusemion	Gahaniella
Atropates	Epaenasomyia
Xanthoencyrtus	Pheidoloxenus
Pauridia	x <u>Coccidoxenus</u> (Gomes, 1941)
Plagiomerus	x <u>Uesleria</u> (Timberlake, 1926)
*Psylledontus	x <u>Bothriophryne</u> (Compere, 1939)
Agromyzaphagus	
Paracalocerinus	2. ARRHENOPHAGINAE
Echthrogonatopus	Arrhenophagus
xIxodiphagus (Gahan, 1934)	

IX. EUPELMIDAE

- *Metapelma
- *Eusandalum
 - Calosota
- *Eupelmus
 - Arachnophaga
- *Eupelmella (fig.103)
- *Anastatus
 - Encyrtaspis
 - Lecaniobius
 - Zaischnopsis

X. EUCHARITIDAE

- *Pseudochalcura
- *Stilbula
 - Lophyrocera
- *Kapala
- *Pseudometagea
- *Orasema

XI. PERILAMPIDAE

- *Euperilampus
- *Perilampus (figs.104,188)

XII. AGAONTIDAE

- *Blastophagus
 - Secundeisenia

XIII. TORYMIDAE

1. IDARNINAE

- Colyostichus
- Sycophila
- Idarnes

2. TORYMINAE

- *Allotorymus
- *Torymus (fig.105)
- *Diomorus
 - Physothorax

3. ERIMERINAE

- Erimerus
- Pseuderimerus

4. MONODONTOMERINAE

- *Liodontomerus
- *Idiomacromerus
- *Platykula
 - Dimeromicrus
- *Monodontomerus
 - Zaglyptonotus
- *Glyphomerus
 - Eridontomerus
- *Pseudotorymus

- Cryptopristus
 Ditropinotus
 Antistrophoplex
 Microdontomerus
 5. MEGASTIGMINAE
 *Megastigmus (fig.106)
 XIV. ORMYRIDAE
 Monobaeus
 *Ormyrus
 Megormyrus
 XV. PTEROMALIDAE
 1. SPHEGIGASTERINAE
 (1) Spalangiini
 *Spalangia
 (2) Cerocephalini
 *Choetospila
 Acerocephala
 *Theocolaxia
 (3) Asaphini
 *Asaphes
 Hyperimerus
 (4) Diparini
 *Dipara
 Apterolelaps
 Spalangiolaelaps
 (5) Lamprotatini
 *Lamprotatus
 *Seladerma
 *Syntomopus
 *Bubekia
 Brachycaudonia
 *Chrysolampus
 Elatus
 Paracarotomus
 (6) Pachyneurini
 *Pachyneuron
 *Pachycrepoides
 *Euneura
 (7) Cratomini
 *Cratomus
 (8) Halticopterini
 Halticoptera
 (9) Spegigasterini
 Trigonogastra
 *Cyrtogaster
 Gyrinophagus
 *Eurydinota
 Heteroschema
 Panstenon

2. PTEROMALINAE

(1) Eunotini

Tomocera

Eunotus

*Scutellista

(2) Pirenini

Pirene

Spathopus

Morodora

Parecrizotes

Stigmatocrepis

Dipachystigma

(3) Brachyscelidiphagini

*Hemadas

(4) Tridymini

*Trigonoderus

Elachertodomyia

*Tridymus

Parasyntomocera

*Systasis

Terobia

*Erixestus

(5) Merisini

*Merisus

*Merisoporus

*Callitula

(6) Rhaphitelini

*Rhaphitelus

(7) Pteromalini

*Pachyceras

*Metacolus

*Dinotiscus

*Rhopalicus

*Amblymerus (fig.107)

Zacalochlora

Platyterma

*Coelopisthia

*Dibrachoides

Belonura

*Urolepis

Eipteromalus

*Trichomalus

*Diglochis

*Tritneptis

Pseudomicromelus

*Dibrachys

*Eupteromalus

*Lariophagus

*Schizonotus

Psilocera

Scymnophagus

*Xenocrepis

Meraporus

*Neopolycelis
 *Psychophagus (fig.108)
 *Cecidostiba
 *Catolaccus
 *Zatropis
 Caenacis
 Pseudocatolaccus
 *Muscidifurax
 *Nasonia
 *Bruchobius
 *Pteromalus
 *Habrocytus
 *Anisopteromalus
 *Trimeromicrus
 *Systellogaster
 Paradibrachys
 Endomychobius
 *Hypopteromalus
 (8) Metastenini
 Hemitrichus
 *Norbanus
 *Metastenus
 *Neocatolaccus
 Eurydinoteloides
 Megatrydymus
 Acaenacis

(9) Cleonymini

*Tomicobia
 *Heydenia
 *Epistenia
 Cleonymus
 Ptinobius
 *Cheiropachus

XVI. EURYTOMIDAE

 Isosomodes
 *Harmolita
 Axima
 Macrorileya
 *Rileya
 Bephratoides
 *Bephrata
 *Prodecatoma
 Phylloxeroxenus
 Chryseida
 *Eurytoma (fig.109)
 *Eudecatoma
 *Systole
 *Bruchophagus

XVII. PODAGRIONIDAE1. PODAGRIONINAE

*Podagrion

2. CHALCEDECTINAE

Chalcedectus

Euchrysia

XVIII. CHALCIDIDAE

1. HALTICHELLINAE

*Haltichella

*Stomatoceras

*Schwarzella

2. BRACHYMERIINAE

Acanthochalcis

*Phasgonophora

*Trigonura

*Brachymeria (fig.110)

3. DIRHININAE

*Dirhinus

4. CHALCIDINAE

Metadontia

*Chalcis

*Spilochalcis

*Ceratosmicra

XIX. LEUCOSPIDAE

*Leucospis (fig.111)

CYNIPOIDEA

I. IBALIIDAE

1. IBALIINAE

*Ibalia (fig.112)

II. LIOPTERIDAE *

1. MESOCYNIPINAE

Paramblynotus

Kiefferiella

III. FIGITIDAE

1. ASPICERATINAE

*Paraspicera

*Prosaspicera

*Callaspidia (fig.113)

2. ANACHARITINAE

Xyalaspis

Acothyreus

*Anacharis

Hexacharis

*Aegilips

3. FIGITINAE

*Neralsia

*Xyalophora

xParaschiza (Weld, 1952)

*Lonchidia

*Melanips

*Sarothrus

Trischiza

*Zygosis

*Figites

Psichacra

*Ganaspis

Hypoethria

*Rhoptromeris

Aglaotoma

*Pseudeucoila (Hexamerocera)

* " (Pseudeucoila)

" (Macrocereucoila)

*Cothonaspis

*Eucoilidea (fig. 114)

IV. CYNIPIDAE

1. EUCOILINAE

*Kleidotoma (Kleidotoma)

* " (Tetrarhoptra)

" (Kleidotomidea)

" (Heptameris)

*Hexacola

Eutrias

*Eucoila

Aporeucoela

Trybliographa (Tetraplasta)

" (Pentaplastidea)

* " (Hexaplasta)

* " (Trybliographa)

2. CHARIPINAE

Lytoxysta

*Charips

*Alloxysta

Glyptoxysta

Hemicrisis

*Phaenoglyphis

3. CYNIPINAE

Saphonecrus

*Synergus

Synophrus

Synophromorpha

*Periclistus

Myrtopsen

*Ceroptres
 *Euceroptres
 *Gonaspis
 *Antistrophus
 *Diastrophus
 *Liposthenes
 *Aylax
 *Aulacidea
 *Gillettea
 *Diplolepis
 *Neuroterus
 Trichoteras
 Phylloteras
 Xystoteras
 *Xanthoteras
 *Acraspis
 *Philonix
 Liodora
 Dros
 *Adleria
 *Amphibolips
 *Andricus (fig.115)
 Besbicus
 Atrusca
 *Disholcaspis
 Antron

*Belonocnema
 Sphaeroteras
 Zopheroteras
 *Loxaulus
 Bassettia
 Eumayria
 *Trisoleniella
 Odontocynips
 Holocynips
 Plagiotrochus
 *Dryocosmus
 Heteroecus
 *Callirhytis

PROCTOTRUPOIDEA

I. EVANIIDAE

*Evania (fig.116)
 *Prosevania
 Evaniella
 *Hyptia

II. GASTERUPTIIDAE

1. AULACINAE

*Aulacostethus
 *Aulacus

2. GASTERUPTIINAE

*Gasteruption (fig.117)

*Rhydinofoenus

III. PELECINIDAE

*Pelecinus (figs.118,195)

IV. VANHORNIIDAE

*Vanhornia (fig.125)

V. ROPRONIIDAE

*Ropronia (fig.126)

VI. HELORIDAE

*Helorus

VII. PROCTOTRUPIDAE

*Proctotrupes

*Disogmus (fig.119)

Phaenoserphus

*Cryptoserphus

*Codrus

VIII. CERAPHRONIDAE

*Ceraphron

Neoceraphron

*Aphanogmus

Ecitonetes

Allomicrops

*Lagynodes

Atritomellus

*Lygocerus

*Conostigmus

*Trichosteresis

*Megaspilus

Conostigmoides

Dendrocerus

IX. DIAPRIIDAE

1. DIAPRIINAE

Solenopsia

Auxopaedeutes

Propantolyta

Myrmecopria

Lepidopria

Adeliopria

*Entomacis

*Aparamesius

Hemilexis

Idiotypa

*Paramesius

*Aneurhynchus

*Psilus

*Spilomicrus	Stylidolon
*Monelata	*Aclista
*Xenopria	Acropiesta
*Phaenopria	Rhynchopsilus
Glyptonota	Atelopsilus
*Acidopria	Paratelopsilus
*Loxotropa	
*Trichopria	X. <u>SCELIONIDAE</u>
Cracinopria	
*Basalys	1. TELENOMINAE
*Diapria (Figs.120,121,193)	Aradophagus
Doliopria	Tiphodytes
Prosynacra	Eumicrosoma
	*Protrimorus
2. CINETINAE	*Telenomus (Aholcus)
Ismarus	* " (Telenomus) (fig.122)
*Oxylabis	*Dissolcus
Acanosema	*Trissolcus
*Cinetus	Hadrophanurus
Propsilomma	
*Zygota	2. BAEINAE
Diphora	Tetrabaeus
Macrohynnis	*Ceratobaeus
*Miota	*Baeus
*Leptorhaptus	*Acoloides
Scorpioteleia	Thoron

3. TELEASINAE

*Teleas

*Paragryon

*Trimorus

*Trisacantha

4. SCELIONINAE

*Sparasion

*Scelio

*Hoploteleia

*Opisthacantha

Oethecoctonus

Paridris

Anteris

Prosanteris

Hadronotus

*Baryconus

Prosapegus

*Ceratoteleia

Pegoteleia

Macroteleia

*Stictoteleia

Synteleia

Pseudanteris

XI. PLATYGASTERIDAE

1. INOSTEMMINAE

Monocrita

Metaclisis

*Acerota

*Allotropa

Triclavus

*Inostemma (fig.123)

*Isostasius

2. PLATYGASTERINAE

*Amblyaspis

*Fidiobia

Amitus

*Isocybus (fig.124)

*Trichacis

*Eritrissomerus

*Platygaster

Xestonotidea

*Sactogaster

*Leptacis

Gastrotrypes

CHRYSIDOIDEA

I. CHRYSIDIDAE

- *Omalus
- *Elampus
- *Diplorrhinos
- *Holopyga
- *Hedychridium
- Hedychrum
- *Chrysis (Chrysura)
- * " (Chrysogona)
- " (Dichrysis)
- * " (Trichrysis)
- * " (Chrysis) (fig.127)
- * " (Pyria)
- *Stilbum (fig.128)
- *Parnopes

II. CLEPTIDAE

- *Cleptes
- Mesitiopterus

BETHYLOIDEAI. BETHYLIDAE

- *Cephalonomia
- Glenosema
- *Scleroderma

- *Laelius
- *Epyris
- *Rhabdepyris
- Holepyris
- Psilepyris
- Chlorepyris
- Xanthepyrus
- Acrepyris
- Anisepyris
- Plastanoxus
- Pristocera
- *Pseudisobrachium
- Disomphalus
- Bethylus
- Digoniozus
- *Goniozus
- *Perisierola
- Parasierola

II. SCLEROGIBBIDAE

- Probethylus

TRIGONALIDAE

- *Orthogonalys
- Poecilognathos
- Lycogaster
- *Bareognathos (fig.129)

SCOLIOIDEAI. TIPHIIDAE

1. TIPHIINAE

*Tiphia (figs. 130,131)

Neotiphia (Neotiphia)

" (Krombeinia)

Paratiphia

Epomidiopteron

2. MYZININAE

Pterombrus

*Myzinum

3. ANTHOBOSCINAE

Lalapa

4. BRACHYCISTIDINAE

*Brachycistis

Brachycistina

Brachycistellus

Quemaya

Colocistis

Glyptometopa

Stilbopogon

Glyptacros

Xeroglypta

Aulacros

Eurycros

Astigmometopa

Aglyptacros

5. METHOCHINAE

*Methocha (Methocha)

6. MYRMOSINAE

*Myrmosa (Myrmosa) (fig.132)

" (Myrmosina)

" (Myrmosula)

II. SIEROLOMORPHIDAE

Sierolomorpha

III. MUTILLIDAE

1. APTEROGYNINAE

(1) Chyphotini

*Chyphotus

Pitanta

2. TYPHOCTINAE

Typhoctes

3. SPHAEROPHTHALMINAE

Protophotopsis (Protophotopsis)

- Photomorphus
 Micromutilla
 Sphaerophthalma
 Photopsis
 *Odontophotopsis
 Tetraphotopsis
 Morsyma
 *Pseudomethoca
 Myrmilloides
 *Dasymutilla (figs.133,134)
 Lomachaeta

 4. MUTILLINAE

 (1) Mutillini
 *Timulla (Timulla)

 (2) Ephutini
 *Ephuta

 IV. RHOPHALOSOMATIDAE

 xRhopalosoma (Brues,1943)
 Olixon

 V. SCOLIIDAE

 *Scolia (Scolia)
 " (Triscolia)
 *Campsomeris (Campsomeris)
- Campsoscolia
 *Dielis (figs.136,137)

 VI. SAPYGIDAE

 1. FEDTSCHENKIINAE

 Fedtschenkia

 2. SAPYGINAE

 *Sapyga (fig. 135)
 Eusapyga

FORMICIDAE (Unless otherwise
 specified, genera marked
 x were seen in Wheeler,
 1910)

 1. DORYLINAE

 *Eciton (Eciton) (figs.143,144)
 " (Nomamymex)
 " (Labidus)
 * " (Neivamymex) (fig.145)
 xLeptanilla (Wheeler, 1932)
 xAenictus (Wheeler, 1930)
 xCheliomymex
 xDorylus

 2. CERAPACHYINAE

 Ceraphachys (Ceraphachys)

*Ceraphachys (Parasyscia)	x <u>Thaumatomyrmex</u> (Weber, 1939)
Acanthostichus (Acanthostichus)	x <u>Wadeura</u> (Weber, 1939)
Ctenopyga	x <u>Myrmecia</u>
3. PONERINAE	x <u>Mystrium</u>
	x <u>Harpegnathus</u>
xStigmatomma	x <u>Streblognathus</u>
Platythyrea	x <u>Parasyscia</u>
*Ectatomma (Ectatomma) Fig. 142)	x <u>Cylindromyrmex</u>
" (Parectatomma)	x <u>Stigmatomma</u>
Proceratium	x <u>Odontoponera</u>
Sysphincta	* <u>Paraponera</u> (fig. 138)
Discothyrea	
xNeoponera (Neoponera) (Wheeler, 1928a)	4. LEPTALEINAE (=PSEUDOMYRMINAE)
*Pachycondyla (Pachycondyla) (fig. 141)	Leptalea (=Pseudomyrma)
Euponera (Euponera)	x <u>Sima</u>
" (Brachyponera)	
" (Trachymesopus)	5. MYRMICINAE
xPonera	* <u>Myrmica</u> (Myrmica)
xLeptogenys (Leptogenys)	" (Manica)
" (Lobopelta)	Progonomyrmex (Progonomyrmex)
xOdontomachus	" (Ephebomyrmex)
x <u>Acanthoponera</u> (Wheeler, 1923)	Stenamma
x <u>Anochetus</u> (Creighton, 1930)	x <u>Aphaenogaster</u> (Aphaenogaster)
x <u>Myopias</u> (Wheeler, 1923)	" (Attomyrma)
x <u>Probolomyrmex</u> (Wheeler, 1928b)	Novomessor
	Veromessor

xPheidole (Pheidole)	xTetramorium
" (Ceratopheidole)	Xiphomyrmex
xEpipheidole	Wasmannia
xSympheidole	Paracryptocerus (Paracryptocerus)
xCardiocondyla	" (Harnedia)
xCrematogaster (Orthocrema)	" (Cyathomyrmex)
" (Crematogaster)	xStrumigenys (Strumigenys)
*Monomorium (Monomorium) (fig.147)	Smithistruma (Wessonistruma)
" (Parholcomymex)	" (Smithistruma)
Xenomyrmex	Trichoscapa
xSolenopsis (Solenopsis) (Weber,1943)	Quadristruma
" (Euophthalma)	xCyphomyrmex (Cyphomyrmex)
" (Diplorhoptrum)	x " (Mycetosoritis)
Epoecus	xTrachymyrmex
xAnergates	*Acromyrmex (Acromyrmex)
xErebomyrma	x " (Moellerius)
Myrmecina	*Atta (fig.139)
xMacromischa	xWheeleriella
Leptothorax (Nesomyrmex)	*Daceton
" (Myrafant)	xRhopalomastix (Wheeler,1929)
" (Dichothorax)	xMelissotarsus (Wheeler,1929)
x " (Leptothorax)	xMessor
xSymmyrmica	*Cryptoceras (fig.140)
xHarpagoxenus	xPristomyrmex
Triglyphothrix	xEpitritus
	xCataulacus

<u>xHolcomymrmex</u>	Camponotus (Tanaemyrmex)
<u>xMyrmicocrypta</u>	* " (Myrmothrix) (figs.146,148)
<u>xSericomymrmex</u>	" (Myrmentoma)
<u>xApterostigma</u>	x " (Colobopsis)
<u>xMycocepurus</u>	" (Myrmaphaenus)
<u>xFormicoxenus</u>	" (Manniella)
<u>xOxygyne</u>	" (Myrmobrachys)
<u>xStrongylognathus</u>	Paratrechina (Paratrechina)
6. DOLICHODERINAE	" (Nylanderia)
<u>xDolichoderus</u> (Dolichoderus)	xPrenolepis
" (Hypoclinea)	xLasius (Lasius)
<u>xLiometopum</u>	" (Chthonolasius)
<u>xIridomyrmex</u> (Newell,1909)	x " (Acanthomyops)
Forelius	xMyrmecocystus
Dorymyrmex (Dorymyrmex)	xFormica (Proformica)
" (Conomyrma)	" (Neoformica)
Tapinoma	* " (Formica)
<u>xLeptomymrmex</u>	xPolyergus
<u>xAzteca</u>	xPseudolasius
<u>xAneuretus</u>	xAcantholepis (Wheeler,1935a)
7. FORMICINAE	xMyrmoteras (Creighton,1930)
Brachymymrmex (Brachymymrmex)	xAcropyga (Wheeler, 1935b)
*Camponotus (Camponotus) (fig.149)	xGesomymrmex
	xOpisthopsis
	xHemioptica

xDimorphomyrmex

xOecophylla

VESPOIDEA

I. VESPIDAE

1. VESPINAE

*Vespa

*Vespula (Vespula) (Fig.150)

* " (Dolichovespula)

2. POLISTINAE

*Polistes (fig.151)

3. POLYBIINAE

*Mischocyttarus (Mischocyttarus)

" (Kappa)

xBrachygastra (Bequaert,1932)

xPolybia (Bequaert,1932)

4. ZETHINAE

Zethus (Zethus)

* " (Zethusculus) (fig.152)

5. MASARINAE (Several misc.specimens examined)

Pseudomasaris (Pseudomasaris)

" (Toryna)

" (Holopticus)

6. EUPARAGIINAE

xEuparagia (Bohart, 1948)

Paramasaris

7. EUMENINAE

*Eumenes (fig.153)

Montezumia

Pachymenes (Pachymenes)

* " (Paranortonia)

*Pseudodynerus

*Monobia

Odynerus

*Pseudepipona

*Rygchium

Pachodynerus

*Ancistrocerus

*Symmorphus

Hypalastoroides

Leptochilus

*Stenodynerus (Stenodynerus)

* " (Parancistrocerus)

Dolichodynerus

Maricopodynerus

Leptochiloides

Pterocheilus (Pterocheilus)

* " (Megapterocheilus)

" (Onchopterocheilus)

" (Micropterocheilus)

POMPILIDAE

1. PEPSINAE

(1) Pepsini

*Chirodamus

Hemipepsis

*Pepsis

*Priocnessus

*Priocnemioides

*Cryptocheilus

Dipogon (Deuteragenia)

" (Dipogon)

*Priocnemis (Priocnemis)

" (Myrmecosalius)

*Calicurgus

(2) Macromerini

*Phanagenia

*Auplopus

Ageniella (Ameragenia)

" (Leucophrus)

" (Nemagenia)

* " (Ageniella)

" (Priophanes)

2. CEROPALINAE

Minagenia

Notocyphus

*Ceropales

3. POMPILINAE

(1) Aporini

Aporus (Aporus)

" (Plectraporus)

Melanaporus

Chelaporus

Allaporus

Psorthaspis

(2) Pompilini

Tastiotenia

Chalcochaes

*Evagetes

*Agenioideus (Agenioideus)

" (Ridestus)

" (Gymnochaes)

*Sericopompilus

*Episyron (fig.154)

*Poecilopompilus

*Tachypompilus

*Anoplius (Lophopompilus)

" (Notiochaes)

" (Anopliodes)

* " (Arachnophroctonus)

*Anoplius (Pompilinus)	Bothynostethus
" (Anoplius)	Pisonopsis
Pompilus (Pompilus)	*Plenoculus
" (Hesperopompilus)	*Solierella
* " (Ammosphex)	*Miscophus
* " (Arachnospila)	Nitelopterus
* " (Anoplochaeres)	Nitela
Aporinellus	(2) <u>Tachytini</u>
Allochaeres	*Tachytes (Tachytes)
Paracyphononyx	" (Tachyplena)
	" (Tachynana)
<u>SPHECOIDEA</u>	" (Tachyoides)
I. <u>AMPULICIDAE</u>	*Larropsis
Ampulex (Ampulex)	*Tachysphex (Tachysphex) (fig.156)
x " (Rhinopsis)	(3) <u>Larrini</u>
(Strandtmann, 1943)	Larra
Dolichurus	Motes (Motes)
	" (Notogonius)
II. <u>SPHECIDAE</u>	
1. ASTATINAE	3. TRYPOXYLONINAE
Diploplectron	Pison (Pison)
*Astata (Astata) (fig.155)	*Trypoxylon (Trypoxylon (fig.157)
" (Dryudella)	* " (Trypargilum)
2. LARRINAE	4. PEMPHREDONINAE
(1) <u>Miscophini</u>	(1) <u>Psenini</u>
*Lyroda	Diodontus (Diodontus)

*Psen (Psen)
 * " (Pseneo)
 *Mimesa (Mimesa) (fig.158)
 * " (Mimumesa)

Pluto

(2) Pemphredonini

*Xylocelia

xAmmoplanops (Pate,1937)

xPulverro (Pate,1937)

*Pemphredon (Pemphredon)

* " (Cemonus)

*Stigmus (Stigmus)

*Passaloecus (fig.159)

*Spilomena

xXysma (Pate,1937)

xAmmoplanus (Ammoplanus)
 (Pate,1937)

" (Parammoplanus)

x " (Ammoplanellus)
 (Pate,1937)

xTimberlakena (Riparena)
 (Pate,1938)

x " (Mojavena)
 (Pate,1938)

x " (Timberlakena)
 (Pate,1938)

5. SPHECINAE

(1) Sphecini

*Spheex (Spheex) (figs.160,189)

*Spheex (Isodontia)

* " (Priononyx)

* " (Palmodes)

* " (Chlorion)

(2) Ammophilini

*Ammophila

*Podalonia (fig.161)

(3) Sceliphronini

*Sceliphron

*Chalybion (fig.162)

(4) Podiini

Podium

6. NYSSONINAE

(1) Mellinini

*Mellinus

(2) Alyssonini

*Alysson (fig.163)

*Didineis

(3) Nyssonini

*Nysson (Nysson) (fig.164)

" (Epinysson)

" (Hyponysson)

Foxia

*Zanysson

Metanysson (Metanysson)

" (Huachuca)

- (4) Gorytini
 Argogorytes (Argogorytes)
 " (Archarpactus)
 *Ochleroptera
 Ammatomus (Ammatomus)
 " (Tanyoprymnus)
 *Sphecius (Sphecius)(fig.165)
 Harpalomellinus
 Trichogorytes
 Dienoplus
 Arigorytes
 Lestiphorus
 Harpactostigma (Harpactostigma)
 " (Arcesilas)
 Psammaletes
 Psammaecius
 *Gorytes (Gorytes) (fig.166)
 * " (Pseudoplisus)
- (5) Stizini
 *Stizus
 *Stizoides
 Bembecinus
- (6) Bembecini
 *Steniolla
 *Stictiella
- *Bicyrtes (fig.167)
 *Microbembex (fig.168)
 *Bembix
 *Epibembex
7. PHILANTHINAE
- (1) Philanthini
 *Philanthus (fig.171)
 xAphilanthops (Aphilanthops)
 (Strandtmann, 1946)
 " (Clypeadon)
 Trachypus
- (2) Cercerini
 *Cerceris (figs.169,170)
 *Eucerceris
8. CRABRONINAE (Numerous misc.
 crabronines were
 examined)
- (1) Crabronini
 Anacrabro
 Entomognathus (Entomognathus)
 " (Toncahua)
 Encopognathus (Encopognathus)
 " (Rhectognathus)
 " (Tsaisuma)
 Lindenius (Lindenius)
 " (Trachelosimus)

Tracheliodes	Ectemnius (Hypocrabro)
Crabro (Paranothyreus)	" (Ectemnius)
" (Synothyreopus)	Lestica (Lestica)
" (Crabro)	" (Solenius)
" (Norumbega)	(2) <u>Oxybelini</u>
Euplilis (Euplilis)	xBelomicrus (Pate,1940)
" (Corynopus)	xEnchemicrum (Pate,1940)
" (Alliognathus)	*Oxybelus (fig.172)
Moniaecera (Moniaecera)	
*Crossocerus (Hoplocrabro) (fig.173)	<u>DRYINIDAE</u>
" (Yuchiha)	1. DRYININAE
" (Crossocerus)	(1) <u>Dryinini</u>
" (Synorhopalum)	Mesodryinus
" (Ablepharipus)	Hesperodryinus
" (Epicrossocerus)	Tetradryinus
" (Blepharipus)	Perodryinus
" (Nothocrabro)	Psilodryinus
" (Stictoptila)	Cyrtogonatopus
x " (<u>Eupliloides</u>) (Pate,1946)	Pristogonatopus
Enoplolindenius (Iskutana)	*Dicondylus (fig.174)
" (Enoplolindenius)	Pseudogonatopus
Ectemnius (Protothyreopus)	Agonatopoides
" (Clytochrysus)	Haplogonatopus
" (Metacrabro)	Eucamptonyx
" (Lophocrabro)	Apterodryinus
	Pachygonatopus
	Chalcogonatopus

*Gonatopus

Neogonatopus

Agonatopus

Epigonatopus

Digonatopus

(2) Bocchini

Bocchus

(3) Anteonini

*Anteon (fig.175)

Chelogynus

Deinodryinus

Prenanteon

Trisanteon

2. APHELOPINAE

*Aphelopus

3. EMBOLEMINAE

Ampulicomorpha

*Embolemus

APOIDEA

I. COLLETIDAE

1. COLLETINAE

(1) Caupolicanini

Caupolicana

Ptiloglossa

(2) Colletini

*Colletes (fig.176)

2. HYLAEINAE

*Hylaeus

II. ANDRENIDAE

1. ANDRENINAE

*Andrena (fig.177)

Megandrena

Ancylandrena

2. OXAEINAE

Protoxaea

3. PANURGINAE

Psaenythia (Psaenythia)

" (Protandrena)

*Perdita

*Panurginus

Pseudopanurgus (Pseudopanurgus)

" (Anthemurgus)

" (Heterosarus)

Nomadopsis

*Calliopsis (Calliopsis)

Calliopsis (Verbenapis)	Nomia (Dieunomia)
" (Perissander)	
Hypomacrotera	3. DUFOUREINAE
III. <u>HALICTIDAE</u>	Conanthalictus (Conanthalictus)
*Halictus (Halictus)	" (Phaceliapis)
" (Saladonia)	" (Sphecodosoma)
*Lasioglossum (Lasioglossum) (fig.178)	Micralictoides
" (Evyllaesus)	Dufourea (Dufourea)
" (Hemihalictus)	* " (Halictoides)
" (Sphecodogastra)	IV. <u>MELITTIDAE</u>
" (Chloralictus)	1. MELITTINAE
" (Dialictus)	Melitta (Melitta)
" (Paralictus)	" (Dolichochoile)
Xeralictus	2. DASYPODINAE
*Sphecodes	Hesperapis (Hesperapis)
*Agapostemon	" (Amblyapis)
*Augochlora (Augochlora)	" (Panurgomia)
" (Augochlorella)	* <u>Dasypoda</u>
*Augochloropsis	3. MACROPIDINAE
2. NOMIINAE	*Macropis (Macropis)
Nomia (Nomia)	
" (Curvinomia)	
" (Epinomia)	
" (Acunomia)	

V. MEGACHILIDAE

1. LITHURGINAE

- *Lithurge (Lithurge)
 " (Lithurgopsis)

2. MEGACHILINAE

(1) Anthidiini

- Trachusa
 *Heteranthidium
 *Paranthidium (Paranthidium)
 " (Mecanthidium)
 *Anthidium (Anthidium)
 Callanthidium
 *Dianthidium
 *Anthidiellum
 Heterostelis
 *Stelis (Stelis)
 " (Protostelis)
 * " (Microstelis)
 " (Pavostelis)
 *Chelynia (Chelynia)
 " (Melanostelis)
 " (Stelidium)
 " (Stelidina)

Dioxys

(2) Megachilini

- Chelostoma
 Chelostomopsis
 *Prochelostoma
 *Heriades (Heriades)
 " (Neotrypetes)
 " (Physostetha)
 *Ashmeadiella (Ashmeadiella)
 " (Titusella)
 " (Arogochila)
 " (Corythochila)
 " (Chilosima)
 " (Cubitognatha)
 *Formicapis
 Robertsonella
 *Hoplitis (Hoplitis)
 " (Hoplitina)
 " (Alcidamea)
 " (Cyrtosmia)
 " (Dasyosmia)
 " (Acrosmia)
 " (Monumetha)
 " (Chlorosmia)
 " (Andronicus)
 Proteriades

*Anthocopa (Anthocopa)	Megachile (Leptorachis)
" (Atoposmia)	" (Pseudocentron)
" (Eremosmia)	" (Acentron)
" (Phaeosmia)	" (Melanosarus)
" (Hexosmia)	" (Sayapis)
" (Xerosmia)	" (Chelostomoides)
*Diceratosmia	*Coelioxys
*Osmia (Osmia)	VI. <u>APIDAE</u>
" (Chalcosmia)	1. ANTHOPHORINAE
" (Cephalosmia)	(1) <u>Exomalopsini</u>
" (Melanosmia)	Exomalopsis (Exomalopsis)
" (Acanthosmioides)	" (Anthophorula)
" (Nothosmia)	Ancyloscelis
*Megachile (Litomegachile) (fig.179)	(2) <u>Nomadini</u>
" (Neomegachile)	*Nomada (Nomada)
" (Cressoniella)	" (Gnathias)
" (Megachile)	" (Phor)
" (Eutricharaea)	" (Heminomada)
" (Delomegachile)	" (Holonomada)
" (Phaenosarus)	" (Laminomada)
" (Megachiloides)	" (Pachynomada)
" (Derotropis)	" (Callinomada)
" (Xeromegachile)	" (Micronomada)
" (Argyropile)	" (Centrias)
" (Xanthosarus)	" (Nomadula)

Hexepeolus	(10) <u>Epeoloidini</u>
Paranomada	*Epeoloides
Hesperonomada	(11) <u>Emphorini</u>
Triopasites	Emphor
Melanomada	*Diadasia
(3) <u>Holcopasitini</u>	*Melitoma
*Holcopasites (Holcopasites)	(12) <u>Eucerini</u>
" (Trichopasites)	*Peponapis
" (Odontopasites)	Xenoglossa
(4) <u>Biastini</u>	Cemolobus
Neopasites (Neopasites)	Anthedonia
" (Micropasites)	Martinapis
(5) <u>Townsendiellini</u>	Florilegus
Townsendiella (Townsendiella)	*Melissodes
" (Xeropasites)	Xenoglossodes
" (Eremopasites)	*Tetralonia
(6) <u>Neolarrini</u>	Eucera
*Neolarra (Neolarra)	(13) <u>Anthophorini</u>
" (Phileremulus)	*Anthophora (Anthophora)
(7) <u>Ammobatini</u>	" (Clisodon)
*Oreopasites	" (Amegilla)
(8) <u>Protepeolini</u>	" (Micranthophora)
Protepeolus	* " (Emphoropsis)
(9) <u>Epeolini</u>	(14) <u>Hemisiini</u>
*Epeolus	Hemisia
*Triepeolus	

(15) Melectini

*Melecta (Melecta)

" (Melectomimus)

" (Xeromelecta)

" (Melectomorpha)

Brachymelecta

Zacosmia

(16) Ericrocini

Ericrocis

2. XYLOCOPINAE

(1) Ceratinini

*Ceratina (Ceratina)(fig.180)

" (Zadontomerus)

(2) Xylocopini

*Xylocopa

3. APINAE

(1) Euglossini

Centris

(2) Bombini*Bombus (figs.182-184)
section Boopobombus

" (Fraternobombus)

" (Bombias)

" (Separatobombus)

" (Cullumanobombus)

section Odontobombus

Bombus (figs.182-184)
section Odontobombus

" (Subterraneobombus)

" (Fervidobombus)

section Anodontobombus

" (Bombus)

" (Pratobombus)

" (Alpinobombus)

*Psithyrus (Psithyrus (fig.181)

" (Ashtonipsithyrus)

" (Laboriopsithyrus)

" (Fernaldaepsithyrus)

(3) Apini*Apis mellifera (figs.185,190,
198)