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Richard C. Newton
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MASSACHUSETTS AGRICULTURAL COLLEGE

Memorandum

Date May 31, 1930. Dept. Bact. & Phys.

To Dr. C. G. Crampton, Fernald Hall

Subject: Mr. Newton's Thesis

I am returning the thesis of Mr. Richard C. Newton with my approval as a member of the Reading Committee.

Although I cannot criticize the subject matter due to a lack of specific knowledge of the subject of Entomology, I do think Mr. Newton has assembled his data and presented them in very good form.

Very truly yours,

Leon A Bradley

Leon A. Bradley
Assistant Professor of Bacteriology

LAB:KP

Signed:

MASSACHUSETTS AGRICULTURAL COLLEGE

Memorandum

Dept. Botany Date, May 24 1930

To Dr Crampton

Subject: Mr Newton Thesis

As far as I can judge this thesis seems to have all the earmarks of the unusually thorough & painstaking quality on problems of real significance characteristic of the studies made under your direction

approved G. C. Crampton
(chairman)

Signed Otto L. Clark

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Richard C. Newton

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C O N T E N T S

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INTRODUCTION

There is at the present time some question as to the exact phylogenetic relationship of the various families making up the order Trichoptera. Most workers are in agreement concerning the general position of the principal families; thus the Hydroptilidae, Rhyacophilidae, and Philopotamidae are generally considered primitive while the Polycentropidae, Psychomyidae, and Hydropsychidae are thought to be quite early offshoots. The Molannidae, Leptoceridae, Odontoceridae, and Calamoceratidae are regarded as later derived families and the Sericostomatidae, Limnophilidae, and Phryganeidae are placed at the top of the order. It is interesting to note that this general grouping of the families corresponds to the two larval forms, thysanuriform and eruciform, which occur within the order. The six primitive families are characterized by thysanuriform larvae while the later evolved groups have eruciform larvae. Krafka (1923) concludes from a study of the heads of Trichopterous larvae that the stem forms of the order are not found in the thysanuriform group but rather in the eruciform group, and he considers the thysanuriform larvae as a specialization rather than a primitive condition among

Trichoptera. This is not in harmony with the evidence derived from the present study of adult forms yet it does emphasize the need of a comparative study of morphology of the different families, based on the heads of adults. There is also some question as to the affiliation of the subfamilies making up the family Sericostomatidae.

Major head characters, such as the presence or absence of ocelli, the number of segments of the maxillary palpi, and the range in length and width of the segments comprising these structures, are used by systematists in practically all keys for determining the families of Trichoptera. This has suggested the possibility of determining, from a study of the external areas of the head capsule and the mouthparts, some new family characters of value in identification as well as adding some links to the disputed phylogenetic relationships of the families. With this point in mind the following study of the heads of Trichoptera has been carried out.

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EXTERNAL MORPHOLOGY

General Discussion of the Head and Appendages of Trichoptera

The heads of Trichoptera are generally small, hypognathous, and from the cephalic aspect tend to be transverse. The labrum and mouthparts are not projected from the head capsule in most families, yet the Phryganeidae and some Limnophilidae (Figs. 1, 2, 4, 5, 7, 8, and 9) have these structures prolonged ventrally. The maxillary palpi are markedly different in the male and female sexes in the Phryganeidae (Figs. 1 and 2), the Limnophilidae (Figs. 8 and 9), and the Sericostomatidae (Figs. 10, 11, 12, and 13). The head capsule is usually slightly smaller in the male than in the female and other less noticeable variations occur in the heads studied.

The Head Capsule: - The external sclerites of the head capsule are the parietals, frons, clypeus, parafrons, postgenae, gula, and labrum. Although a true sclerite of the head capsule, the labrum is closely associated with the mouthparts and will be discussed with these appendages. The sutures that demark the sclerites are distinct in the lower families but unfortunately they are faint and may be entirely lost in higher members, and new sutures frequently appear which shift from the original position, making it impossible to determine the exact homologies in comparing similar areas in a number of heads. Such migrations of

sutures should be studied through a series of graded forms before the areas that they bound can be identified with certainty.

The parietal region is situated dorsally between the large lateral compound eyes. This region is generally flat or slightly convex above and is bounded anteriorly by the antennal fossae (a). Sense areas, frequently bearing hairs, may occur within the parietals and are indicated by the faintly dotted lines in all figures (Figs. 1-3, 6-10, 12, 15, 18-28, 30-33). The coronal suture (cs) when present extends anteriorly from the occipital foramen (Figs. 3 and 29, of) and divides the parietal area in the primitive heads (Figs. 28, 30, 31, and 32). The ocelli (Figs. 1-9, 28-33, o) may be present or absent, but when present they are always three in number. The median ocellus (o) is situated between or slightly caudad of the antennal fossae (a) usually in the frons (f) while the lateral ocelli (o) are in the parietal area laterad of the coronal suture (cs). The parietal region is bounded posteriorly by the anterior sutures demarking the wart-like tubercles (Figs. 1-9, w) in the heads of higher Trichoptera. These sutures are not always distinct and when this is the case the sutures are indicated in all figures by the longer broken lines (Figs. 1-12, 14, 15, 17, 20, 23, 24, and 33). The wart-like tubercles (w) do not occur within the parietal region but in the extreme anterior part of the postgenae (Fig. 3, pgs). These areas are usually

convex and bear numerous stout setae. Other tubercles, similar in appearance to the areas labeled w but usually smaller, occur caudad of each antennal fossa (a) in some species (Figs. 11, 16, and 23). Such areas are distinctly within the parietal region. In the Odontocerid (Fig. 16,v) a highly specialized membranous sense area occupies a position similar to that occupied by the wart-like tubercles (w) in the other heads considered. Due to specialization there is some doubt as to the exact homologies of all the areas labeled w, especially in the more intermediate heads. The exact homologies of the areas labeled w in the Sericostomatidae (Figs. 10, 11, 12, and 13), the Calamoceratidae (Fig. 14), the Leptoceridae (Fig. 17), the Hydropsychidae (Fig. 23), and the Hydroptilidae (Fig. 33) have not been determined. The postcranial area (pc) seems to occupy this same region in the heads of lower Trichoptera (Figs. 28, 29, 30, and 31) but from a posterior view the postcranial area (pc) is seen to be clearly demarked from the postgenae (pga) by a distinct laterocephalic or paracephalic suture (lc). The postcranial area (pc) is therefore more closely associated with the parietal area than with the postgenae (pga) and is considered a part of the parietal area in this paper. There is some doubt as to the correct homologies of all the areas labeled pc in the intermediate heads, as the Leptoceridae (Figs. 18 and 19), the Hydropsychidae (Figs. 21 and 22), and the Polycentropidae (Figs. 25, 26, and 27).

It is difficult to determine whether these regions are homologous with the postcranial areas (pc) occurring in primitive heads, or the wart-like tubercles (w) occurring in the more specialized heads since they are not demarked by a laterocephalic suture.

The antennal fossae (a) vary in size and outline. They may be extremely small and widely separated (Fig. 12), or of medium size (Figs. 1, 4, and 5), or they may be large, extending into the frontal region (Figs. 17 and 19). Within the family Hydropsychidae (Figs. 21, 22, and 23) the antennal fossae (a) approach each other mesally and unite in the genus Macronema (Fig. 23). They are also closely approximated in some Polycentropidae (Fig. 27). An antennifer (Fig. 23, x) appears as a heavily chitinized projection in each antennal fossa of practically all Trichopteran heads. It usually occurs on the ventro-lateral margin although in some heads it is noticeably more ventral in position (Figs. 21, 22, 23, and 28) and varies in its length. The scape (sc) or basal antennal segment pivots on the antennifer (x) in the antennal fossa (a). It is larger than the following antennal segments and ranges greatly in both length and width. It may be extremely short and broad (Figs. 4 and 14) or long and slender (Figs. 11-13). The antennae may be short and robust, or long and slender, and furnish characters of value in identification. They have been omitted in this study.

The frons (f) is a median area demarked by the frontal sutures (fs) which are distinct in primitive heads (Figs. 28, 30, 31, and 32) and may be distinct in the heads of higher Trichoptera (Fig. 5) or may be partly lost (Figs. 1, 8, 12, 15, 20, and 25). In some members, the frontal sutures are entirely absent (Fig. 4) and when this is the case the frontal pits (fp) are of value in delimiting the frons since the frontal pits (fp) always occur on the frontal sutures in primitive insects and are less variable in their position than are the sutures. New or secondary sutures, closely resembling the original frontal sutures, occur in the Odontoceridae shown in Figure 16 and cause the frons (f) to appear to shift cephalad. These sutures are obviously secondary since traces of the true frontal sutures (fs) are faintly discernible, extending cephalad of the frontal pits. Similarly the distinct sutures labeled as the frontal sutures (fs) in the Polycentropidae shown in Figure 26 must be secondary if the smaller sutures extending from the lateral frontal pits (fp) are the true frontal sutures. In the Leptocerid shown in Figure 17 the antennal fossae have extended cephalad crowding out the frontal sutures and bound and demark the frons. The frons is usually demarked anteriorly by a fronto-clypeal suture. When this suture is not present the frontal pits are generally considered to demark the anterior boundary of the frons. Sense areas bearing numerous setae frequently occur within the frons and are indicated by the faintly dotted lines. These areas vary in their size and

situation within the frons (Figs. 8, 9, 11, 18, 19, 23, 25, 27, 28, 30, 31, and 33).

The clypeus (c) is a median area cephalad of the frons from which it is clearly separated by a fronto-clypeal suture in the Leptoceridae (Figs. 17, 18, and 19). In other forms the clypeus is frequently fused with the frons forming a fronto-clypeus (Figs. 1, 2, 4, 5, 15, 20, 21, 25-27, f and c), and when this is the condition, the clypeus is considered the region anterior to the frontal pits. In some heads the clypeal region becomes divided by an anteclypeal suture into an anteclypeus (ac) and a postclypeus, frequently called the epistoma (e) (Figs. 6-14, 22, 23, 28, and 30-32). The anteclypeus frequently becomes more closely associated with the labrum (l) than with the epistoma (e) to which it originally belonged. In the Limnophilidae and the Sericostomatidae the anteclypeus and the labrum frequently become narrowed and elongated (Figs. 6, 7, 8, 9, 11, 12, and 13).

The parafrons (pf in all figures) is the area laterad of the frons or the fronto-clypeus (f and c) in heads where the frons and clypeus are fused. The extreme anterior portion of the parafrons includes the gena or cheek. In some Trichoptera the genal region becomes elongated to form a genal process (Figs. 6 and 7, gs). Sense areas, bearing setae, often occur within the parafrons (Figs. 8, 9, 10, 12, 15, 16, 18, 19, and 20). A suture extends the length of the parafrons

in some heads and it may be distinct (Figs. 5, 11, and 13) or it may fade out (Figs. 1, 2, and 33). It is possible that these sutures are traces of the laterocephalic or paracephalic sutures (lc) that extend from the postcranial areas (pc) in the heads of primitive Trichoptera. However, in the primitive heads studied, the laterocephalic sutures are not observed to extend cephalad of the antennal fossae (Figs. 28, 30, 31, and 32) except in Polycentropus (Fig. 25) where faint sutures extend from the regions labeled pc cephalad around the antennal fossae and join with the frontal sutures below the antennal fossae. If these are laterocephalic sutures extending into the parafrons it is possible that the sutures found extending the length of the parafrons are prolongations of the laterocephalic sutures. In the Calamoceratid, Phylloicus (Fig. 14), and in some Leptoceridae (Figs. 17, 18, and 19) the area laterad of the frons is curiously modified by secondary sutures to form a triangular raised region which in some members of the Leptoceridae (Figs. 18 and 19) bear sense areas with numerous setae. This highly modified area is probably homologous with the parafrons.

The postgenae (Figs. 3 and 29, pgs and pga) occupy the caudal region of the head on either side of the occipital foramen (of) and of the gula and the submentum (sm). An indistinct suture demarks an area laterad of the postgenae labeled r in Philopotamus (Fig. 29). A similar area

labeled r is demarked by a distinct suture in the head of Neuronia (Fig. 3). This area becomes elongated extending posteriorly around the compound eye and in the Limnophilidae (Figs. 6, 7, 8, and 9, r) and Sericostomatidae (Figs. 10, 11, 12, and 13, r) it appears wart-like, bearing numerous stout setae. Indistinct sutures lead to the gular pits (gp) on either side of the submentum (sm) and the caudal portion of this demarked area bears a ventral fossa for receiving the stipes of each maxilla. The area, which is known as the hypostoma, is clearly defined in the head of Philopotamus (Fig. 29) but is not as distinct in Neuronia (Fig. 3). Anterior to the gular pits (gp) but caudad of the occipital foramen (of) this same suture demarks a small area which corresponds to the paragula in other insect heads. The paragula is not clearly demarked in Neuronia (Fig. 3) but the area caudad of the occipital foramen is probably homologous with the paragula.

The gula is a ventral median area (Figs. 3 and 29) demarked laterally by the gular pits (gp). This area is extremely short in Trichoptera extending from the occipital foramen (of) to the gular pits (gp) which demark its cephalic extent.

The occiput (Figs. 3 and 29, oc) is a small median area cephalad of the occipital foramen (of) which borders its caudal limits in the heads of Trichoptera. In Neuronia

(Fig. 3) the occiput is bounded laterally by the portion of the postgenae which forms the wart-like tubercles (w). The wart-like tubercles also bound the occiput anteriorly for they extend mesally but do not quite meet, leaving a small cephalic portion of the occiput unbounded from which the coronal suture (sc) extends forward, dividing the parietals. In Philopotamus (Fig. 29) the occiput (oc) is bounded laterally by the postcranial areas which extend mesally as do the wart-like tubercles (w) in Neuronia (Fig. 3). The postcranial areas do not meet on the median line thus leaving a small unbounded portion from which the coronal suture extends anteriorly.

The occipital foramen (Figs. 3 and 29, of) is the opening through which the esophagus and ventral nerve chain pass to the thorax and abdomen. In Philopotamus (Fig. 29) the occipital foramen (of) is transverse in outline with the anterior margin moderately concave. The lateral and posterior margins are rounded. The posterior margin is interrupted on the median line. In Neuronia (Fig. 3) the occipital foramen is transversely oval in outline. It is open on the caudal median line next to the gula, as is the case in Philopotamus.

The Mouthparts: - Although the labrum (l) is in reality a portion of the head capsule, cephalad of the clypeus or anteclypeus, it is closely associated with the mouthparts and is therefore treated under this heading. The labrum varies greatly in size and shape within the order Trichoptera and

may be broader than long (Figs. 14, 17, 18, 20, 21, 22, 23, 27, and 28) or greatly elongated and narrowed (Figs. 1, 2, 4, 5-9). In some species it is very small (Figs. 24, 25, and 26) and it is frequently membranous at the anterior margin.

The mandibles (m) are best developed in the family Philopotomidae and Rhyacophilidae (Figs. 28, 30, 31, and 32). They are small in other families (Figs. 15, 17, 18, 21, 23, 25, and 27) and are atrophied or rudimentary in the Phryganeidae (Figs. 1, 2, 4, and 5) where they appear as small useless prolongations laterad of the elongated labrum (l). In a few Trichoptera the mandibles are entirely lost (Figs. 6-9, 11-14, 16, 19, 20, and 26).

While the primitive Trichoptera have mandibles, these insects are probably unable to take solid food in the adult stage. Some can suck liquids, but a large majority probably never feed as adults and live but a short time.

The maxillae are usually reduced, with membranous, lobe-like galeae while the maxillary palpi (mp) are greatly developed. In Dipseudopsis, however, the maxillae are well developed, according to Ulmer (1905) and the galeae are as long as the galeae found in certain primitive microlepidoptera such as Mnemonica. In Philopotamus (Fig. 29) the small stipes (s) articulates in a ventral fossa of the hypostoma. The galeae (g) are membranous and extend mesally from each stipes.

In Philopotamus, the galeae are visible only from the posterior view of the head. In Neuronia (Fig. 3) the cardo (ca) is a long slender structure attached to the stipes (s) which is also elongated and narrowed but widens distally at the attachment with the maxillary palpus (mp). The galea (g) is given off from the stipes (s) and lies laterad of the elongated labrum (Fig. 2, 1). The maxillary palpi (mp) are five-segmented in all families of Trichoptera except the Phryganeidae (Fig. 2) when the males have the maxillary palpi four-segmented, the Limnophilidae (Figs. 6, 7, and 9) where the males have the maxillary palpi three-segmented and the Sericostomatidae (Figs. 11, 12 and 13) where the maxillary palpi of the males vary from one to three segments. The length of the various segments vary in all members and may be densely clothed with hairs. These characters are used in classifying the order. The last maxillary palpal segment is long in several families, as the Hydropsychidae (Figs. 21, 22, and 23), the Psychomyidae (Fig. 24), the Polycentropidae (Figs. 25, 26, and 27), and the Philopotamidae (Fig. 28). In the Odontocerid (Fig. 16) the first, second, third and fourth segments of the maxillary palpi are extremely wide, while the last segment is elongated. These segments are all strongly clothed with hairs. In the males of the family Sericostomatidae the maxillary palpi are greatly modified. They may be one-segmented and membranous (Fig. 12), two-segmented, the basal segment being broad,

flattened and sclerotized along a median line, while the distal or second segment is rounded, and membranous, bearing specialized eversible sense areas at the tips (Fig. 11), or the maxillary palpi may be three-segmented, the basal segment being elongated and sclerotized, the second segment sclerotized but short, and the distal segment membranous and club shaped, and in the living insect held masking the face in specialized pits or depressions (d) on the frons (Fig. 13).

The labium or under lip is greatly reduced except for the labial palpi (Figs. 3 and 29). The submentum (sm) is the membranous median area anterior to the paired gular pits (gp). Its cephalic boundary is indicated by a faint fold in the membrane demarking the membranous mentum (mn), not labeled in Philopotamus. Within the mentum (mn) two sclerotized areas occur, the palpigers (pg) to which the three-segmented labial palpi (lp) are attached. Other structures of the labium are lost. In Neuronia (Fig. 3) the membranous mentum (mn) is elongated in connection with the elongation of the other mouthpart structures, so that the sclerotized palpigers (pg) are brought forward. The labial palpi (lp) are short and broad in Neuronia (Figs. 1, 2, and 3) and the segments tend to be spoon-shaped. In the males of the family Sericostomatidae (Figs. 11, 12, and 13) the

labial palpi are longer than the maxillary palpi. They are also greatly elongated in Psilotreta (Fig. 16) of the family Odontoceridae.

The Primitive Trichopteran Head

In order to determine which of a large number of head characters are primitive, one must consider both the ancestral and intermediate forms that lead to the group under consideration. The occurrence of the antennifer in lower insects and also in Trichoptera and some higher orders cannot be interpreted otherwise than as primitive. Similarly the occurrence of the laterocephalic or paracephalic sutures (lc) described by Crampton (1917) as being found in the heads of lower insects, must be considered an extremely primitive character in the Trichopterous heads in Figures 25, 28, 30, 31, and 32. The presence of mandibles are also clearly indications of primitiveness within the order. The wide labrum, common of certain Orthopteroid insects, the presence of distinct sutures and of three ocelli, are all characters retained from primitive insect ancestors.

The ancestral Neuroptera are synthetic types giving rise to the ancestors of the Mecoptera, which in turn give rise to the Diptera on the one hand and to Trichoptera with the Lepidoptera on the other, according to Crampton (1921), who observed that certain Neuroptera, as the genus Oliarces, have retained a type of head capsule closely resembling the

primitive Trichopteran head Philopotamus (Fig. 28). He also observed that the Ithoniidae and other Neuroptera have characters in common with Trichoptera and Lepidoptera. It is logical, therefore, to consider characters of these Neuroptera as primitive when they reappear in Trichoptera.

The Mecoptera likewise have characters in common with Trichoptera that can be considered primitive, although the Mecoptera have developed along different lines than the Trichoptera. Certain Mecoptera exhibit the ectocardine condition of the maxillae and this same condition is found present in the maxillae of certain Trichoptera, according to Crampton (1923). It is also of interest to note that the Mecoptera commonly exhibit the elongation of the genae into a genal process and this is strongly exhibited in many members of the family Limnophilidae (Figs. 6 and 7, gs).

Certain lower forms of Lepidoptera, while specialized along lines that place them unquestionably within this order, retain a few more primitive characters than are found in the lowest Trichoptera. These Lepidopterous forms are of importance in determining primitive characters in the Trichoptera. Thus the head capsule of the micropterygid Mnemonica resembles in outline the head capsules of Philopotamus (Fig. 28) and the Hydrophilidae (Fig. 33). The distinct labrum, anteclypeus, and postclypeus of Mnemonica are exhibited by the Rhyacophilidae (Figs. 30 and 31), while the widely separated ocelli occur in the Hydroptilidae in

Figure 33. Large mandibles occur in the Micropterygidae and the nearest Trichoptera approaching this condition are the Rhyacophilidae, Philopotamidae, and one or two of the intermediate families. The Micropterygidae have the galea greatly elongated, a condition unusual in the caddice flies, yet the galea of the Trichopteran Dipseudopsis is as long as the galea in Mnemonica.

Description and Variation of Heads within the Families

A large part of the material selected for this study was obtained from Staudinger and Bang-Haas, Germany, and are species of northern Europe. Some species native to New England were also used, while the representative of the family Calamoceratidae, kindly furnished by Mr. Nathan Banks, was collected in South America. The descriptions and discussions of head variations are based on these specimens.

Phryganeidae (Figs. 1, 2, 4, and 5): - Members of this family have in common three large ocelli, a fusion of the clypeus and frons to form the fronto-clypeus, a greatly elongated labrum, and small rudimentary mandibles. The segments of the maxillary palpi are similar in appearance, five-segmented in the females and four segmented in the males.

Neuronia (Figs. 2 and 4). There is a marked variation in the heads of Neuronia posticus Walker (Fig. 2) and Neuronia pardalis Walker (Fig. 4). The coronal suture (cs)

is indistinct in N. posticus but is distinct in N. pardalis. N. posticus has indistinct frontal sutures (fs) demarking a definite fronto-clypeus (f and c) and parafrons (pf), both of which are indefinitely indicated in N. pardalis because the frontal sutures (fs) are entirely lost except for frontal pits (fp). These two species also have noticeable variation in the size and shape of the scape (sc), the length of the labrum (l) and the absence of a suture in the parafrons (pf) and sense areas in the parietals in N. pardalis.

Phryganea grandis (Fig. 5) has a distinct coronal suture (cs) which disappears cephalad of the lateral ocelli (o). The fronto-clypeus (f and c) and parafrons (pf) are clearly defined by frontal sutures (fs) and a distinct suture extends the length of the parafrons (pf). There are marked differences in the shape of the scape (sc) and the outline of the antennal fossae (a) in Neuronia and Phryganea and the labrum of Phryganea has the sides more nearly parallel.

In comparing the heads within the family there seems to be as great a difference within the species as in the two genera. However, the differences between genera observed in the shape of the scape (sc) and the labrum (l) are obviously of a more fundamental character than the presence or absence of sutures.

Limnophilidae (Figs. 6, 7, 8, and 9): - All the members of Limnophilidae have three ocelli; the maxillary palpi are similarly formed, cylindrical, five-segmented in the females and three-segmented in the males. The anteclypeus has become separated from the epistoma and is closely associated with the narrow elongated labrum. Wart-like tubercles are present in the posterior head region.

In the species Carboricus punctatissimus Walker (Fig. 6) the coronal suture (cs) is distinct and divides the parietal region. The frontal sutures (fs) extend into the parafrons (pf) rather than to the frontal pits (fp). The genal region is prolonged into conspicuous genal processes (gs). Sense areas occur within the parietal region between the lateral and median ocellus (o). The wart-like tubercles (w) occur caudad of the parietal region and the area (r) extends posteriorly around the compound eye.

The species Astenophylax argus Harris (Fig. 7) has but a slight indication of the coronal suture (cs). The frontal sutures (fs) while not complete extend toward the frontal pits (fp) and indicate the frons (f), the epistoma (e) and the parafrons (pf). The genal process (gp) is prolonged but not to the same extent as that observed in C. punctatissimus (Fig. 6). The labrum (l) and the mouthparts are elongated. Sense areas occur within the parietal region between the median and lateral ocelli (o). The wart-like tubercles (w) and the specialized areas labeled r occur caudad of the parietal area and compound eyes.

The coronal suture (cs) is lost in Limnophilus griseus L. (Fig. 9). The faint frontal sutures (fs) extend from the antennal fossae (a) to the cephalic frontal pits (fp) demarking the frons (f), epistoma (e) and the parafrons (pf). Sense areas are located in the frons (f) and the parafrons (pf); also between the lateral and median ocelli (o). The wart-like tubercle (w) occurs posterior to the parietal region, while the specialized area labeled r extends posteriorly around the compound eyes and is visible ventrally as well as dorsally from the cephalic aspect.

The three genera of the Limnophilidae considered show similarities in the general contour of the head capsule, the shape of the antennal fossae (a) and in the size and outline of the scape (sc). The close association of the anteclypeus (ac) and the labrum (l), also the absence of mandibles, are common to the Limnophilidae.

The outstanding differences are the partial loss and variation of the sutures, the prolongation of the genal process (gp) in C. punctatissimus and A. argus, the elongation of the labrum in A. argus and L. griseus and the widely separated lateral ocelli (o) in L. griseus. Sense areas occur within the frons (f) and the parafrons (pf) in L. griseus and the frontal sutures (fs) extend from the antennal fossae (a).

Sericostomatidae (Figs. 10, 11, 12, and 13): - The ocelli are usually absent in the family Sericostomatidae. The maxillary palpi are five-segmented in the females, but

vary from one to three segments in the males where they may be clavate or flattened masking the face. Within both sexes the palpi are strongly clothed with hairs. The scape (sc) is extremely variable throughout the family and may be short (Fig. 10) or extremely long (Figs. 11 and 13). In some species it is longer than the head and may be furnished with spines. Wart-like tubercles occur on the posterior region of the head.

The female of the species Sericostoma turbatum McLachlan (Fig. 10) has no coronal suture and the frontal sutures (fs) are indistinct and extend mesally from the antennal fossae (a) to about the middle of the frons (f) where they again diverge in extending to the anterior margin of the head capsule. These frontal sutures (fs) are probably secondarily formed since they do not run to the frontal pits (fp) which are situated laterad of them. An anteclypeal suture divides the clypeus into a posterior region, the epistoma (e) and the anteclypeus (ac) closely associated with an extremely short labrum (l). The parafrons (pf) is extremely wide because of the mesal direction of the frontal sutures (fs). Each parafrons (pf) bears a large sense area. The maxillary palpi are five segmented, the segments being cylindrical and similar except for the short basal segment.

In the male of the species Mormomyia vernalis Banks (Fig. 12) the coronal suture (cs) is clearly demarked. The

parietal bears a sense area caudad of each small antennal fossa (a). The scape (sc) is long. The frontal sutures (fs) extend from a median point anterior to the antennal fossae (a) to the widely separated frontal pits (fp). A ridge extends along the median line in the frons (f). The parafrons (pf) is narrow and bears a small sense area. An anteclypeal suture divides the clypeus into a posterior region, the epistoma (e) and the anteclypeus (ac), closely associated with the short and pointed labrum (l). The maxillary palpi (mp) are entirely membranous, short and one-segmented, tapering to a point. The labial palpi (lp) consist of three rather slender segments and are longer than the maxillary palpi (mp).

In the male of the species Lepidostoma hirtum F. (Fig. 11) the coronal suture (cs) is clearly demarked. Two wart-like tubercles bearing sense areas are caudad of the antennal fossae (a). The scape (sc) is long, cylindrical and slightly wider at its distal end. Cephalad of the antennae are raised sense areas. Frontal sutures extend but a short distance from the frontal pits (fp) so that the frons (f) is not clearly defined. The median line of the frons (f) is raised to form a ridge extending to the anteclypeus (ac). Clearly defined sutures traverse the length of the indefinitely defined parafrons (pf). The clypeus is divided into the epistoma (e) and the anteclypeus (ac) closely associated with a narrow pointed labrum (l). The maxillary palpi are two-segmented, the first segment being

extremely broad, flattened and sclerotized in the median area. The second segment is also membranous but is smaller and rounded. The labial palpi (lp) are long, slender and three-segmented. They are longer than the maxillary palpi (mp).

The male of the species Goera pilosa F. (Fig. 13) has a slight indication of the coronal suture (cs) at the posterior region of the head. A specialized area (w) may possibly be homologous with the similarly placed areas labeled w in the parietal region of the heads discussed in Figures 11 and 12, but if homologous this specialized area has shifted cephalad in G. pilosa. The antennal fossae (a) are small, widely separated and each supports a long cylindrical but slightly curved scape (sc). Frontal sutures are lost but distinct sutures traverse the poorly demarked parafrons (pf). The frons is similarly indefinitely defined and has two parallel depressions (d) separated by a median ridge. The depressions are for receiving the distal clubbed segment of the maxillary palpi (mp). The frontal pits (fp) are situated far cephalad at the ends of the depressions (d). The anteclypeus (ac) is closely attached to the slightly elongated lobe-like labrum (l). The maxillary palpi (mp) are three-segmented. The first segment is of moderate size and is sclerotized as is the second, small, ring-like segment. The third segment, which is the largest, is membranous, clavate, and has a mesal fold in the membrane. The maxillary palpi are held masking

the face in the living insect, while the third segment fits into the frontal depression (d). The labial palpi (lp) are three-segmented. The first segment is short, the following two are long and cylindrical, making the labial palpi (lp) longer than the maxillary palpi (mp).

The genera of the family Sericostomatidae show extreme variations in the outline of the head capsule and in the modification of the maxillary palpi (mp) which varies from a membranous one-segmented structure (Fig. 12) to a partly sclerotized three-segmented palpus (Fig. 13). The frons (f) is extremely variable in its modifications within the male heads studied (Figs. 11, 12, and 13). The frontal pits are cephalad and similarly situated in the genus Lepidostoma (Fig. 11) and Goera (Fig. 13) while in Mormomyia (Fig. 12) the frontal pits (fp) are widely separated. These variations in the Sericostomatidae would seem to justify the possibility of more family characters, especially if such variations are paralleled by others as great within the thorax and abdomen.

Similarities within the three genera (Figs. 11, 12, and 13) are seen in the long cylindrical scape (sc), the small and widely separated antennal fossae (a) and a tendency for a median ridge, extending the length of the frons (f).

Calamoceratidae (Fig. 14): - Members of the family Calamoceratidae are without ocelli. The maxillary palpi are five-segmented in both the males and the females. The labial palpi are three-segmented and short.

The species Phylloicus bromeliarum Müll. (Fig. 14) has the wart-like tubercles (w) rather faintly demarked in the posterior region of the head. The coronal suture is absent and the antennal fossae (a) are large and circular in outline. The scape (sc) is short and bulbous. The frons (f) is demarked by the anterior margins of the antennal fossae (a) although the frontal sutures (fs) extend from the rather posteriorly situated frontal pits (fp) in a latero-ventral direction to the bases of the maxillary palpi (mp) and demark lateral convex areas anterior to the antennae. An anteclypeal suture demarks a transverse anteclypeus (ac) from the epistoma (e). The labrum (l) is unusually broad. The maxillary palpi (mp) are five-segmented with the fourth segment very short and bead-like. The labial palpi (lp) are short and broad.

Odontoceridae (Figs. 15 and 16): - The ocelli are absent in the family Odontoceridae. The maxillary palpi are five-segmented in both the males and females and are clothed with hair.

Odontocerum albicorne Scopoli (Fig. 15) has a sharply defined coronal suture (cs) dividing the parietals. Wart-like tubercles (w) occur posterior to the parietals. Caudad of the antennal fossae (a) and extending mesally are two humps between which the coronal suture (cs) passes. Each of these humps bears a small oval sense area. The scape (sc) is large, elongate and widens distally and bears a sense area at its distal end. The frontal sutures (fs)

are faint and extend from the antennal fossae (a) to the frontal pits (fp) and the bases of the mandibles (m) demarking a bell shaped fronto-clypeus (f and c) and a large parafrons (pf). A sense area occurs within each parafrons (pf). Similar small areas are located within the clypeal region (c) caudad of the mandibles (m). The maxillary palpi (mp) are five-segmented, each segment being cylindrical while the last two segments are slender and more elongated than the preceding segments. The labial palpi (lp) are three-segmented.

The species Psilotreta frontalis Banks (Fig. 16) has a coronal suture (cs) extending far forward between the widely separated antennal fossae (a). Arms that appear as frontal sutures connect with the coronal suture. However, as these arms do not extend to the frontal pits (fp) which are laterad of them, the sutures are probably secondarily formed demarking a small cephalic frons (f). The true frontal sutures (fs) can be seen as faint lines extending caudad of the frontal pits (fp). They indicate the parafrons (pf) which contains a sense area. A faint suture also extends cephalad of each antennal fossa (a) into the parafrons (pf). Within the parietal region a special membranous area (v) is formed which is strongly clothed with hairs. This area is probably not homologous with the wart-like tubercle (w) which occupies a similar position in the genus Odontocerum (Fig. 15). Wart-like areas occur caudad of the antennal fossae (a) within the parietals. The clypeus (c) is probably not the true

clypeus which would be the area cephalad of the frontal pits (fp) as in the genus Odontocerum (Fig. 15) but rather an anteclypeus. The labrum (l) is short. The maxillary palpi are five-segmented, the first three segments being unusually short and broad while the fourth segment is short and appears twisted in giving off a long tapering fifth segment. The maxillary palpi (mp) are strongly clothed with hairs so that the segmentation can not be observed. They are held over the head and mask the face in the living insect. The labial palpi (lp) are three-segmented, the first segment is the shortest and is followed by two long slender segments, making the labial palpi (lp) unusually long in this highly modified head.

The two species, O. albicorne (Fig. 15) and P. frontalis (Fig. 16) have little in common other than the similar outline of the head capsules and the size and general outline of the scapes (sc). The frons (f), parafrons (pf), and clypeal areas (c) are extremely unlike in the two heads, as well as the maxillary and labial palpi. From head characters alone these two species cannot rightly be considered members of the same family.

Leptoceridae (Figs. 17, 18, and 19): - The ocelli are always absent in the family Leptoceridae. The antennal fossae (a) are large and extend into the frons (f) which they frequently border. The scape (sc) is large and tapers at its distal end. The clypeus is demarked from the frons by a

fronto-clypeal suture. The labrum is about as broad as long and is rounded anteriorly. The maxillary palpi are hairy, five-segmented in both the males and the females, with long and slender segments. The labial palpi are three-segmented and short.

In Leptocella (Fig. 17) faint sutures demark a large area (w) in the posterior region of the head which may correspond to the wart-like tubercles (w) occurring in the heads of other forms (Figs. 1, 2, and 3). The coronal suture is absent. The antennal fossae (a) occupy a large portion of the head and encroach upon the frons (f) in extending to very near the anteriorly situated frontal pits (fp). The clypeus (c) is demarked from the frons (f) by a fronto-clypeal suture and appears broad and narrow. The labrum (l) is as broad as long, and is membranous at its rounded anterior margin. Laterad of the frontal pits (fp) an area is demarked which is strikingly similar to the area labeled pf in the representative of the family Calamoceratidae (Fig. 14) but which does not quite reach the margin of the compound eye in Leptocella. This whole area is probably the parafrons (pf) demarked by secondary sutures. Mandibles (m) are quite large and can be observed laterad of the labrum (l). The maxillary palpi (mp) are five-segmented, each segment being cylindrical, long and slender. The basal maxillary segment is slightly the broadest. The three-segmented labial palpi (lp) are small in Leptocella.

In the species Leptocerus albifrons L. (Fig. 18) the coronal suture (cs) is distinct. Arms extend from the coronal suture (cs) within the region generally considered the parietals to the posterior margin of each antennal fossa (a). These arms of the coronal suture are either secondarily formed sutures or the frontal sutures shifted caudad. If the latter is the true interpretation, the frons (f) would be the median area between these sutures. The area laterad of the coronal suture (cs) is again divided by a suture extending from the posterior portion of the parietal area to the antennal fossae (a). The more median of these two demarked lateral areas bears a large anteriorly situated sense area; the distal area demarked is bounded laterally by a suture similar in position and possibly homologous with the paracephalic sutures which demark the postcranial areas (pc) in the heads of primitive Trichoptera. However, this may be merely a convergence brought about by secondarily formed sutures. This area labeled pc in Leptocerus (Fig. 18) also contains a sense area. The scape (sc) is large and similar to the scape (sc) in Leptocella (Fig. 17) although because of the smaller antennal fossae (a) in Leptocerus the base of the scape fills a much greater portion of this socket. The frons (f) is not demarked by frontal sutures but as in Leptocella (Fig. 17) this median area is demarked by the antennal fossae (a) and by specialized lateral

regions, bearing sense areas which are homologous with the parafrons (pf) of other heads studied. Frontal pits (fp) are situated anteriorly on the fronto-clypeal suture demarking the clypeus (c). The labrum (l) is closely united with, but demarked from, the clypeus (c) by a faint suture. It bears an anterior membranous lobe at its margin. The mandibles (m) are situated laterad of the clypeus (c). The maxillary palpi (mp) are five-segmented; the basal segment is slightly stouter than the following. The second and third segments are extremely long, and are much longer than the corresponding segments in the maxillary palpi in Leptocella (Fig. 17). The labial palpi (lp) are three-segmented and small.

The species Oecetina avara Banks (Oecetodes avara) (Fig. 19) has a coronal suture (cs) demarking lateral parietal regions, each of which is again divided by a secondary suture. Both the more median of the lateral areas and the more distal, labeled pc because of its resemblance to the postcranial areas (pc) in primitive heads (Figs. 30 and 31), bear an anteriorly situated sense area indicated by the faintly dotted lines. Cephalad of the coronal suture (cs) a median region is demarked by sutures and this region likewise contains a sense area. The antennal fossae (a) are very large and extend to near the anteriorly situated frontal pits (fp), thus bounding the frons (f) as was the condition observed in Leptocella (Fig. 17) and Leptocerus (Fig. 18). The frons (f) has a

centrally raised area demarked by sutures and containing two sense areas. The specialized region laterad of the frons (f) is similar to the regions labeled pf in Leptocella (Fig. 17) and Leptocerus (Fig. 18) and is probably the parafrons (pf). The frons (f) is separated from the broad narrow clypeus (c) by a fronto-clypeal suture extending between the genae. The labrum (l) is much narrower than the clypeus (c) and is rounded and membranous at its cephalic margin. The mandibles are absent. The five-segmented maxillary palpi (mp) have the basal segment stouter than the following ones. The second segment is longer than the following three, but is shorter than the corresponding segment in Leptocerus (Fig. 18). The three-segmented labial palpi (lp) are small.

The three genera, Leptocella (Fig. 17), Leptocerus (Fig. 18), and Oecetina (Fig. 19) have many characters in common, as the general contour of the head capsule, the large antennal fossae (a) bordering the frons (f), and the demarked clypeus (c). The maxillary palpi (mp) are long and slender throughout the family Leptoceridae. Leptocella (Fig. 17) differs from Leptocerus (Fig. 18) and Oecetina (Fig. 19) in having the large areas (w) within or posterior to the parietals. Leptocella (Fig. 17) resembles Oecetina (Fig. 19) more closely than Leptocerus (Fig. 18) in having the antennal fossae (a) much larger than the base of the scape (sc), the clypeus (c) closely associated with the head capsule, and a noticeable similarity in the segmentation of the maxillary

palpi (mp) and in the size and shape of the labrum (l). Leptocerus (Fig. 18) has the clypeus (c) more closely associated with the labrum (l), the second and third segments of the maxillary palpi (mp) long and slender and the parietals containing the postcranial areas (pc) rather than the areas labeled w as in Leptocella (Fig. 17). The parietals are modified and contain sense areas in both Leptocerus (Fig. 18) and Oecetina (Fig. 19).

Molannidae (Fig. 20: - Members of the family Molannidae are without ocelli. The maxillary palpi are composed of five rather wide segments, the basal and second segments of which are extremely wide and short.

In Molanna angustata Curtis the coronal suture (cs) extends cephalad from the posterior region of the head but fades out and is lost anteriorly. Wart-like tubercles (w) convex and faintly bounded by sutures occupy the posterior head region. The antennal fossae (a) are small and are widely separated while poorly defined sutures separate them. Frontal sutures (fs) are indistinct and extend to the frontal pits (fp) demarking a median fronto-clypeus (f and c) and the lateral parafrons (pf) within each of which is a large sense area. Faint traces of secondary sutures can be observed caudo-laterad of each antennal fossa (a) while anterior to each antennal fossa (a) a faint suture extends out into the parafrons (pf). The labrum (l) is moderately wide rounding to the anterior margin which bears a short

truncated membranous portion. The maxillary palpi (mp) are five-segmented; the basal segment is broad and extremely short, the following is narrower and bead-like, while the last three segments are cylindrical and of about equal length. Labial palpi (lp) are three-segmented. The basal segment is short, the second and third equal in length and longer than the first segment.

Hydropsychidae (Figs. 21, 22, and 23): - All the members of the family Hydropsychidae are without ocelli. The scape is usually short but in the genus Macronema (Fig. 23) it is unusually large. The maxillary palpi are five-segmented and are long and slender in both sexes. The basal segment is always short, the second segment is longer, the next two are usually similar, while the last is extremely long, whip-like and subsegmented.

In Hydropsyche (Fig. 21) the coronal suture is lost while lateral secondary sutures faintly indicate a lateral area suggestive of the postcranial area (pc) seen in the primitive Trichoptera (Figs. 28, 30, 31, and 32). One of these sutures extends from the postcranial area (pc) to the caudal margin of the antennal fossa (a) and demarks a median parietal region within which are located three sense areas, one occurring caudad of each antennal fossa (a) while a median sense area lies slightly anterior to, but between, the lateral ones. Frontal sutures (fs) extend from the anterior margin of the antennal fossae (a) through the frontal pits (fp) to the

bases of the small inconspicuous mandibles (m) demarking the broad fronto-clypeus (f and c) and the lateral parafrons (pf). The labrum (l) is separated from the fronto-clypeus (f and c) by a faint suture; it is broad and has an anterior membranous lip. The maxillary palpi (mp) are long and five-segmented, the basal segment is short, the second is longer, while the third and fourth are of equal length, shorter than the second segment but longer than the first, and are followed by a fifth long whip-like segment. The labial palpi (lp) are three-segmented; the two basal segments are short and broad while the last segment is longer and more slender.

In Hydropsyche (Fig. 22) a faint coronal suture (cs) is present. Lateral sutures demark a postcranial area (pc) in the parietals. The antennal fossae (a) are greatly enlarged, almost uniting with each other. They extend cephalad and shorten the frons (f) which is demarked laterally by short frontal sutures (fs) extending to the frontal pits (fp). An anteclypeal suture divides the broad and narrow anteclypeus (ac) from the epistoma (e). The labrum (l) is small and membranous at its tip. The maxillary palpi (mp) are similar in appearance to the maxillary palpi (mp) described for Hydropsyche in Figure 21. The labial palpi (lp) are slender and three-segmented. Mandibles are absent.

In Macronema zebratum Hagen (Fig. 23) the contour of the head differs from the two heads of the genus Hydropsyche (Figs. 21 and 22). The coronal suture is absent but in the

posterior parietal region there are small areas (w) which are probably not homologous with the wart-like tubercles (w). A large wart-like area also occurs caudad of each scape (sc). The antennal fossae (a) are united and each has an unusually long antennifer (x) attached anteriorly, which pivots with a wide scape (sc). The frontal sutures (fs) are distinct and pass through the frontal pits (fp) in extending to the base of the mandibles (m). Two sense areas occur within the frons (f) while the parafrons (pf), laterad of the frons (f), is without sense areas. An anteclypeal suture divides the clypeus into the postclypeus or epistoma (e) anterior to the frontal pits (fp), and the anteclypeus (ac) extending between the bases of the mandibles (m). The labrum (l) is broad and bluntly pointed by a membranous flap. The maxillary palpi (mp) are five-segmented, resembling the maxillary palpi (mp) in the genus Hydropsyche (Figs. 21 and 22) except that the second segment is not longer than the following two segments. The labial palpi (lp) are three-segmented, the first two segments being shorter and broader than the distal segment.

The two species in the genus Hydropsyche (Figs. 21 and 22) show variation in the size of the compound eyes and the antennal fossae (a). The antennal fossae (a) are closely approximated in the Hydropsyche species in Figure 22. This Trichopteron also has the clypeus divided into an epistoma (e) and a narrow anteclypeus (ac) by an anteclypeal suture, a condition that occurs in the genus Macronema (Fig. 23).

Other variations within the genus Hydropsyche are in the arrangement of sense areas in the parietal region and the presence or absence of a faint coronal suture (cs). The size and outline of the labrum (l) is also variable within the genus.

Macronema zebratum (Fig. 23) has the head capsule differing in outline from the two heads considered in the genus Hydropsyche (Figs. 22 and 23). The antennal fossae are united in M. zebratum and the large scapes (sc) pivot on unusually long antennifers (x). The frons (f) is longer than the corresponding region in the genus Hydropsyche and has two sense areas beneath the antennifers (x). While the heads of Macronema differ extremely from the heads in the genus Hydropsyche, the maxillary palpi (mp) and the labial palpi (lp) are strikingly similar in both genera. Some of the differences, as the union of the antennal fossae (a), the division of the clypeus into the epistoma (e) and the anteclypeus (ac), and the large antennifers (x) which occur in the Macronema are present to a much less degree in the genus Hydropsyche in Figure 22. This species, although clearly a Hydropsyche, thus suggests a few of the modifications observed in the genus Macronema.

Psychomyidae (Fig. 24): - The maxillary palpi are five-segmented in both sexes within the family Psychomyidae. The last segment is long and subsegmented. Ocelli are never present.

Lype phaeopa Steph. (Fig. 24) has the compound eyes unusually large and approximated. The coronal suture is absent. Wart-like tubercles (w) are situated in the posterior region of the head. Within the parietal region there are two large laterally situated sense areas, and a larger median one which extends cephalad between the small widely separated antennal fossae (a). The scape (sc) is medium sized and widest at its distal end. Frontal sutures (fs) extend from between the antennal fossae (a), where they join with each other, to the frontal pits (fp). The anterior end of the demarked fronto-clypeal region (f and c) is closed by the suture demarking the clypeus from the labrum (l). The labrum (l) appears as a narrow spear-like flap. The parafrontal sutures (pf) are wide and are subdivided by a secondarily curved suture extending from the base of the antennifer to the frontal pit (fp). The maxillary palpi are five-segmented; the basal segment is short while the distal segment is long and subdivided. The labial palpi are made up of three wide segments.

Polycentropidae (Figs. 25, 26, and 27): - The ocelli are never present in the family Polycentropidae. The maxillary palpi are five-segmented in both the sexes, the first two segments being very short while the last segment is long and subsegmented.

In Polycentropus flavomaculatus Pictet (Fig. 25) the coronal suture is absent. Faint lateral sutures occur in the parietal region and demark the lateral area (pc) suggestive of and possibly homologous with the postcranial areas occurring in primitive Trichopteron heads (Figs. 28, 30, 31, and 32). Faint sutures extend from the postcranial areas (pc) laterad of the small antennal fossae (a) to join with the faintly demarked frontal sutures (fs). Within the median parietal region caudad of the antennal fossae (a) is situated a large sense area. The scape (sc) is small and is hardly wider than the following antennal segments. Within the fronto-clypeus (f and c) demarked by the frontal sutures (fs) and just cephalad of the antennal fossae (a) are situated two closely approximated sense areas. The parafrons (pf) is extremely narrow, its widest point being slightly caudad of the frontal pits (fp). The labrum (l) is small and triangular, with a slightly rounded membranous apex. The first two segments of the maxillary palpi (mp) are short; the third segment is more than twice as long as the fourth, while the fifth segment is very long and subsegmented. The small labial palpi are three-segmented.

Polycentropus confusus Hagen ? (Fig. 26) has the coronal suture (cs) ending just caudad of the large antennal fossae (a). Faint lateral sutures demark the possible postcranial areas (pc) which bear sense areas. A large sense area also occurs within the parietal region posterior to the antennal fossae (a).

The scape (sc) is larger than the scape (sc) in P. flavo-maculatus (Fig. 25) and is widest at its base. Secondary sutures usually considered the frontal sutures (fs) demark a fronto-clypeus (f and c). These cannot be the true frontal sutures as they extend mesad of the frontal pits (fp) and cause them to appear in the parafrons (pf). Traces of the original frontal sutures are still retained leading from the frontal pits (fp) and these sutures and the frontal pits (fp) indicate the true parafrons (pf). The labrum (l) is narrow, spear-shaped and slightly membranous at the tip. The maxillary palpi (mp) have the first two segments short, the third segment longer than the fourth while the fifth segment is the longest and is subsegmented. The labial palpi (lp) are small.

The species Phylocentropus placidus Banks (Fig. 27) has a distinct coronal suture (cs) from which arms extend almost at right angles caudad of the antennal fossae (a). A lateral region (pc) is demarked in the parietals and a small sense area is mesad of this region. Other sense areas occur between the branches of the coronal suture (cs) and the antennal fossae (a). The antennal fossae (a) are closely approximated being separated only by a narrow sclerotized area. The scape (sc) is large and broadest at the base. Distinct frontal sutures (fs) demark the median fronto-clypeus (f and c) and the lateral parafrons (pf). The frontal pits (fp) are within the frontal sutures (fs). Mandibles (m) are situated

laterad of the broad labrum (l). The anterior margin of the labrum (l) is truncated and membranous. Maxillary palpi (mp) have the two basal segments very short, the third segment longer than the fourth, and the fifth segment very long and subsegmented. The labial palpi are extremely short.

There are noticeable variations in the heads of Polycentropus flavomaculatus (Fig. 25) and Polycentropus confusus (Fig. 26). P. flavomaculatus has no coronal suture, the antennal fossae(a) are small and the scape (sc) is but little wider than the following antennal segments. In P. confusus (Fig. 26) there is a distinct coronal suture (cs), the antennal fossae (a) are larger than the fossae in the species P. flavomaculatus and the scape (sc) is likewise larger and broader at its base. The labrum (l) is small and triangular in P. flavomaculatus while in P. confusus it is small and spear-shaped.

The species Phylocentropus placidus (Fig. 27) differs from the two species in the genus Polycentropus in having closely approximated antennal fossae (a) and the scape (sc) large and bulb-like. The labrum (l) is much broader than the corresponding sclerites in either P. flavomaculatus or P. confusus. P. confusus, however, shows a tendency for the enlarged scape (sc) and approximating antennal fossae (a) that are present in Phylocentropus placidus.

Philopotamidae (Fig. 28): - Three ocelli are always present in the family Philopotamidae. The scape is small and

the maxillary palpi are five-segmented. The basal segment is short while the fifth segment is long and subsegmented.

In Philopotamus (Fig. 28) a coronal suture (cs) divides the parietals. Forks of the epicranial suture caudad of the antennal fossae (a) extend to the bases of the lateral ocelli (o). The median ocellus (o) is between the branches of the epicranial suture (cs). A postcranial area (pc) is demarked by a wide laterocephalic suture (lc) extending laterad of each antennal fossa (a). Sense areas occur on either side of the coronal suture (cs). Frontal sutures (fs) extend from the antennal fossae (a) to the anteriorly situated frontal pits (fp) demarking the frons (f) and the parafrons (pf). The epistoma (e) is anterior to the frontal pits (fp) and is separated from the anteclypeus (ac) by a distinct anteclypeal suture. The labrum (l) is separated from the anteclypeus by a faint suture; it is broadly rounded with a membranous margin. Mandibles (m) are laterad of the labrum. The maxillary palpi (mp) have the basal segment short, and the distal segment long, whip-like and subsegmented. The labial palpi (lp) are three-segmented.

Rhyacophilidae (Figs. 30, 31, and 32): - Members of the family Rhyacophilidae have three ocelli. The maxillary palpi are five-segmented in both sexes. The first two segments are short and thick, the third segment is the longest and is frequently slightly shorter than the fourth and fifth segments together. Mandibles are usually quite large.

In the species Rhyacophila nubila Zetterstedt (Fig. 30) the coronal suture (cs) or stem of the epicranial suture divides the parietals. The epicranial suture branches caudad of the antennal fossae (a) and an arm extends to the posterior margin of each antennal fossa (a). The lateral ocelli (o) are situated on either side of the coronal suture (cs) while the median ocellus (o) is between the antennal fossae (a). Sense areas occur around the arms of the epicranial suture cephalad of the median ocellus (o). The scape (sc) is large and widens distally. The postcranial area (pc) is demarked by faint laterocephalic sutures (lc) which extend cephalad along the margin of the compound eye. Faintly demarked frontal sutures (fs) reach from the anterior margin of the antennal fossae (a) through the frontal pits (fp) to the fronto-clypeal suture and demark a broad frons (f) and a narrow parafrons (pf). Sense areas are located in the frons (f) next to the frontal sutures (fs). An anteclypeal suture divides the clypeus into the epistoma (e) and the anteclypeus (ac) which extends between the bases of the mandibles (m). The anterior margin of the anteclypeus narrows and a faint suture demarks the small spear-shaped labrum (l). The maxillary palpi (mp) are five-segmented. The first two segments are short while the second segment is wider and more rounded than the first. The third segment is cylindrical and is longer than either the cylindrical fourth or fifth segments. The labial palpi (lp) are quite large and the segments are of about equal length.

The Rhyacophila shown in Figure 31 has the coronal suture (cs) dividing the parietals. Lateral ocelli (o) are laterad of the coronal suture (cs) while the median ocellus (o) lies between the antennal fossae (a) to which arms of the epicranial suture extend but do not quite meet. The postcranial areas (pc) are demarked by an unusually wide laterocephalic suture (lc) which extends laterad of the antennal fossae (a). A sense area is located caudad of each ocellus (o), also back of each antennal fossa (a). The scape (sc) is large, cylindrical and slightly broadest at the distal end. Frontal sutures (fs) are distinct and demark a broad frons (f) bearing laterally situated sense areas, and the parafrons (pf). The frontal sutures (fs) are cephalad and a suture divides an epistoma (e) and a broad anteclypeus (ac) extending between the bases of the mandibles (m). The anteclypeus (ac) narrows anteriorly and is delimited by a faint suture from the small labrum (l). The maxillary palpi (mp) are five-segmented, the first two segments are short, the second being more rounded than the basal segment, while the following are cylindrical. The third segment is longer than the fourth and fifth segments. Labial palpi (lp) are three-segmented.

In Glossosoma (Fig. 32) the coronal suture (cs) extends cephalad to sense areas located between the antennal fossae (a). Postcranial areas (pc) are demarked by the wide laterocephalic sutures (lc) which extend toward the parafrons (pf). Lateral ocelli (o) are situated anterior to the

postcranial areas (pc). A sense area is located laterad of the coronal suture and slightly caudad of the lateral ocelli (o). The median ocellus (o) is between the antennal fossae (a). The scape (sc) is large and cylindrical. Frontal sutures (fs) demark a frons (f) in passing from the antennal fossae (a) through the frontal pits (fp). The parafrontal sclerites (pf) demarked by the frontal sutures (fs) are narrow. The epistoma (e) is the region anterior to the frontal pits (fp). The anteclypeus (ac) is not definitely defined yet a suture in the triangular labrum (l) may possibly indicate this region. Mandibles are small. The maxillary palpi are similar to the maxillary palpi (mp) described for the Rhyacophila in Figures 30 and 31. The labial palpi (lp) are small and three-segmented.

The two described species of Rhyacophila (Figs. 30 and 31) are strikingly similar. Slight variations occur in the outline of the labrum (l), the distinctness of frontal and paracephalic sutures, the situation of sense areas, and the size and shape of the scape (sc). The genus Glossosoma (Fig. 32) closely resembles the genus Rhyacophila, the most noticeable modification being in the labrum (l), and the poorly defined anteclypeus. The frontal pits (fp) are not as far cephalad as the frontal pits in the species of Rhyacophila. The median ocellus (o), however, is extremely cephalad in Glossosoma (Fig. 32).

Hydroptilidae (Fig. 33): - The ocelli may be present or absent within the family Hydroptilidae. The heads are transverse and the scape (sc) is rarely much wider than the following antennal segments. The maxillary palpi are five-segmented in both sexes. The first two segments are extremely short, the third and fourth are of about equal length and are longer, while the distal segment is the longest.

In the species Agraylea multipunctata Curtis the coronal suture (cs) is faint and fades out before reaching very far cephalad. The lateral ocelli (o) are widely separated while the median ocellus (o) is caudad of the small antennal fossae (a). Secondary sutures demark an area (w) on either side of the parietal region which are wart-like in appearance and bear dense hairs. The median portion of the parietals is occupied by a large sense area. The scape (sc) is small, longer than broad but little wider than the following antennal segments. Frontal sutures (fs) demark a frons (f) and a wide parafrons (pf). The frontal pits (fp) are extremely cephalad near the fronto-clypeal suture demarking a broad clypeus (c) which is but faintly demarked from the labrum (l). The labrum (l) has a membranous anterior margin. A suture extends caudad from the gena into the parafrons (pf). The maxillary palpi (mp) are cylindrical, the first two segments are extremely short, so that only the second segment is visible, while the following three are longer; the fifth segment is longer than the fourth, and the fourth segment is slightly longer than the third. The labial palpi (lp) are three-segmented, the distal segment being the longest.

FAMILY RELATIONSHIPS BASED ON HEAD CAPSULE

The extreme variations in the sclerites and mouthparts have already been considered under the general discussion of the head and appendages. The reasons for considering certain characters as primitive have been explained and the descriptions and variations of the heads within the families have also been considered to show the characters common to, and the variations within the families.

In considering the family relationships, conclusions should be drawn from the study of a number of heads since both primitive and specialized characters commonly occur together in most Trichoptera. Thus in Neuronia posticus (Fig. 2) the presence of frontal sutures (fs) and large ocelli (o) are primitive characters while this Trichopteran also exhibits an elongated labrum (l), its maxillary palpi are four-segmented in the males rather than five-segmented, and the segments of the labial palpi (lp) are spoon-shaped, these being indications of specialization. No two characters have the same importance in determining whether a head is primitive or specialized. In N. posticus (Fig. 2) the primitiveness indicated by the presence of ocelli (o) and distinct frontal sutures (fs) is outweighed by the specialization seen in the greatly elongated labrum (l), the four-segmented maxillary palpi and the spoon-shaped segments of the labial palpi so that this head is considered highly specialized.

There is frequently a wide range of structural differences within families. The two heads representing the family Odontoceridae (Figs. 15 and 16) show more variation of a fundamental nature than is found in the heads of some different families, as for example the heads of the Calamoceratidae (Fig. 14) and the Leptoceridae (Fig. 17). The heads within the family Polycentropidae (Figs. 25, 26, and 27) however, can be seen to clearly resemble each other in the general outline of the head capsule, the fusion of the frons and clypeus to form the fronto-clypeus (f and c), and the strikingly similar segmentation of the maxillary palpi (mp).

The family Rhyacophilidae (Figs. 30, 31 and 32) contains the largest number of primitive head characters shown in the branched epicranial suture, the presence of three ocelli (o), the postcranial area (pc) bounded by a wide laterocephalic suture (lc), the closely associated frons (f) and epistoma (e), the cephalad frontal pits (fp) through which the frontal sutures extend to the antennal fossae, the broad anteclypeus (ac), the large mandibles (m) and the relatively simple segmentation of the maxillary palpi (mp). Slight indications of specialization are exhibited in the sense areas within the frons (f) (Figs. 30 and 31), the short rounded second segment of the maxillary palpi and the modified labrum (l) and anteclypeus (ac) in the genus Glossosoma (Fig. 32).

The Philopotamidae (Fig. 28) appear to be closely related to the Rhyacophilidae as they exhibit most of the primitive characters occurring in the Rhyacophilidae and in Philopotamus the contour of the head capsule closely resembles the head of Mnemonica, a genus of the Micropterygidae. Philopotamus has a broad labrum (l) which appears more primitive than the corresponding structure in the members of the Rhyacophilidae. Yet in the long distal segment of the maxillary palpi (mp), Philopotamus exhibits a fundamental specialization not observed in the family Rhyacophilidae and for this reason it cannot be considered as primitive as Rhyacophilidae.

The family Hydroptilidae (Fig. 33), is closely related to the more primitive families, Rhyacophilidae and Philopotamidae. The head capsule is primitive in outline, in Agraylea resembling the heads in the genus Mnemonica of the Micropterygidae. Agraylea is likewise primitive in having the lateral ocelli (o) widely separated, the clypeus broad, distinct frontal sutures (fs) extending from cephalic frontal pits to the antennal fossae (a), and similar segmentation of the maxillary palpi (mp). Two very primitive characters, namely the postcranial areas (pc) and the laterocephalic sutures (lc) are absent in Agraylea while specializations are observed in the wart-like areas (w) in the posterior region of the head, the large sense area in the parietals, and possibly in the secondary suture within

the parafrons (pf). Because Agraylea has lost these fundamental primitive characters, and in some members the ocelli are also absent, it must be considered a higher type of head than is exhibited by either Rhyacophilidae or Philopotamus.

The families Polycentropidae (Figs. 25, 26, and 27) and the Hydropsychidae (Figs. 21, 22, and 23) show resemblances in having an area in the posterior parietals labeled pc and suggesting the postcranial areas occurring in primitive heads. The maxillary palpi (mp) are slender and indicate specialization in their segmentation, especially in the elongated, slender distal whip-like segment and the short fourth segment. It is difficult to determine from the heads studied which of these two families is the more primitive. The head capsule in the members of the family Polycentropidae resembles in outline the primitive head of Philopotamus (Fig. 28) and Agraylea (Fig. 33). The genus Hydropsyche (Fig. 22) likewise resembles more these primitive Trichoptera in the outline of the head and although Hydropsyche (Fig. 22) shows extreme modification in the elongated and approximated antennal fossae (a) and the cephalic frons (f) at the same time it retains the division of the clypeus into the epistoma (e) and the anteclypeus (ac) which is the primitive condition exhibited in both the Philopotamidae and Rhyacophilidae. The modified Macronema (Fig. 23) likewise has the clypeus divided into the epistoma (e) and the anteclypeus (ac) and the mandibles (m) are noticeable. In the

Polycentropidae (Figs. 25, 26, and 27) the frons and clypeus have fused to form the fronto-clypeus (f and c) and the labrum is generally small except in Phylocentropus (Fig. 27). This would seem to indicate that the Polycentropidae are slightly more specialized than the Hydropsychidae.

The Psychomyidae (Fig. 24) as represented by Lype do not exhibit many indications of primitiveness. The family has been considered related to the Hydropsychidae and Polycentropidae because of the long distal segment of the maxillary palpi (mp). The segments making up the maxillary palpi are unlike the segments observed in Hydroptilidae and Polycentropidae, the only resemblance being in the long distal segment. Lype exhibits specialization in the fusion of the frons and clypeus to form the fronto-clypeus (f and c), the wart-like areas (w) in the posterior region of the head, and the unusually small labrum (l). While the resemblance to the Hydroptilidae and Polycentropidae is extremely slight the head of Lype appears more closely related to these families than any others.

The families Molannidae (Fig. 20) and Odontoceridae (Fig. 15), while exhibiting many specializations, present slight suggestions of primitiveness in some features, such as the general segmentation of the maxillary palpi (mp) and in the fusion of the frons and clypeus. It is difficult to determine from the heads alone which of these two families is the more primitive. The genus Odontocerum (Fig. 15) has

conspicuous mandibles (m) and the frontal sutures (fs) are less modified than are the frontal sutures in the head of Molanna (Fig. 20) which is without mandibles. Modifications are exhibited in the first two segments of the maxillary palpi (mp) within the genus Molanna. The genus Psilotreta (Fig. 16) of the Odontoceridae is extremely modified and possesses no head characters in common with either of these families.

The families Calamoceratidae (Fig. 14) and Leptoceridae (Figs. 17, 18, and 19) exhibit more primitive characters than do the Molannidae and Odontoceridae in having an unusually broad labrum (l) and in having in the Calamoceratidae the clypeus divided into the epistoma (e) and an extremely broad and narrow anteclypeus (ac). This division of the clypeus occurs in primitive heads and would indicate that the Calamoceratidae are more primitive than the Leptoceridae which have the clypeus separated from the frons (f) but undivided, extremely wide, and narrow. Other differences between these two families are seen in the wart-like tubercles (w) occurring in Calamoceratidae (Fig. 14) and in Leptocella (Fig. 17) but not in the other representatives of the Leptoceridae (Figs. 18 and 19). The segmentation of the maxillary palpi (mp) likewise varies in these two families and the small bead-like fourth segment of the maxillary palpi in Calamoceratidae does not resemble the corresponding segment of the maxillary palpi in the family Leptoceridae. Because the maxillary palpi

appear extremely modified as well as the parafrons (pf) in these two families and because the antennal fossae (a) are unusually large, demarking the frons (f) these families are considered more specialized than the families Molannidae and Odontoceridae previously discussed. The Calamoceratidae are probably more primitive than the Leptoceridae as is suggested by the division of the clypeus into the epistoma (e) and anteclypeus (ac).

The heads are highly modified in the families Limnophilidae (Figs. 6-9), Phryganeidae (Figs. 1-5), and Sericostomatidae (Figs. 10-13) and are being considered together because they exhibit sexual dimorphism in the segmentation of the maxillary palpi (mp). The Limnophilidae and Phryganeidae show primitiveness in having ocelli (o) while specialization is exhibited in the elongated labrum (l). The Limnophilidae and Sericostomatidae both show indication of primitiveness in having the clypeus divided into the epistoma (e) and the anteclypeus (ac). In the Phryganeidae the clypeus is fused with the frons to form the fronto-clypeus (f and c); a condition never present in primitive heads. The Sericostomatidae, however, exhibit extreme modifications in the maxillary palpi (mp) in the males (Figs. 11, 12, and 13), also in the faint sutures demarking the frons, the elongated scape (sc) and in the absence of the ocelli (o). These fundamental specializations seem to indicate that the

Sericostomatidae are more modified than either the Limnophilidae or Phryganeidae. The affiliations of the subfamilies of the Sericostomatidae are questioned by many workers and probably justly so, if the extreme range of variation occurring in the heads is carried over into the other body divisions. The Phryganeidae and Limnophilidae do not show the extreme sexual dimorphism that occurs in the maxillary palpi in the Sericostomatidae. Within the Limnophilidae the elongated genal process (gs), the occurrence of sense areas in the parafrons (pf), and the close association of the anteclypeus (ac) with the labrum (l) are specializations which do not occur in the Phryganeidae. The Phryganeidae on the other hand exhibit the greatly elongated labrum (l) and the ventrally prolonged mouthparts to a much greater degree than is exhibited in the heads of the Limnophilidae.

It is evident that the greater the number of heads studied, and the larger the number of primitive and specialized tendencies considered within each head, the more accurate the conclusions as to family relationships within the order will be. Krafka (1923) studied the family relationships of the order from a consideration of the frontoclypeus and the chaetotaxy of this region in larval heads and his conclusions contradict the evidences of relationship derived from studies of the adults. The variations already observed in the adult heads show that conclusions concerning phylogenetic relationships of the families cannot be determined accurately from the study of any one region unless a large number of the synthetic forms are available for study.

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ABBREVIATIONS

a	antennal socket
ac	anteclypeus
c	clypeus
ca	cardo
cs	coronal suture
d	depression
e	postclypeus or epistoma
f	frons
f and c	fronto-clypeus
fp	frontal pits
fs	frontal suture
g	galea
gp	gular pits
gs	genal process
l	labrum
lc	laterocephalic or paracephalic suture
lp	labial palpus
m	mandible
mn	mentum
mp	maxillary palpus
o	ocellus
oc	occiput
of	occipital foramen
pc	postcranial area
pf	parafrons
pg	palpiger
pga) pgs)	postgena
r	demarked area
s	stipes
sc	scape
sm	submentum
v	sense area
w	wart-like tubercles
x	antennifer

EXPLANATION OF PLATES

1. Neuronia postica Walker, Female.
2. Neuronia postica Walker, Male.
3. Neuronia postica Walker, Male, posterior view.
4. Neuronia pardalis Walker, Male.
5. Phryganea grandis L., Male. Staudinger and Bang-Haas.
6. Caborius (Allophylax) punctatissimus Walker, Male. Determined by Banks.
7. Astenophylax argus Harris, Male.
8. Limnophilus griseus L., Female. Staudinger and Bang-Haas.
9. Limnophilus griseus L., Male. Staudinger and Bang-Haas.
10. Sericostoma turbatum McLachlan, Female. Staudinger and Bang-Haas.
11. Lepidostoma hirtum Fabricius, Male. Staudiner and Bang-Haas. Determined by Navas.
12. Mormomyia vernalis Banks, Male. Determined by Banks.
13. Goera pilosa Fabricius, Male. Staudinger and Bang-Haas.
14. Phylloicus bromeliarum Fr. Müller. Determined by Banks.
15. Odontocerum albicorne Scopoli. Staudinger and Bang-Haas. Determined by Navas.
16. Psilotreta frontalis Banks. Determined by Banks.
17. Leptocella sp.
18. Leptocerus albifrons L. Staudinger and Bang-Haas.

19. Oecetina avara Banks. Determined by Banks.

20. Molanna angustata Curtis. Staudinger and Bang-Haas.

21. Hydropsyche sp.

22. Hydropsyche sp. Determined by Banks.

23. Macronema zebratum Hagen.

24. Lype phaeopa Stephens. Staudinger and Bang-Haas. Determined by Ulmer.

25. Polycentropus flavomaculatus Pictet. Staudinger and Bang-Haas.

26. Polycentropus confusus Hagen ? Determined by Banks.

27. Phylocentropus placidus Banks. Determined by Banks.

28. Philopotamus sp.

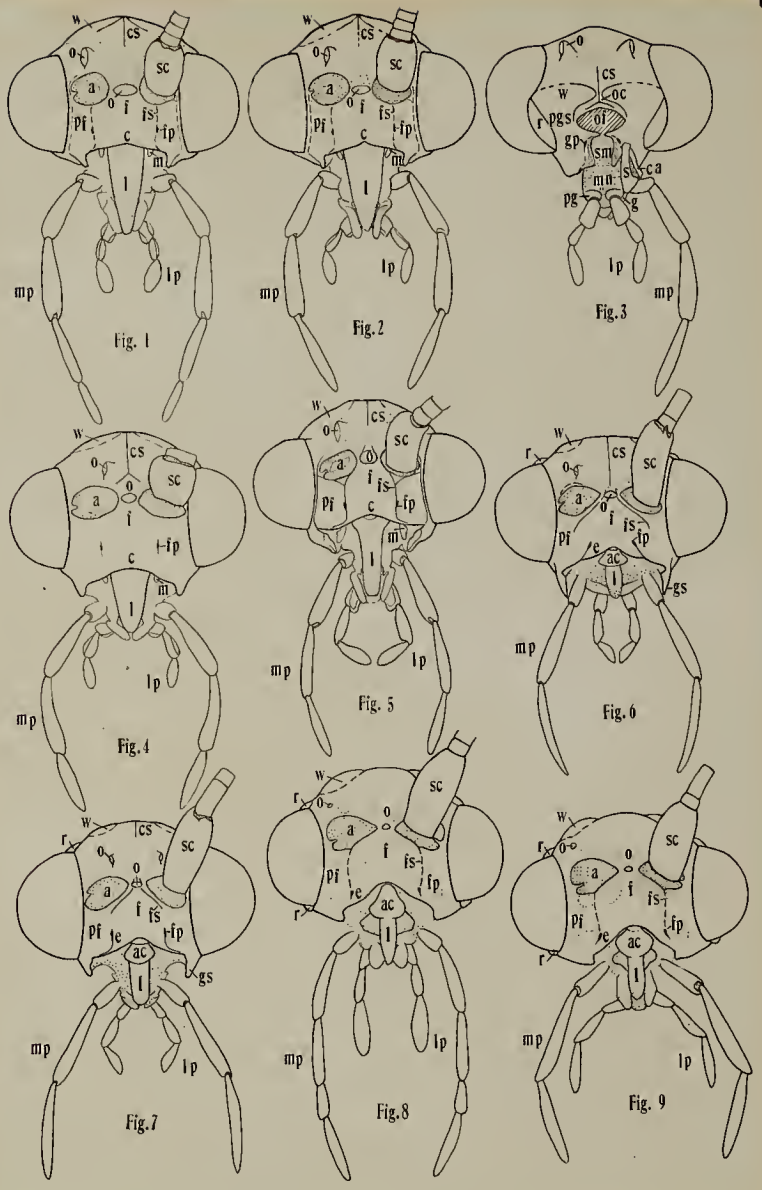
29. Philopotamus sp., posterior view.

30. Rhyacophila nubila Zetterstedt. Staudinger and Bang-Haas.

31. Rhyacophila sp. Determined by Banks.

32. Glossosoma sp. Determined by Banks.

33. Agraylea multipunctata Curtis. Staudinger and Bang-Haas. Determined by Ulmer.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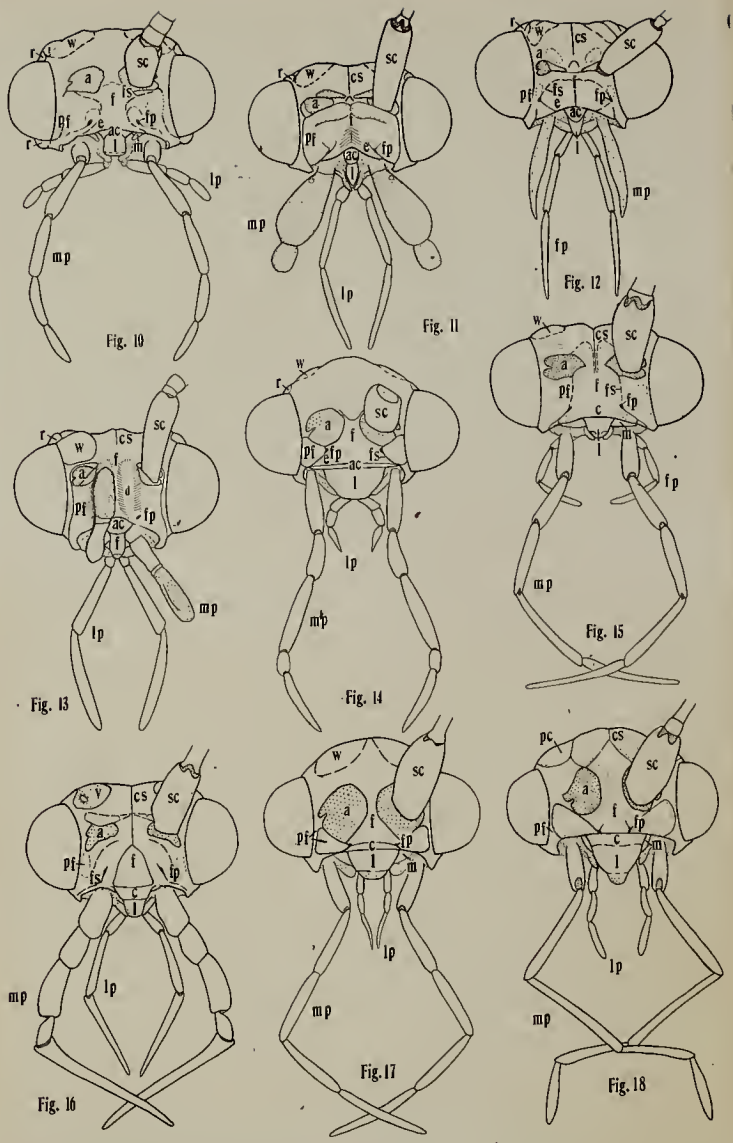

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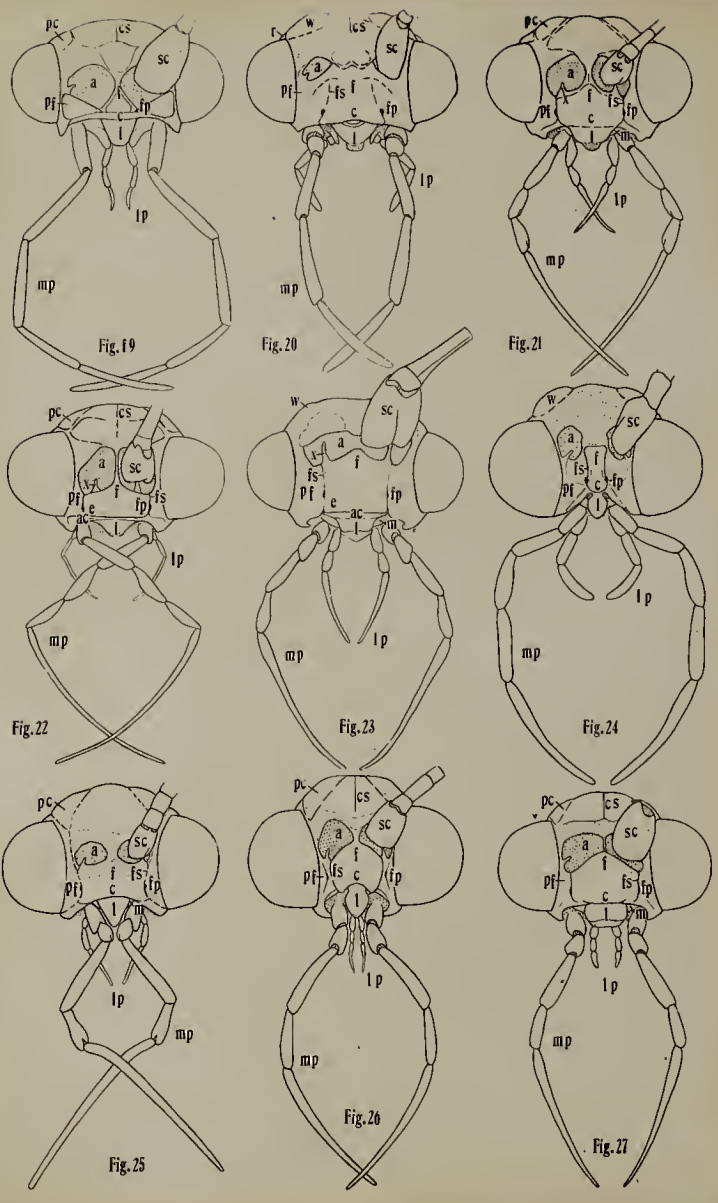
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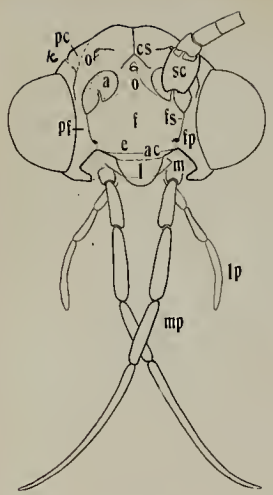

Fig. 28

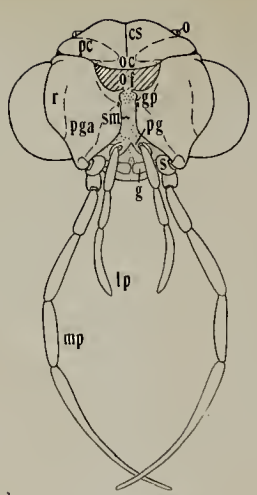

Fig. 29

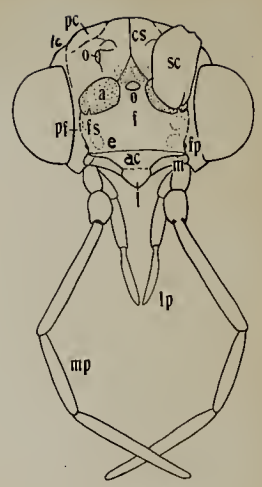

Fig. 30

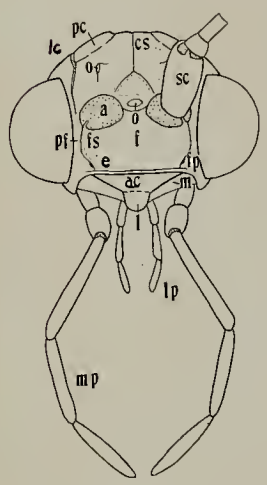

Fig. 31

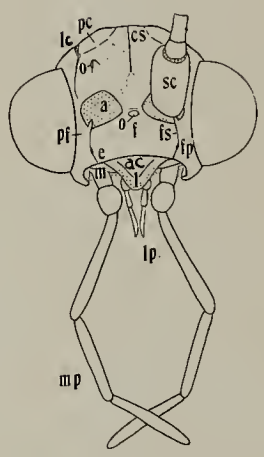

Fig. 32

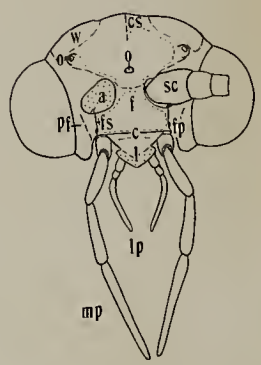

Fig. 33


HUNTING