HOMOPTEROUS STUDIES. PART II.

Morphological Studies of the Superfamily Jassoidea.

ERIC. S. COGAN, M. A.

Introduction.

The Superfamily Jassoidea comprises a large number of small or comparatively small Homopterous insects, which agree in respect to the character of the hind tibiæ. The latter are prismatic in shape and are armed with a row of spines on their posterior margins. The head varies in shape and may be angular or rounded, produced or shortened. The eyes are located on the lateral margins of the head, and the breadth across them is frequently the widest part of the body. The antennæ are usually inserted on the face between the eyes. The thorax varies considerably, but in all the pronotum is the most pronounced region. There are two pairs of wings, the first pair being developed as tegmina and are usually coriaceous, while the second pair may be membranous. In some forms the elytra are reduced in size.

The superfamily is generally subdivided into four subfamilies, viz.: Bythoscopidæ, Tettigoniellidæ, Jassidæ and Typhlocybidæ, the subdivision of the first three being based on the location of the ocelli, and of the last, on the character of the venation of the elytra. In the Bythoscopidæ, the ocelli are situated on the front below the border of the vertex; in the Tettigoniellidæ they are on the disk of the vertex, while in the Jassidæ they are to be found on the border of the vertex or between the latter and the face. In the three subfamilies mentioned, the elytral nervures fork on the disk, while in the Typhlocybidæ the nervures fork at the base and run to the apex of the elytron without further dividing. Again in the last named family the ocelli may or may not be present. The various subfamilies are further subdivided into a number of genera, and frequently into tribes and divisions.

The chief object of this investigation has been to obtain a definite understanding of the external and internal anatomy for the group generally and to establish homologies with the

other Homopterous families. Very little work has been done on the anatomy of the Jassids, and as far as the writer is aware, no complete treatment of any phase of the morphology has yet been offered. Considerable work has been accomplished on the other Auchenorrhynchous families by Muir, Kershaw, Licent, Pantel, Bugnion, Sulc and others, but the only treatment of the Jassoid anatomy is to be found in the general discussions of systematic works on the group. Thus the works of Signoret, Burmeister, Flor, and Melichar contain general discussions of the external anatomy, which are necessary for taxonomic purposes. The wings and their structure have been ably treated by Metcalf, and only mention will here be made of this phase.

Since the only work on the external anatomy of the Jassoidea has been done by systematists and for taxonomic purposes, Professor Osborn suggested to the writer that an investigation into the morphology of the group would be of some avail, and accordingly the work was undertaken. The scope of the investigation is confined to the four families. A common and seemingly generalized species was selected from each family and in the main the studies here noted were conducted on these. the Bythoscopidæ, Agallia sanguinolenta was selected chiefly because the material, both adult and nymph, was abundant and readily obtainable; the same may be said of Draeculacephala mollipes for the Tettigoniellidæ, Deltocephalus inimicus for the Jassidæ, and Empoasca mali for the Typhlocybidæ. In many cases species belonging to other genera were studied and compared with the above where such was necessary. To Professor Osborn the writer wishes to express his indebtedness for directing the investigation, and for helpful criticism and suggestion.

METHODS.

The material for gross dissection was killed and preserved in a 4 per cent. solution of Formalin and found to be quite satisfactory. Some specimens were killed in hot water and preserved in 70 per cent. alcohol. In many cases material which had recently been collected in the field was killed in 100 per cent. alcohol and dissected and examined immediately. All dissection was accomplished by means of a Bausch and Lomb binocular microscope. For the dissection of the smaller

insects, a shallow dissecting pan made by filling a watch glass with paraffin, proved very convenient. The study of many of the chitinized parts was facilitated by previously boiling the specimens in a 10 per cent. solution of potassium hydroxide, washing in water and examining in glycerine or alcohol. The former proved very suitable, and has the advantage in that it evaporates very slowly. In the dissection of the reproductive organs and the digestive apparatus, normal salt solution was used to float out the organs. Some of the immature forms were conveniently studied by simply killing in Xylol and mounting in balsam almost immediately. Certain structures, such as the tracheal system, show up clearly when treated by this method.

Material for sectioning was killed mainly by two methods. Hot water was used where the insect has recently moulted and the chitin had not yet hardened. Carnoy A (Glacial acetic acid one part, to absolute alcohol three parts) proved to be a very good fixing fluid. Practically all the material for sectioning was killed by this method. Delafields haematoxylin and eosin were the stains used for staining sectioned material. Staining in toto did not prove satisfactory. Picric acid for staining chitin was used to some extent. The material was embedded and cut in paraffin with a melting point of 55 C.

THE HEAD.

External Anatomy. (Pl. XXI, XXII, Figs. 1, 2, 3, 4, 5, 7, 25–31).

The different regions of the Jassoid head have been well defined by systematists in the group and before proceeding to a discussion of the structure, it will be as well to outline these regions, which now, for the most part, are of interest because of their place in the taxonomy of the superfamily. The dorsal region, i. e., the portion of the head between the compound eyes is termed the vertex (v), and in some of the families it bears the paired ocelli (o). Although not a definite sclerite, it serves as a good "landmark" for descriptive purposes. The region from the anterior edge of the vertex to the first apparent transverse "suture" is regarded as the front ("frons"); its lateral margins are limited by the longitudinal sutures which run from the antero-lateral edges almost to the antennæ and frequently to the anterior edge of the head. Attached to the

anterior edge of the frons is the broadly rectangular clypeus, and at the distal edge of the latter is seen the small peglike labrum. At the sides of the frons and clypeus, two small semi-circular plates are seen, these are the loræ. The genæ are the large regions extending from beneath the eyes to the anterior edge of the clypeus and completely surrounding the loræ. The rostrum or beak projects from under the surface of the clypeus and encloses the setæ. The head is greatly deflexed with the result that the rostrum lies between the anterior coxæ and projects in a caudal direction.

The same regions as are seen in the Jassoid head are to be differentiated in the Cicada, or any other of the Auchenorrhynchous Homoptera. In 1896 Marlatt drew attention to the fact that the frons of Cicada septendecim was really the clypeus, that the clypeus and labrum constituted the labrum, and that the loræ were the external representatives of the mandibles, while the genæ were the corresponding pieces of the maxillæ. No attempt was made to homologise the various parts, until the work of Muir and Kershaw appeared in 1911. From a study of the external and internal anatomy as well as the development and embryology of both Homopterous and Heteropterous forms, these authors concluded that the "frons of many writers was the clypeus, and their clypeus was the labrum. The loræ have no connection with the mandibles, but are lateral developments of the clypeal region. The dorsal and outer pair of setæ are the mandibles, developed direct from the first pair of appendages behind the stomodaeum of the embryo, and articulated in their normal position, viz., on the oral margin between the clypeus and the maxillæ. The ventral and inner pair of the setæ are part of the maxillæ developed directly from the distal joint of the second pair of appendages behind the stomodaeum of the embryo, the basal joint being directly developed into the maxillary plate." In a paper on the Development of the Mouthparts in Homoptera, the same authors conclude that "(1) The mandibles and maxilla arise as in other insects, the former being articulated in an approximately normal position. (2) The Homopteran and Heteropteran mouthparts arise and develop in the same manner. (3) There is no mandibular plate. (4) The tentorium agrees essentially with that of other insects. (5) The maxillary seta does not represent the palpus, but may be a development

of the palpifer or the combined lacinia and galea. (6) The maxillary-plate represents the cardo and stipes." In their discussion of the Homology of the Hemipterous mouthparts, no reference is made to the Jassoidea, except that the Tettigoniellids can be easily homologised with the Cicada. Beyond this reference to the Jassoid head the writer has been unable to find further treatment of the subject.

In the following discussion of the Jassoid head, the fixed parts will be considered first and then the free or movable parts.

Fixed Parts of the Head. (Pl. XX, Figs. 1, 2, 3, 4, 5).

The Jassoidea agree with the other Hemipterous families in the general arrangement of the head and mouthparts. The head is greatly deflexed and the mouthparts are attached to the caudo-ventral portion of the capsule, with the result that the beak or so-called proboscis is directed caudally between the first pair of thoracic legs.

Head-Capsule.—As in a generalised insect, the head of the Jassid is composed of a number of sclerites, which have become united to form the head-capsule, and this becomes the external skeleton of the head. To this capsule, the various appendages of the head are attached and articulated. In the head it will be found that no trace of the primitive sclerites forming the head-capsule is to be found, for they have either disappeared or amalgamated with other sclerites. The various regions on the Jassoid head were indicated before, and only those areas which can be definitely recognized as sclerites will be considered here.

The dorsal region (v) of the head (i. e., the vertex) is not separable from the front or frons (Fr), and there is no trace of a suture between them, as one would expect. Together with the genæ and occiput, the vertex and front constitute the epicranium.

The vertex (v) varies considerably in size from a mere narrow region in the Bythoscopidæ to a greatly elongated area in the Tettigoniellids (especially in the Tribe Dorydini). It usually bears the paired ocelli (o); thus in the Family Tettigoniellidæ they are located on the disk or surface, in the Jassidæ on the cephalo-lateral margin near the eyes, and in the Typhlocybidæ (when present) also on the cephalo-lateral margin. But in

the case of the Bythoscopidæ they have been carried over and down on the face, while the dorsal surface of the vertex is greatly reduced.

The Front, although a true sclerite, is not readily differentiated from the following sclerite—the clypeus (clyp.)—the suture between them being obsolete, but its position can be judged by the fact that the anterior arms (i. a.) of the tentorium are invaginated on each side, where the suture should normally end. The front usually, at least in the more generalized insects, can be identified owing to the fact that it bears the median ocellus, but no trace of such an ocellus is to be found in the Jassid head. The frontal region ("frontal ridge") then would be the area between the cephalic margin of the head and a transverse line connecting the invaginations of the anterior arms of the tentorium. In the Jassoid head these invaginations occur at the cephalic end of the maxillary suture, on the so-called mandibular plates or loræ. Its lateral margins would be defined by the longitudinal sutures on either side of the head.

The clypeus (clyp.) is the sclerite attached to the frons along its anterior margin. In the Jassid head as in other Homoptera, it is not easily distinguished from the front; it is a broadly rectangular sclerite, generally somewhat convex with its lateral margins developed into two plates (loræ) which attach along the sides of the labrum. These two plates (the loræ or so-called mandibular plates) have long been regarded as the external pieces of the mandible, although in reality they have no connection with the mandibles. Muir and Kershaw have shown conclusively in their work on the development of the mouthparts of the Homoptera, that the mandibles become enclosed within the head in the course of development. true suture exists where these two plates are in relation to the labrum, but their basal portion is attached strongly to the middle piece of the clypeus. If we consider the mesal piece as the clypeus proper, then the lateral developments might be regarded as the antecoxal pieces of the mandible.

The labrum (labr.) is the upper lip and is attached to the anterior margin of the clypeus. It constitutes the roof of the mouth and is differentiated with difficulty from the clypeus. However the anterior margin of the clypeus is connected with the pharynx by two small developments of the tentorium, and these

mark the region where labrum and clypeus meet. The shape of the labrum is broadly rectangular, with the anterior margin generally rounded off, and forming a covering for the basal joint of the labium. Projecting from under its anterior margin and fitting into the groove at the base of the labium is the small, peglike epipharynx (epi.). On an external view the epipharynx appears as part of the labrum, but on close examination it will be seen to run back as the dorsal wall of the pharynx.

The Occiput or the posterior part of the dorsal surface of the head can not be differentiated from the vertex. However, by viewing the head in its caudal aspect it may be seen as the large sclerite surrounding the occipital forearm. Attached to the ventral surface of the occiput, is the gula or gular region, which is very small in the Jassoid head, owing to the deflection. The gula consists of a small membrane attached at one end to the base of the occiput and at the other to the basal joint of the labium.

The Genæ proper cannot be distinguished from the maxillary plates—an amalgamation of the two sclerites taking place early in the development of the insect's head. No trace of a suture is to be found and we can only refer to the genæ in general terms as that region surrounding the compound eyes on either side of the face and attached to the maxillary plates, for the greater part.

Ocelli.—The ocelli (o) where present are two in number. As stated before, in the Tettigoniellidæ (Fig. 5), they are located on the mid-dorsal surface of the vertex, while in the Bythoscopidæ they are situated on the face (Fig. 3). The position in the case of the last named family is probably owing to development of the epicranium, which occupies the greater part of the dorsal region of the face. However, in the Jassidæ and Typhlocybidæ (where present), the ocelli are located on the cephalo-lateral margins of the head. On examining the internal structure of the head, it will be found that branches of the dorsal arms of the tentorium proceed to the head just beneath the ocelli. This was found to be the case in practically all the forms examined. The ocelli are small, clear, circular or oval structures, which are generally raised above the general level of the head. Frequently they are colorless or glassy, but in some cases they are pigmented with red or black.

Compound Eyes—The compound eyes (E) occupy the greater part of the dorsal aspect of the head at the sides of the vertex. They are large oval or semicircular bodies, which extend back to the anterior margin of the pronotum. In the immature forms they are relatively larger than in the adult and are more rounded. The character of the facets is the same as that of a generalised insect, although the number of these facets is exceedingly great.

Movable Parts of the Head. (Pl. XX, XXI, Figs. 6,7,13,16,17).

Antennæ (Figs 18–21).—The antennæ (A) are for the most part setaceous in form; structurally there is very little difference between the morphology of the antennæ in the various forms, although it will seem as well to indicate here the more important The number of segments or joints varies considerably and frequently cannot be distinguished at the distal ends. basal segment and those adjoining it are the most modified In the males of Idiocerus (Bythoscopidæ) the distal joints of the antennæ are developed into small oval plates, which Hansen has regarded as sensory structures. In many of the Tettigoniellids and Jassids, small hairs or spines are developed on the basal joints of the antennæ. The antenna of Deltocephalus inimicus figured shows this structure (Fig. 19). These spines may have some sensory function, although no trace of sense cones were found on them. The antennæ are inserted on the face between the compound eyes and the longitudinal suture of the front. In some cases the point of insertion may be a deep cavity, in others it may be shallow. some of the Bythoscopidæ the cavity is overlapped by a distinct ledge.

Labium—(Pl. XX, Figs. 9, 13). The beak or proboscis of the Jassid mouthpart is the labium or lower lip. It is relatively short and thick, circular in outline, and is three-jointed. The distal joint, or tip of the labium is the largest, the proximal the smallest and the middle is about intermediate in size between the two. Externally the labium appears to emerge from under the labrum, but a closer examination will reveal the fact that the tip of the epipharynx, a small, peg-like structure, which is attached to the anterior end of the labrum, fits into a narrow groove on the surface of the labium and gives it some means of support in one direction. Ventrally the labium

is attached by its strong lateral and central muscles to the gula and to the body of the tentorium. The membrane of the proximal joint is developed into a central chitinous rod, to which attach the central muscles (c); at the sides the muscles attach directly to the basal joint at one end and to the gula The labium forms the floor of the mouth, and encloses the mandibular and maxillary setæ. As the mouthparts of the Jassid are fitted for sucking, the two pairs of setæ are in close relation in the trough which runs the full length of the labium. This trough is shallow, and closed for the greater part beyond the epipharynx. The maxillary setæ form the sucking tube through which the plant juices are drawn. It is quite possible that the mandibles form the piercing organs, by means of which the maxillæ are enabled to function. Two sets of muscles are to be found in the labium circular (c. m.) and longitudinal. The longitudinal muscles enable a back and forward movement, such as protrusion and withdrawal, while the circular muscles allow of an up and down movement. The attachment of the labium to the gula is not very strong and frequently on removing the head from the body, the labium will remain attached to the anterior edge of the prosternum. The setæ are capable of withdrawal from the trough of the labium, and may be free—this is often the case in nymphal forms. At the anterior edge of the labrum where the setæ emerge from the head capsule into the labium, a small membrane covers the entrance to the labium, making the structure airtight. This is necessary when it is considered that the plant juices constituting the food of the insect must be sucked up into the pharynx.

The tip of the labium is rounded and the setæ are protruded through a small hole at the end. The external region of the labium is chitinized, and is set with numerous hairs or spines. In feeding, the labium is applied to the plant leaf or tissue and forms a guide for the setæ. It however, does not enter the plant tissue. It is quite possible that the close application of the labium to the plant will render the connection airtight so that the juices may more readily be sucked up.

Maxillæ—(Pl. XX, Figs. 7, 17, 5, 4, 3). If the head of a Jassid be examined, two large plates (mx. pl.) forming the sides of the face and the lateral covering of the mouth, will be

found. These are the maxillary plates (mx. pl.), and they occur in all Homoptera. Although the maxilla are fused with the genæ, they can be distinguished from the latter in that they articulate with the maxillary setæ (mx. s.), which are enclosed within the head-capsule. The maxillary plates extend around the sides of the face and constitute the border; they completely surround the clypeus and meet anteriorly beneath the labrum, where they are connected by a membrane. At the sides the plates are turned down and under, forming the part of the ventral surface of the head. Distally they turn back on the under side of the head, and develop into two rectangular chitinous plates—with which the maxillary setæ articulate. The maxillary setæ are attached to these chitinous plates, which in turn are hinged to the body of the tentorium (t. b.).

The maxillary setæ (mx. s.) resemble the setæ of other Homoptera; they are long and slender for the most part, but their proximal basal region is swollen, and attaches to a small tendon (t.), which passes dorsally into the retractor muscles (mx. r.) of the setæ. A membrane sleeve surrounds the seta, as far as the entrance to the labium. The strong protractor muscles (mx. p.) of the maxillary setæ are attached to the maxillary plate, while the retractor muscles attach to the head-capsule at the sides of the occiput. The articulation of the seta is on the inner side of the maxillary plate and it can easily be seen by reference to the figure (Pl. I, Fig. 7) how the maxillæ can be worked forward and backward.

The exact homology of the maxilla in Homoptera is a question on which no little discussion has arisen. The amalgamation of the maxillary plate with the genæ, would lead one to believe at once that the whole of the plate at that side of the clypeus constitutes the gena, but on examining the internal structure, and the connection of the maxillary plate with the maxillary seta, it can readily be seen that the maxillary seta is intimately connected with the maxillary plate. Added to this the invaginations of the posterior arms of the tentorium are to be found at the sides of the occipital foramen, and are adjacent to the attachment of the maxillary plates with their setæ. In all the insects so far examined, the invaginations of the posterior arms of the tentorium have always been associated with the point of attachment of the maxilla.

Mandibles—(Pl. XX, Figs. 6, 16, 2, 4, 3). Viewing the head on the inside from its caudal aspect, the two pairs of setæ, viz., the mandibular (m. s.) and maxillary setæ, can be seen attached to the head capsule. These two pair of setæ are in rather close relationship, but with careful dissection it will be seen that the more dorsal pair are articulated with head-capsule, between the maxillary plate and the clypeus. The posterior end of the mandible is produced into a small tendon (t) to which attach the strong retractor muscles (m. r.) which attach in turn to the head-capsule at the sides of the occipital foramen. small tendonous rod (m. a.) connects the mandibular seta with the latero-posterior edge of the clypeus. While the mandibular seta is intimately related to the maxillary seta in the labium, the two are separate within the head-capsule. The mandibles are capable of being withdrawn and protruded within limits owing to the muscles, which are connected with the posterior The retractor muscles (m. r.) attach to the head capsule on the inner side of the clypeus. The position of the invagination of the anterior arms of the tentorium, which are associated with the mandibles, enables one to homologise the mandibular setæ in the Jassoidea with the mandibles in the Cicadidæ and other Homoptera.

The identity of the mandibular plate or lora, has been well demonstrated by the work of Muir and Kershaw on the development of the Homopterous head, wherein it is shown that the mandibles become completely enclosed within the head-capsule. Although this question has been much discussed, from various points of view, it seems to the writer clear that the evidence favors the interpretation of the mandibular setæ as representing the entire mandible. The articulation of the mandibular setæ viz.. between the clypeus and the maxilla is the normal position, and further the invagination of the anterior arms of the tentorium add additional weight to the interpretation.

The structure and morphology of the mandibular seta resembles very much that of the general Homopteron; the tips are barbed, with the barbs (b. a.) pointing backward. As stated before, their function is probably that of piercing the plant, to enable the maxillæ to perform the sucking function. Like the maxillary, the mandibular setæ are surrounded for their proximal half with a membranous sleeve.

Internal Anatomy. (Pl. XX, Figs. 2, 3, 4, 5, 8, 9, 10, 11; Pl. XXI, Fig. 22).

In the following discussion of the internal anatomy of the head, those structures previously mentioned will be omitted and only the parts which pertain directly to the internal structure will be considered.

Tentorium—(Figs. 4, 5). In the heads of all insects there is to be found a definite arrangement of supporting, chitinous structures, which owe their origin to three pairs of primary invaginations of the body wall. The structure itself consists of a system of rod or plate-like bodies, which constitute the tentorium or internal head skeleton. In the Jassid head this skeleton is present, but in some respects it has been modified. The three pairs of arms which compose the tentorium are known respectively as the anterior, dorsal and posterior arms. anterior arms (i. a.) are invaginated on the cephalo-lateral edges of the clypeus; in the Jassid head this invagination is to be found at the upper corner of the so-called mandibular plate; it persists as an opening and can be distinctly seen in a specimen which has been boiled in KOH. In many insects the points of the invaginations do not persist in the adult. The anterior arms (i. a.) are always associated with the mandibles. and in the Jassid head they are to be found near the articulation of the mandibular setæ. The dorsal arms (d. a.) are invaginated beneath the antennæ and are easily seen in the head of Deltocephalus inimicus or any Jassoid. They are always associated with the antennæ, and in this case they occupy their normal position. While the invaginations themselves are not readily seen, the arms are quite prominent. The posterior arms (i. p.) are invaginated at the sides of the occipital foramen and are near the attachment of the maxilla. The upper ends of the posterior arms are connected by a chitinous bridge (the maxillary bridge of Muir and Kershaw), which is the body of the tentorium (t. b.). The latter divides the occipital foramen into two parts.

In the Jassoid head the parts of the tentorium have been modified to a certain extent, but nevertheless they can readily be homologised with the corresponding structures in the Cicada and other Homoptera. From the invagination of the anterior arms, on either side of the head, two small chitinous structures run forward to the anterior edge of the clypeus; here they attach to the dorsal region of the clypeus, and at the same time are connected with one another by a narrow bridge, which is scarcely visible. From the anterior region of the pharynx two small tentorial structures attach to the anterior arms and form the chief means of support of the pharynx.

The posterior arms, the invaginations of which are connected by the body of the tentorium (t. b.), run forward along the ventral region of the head, as far as the salivary pumping apparatus (s. p.), where they attach on either side to the The body of the tentorium is very prominent and on either side it forms a means of support for the maxilla, to which it is attached. Its median portion supports various muscles, including those of the salivary pump and the labium. Passing up from the invagination, the posterior arms nearly surround the occipital foramen and join with the corresponding The connection is not so very prominent, and in all the forms examined, the junction was confined to a mere tendon. The dorsal arms, which are to be found beneath the antennæ, are quite prominent in the dorsal region of the head. The size of the dorsal arms varies somewhat in different species: in Draculecephala mollipes they are short and branched, while in Deltocephalus inimicus and Agallia sanguinolenta they are much longer. Between the invaginations of the dorsal and anterior arms, small tendonous plates are to be seen.

In the Jassoid head, the correlation between the tentorial structures and the appendages of the head is to be found and forms the basis for their interpretation.

Epipharynx—(Pl. XX, Figs. 14, 1, 2, 3, 15). The anterior end of the dorsal plate of the pharynx is differentiated into the epipharynx (ep.), which is seen externally as the small peg covering the base of the labium. This structure is closely related to the labrum and in fact, the separation of the two is a difficult matter. The pharynx (ph.) continues along the under side of the labrum and passes out as the epipharynx. The epipharynx is fused with the anterior edge of the labrum, but a trace of the former condition can be seen.

Hypopharynx—(Pl. XX, Figs. 8, 15). The anterior end of the ventral plate of the pharynx is the hypopharynx (hyp.) and is a prominent structure in the mouth-cone of the Jassid.

It is broadly spoon-shaped, with the anterior end slightly pointed. Beneath it, the salivary pumping apparatus (s. p.) occurs and is in close relationship with its lower surface. The hypopharynx is heavily chitinized. The opening of the pharynx into the suction canal of the labium is surrounded by hypodermis, which encloses the setæ.

Pharynx—(Pl. XX, Fig. 5). The chitinous pharynx, as in all Hemiptera, constitutes a pumping apparatus, by means of which plant juices and other food are withdrawn into the digestive canal. The pharynx is a comparatively short, simple, chitinous tube, supported by strong muscles. The dorsal plate is somewhat elastic, and is capable of being withdrawn from the ventral plate by the pharyngeal muscles (ph. m.), which attach to the head-capsule along the inner surface of the clypeus. Apparently the pharynx is about the most powerful organ of the head, as the preponderance of pharyngeal muscles is obvious. The pharynx passes back over the body of the tentorium into the membranous esophagus.

The Salivary Pumping Apparatus—(Pl. XX, Figs. 8, 15). This characteristic Hemipterous structure is to be found beneath the base of the hypopharynx. It consists essentially of a broad spoon-shaped structure, into which fits the plunger (p.); the latter is slightly smaller than the spoon or barrel (b. a.) and functions as the driver of the apparatus. The plunger is developed backward into a thick rod (r.), to which attaches at its end the protractor muscles (p. p. s.): The united salivary ducts (s. d.) open into the base of the barrel, and by the forward motion of the plunger the saliva is forced forward through a small canal (s. d. h.), which leads to the anterior edge of the hypopharynx. At their entrance to the barrel the salivary ducts are chitinized. The protractor muscles (p. p. s.) of the plunger rod attach to the body of the tentorium, while the retractor muscles (p. r. s.) attach on the under side of the rod at one end and to the maxillary plates at the other. plunger is thus capable of a forward and backward motion, by which means the saliva is pumped into the canal.

Salivary Glands—(Pl. XXI, Fig. 22). In the Jassoid head four separate salivary ducts are to be found; two pairs unite behind the salivary pump into one common duct, but farther back they separate into two pairs, which continue along the

floor of the mouth into the thorax. Both pairs of ducts end in glands, which are long structures, normally located in the abdomen. Each gland is whitish, and rather narrow. The salivary glands secrets the saliva which is carried forward into the pump and thence into the sucking tube.

THE THORAX.

The structure of the thorax was not studied in any degree of detail, and only reference to the more striking features will here be made. As in a generalised insect the thorax is composed of three segments, in order, the pro-, meso- and meta-thorax. The prothorax has undergone considerable modification and the traces of the sclerites seem to have been entirely lost. The dorsum or tergum is the large piece on the dorsal surface; it overlaps the mesonotum. Laterally the prothorax shows little differentiation into episternum and epimeron. sternal region is reduced to a small piece, which bears the small chitinous apophyses. At the sides the first pair of legs are The mesothorax is large and well developed, comprising a number of sclerites, which are separated with difficulty. Laterally it bears the tegmina and beneath the second pair of legs. The episternum and epimeron are easily recognised in this segment. A noticeable feature of the mesothorax is the great development of the musculature; the large wing muscles are very prominent. The apophyses are strongly developed. The metathorax is striking because of the great development in size of the hind coxæ; the latter are supported by very strong muscles. The sternal surface of the metathorax is almost completely overshadowed by the large coxæ.

THE ABDOMEN.

The Jassid abdomen is composed of at least eight segments, of which the first seven bear spiracles. Each abdominal segment is composed of a dorsal tergite and a ventral sternite, the two being connected by pleural membranes.

The modification of the posterior end of the abdomen for reproductive purposes has brought about a reduction in the number of apparent segments and many of these are recognised with difficulty. In the female the last abdominal segment is known as the pygofer (pyg.); through its dorsal region the anal tube (an. t.) opens to the exterior. The ventral portion almost completely encloses the ovipositor (ovp.) which is generally a long, rather slender, heavily chitinized organ, hinged to the caudal end of the preceding segment. In its simplest form the ovipositor consists of two strong ventral valves (v. v.), which on being spread apart, expose the two inner valves (i. v.). The latter constitute the main part of the ovipositor and are small, sharp, slender pieces, which fit close together and so form a channel through which the ova may be extruded. The tip of the inner valves are barbed or sickle-shaped. The vagina opens into the anterior end of the channel. Beneath the inner valves are two large pieces which fit close together and compose the dorsal valves of the ovipositor. (d. v.).

The posterior region of the female abdomen as well as that of the male, shows a great deal of variation in the modification and advantage is taken of this for taxonomic purposes. The ventral abdominal segment just anterior to the ovipositor frequently shows a great deal of variation in shape. In the majority of the forms examined, however, the essential details of the female genital armature do not differ strikingly from the above.

In the male the last dorsal segment is known as the pygofer, and as in the female, the anal tube opens on it. Ventrally, the posterior of the abdomen is modified into a series of plates which afford protection for the penis. The uppermost of these plates is connected with the preceding abdominal segment and constitutes the valve (g. v.); it is generally triangular in shape, and extends about half way over the plates beneath. The latter are the genital plates (g. pl.) and are two long, somewhat rectangular pieces, which cover over the penis and penis guides. genital plates vary considerably in size and shape, and advantage is taken of this character in the differentiation of species. copulation the ventral valve bends down so as to allow the genital plates to spread apart, and the penis, with its accompanying guides is brought into action. The penis (pen.) is an elongate slender structure, which is strongly chitinized. It is hinged at the base of the pygofer, and is capable of considerable motion in a ventral direction.

Internal Anatomy.

The Digestive System. (Pl. XXI, Fig. 22; Pl. XXII, Fig. 34).

The chitinous pharynx passes back into the membranous esophagus (e. s.), which is a relatively short simple tube. In the metathorax, where the esophagus enters the midintestine, a constriction is noticed and a large food reservoir is developed. The latter structure is comparable to the food-reservoir of certain Fulgoridæ and Cercopidæ. The food-reservoir is a bilobed or double U-shaped structure, which opens into the intestinal coils; its function is probably that of a storage reser-From the reservoir the alimentary canal continues as a long, convoluted tube (m. i.) of small diameter; the length of midintestine is about two and a half times that of the body. It ends in the short rectum without differentiating into either colon or ileum. The rectum continues to the anus, which is located on the dorsal surface of the last abdominal segment.

Opening into the midintestine (m. i.) are the long Malpighian tubules (mp. t.); these are difficult to detect in the Jassid, but at length may be seen among the coils of the intestine. are about the same length as the body and are of small diameter. There are only two pairs so far as was observed.

The food reservoir (f. res.), or crop, in Deltocephalus inimicus occurs entirely within the abdomen and does not enter the thorax. This seems to be the general condition, although in some forms it is to be found penetrating the thoracic region In some forms it occupies a great part of the anterior region of the abdominal cavity.

The digestive system may be readily dissected out of preserved specimens, although some little difficulty is experienced in keeping the coils of the intestine intact. It was noticed that in specimens which had been cleared in carbolturpentine, there was a tendency on the part of the food reservoir to swell up and telescope through the dorsal wall of the abdomen.

The opening of the alimentary canal to the exterior, i. e., at the anus, is on the last abdominal segment and in the majority of individuals examined it was noticed that the anal orifice was beset with hairs and strong spines. The anal tube is a small structure, which is heavily chitinized. It conveys the feces to the exterior. In most individuals the anal tube is two-jointed. the basal joint being the longest.

Tracheal System. (Pl. XXII, Fig. 33).

The Tracheal System consists of the main trunk (m. t.) system connected with the spiracles (spi.). There are in most forms nine pairs of spiracles; two thoracic, and seven abdominal (I-VII), although in some species the abdominal number may be only six. The thoracic spiracles (t. spi.) are at first rather difficult to detect, but may be found below the wings on the episterna as two small, unprotected holes. On the abdomen the spiracles (ab. spi.) appear as small, elongate, narrow holes, located on the anterior halves of the segments, near the pleural membranes. Each spiracle connects with the main trunk system by a short tube.

The main trunk system (m. t.) comprises the two lateral tubes, which run down the sides of the body and anastomose. The two longitudinal trunks are connected by transverse trachea in the meso- and meta-thorax. The anastomosis in the thoracic trachea is best shown by reference to the Figure (Pl. XXII, Fig. 33). Two large transverse tubes connect the longitudinal trunks in the mesothorax, while in the metathorax the two transverse tubes do not open directly into the main trunks, but connect with the spiracle tube. A small tracheal tube runs between the two thoracic spiracles and gives off the branches which run to the wings. In the nymphs these tubes are very evident, although in the adult they are not so prominent. At the caudal end of the body the two trunks are in close relationship by means of their smaller branches, but no distinct tracheal connection is seen.

From the main longitudinal trunks arise the three systems of branches, the dorsal, visceral and ventral, which ramify through each segment, and portion of the body. Two strong branches are seen in the head, and supply the antennæ, mouthparts and the viscera of the head with trachea. Branches of the dorsal system can frequently be found in the dorsal muscles of the thorax, and in the peripheral region of the dorsum. The visceral system of branches supports the digestive apparatus and the reproductive organs, while the ventral system is closely connected with the nervous system and the ventral musculature.

Reproductive System. (Pl. XXII, Figs. 35, 36).

Female Organs—The paired ovaries (ov.), are normally located in the third segment of the abdomen, but frequently they occupy the greater portion of the abdominal cavity. Each ovary consists of six ovarian tubes (o. t.) or tubules, although this number is subject to some variation. Holmgren, who has studied the female organs in some detail gives the number of ovarian tubules in a Thamnotettix as twelve or two pairs of six each. Each ovarian tube (o. t.) is attached at a common point to the suspensor (sus), which in turn is supported by a tracheal branch in the dorsal region of the body. The length of the ovarian tubule varies greatly, but it frequently exceeds the abdomen; in many cases, as just before oviposition, the abdomen will be greatly distended by the numbers of eggs in the ovaries and on first examination it would seem that the whole abdominal cavity was filled with ova. In some cases the ovarian tubes may be pressed into the thoracic region, previous to oviposition. All the ovarian tubes unite caudally in a common oviduct (Ovd.) which is short and broad, although in some forms e. g. Cicadula, it may be long. The oviduct is frequently constricted before the opening of the receptaculum seminorum (rec. sem.) which is a semi-circular structure, lying to the side of the oviduct. The size of the receptaculum seminorum varies and may be large or small. Beyond the receptaculum seminorum the oviduct receives two pairs of accessory glands (ag1, ag2), which are very long and extend back into the abdomen. The vagina which is the terminal portion of the oviduct, opens into the ovipositor, through which the ova are extruded.

Male Organs—(Pl. XXII, Fig. 35). In the male each testis is composed of a varying number (usually six) follicles (f.). The testes which are located at the posterior end of the abdomen are yellowish in color, and are frequently enclosed in a whitish membrane. Each follicle is about three times as long as broad, and opens into the vas deferens (v. d.) by a separate duct. The vasa deferentia are about four times as long as broad and unite to form the ejaculatory duct (e. d.), which is merely a dilation before the penis or copulatory organ. Small accessory glands (a. g.) enter the vasa deferentia just before the ejaculatory duct.

Musculature System.

The most noteworthy features of the musculature system are the powerful muscles of the posterior region of the abdomen. The pygofer bears the muscles which support and work the strong ovipositor. The longitudinal muscles of the abdomen comprise the small ventral muscles of the body wall and the dorsal muscles. They are segmentally arranged. The lateral muscles of the abdomen are poorly developed and are confined to small strands which are situated along the sides of the body.

Nervous System.

The central nervous system (Pl. XXII, Fig. 32) consists of the brain (supraesophageal ganglion), the subesophageal ganglion, and the thoracic ganglion, with their attendant nerves and commissures.

The Brain (Br.) is relatively large and occupies the greater part of the dorsal region of the head. It emits two pairs of large nerves, which innervate the eyes (On.) and antennæ (An.) respectively. The brain is connected with the subesophageal ganglion by the circumesophageal commissures, which are rather small and not easily recognised. From the subesophageal ganglion small nerves pass to the maxillæ and labium.

The Thoracic Ganglia (T. G.) are fused into one large ganglion, located on the floor of the mesothorax. Small commissures connect the thoracic ganglion with the subesophageal, although the two appear to be continuous. Numerous nerves originate from the thoracic ganglion and pass to the legs, the dorsal muscles and the digestive apparatus.

There are no abdominal ganglia, but two strong nerves are seen passing back from the thoracic ganglion to the caudal end of the body. These two main abdominal nerves (Abd. N.) arise close to one another and are probably the result of the separation of the abdominal ganglia and commissures. They become widely separated as they pass down the body on either side of the median line. Each abdominal segment is supplied with nerves from these two main commissures and in addition the reproductive organs, the digestive apparatus and the excretory system are innervated.

While the Jassid nervous system does not differ very much from that of a generalized insect, it shows a specialization in the absence of the abdominal ganglia. However, this is not an unusual state for the Homoptera, as Kershaw has shown that in the Fulgorid Pyrops candelaria, the structure and morphology of the nervous system is essentially the same. The abdominal ganglia have probably migrated forward and fused with the thoracic ganglia, leaving the abdominal commissures in their former position.

Circulatory System.

The Circulatory System so far as observed, consists of a long tube, or dorsal vessel, which runs the full length of the body, from the brain to the last abdominal segment. In general it is an undifferentiated tube, in which the blood circulates. The pulsation of the dorsal vessel may be observed by placing a living specimen under the binocular microscope, and watching the rhythmic movements of the abdomen. The vessel reaches the brain, which it supplies with blood and then apparently divides into two branches which pass into the body cavity.

Conclusions.

The studies enumerated above have led me to the conclusion that the Jassoidea can be homologised with the other Homopterous families. The head differs very little from the fundamental and generalised plan of the Cicada, and while the Jassid does not show the development of the prominent sulci, the structure of the mouthparts and head is very similar. The mandibular setæ represent the mandibles and the maxillary setæ, together with the maxillary plate constitute the maxillæ. While for systematic purposes we have been applying general terms to the regions of the head, it would seem impossible to change the nomenclature, so as to correspond with the morphological details. The labrum and clypeus are scarcely distinguishable from one another and the epipharynx is closely related to the labrum. The tentorium is present and the invaginations occur as in all insects. There is a well-developed salivary pumping apparatus. The epicranium is subject to some modification in size. There is a well developed nervous system, which is almost entirely cephalo-thoracic. The digestive system, in the development of a food-reservoir agrees with the other Auchenorrhynchous Homoptera. In general the plan and morphology of the internal organs follows that of a generalised Hemipteron, and the various modifications which occur in structure are just as likely to be specific as well as generic.

LITERATURE CONSULTED.

1833: **Dufour.** Recherches anatomiques et physiologiques sur les Hemipteres.

1860. Flor. Rhynchoten Livlands Vol. 1

Fieber. Les Cicadines d'Europe. Introduction, pp. 8-31. 1875.

Gise. Die Mundtheile der Rhynchoten. Archiv. f. Naturg. Vol. XLIV. 1883. Beitrage zur Kenn. des Rhynchotenrussels. Archiv. f. Naturg. 1885. Wedde. (2) LI.

Miall and Denny. The Structure and Life History of the Cockroach. 1886.

1896. Hyatt. Cicada Septendecim, its mouthparts and terminal armour. Am. Mo. Mic. Journ. Vol. XV. id. Vol. XVII. Marlatt. The Hemipterous Mouth. Ent. Soc. Wash. Vol. III. pp. 241-250. 1896.

Melichar. Cicadinen von Mittel-Europa. 1896.

1896. The Phylogeny of Hemiptera. Ent. Soc. Wash. Vol. III. pp. Osborn. 185-190.

Melichar. Cicadinen von Mittel-Europa. Packard. Text Book of Entomology. 1896.

1898.

1898-1899. Holmgnen. Beitrage zur Kenntnis der Weiblichen Geschlechtorgane der Cicadanen. Zool. Jahrb. Abt. fur Syst. XII.
1902. Comstock and Kochi. The Skeleton of the Head of Insects. Am. Nat.

Vol. XXXVI

The Structure of the Hemipterous Mouth. Science. Vol. XIX. 1902. Smith. No. 478.

1904. Haller. Lehrbuch der Vergleichenden Anatomie.

Bugnion. L'Appareil Salivaire des Hemipteres. Arch. D'Anat. Mic. Vol. X. 1908. pp. 227-268

1909

Berlese. Gli Insetti. Vol. I.
Gadd. Zur Anatomie der Cicaden und Tettigonia viridis. Revue Russe d'Entom. X. No. 3. pp. 205-213.
Faure-Fremiet. Contribution a L'Etude des Glandes Labiales des Hydrocorises. Ann. des Sci. Nat. Zool. N. S. 9. Vol. XII. 1910.

1910.

1910. Kershaw. A Memoir on the Anatomy and Life History of the Homopterous Insect, Pyrops candelaria. Zool. Jahrb. Abth. f. Anat. XXIX. pp. 105-124. Pantel and Licent in Bull. Soc. Entom. de France. pp. 36-39. 1910.

Bugnion and Popoff. Les Pieces Buccales des Hemipteres (Prem. Partie). 1911. Arch. Zool. Exper. et General. 5e Serie, Vol. VII. pp. 643-674.

1911.

Licent. Signification de la dilation proventriculaire chez les Homopteres superieurs. Bull. Soc. Entom. France. pp. 48-52, 284-296.

Uber Respiration, Tracheensystem und Schaumproduktion der 1911. Sulc. Schaumcikadenlarven. (Aphrophorinae-Homoptera). Zeits. f. Wissensch. Zool. Band. 99. pp. 147–188.

1911.

1911.

Muir and Kershaw. On the Homologies and Mechanism of the Mouth-Parts of Hemiptera. Psyche. Vol. XVIII. No. 1, pp. 1-12. pl. 1-5.

Muir and Kershaw. On the later Embryological Stages of Pristhesancus papuensis. Psyche. Vol. XVIII. No. 2, pp. 75-79. Pl. 9-10.

Muir and Kershaw. The Development of the Mouthparts in the Homoptera 1912. with observations on the Embryo of Siphanta. Psyche. Vol. XIX. No. 3. pp. 77-89.

Kershaw. Anatomical Notes on a Membracid. Ann. Soc. Entom. Belgique. 1913.

T. 57. pp. 191-201.
Kershaw. The Alimentary Canal of Flata and Other Homoptera. Psyche, Vol. XX. No. 6. pp. 175-187. Pl. 5-6.
Tower. The External Anatomy of the Squash Bug, Anasa tristis DeG. Ann. Ent. Soc. Amer. Vol. VI. pp. 427-437. Pl. LV-LVIII.
Kershaw. The Alimentary Canal of a Cercopid. Psyche, Vol. XXI. No. 2. pp. 457-79. Pl. 4 1913. 1913.

1914.

Kershaw. The Alpp. 65-72. Pl. 4. 1914.

1915.

Tower. The Mechanism of the Mouthparts of the Squash Bug, Anasa tristis DeG. Psyche, Vol. XXI. No. 3. pp. 99-108. Pl. 1-11.

Peterson. Morphological Studies of the Head and Mouthparts of the Thysanoptera. Ann. Ent. Soc. Amer. Vol. VIII. No. 1. pp. 22-57. Pl. 1-7.

Martin. The Thoracic and Cervical Sclerites of Insects. Ann. Ent. Soc.

Amer. Vol. IX. No. 1.

1916.

ABBREVIATIONS.

A.—Antenna.

Ab. Spi.—Abdominal Spiracle.

Ag.—Accessory gland. An.—Anus.

An. t.—Anal tube. A. N.—Antennal Nerve.

a. m. s.-Articulation of the mandibular

seta.

Abd. n.—Abdominal nerve.

Br.—Brain.

BA.—Barrel of salivary pump.

ba.—Barbs of mandibular seta. C. C.—Circumesophageal commissure. C.—Central muscles of labium.

c. m.—Circular muscles of labium. Clyp.—Clypeus. D. V.—Dorsal valve of ovipositor.

E.—Eye.

E. d.—Ejaculatory duct.

Es.—Esophagus.

E. p.—Entrance to penis.

ep.—Epipharnyx.
G. Pl.—Genital plate of male.
G. V.—Genital valve of male.

F.—Follicle.

Fr.—Front.

F. Res.—Food Reservoir. Hyph.—Hypopharynx.

i. a.—Invagination of the anterior arms of tentorium.

i. d.-Invagination of dorsal arms of tentorium.

i. p.—Invagination of the posterior arms of the tentorium.

i. v.—Inner valve of ovipositor. L.—Lateral muscles of labium.

lab.-Labium.

labr.—Labrum

lab. ms.—Labial muscles.

m. a.-Attachment of mandibles to head-capsule.

mx. a.—Attachment of maxilla to headcapsule.

md.—Mandible.

mx.—Maxilla. mi.—Midintestine.

m. p.—Protractor muscles of mandibular seta.

mx. p.—Protractor muscles of maxillary seta.

m. t.-Mandibular tendon.

mx. t.-Maxillary tendon.

Mx. pl.—Maxillary plate.

M. T.—Main Trunk of tracheal system. Mp. T.—Malpighian Tubules.

m. r.—Retractor muscles of mandibular

mx. r.-Retractor muscles of maxillary seta.

O.—Ocellus.

O. N.—Ocular nerve.
O. T.—Ovarian tubes.

Ov.—Ovary

Ovd.—Oviduct.

Ovp.—Ovipositor.
O. F.—Occipital foramen.

Pen.—Penis.

P.—Plunger of salivary pump.

Ph.—Pharynx.
Ph. m.—Pharyngeal muscles.
Pl. c.—Plates of Clypeus.

Pyg.—Pygofer.
pps.—Protractor muscles of salivary pump.

prs.-Retractor muscles of salivary pump.

R.—Rod of plunger.
Rec Sem.—Receptaculum Seminorum.

Rec—Rectum.

S.—Seta.

sg.—Salivary gland. sd.—Salivary duct.

Subg.—Subesophageal ganglion.

s. p.—Salivary pump.
sd. h.—Salivary duct to Hypopharynx.

Sd. n.—Salivary duct to H
Sus.—Suspensor.
T.—Tendon.
T. Spi.—Thoracic spiracle.
Tes.—Testis.
Tg.—Thoracic ganglion.

ta.—Arms of tentorium. tb.—Body of tentorium. ts.—Tentorial support.

tr.—Trachea. V.—Vertex.

VV.—Ventral valve of ovipositor.

Vag.—Vagina. V. D.—Vas Deferens.

EXPLANATION OF PLATES.

PLATE XX.

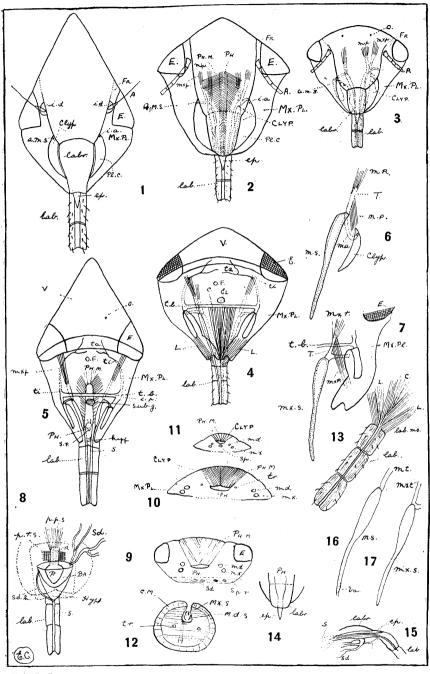
- Ventral view of head of Draeculacephala mollipes. Fig. 1.
- Head of Deltocephalus inimicus. Ventral view. Head of Agallia sanguinolenta. Ventral view. Fig.
- Fig. 3.
- Fig. Head of Deltocephalus inimicus. Caudal aspect. 4. Fig. 5. Head of Draeculacephala mollipes. Caudal aspect.
- Fig. Mandible of Deltocephalus inimicus.
- $\frac{6}{7}$. Fig. Maxilla of Deltocephalus inimicus.
- Fig. Salivary pumping apparatus of Deltocephalus inimicus.
- Cross section through head and eyes of Deltocephalus inimicus. Cross section through pharnyx of Deltocephalus inimicus. Fig. 9. Fig. 10.
- Fig. 11. Cross section through anterior of clypeus of Deltocephalus inimicus.
- Cross section through labium of Draeculacephala mollipes.
- Fig. 12. Fig. 13. Fig. 14. View of labium of Draeculacephala mollipes.
- Labrum and epipharynx of Draeculacephala mollipes.
- Side view of salivary pumping apparatus of Deltocephalus inimicus. Mandibular seta of Deltocephalus inimicus. Fig. 15.
- Fig. 16.
- Maxillary seta of Deltocephalus inimicus. Fig. 17.

PLATE XXI.

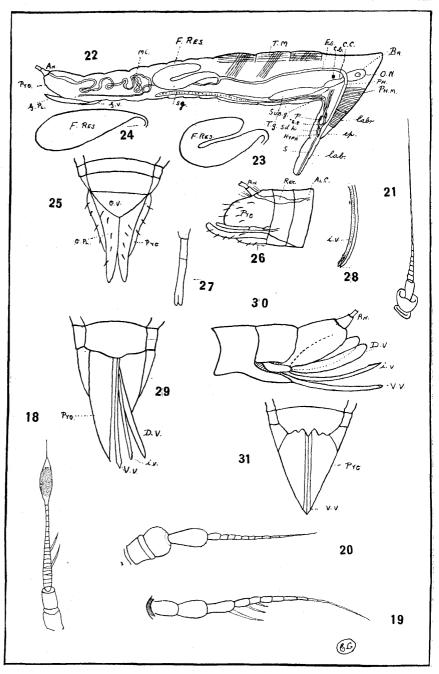
- Fig. 18. Antenna of male Idiocerus.
- Antenna of Deltocephalus inimicus.
- Antenna of Cephalelus infumatus. Antenna of Gypona sp.
- Fig. 19. Fig. 20. Fig. 21. Fig. 22. Longitudinal median section through Draeculacephala mollipes (semidiagrammatic).
- View of food reservoir.
- View of food reservoir.
- Ventral view of genitalia of Phlepsius irroratus. (male.)
- Side view of male genitalia of Phlepsius irroratus.
- Penis of Deltocephalus inimicus.
- Side view of inner valves of ovipositor of Deltocephalus inimicus.
- Fig. 23. Fig. 24. Fig. 25. Fig. 26. Fig. 27. Fig. 28. Fig. 29. Ventral view of female genitalia of Draeculacephala mollipes. (Valves of ovipositor dissected free).
- Side view of ovipositor and female genitalia of Deltocephalus inimicus. Fig. 30.
- Ventral view of female genitalia of Phlepsius irroratus. Fig. 31.

PLATE XXII.

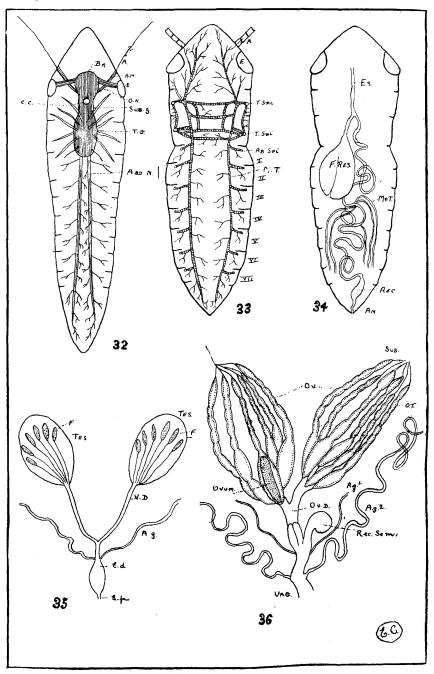
- General dissection of Central Nervous System of Draeculacephala Fig. 32. mollipes (semi-diagrammatic).
- General dissection of the tracheal system of Deltocephalus inimicus. Fig. 33. (Semi-diagrammatic.)
- Fig. 34. View of digestive system of Athysanus exitiosus.
- Fig. 35. General dissection of the male reproductive organs.
- Fig. 36. General dissection of the female reproductive organs.



Eric S. Cogan.



Eric S. Cogan.



Eric S. Cogan.