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The  
Morphology and Phylogeny  
of  
AUCHENORHYNCHOUS  
HOMOPTERA  
(Insecta)

By  
SOL KRAMER

NAT.  
HIST.

THE UNIVERSITY OF ILLINOIS PRESS  
URBANA, 1950

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THE MORPHOLOGY AND PHYLOGENY OF  
AUCHENORHYNCHOUS HOMOPTERA

Illinois Biological Monographs, Vol. XX, No. 4  
Published for the Graduate College, University of Illinois

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The  
Morphology and Phylogeny  
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AUCHENORHYNCHOUS  
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## ACKNOWLEDGMENTS

The writer wishes to acknowledge his gratitude and appreciation to Dr. William P. Hayes, under whose direction this study was undertaken. He has shown an enthusiastic interest in the progress of this study from its inception and contributed a critical and valuable reading of the original manuscript. Further thanks are extended to Dr. Hayes for his help in obtaining financial aid and other assistance which enabled the writer to devote a maximum of time to studies and research during two years at the University of Illinois.

Appreciation is also expressed to Dr. H. H. Ross of the Illinois State Natural History Survey, to Dr. Charles D. Michener of the American Museum of Natural History, to Dr. J. W. Evans of the British Museum and Louise M. Russell of the U.S.D.A. Bureau of Entomology and Plant Quarantine for providing specimens used in this study; to Dr. P. W. Oman of the U. S. National Museum for specimens and identifications; and to Dr. Kathleen C. Doering of the University of Kansas for determinations.

Assistance in interpreting the homologies of the mouthparts of several Homoptera was provided by R. E. Snodgrass during the writer's studies in his laboratory at the U. S. National Museum during the summer of 1947, and this assistance is gratefully acknowledged. Sincere thanks are also expressed to Miss Ruth Keller for typing the major portion of the original manuscript.

An additional note of thanks is due to Dr. Evans for a critical reading of the manuscript, much helpful discussion and other kindnesses, during the writer's stay in England in 1948-49, while preparing this study for publication. Considerable additional information was thus made available.



## CONTENTS

INTRODUCTION .....	1
NOTES ON CLASSIFICATION.....	3
MATERIALS AND METHODS.....	6
THE SCLERITES, APPENDAGES, AND MUSCLES OF THE HEAD OF	
AUCHENORHYNCHA .....	8
<i>Scolops pungens</i> Germar (Fulgoridae).....	8
<i>Tibicina septendecim</i> (Linn.) (Cicadidae).....	11
<i>Lepyronia quadrangularis</i> (Say) (Cercopidae).....	13
<i>Aulacizes irrorata</i> (Fabr.) (Cicadellidae).....	14
<i>Ceresa bubalus</i> (Fabr.) (Membracidae).....	16
THE THORACIC SCLERITES, WINGS, AND LEGS OF AUCHENORHYNCHA.....	18
<i>Scolops pungens</i> .....	18
<i>Tibicina septendecim</i> .....	21
<i>Lepyronia quadrangularis</i> .....	23
<i>Aulacizes irrorata</i> .....	25
<i>Ceresa bubalus</i> .....	27
THE THORACIC MUSCULATURE OF <i>Ceresa bubalus</i> .....	31
ABDOMINAL SEGMENTS OF AUCHENORHYNCHA.....	37
<i>Scolops pungens</i> .....	37
<i>Tibicina septendecim</i> .....	40
<i>Lepyronia quadrangularis</i> .....	43
<i>Aulacizes irrorata</i> .....	45
<i>Ceresa bubalus</i> .....	47
THE ABDOMINAL MUSCULATURE OF <i>Ceresa bubalus</i> .....	51
THE PHYLOGENY OF AUCHENORHYNCHA.....	54
Phylogenetic Considerations of Previous Authors.....	54
Discussion .....	62
BIBLIOGRAPHY .....	71
LIST OF ABBREVIATIONS.....	76
PLATES WITH EXPLANATIONS.....	79





## INTRODUCTION

Comparative studies of insect structure and resulting classifications based on phylogeny have been few in comparison to the amount of material available for study. Handlirsch (1906-08) was able to establish the minimum geologic age of many groups of insects through paleontological studies, and he considerably modified the prevalent conceptions of his day concerning the ordinal relationships of insects. Although Tillyard (1930), Carpenter (1930), and others have attacked this problem, fossil insects are meager in comparison to other animal fossils and many gaps still exist in this line of evidence. Consequently, the insect taxonomist must depend on morphological, physiological, ecological, and zoogeographical sources for his evidence of insect relationship. It should be added that the vast numbers of insect species and groups, ordinarily a handicap, is of decided advantage in phylogenetic studies. Insects have retained in varying degree many primitive characters and their large numbers increase the possibility that there may be derived from existing forms, composite pictures of ancestral types which will clarify relationships.

Just such an attack on the problem of insect phylogeny, through extensive comparative studies of present-day forms, has been made by Crampton (1924). During the past forty years he has undertaken studies of relationship throughout the Insecta, based upon diverse characters, such as the head capsule, thoracic sclerites, wing articulation, abdominal segments and appendages, and genitalia, as well as on the characters of wing venation and mouthparts previously relied upon. His studies, which provided important new concepts of insect phylogeny, have done much to lay the groundwork for future investigation. It should be noted, however, that Crampton's studies were devoted primarily to the broader relationships of insects, and his resulting classification concerns the relationships of the higher categories such as subclasses, superorders, and orders. The problems of phylogeny within the orders of insects, concerning families and lower groupings, remain virtually unsolved.

This comparative study of the Auchenorhyncha is an endeavour to examine one such problem of relationship. One species from each of five families of Auchenorhyncha has been selected for detailed study. Some of the material presented here has been dealt with by others, but much of it is new. Relationships of structure have been indicated by many original drawings, and these studies of the structure of representative Auchenor-

rhyncha have for the first time been incorporated into and compared in a single work. The writer has further included a detailed account of the musculature of the membracid representative, *Ceresa bubalus*.

This investigation represents only a preliminary effort toward the understanding of relationships within the Auchenorhyncha. Through it, the writer has been impressed with the little that is known concerning the functional significance of particular structural modifications. Snodgrass (1935), Weber (1933), and others have done a good deal to emphasize the importance of ascertaining the functional value of anatomical facts, and the value, wherever possible, of supplying reasons for existing structures. Such comparative functional studies should be integrated with morphological studies within the lower categories of insects, if we are to approach some understanding of what has been taking place in the evolution of insects. In this connection it would not be amiss to point out that comparative studies of behavior patterns in some groups of arthropods, such as bees, wasps, spiders, etc., have provided valuable characteristics for the systematist. Such work is based on the assumption, as Lorenz (1939) has pointed out, that "the concept of homology, useful in morphology, is just as applicable to inherited behavior-patterns as to bodily characteristics." Sound classifications should be based on the integration and evaluation of all ascertainable phylogenetic evidence.

The large numbers of insect species have in some measure precluded these studies by systematists. It is nevertheless true that the systematist who specializes in a particular group of insects is in the best position to answer such questions, for he is most intimately acquainted with the many species represented and their diverse modifications of structure and behavior. Future attempts to provide reasons for structure, even though our efforts be faulty, will lead the more quickly to an understanding of what has been taking place in the diverse auchenorhynchous groups of insects, and to a greater comprehension of the Homoptera in general. It is hoped that this study will stimulate questions among taxonomists in these insect groups, and will provide some morphological basis for their answers.

## NOTES ON CLASSIFICATION

In a work on the general classification of animals, Dumeril (1806) separated the Hemiptera into six families. Two of these families, the Collirostreres or Auchénorhynques,\* comprising the cicadas, membracids, cicadellids, fulgorids, and cercopids, and the Plantisuges or Phytadelges, comprising the aleyrodids, chermids, aphids, and coccids, represent in part the Homoptera as we know them.

Westwood (1840), adopting Latreille and Burmeister's view as to the division of Homoptera into three primary sections, named these sections on the basis of differences in the number of tarsal joints as follows:

1. Trimera. Tarsi 3-jointed: antennae minute, setigerous, wings areolate (*Cicada*, Linnaeus).
2. Dimera. Tarsi 2-jointed: antennae moderate, filiform, 5-10 jointed: wings subareolate (*Aphis*, Linn. and *Psylla*, Geoffr.).
3. Monomera. Tarsi 1-jointed: antennae 6-25 jointed: wings not areolate (*Coccus*, Linn.).

The Dimera contain the families Psyllidae, Aphidae, and Aleyrodidae; the Monomera contain the Coccidae; while the Trimera contain the Cicadidae, Fulgoridae, and Cercopidae.

Amyot and Serville (1843) in their work on the classification of Hemiptera separated the Homoptera as a suborder, and divided the latter into sections, Auchénorhynques and Sternorhynques. The former section contains the Trimera of Westwood, while the latter comprises both the Dimera and Monomera.

Buckton (1889) grouped the cicadas, membracids, fulgorids and jassids into a single family, Tettigiidae, which he separated from the Aphidae, Coccidae, etc. Following Latreille, who had divided the Cigalles or Cicadae into two groups separating the singing from the nonsinging forms, "les Chanteuses" and "les Muettes," Buckton separated the Tettigiidae into two subfamilies. The subfamily Stridulantia contained the tribes Tibicinae and Cicadinae, while the subfamily Silentia contained the tribes Membracinae, Fulgorinae, Cercopinae, and Jassinae. In this connection it is interesting to note a recent comment by Evans (personal communication, 1948) concerning a broadcast given by Ossiannilsson from Stockholm of the amplified songs of jassids and cercopids, which sounded like the songs of cicadas and frogs. He adds that Ossiannilsson

---

\*This name refers to the apparent origin of the beak or proboscis, from the "neck" or cervical region, as contrasted with the Sternorhyncha in which the proboscis seemingly arises from the prothoracic sternal region.

had previously published a paper (Opusc. entom., 1946; 82) in which he gives a preliminary note on sound-producing organs in the Homoptera. Evans (1946b) had not seen this paper when he called attention to a supposed tymbal in an aetalionid, *Darthula hardwickii* Gray.

Distant (1906) has pointed out that Westwood recognized only three families of Auchenorrhyncha: the Cicadidae, Fulgoridae, and Cercopidae. Stal divided this group into four families: Stridulantia, Cercopida, Jassida (including membracids), and Fulgorida, and in this view he was supported by Hansen. Although Distant treats the Membracidae as a separate, fifth family of the Auchenorrhyncha, he adds that both Stal and Hansen may possibly be right, on morphological grounds, in relegating the membracids to a subfamily of the Jassidae.

According to China (1927), the family Peloridiidae was erected for a primitive insect *Peloridium hammoniorum* taken on Navarin Island, Tierra del Fuego, described by Breddin in 1897, and assigned to the Heteroptera. In 1924 a new genus and species of this family, *Xenophyes cascus*, taken in New Zealand, was described by Bergroth. In the same year another new genus and species, *Hemiodoecus leai*, taken at Hobart, Tasmania, was described by China.

Myers and China (1929) concluded that the Peloridiidae were more closely allied with the Homoptera. This conclusion was primarily on the basis that the only character clearly separating the Heteroptera from the Homoptera was the presence of the gula, absent in the Homoptera and the Peloridiidae. They suggested a new series, Coleorrhyncha, for the Peloridiidae, to be placed at the base of the Homoptera. The classification of Hemiptera, based on key characters, was modified by them as follows:

Gula present .....	HETEROPTERA
Gula absent .....	HOMOPTERA
Rostrum arising from base of head	
Base of rostrum sheathed by propleural structures.....	COLEORHYNCHA
Base of rostrum entirely free from prothorax.....	AUCHENORHYNCHA
Rostrum arising between or caudad of fore coxae.....	STERNORHYNCHA

More recently Evans (1946a), as a result of extensive taxonomic and morphological studies of the leaf-hoppers and related Auchenorrhyncha, proposed a separation of this group into three divisions, as follows:

1. Tegula almost always present; middle coxae elongate, articulated far apart, free and capable of lateral movement; hind coxae immobile; wing without a marginal vein..... Fulgoromorpha
- Tegula absent; middle coxae short, articulations near together; hind coxae mobile; wing with a marginal vein.....2
2. Head with a swollen postclypeus, the crown with a small triangular frons bearing a median ocellus.....Cicadomorpha

Head with a large but not necessarily swollen postclypeus, which may or may not be distinct from the frons; frons without a median ocellus. . . . . Jassidomorpha

He then subdivides the Jassidomorpha into two superfamilies as follows:

In the head, the anterior arms of the tentorium fused with the posterior arms; hind coxae short, conical, not transversely dilated; hind tibiae with one or a few spurs but lacking spines . . . . . Cercopoidea

In the head, the anterior arms of the tentorium not in contact with the posterior arms; hind coxae transverse, laterally dilated; hind tibiae armed with spines, some of which may be mounted on enlarged bases. . . . . Jassoidea  
(includes the Membracidae)

In his most recent study Evans (1948) reiterated his concept that the membracids belong to the jassoid complex, and divided the membracids into three families, the Nicomiidae, Lamproteridae, and Membracidae.

## MATERIALS AND METHODS

The procurement of properly preserved and adequate numbers of specimens constitutes a major problem for such a study. Proper preservation, essential for the study of insect musculature, is sometimes obtained by chance when live specimens are dropped into 70 per cent alcohol. But for the most part this method is inadequate. The musculature of some insects used in this study, first dropped into steaming water and then into 70 per cent alcohol, was fairly well preserved. By far the best method of preservation, on the basis of comparative tests with *Ceresa bubalus*, is to drop live specimens into steaming water and then transfer to a 5 per cent solution of chloral hydrate where the insects may be stored indefinitely. Steaming water, followed by Bouin's fluid for 24 hours, then storage in 70 per cent alcohol gives almost equally good results.

A variety of dissecting tools were made by grinding, on carborundum and oilstone, stainless steel, surgical needles into extremely fine points, probes, or scalpels and placing these into lightweight, dental broach holders. A pair of microdissecting scissors, the blunt ends of which were ground down almost to needlepoint, proved very useful.

Dissections were performed underneath 50 per cent alcohol in metal pillboxes,  $\frac{3}{4}$  inch high by 2 to 3 inches in diameter, bedded with paraffin wax. As many as a score of dissections were made for each figured drawing. The drawings were first made on cross-section paper, but later tracing paper, underneath which a cross-section guide had been placed, was used. An ocular micrometer proved to be an invaluable aid for this work.

For the dissection of the smaller insects in this study, an adaptation of a method described by Guyer (1947, p. 92) proved very helpful. Longitudinal, or cross-sections of small insects, or of parts of insects such as the head, thorax, etc. were imbedded in paraffin wax. In imbedding, a small area of paraffin is first melted with a hot needle or scalpel. The section of the insect which has been removed from 70 per cent alcohol, and blotted to remove excess liquid, but allowed to remain moist, is immersed in the liquid paraffin up to the upper surface of the insect section. The paraffin around the insect section is again melted so that it securely grips the section when it sets. The dissecting pan is then flooded with 50 per cent alcohol. Any paraffin which has run into the muscles or other internal parts may be readily picked away with a needle. Dissections of minute muscles and parts, which might have been extremely difficult, were greatly facilitated by the use of this technique.

Another method which was of value in muscle study was an eosin staining and oil of wintergreen clearing procedure which I have recently

described (Kramer, 1948). This technique enables one to view the position and relationship of muscles in the thorax and abdomen directly through the body wall of the insect. It was particularly useful when used to ascertain the position of muscles in such smaller structures as the labium, and segments of the leg of *Ceresa bubalus*.

## THE SCLERITES, APPENDAGES, AND MUSCLES OF THE HEAD OF AUCHENORHYNCHA

### *Scolops pungens* Germar (Fulgoridae)

Long considered as a single family Fulgoridae, the fulgorids have more recently been given superfamily rank (Fulgoroidea) and have been considered to represent as many as eighteen families. The modifications of the head in this group are of particular interest since the head has been interpreted by past writers to represent both specialized and generalized modifications in the Homoptera.

The head of *Scolops pungens* is shown in frontal view in figure 7. The median striated area is the postclypeus (pclp), beneath which is the anteclypeus (aclp). The small labrum (lm) is suspended from the anteclypeus, and the lorae (lor) lie laterad of the clypeal area. Above, the frontal region or frons (fr), prolonged dorsally into a cephalic process, is separated from the postclypeus by the epistomal suture (est). The frons contains three ridges or carinae medially and a pair laterally, the latter extend down through the clypeal region. The prominent compound eyes (e), lateral ocelli (oc, Fig. 6) and antennae (ant, Fig. 8) all lie laterad of the frontal region.

The elongate region, posterior to the lorum and anteclypeus is termed the maxillary plate (mxp, Fig. 8). The labium (lb) is suspended by a membrane from the posterior edge of the maxillary plate and the hypopharynx (not seen). Both the lorum and the maxillary plate are separated from the genal region above (ge) by a definite internal ridge which apparently represents the subgenal suture (sgs). The presence of the subgenal suture in this fulgorid, partly present or absent in other fulgorids, is particularly noteworthy. The line separating the lorum and anteclypeus from the maxillary plate has sometimes been referred to as the genal suture, but this is a misnomer since the maxillary plate is merely closely approximated to the margins of the lorum and anteclypeus and is in no way joined to them.

The mandibular stylet (mds), sometimes called mandibular seta, or mandibular bristle, is shown in figure 12. It consists of a comparatively broad basal portion and a narrow bristle-like terminal portion. The retractor muscle (rmds), originating on the vertex of the head capsule, is inserted on the base of the mandibular stylet by means of an elongate tendon. The base of the stylet gives rise to another arm, termed the lever



( $lvr_1$ ), which articulates with the lorum at the point where the subgenal suture meets the epistomal suture. On this lever is inserted the protractor muscle ( $pmds$ ) which originates on the ventral and anterior margins of the lorum.

The maxillary stylet ( $mxs$ , Fig. 15) is likewise broader at the base and narrows to a long terminal bristle. It possesses a long retractor muscle ( $rmxs$ ) originating on the vertex of the head and a protractor muscle ( $pmxs$ ) originating on the maxillary plate. A membrane ensheaths the protractor muscle and forms an enclosed lobe with the maxillary plate. The base of the stylet is enclosed in a pouch formed by this maxillary lobe, the hypopharyngeal wing plate ( $hwp$ ), and the posterior tentorial bridge ( $tb$ ), but the stylet is actually outside the head capsule. A sclerotized lever ( $lvr_2$ ) runs from the base of the stylet to an apodeme of the head capsule, apparently a part of the posterior tentorial bridge. The muscles and levers of both the maxillary and mandibular stylets are thus within the head capsule; whereas the stylets alone are in pouchlike chambers outside the head capsule. It should be noted that the mandibular and maxillary stylets of this fulgorid each possess single protractor and retractor muscles.

The labium (Fig. 17) appears to consist of four parts. A basal segment invaginates inwardly to form an apodemal process. Beyond this basal segment there are a pair of sclerites on the posterior wall of the labium and these are followed by two long segments. Anteriorly, the labium possesses a groove along its entire length in which the bristles of the mandibular and maxillary stylets lie. Apart from a narrow, median, sclerotized rod, this groove is membranous. Protractor muscles ( $plb$ ) and retractor muscles ( $rlb$ ) of the labium, originating on the margins of the hypopharyngeal wing plates, respectively, are inserted on the apex and the base of the apodemal process of the first segment. A median section of the labium (Fig. 14) reveals a pair of muscles ( $mlb_1$ ) going from the paired sclerites of the posterior wall to the median sclerotized process of the anterior groove, a second pair ( $mlb_2$ ) from the median sclerotized process of the groove to the posterior wall, another small pair ( $mlb_3$ ) from the lateral edge of the anterior groove to the posterior wall, and a fourth group of muscles ( $mlb_4$ ) running from the median sclerotized process to the posterior wall.

The hypopharynx is best seen in a median section of the head (Fig. 13). Laterally the hypopharynx sends a pair of chitinous plates, termed hypopharyngeal wing plates, dorsally where they meet the tentorial bridge ( $hwp$ , Fig. 9). Muscles ( $dsyr$ ) originating on the hypopharyngeal wing plates are inserted on an apodemal process of the salivary syringe ( $syr$ ) which is located in the hypopharynx. A pair of salivary ducts ( $sld$ ) from

the salivary glands unite to form a common median duct which empties into the salivary syringe. The saliva is discharged through the ventral tip of the hypopharynx into the salivary channel formed by the maxillary stylets which come together at this point.

The dorsal or anterior wall of the hypopharynx forms the posterior or ventral wall of the sucking pump (pmp). As Snodgrass has shown this is not the true mouth but a portion of the preoral cavity termed by him the cibarium. The anterior wall of the sucking pump is formed by the inner epipharyngeal wall of the clypeus. This anterior wall of the sucking pump gives off a series of tendons medially on which are inserted the large dilator muscles (dlclp) originating on the postclypeus.

Of considerable significance are the lateral arms of the hypopharynx (lh) which extend to the lorae (Figs. 9 and 10). These connecting sclerotized arms between the hypopharynx and lorae are very small in comparison to the broad connection existing in the other homopteran families to be considered.

The tentorial structure consists only of a posterior tentorial bridge (tb, Figs. 9 and 16) extending from the dorsal tips of the hypopharyngeal plates across the posterior opening of the head capsule. Unlike the cicadid, cercopid, cicadellid, or membracid, there is an apodemal connection between the head capsule and this tentorial bridge. In other Homoptera, as far as has been ascertained, the posterior bridge extends across the occipital foramen, but the original connections with the head capsule have been lost. In *Oliarus aridus* (Fig. 11) an actual invagination or tentorial pit (ptp) appears to exist on either side of the tentorial bridge between the hypopharyngeal wing plate and the maxillary plate.

The antenna (Fig. 7) consists of a small basal segment or scape (scp), followed by a large bulblike pedicel (pdc) and a threadlike, single segmented flagellum (fl). Three antennal muscles (mant), inserted on the scape, have a common origin on the tentorial bridge (Fig. 9).

It is interesting to note the various modifications of the postclypeus and the lorae found in the fulgorids. As indicated previously, Evans, Spooner, and others have considered the lorae to be lateral modifications of the postclypeus. Figures 2, 3, and 5 show some of these modifications. In these fulgorids the lorae, more or less, completely merges with the postclypeus. Of significance in homologizing this lorae area throughout the Homoptera is the fact that the protractor muscles of the mandible always originate on this region of the head however it may be developed, as shown in the lateral views of an undetermined species of *Acalonia* (Fig. 1) and *Ormenis pruinosa* (Fig. 4). This will be a more fully discussed in a later section on phylogeny. *Oliarus aridus* is shown (Fig. 6) to indicate the presence of a median ocellus. A median ocellus is

apparently present among the fulgorids only in the subfamily Cixiinae, and only in the Cicadidae of other Auchenorrhyncha.

*Tibicina septendecim* (Linn.)  
(Cicadidae)

Because of their large size, the head and mouthparts of the Cicadidae have been the subject of more studies than any of the other Homoptera, so that this group is fairly well known. Marlatt (1895), Snodgrass (1921, 1927), Myers (1928), Evans (1938, 1940), Butt (1943), and others have made studies of representatives of this family. A description of *Tibicina septendecim* together with additional drawings, however, is included here for comparative study and interpretation.

The most conspicuous feature of the head is the greatly enlarged postclypeus (pcp, Fig. 19). A strong internal ridge is present medially and it is demarked from the anteclypeus (acp) by a very definite suture. It is at once apparent that in this respect the head of this cicada has reached a far greater development than shown among the fulgorids. The dominance of the clypeal area in this and the remaining families of Auchenorrhyncha is in marked contrast to that found in the fulgorids where the clypeal area, although fairly well developed, occupies a considerably smaller portion of the total head area. The loreal areas (lor) extend dorsally almost as far as the postclypeus itself. Internally a strong apodemal ridge (clr, Fig. 25) is present between the lorum and postclypeus. The labrum (lm) fits over the basal portion of the median groove of the labium (lb).

On the dorsal surface of the head (Fig. 26) three ocelli (oc) are present. A median ridge runs from the back of the head to just behind the median ocellus and sends two, somewhat faintly divergent ridges anteriorly. The triangular region (fr) containing the median ocellus evidently represents the frontal area. The anterior dorsal dilator muscle of the pharynx (phym<sub>1</sub>, Fig. 18) originates on the anterior margin of this triangular frontal area.

The mandibular stylet (Fig. 28) possesses retractor muscles (rmds) inserted on an internal tendon given off by the elongate arm of the base, which go to the dorsal part of the head. Mandibular protractor muscles (pmds) originating on the lorum are inserted on the considerably enlarged lever and apodeme of the stylet. The lever (lvr<sub>1</sub>, Fig. 25) articulates with the dorsal-most portion of the lorum just below the point where the anterior tentorial arm (at) invaginates inwardly.

The maxillary stylet (Fig. 23) varies considerably from that found in the fulgorid. Instead of one retractor muscle there are now two (rmxs<sub>1</sub> and rmxs<sub>2</sub>), with separate insertions on the base of the stylet and sep-

arate origins on the dorsal wall of the head. In addition to the protractor muscle (pmxs) originating on the maxillary plate, the strongly sclerotized lever of the maxilla ( $lvr_2$ ) also bears a protractor muscle (pmxl) originating on the maxillary plate and a retractor muscle (rmxl) originating on the posterior tentorial bridge.

The labium (Fig. 21) consists of three segments: a basal segment, an expanded middle segment, and an elongate terminal segment. A pair of median protractor muscles (plb) inserted on the apex of the apodemal process and a pair of lateral retractor muscles (rlb) inserted on the basal segment both run to the hypopharyngeal wing plate. A median section of the labium (Fig. 22) indicates that there are three pairs of muscles, one pair ( $mlb_1$ ) extends from the terminal margin of the first segment to the sclerotized rod and apodeme of the anterior median groove, a second pair ( $mlb_2$ ) from the sclerotized rod to the lateral wall of the middle segment, and a third pair ( $mlb_3$ ) from the median rod to the dorsal wall of the middle segment. No muscles were seen in the terminal segment.

The hypopharynx (hph, Fig. 18) contains the salivary syringe (syr) and gives rise posterolaterally to the greatly enlarged hypopharyngeal wing plates (hwp, Fig. 20) upon which the dilator muscles of the syringe lever (dsyr) are attached. The comparative size of the hypopharyngeal wing plates is seen in figure 27. United with the main body of the wing plate laterally is a thin sclerotized plate which appears to be an apodemal process (mxap, Fig. 20) of the maxillary plate. The lever of the maxillary stylet articulates with this apodeme, and not directly with the maxillary plate as has heretofore been figured and described by some writers. These two posterior plates, together with anterior membranes which meet where the dorsal tip of the hypopharyngeal wing plate unites with the lateral extremity of the posterior tentorial bridge, form the pouch which contains the mandibular and maxillary stylets.

The anterior wall of the hypopharynx forms the ventral, cup-shaped floor of the sucking pump. To the roof of the sucking pump, which nests concavely in the ventral floor, are attached the large dilator muscles (dlclp). Contraction of these muscles arches the roof convexly and creates the pressure which sucks the food into the preoral cavity. As can be seen by lifting or removing the anteclypeus, the hypopharynx is broadly joined laterally to the lorae. The tentorium in this cicada (Fig. 25) consists of a posterior tentorial bar or bridge (tb) from which two arms (at) run anteriorly to the anterior tentorial pit (atp, Fig. 19). Each of these anterior arms gives off a dorsal arm (dt), to the apex of which the antennal muscles are attached. The antenna consists of a basal scape, a pedicel, and a terminal threadlike flagellum.

*Lepyronia quadrangularis* (Say)  
(Cercopidae)

The study of the head and mouthparts of this family of Homoptera, aside from that included in the study of the external structure and biology of *Lepyronia quadrangularis* made by Doering (1922), has received almost no attention.

The postclypeus (pclp, Fig. 29) of *Lepyronia quadrangularis* is again characteristically striated. There is no suture separating the anteclypeus (aclp) from the postclypeus as occurs in the cicada, but its distinctness is indicated by lateral indentations. The anteclypeus is elongated ventrally beyond the head capsule over the basal segment of the labium (lb). The labrum (lm) suspended from the anteclypeus lies over the median groove of the middle segment of the labium. Dorsally the postclypeus continues into a quadrangular area (fclp, Fig. 31) in which is incorporated the frontal region or frons. That this quadrangular area represents some part of the frontal region is substantiated by the anterior dorsal dilator muscle of the pharynx (phym<sub>1</sub>, Fig. 30), which takes its origin from this region. The vertex (vx, Fig. 31) contains a pair of ocelli (oc). The head of *Lepyronia quadrangularis* is acutely angular, when viewed from the side, with the frons and vertex making up the dorsal surface. The ventral surface, comprising the clypeal area and labrum, slants posteriorly (Fig. 30).

The mandibular stylet (Fig. 34) is similar to that found in the cicada. The protractor muscles (pmds) originating on the lorum are inserted on the lever of the mandible (lvr<sub>1</sub>) and the retractor muscle (rmds) is inserted on the narrow arm of the base of the stylet. The lever articulates with the upper corner of the lorum, but it is situated a considerable distance beneath the anterior invagination of the tentorium.

The maxillary stylet (Fig. 33) is drawn with the protractor muscles (pmxs) of both the base of the stylet and lever (lvr<sub>2</sub>) enclosed within the membranous sheath of the maxillary plate to show the relationship of these parts. A pair of retractor muscles (rmxs) is inserted on the base of the stylet. The lever also possesses a retractor muscle similar to that in the cicada and in fact the entire musculature of the maxillary stylet is similar to that of the cicada. The lever of the stylet articulates with the apodemal plate of the maxillary lobe (mxap, Fig. 32) and not to the maxillary lobe itself.

The three-segmented labium (Fig. 37) is comparatively short and thickened. The protractor (plb) and retractor muscles (rlb) are similar to those already described in the fulgorid and cicada. Five pairs of transverse muscles are seen in the basal and middle segments but there are apparently no muscles in the terminal segment.

The mouthparts (Fig. 30) are very similar to those described for the cicada. The salivary syringe (syr), however, is well developed and comparatively large. The dilator muscles of the salivary syringe (dsyr) are of unusual size and are seen to occupy a very large proportion of the posterior head opening (Fig. 32).

The tentorium, as in the cicada, consists of a posterior tentorial bridge (tb, Fig. 32), and a pair of anterior arms (at, Fig. 34), each with a short dorsal arm (dt). The antennal muscles (mant) originate on the apex of the dorsal tentorial arm.

The left half of the head of *Lepyronia quadrangularis*, with the lower part of the postclypeus, the anteclypeus, labium, and labrum dissected away, is shown in figure 35 to reveal the relationship of the lorum (lor) to the hypopharynx (hph). There is a broad ridge, normally covered by the anteclypeus, which joins the lorum to the hypopharynx. This connection between the lorum and hypopharynx is similar to that which is present in the cicada. In addition there exists an internal ridge or apodeme where the lorum and postclypeus meet, termed the clypeal ridge (clr, Figs. 34 and 35).

A cross-section of the head through the sucking pump, stylet pouches, and muscles of the mouthparts is shown in figure 36 to indicate their relationships.

*Aulacizes irrorata* (Fabr.)  
(Cicadellidae)

Evans has made a comprehensive taxonomic and morphological study of this group over a period of ten years and in 1938 provided a valuable evaluation of intrarelations of this family based on an analysis of their morphological characters. He considers that the external structures of the head are second in value only to the venation of the wings for purposes of comparative studies and the determination of phylogenetic relationships. Although this group is here designated as a family for purposes of uniformity, he considered it to be a superfamily, the *Jassoidea*, and divided it into twenty-one separate families. Later (1948) he reduced the familial divisions to eight, including three families of membracids.

The head of *Aulacizes irrorata* is in many respects similar to the cercopid, *Lepyronia quadrangularis*. The clypeal region, however, is a little larger and bulges out considerably more than in the cercopid. In ventral view (Fig. 38) the large striated postclypeus (pclp), although merged with the anteclypeus (aclp) beneath, is demarked from it by lateral indentations. Laterad of the anteclypeus are the loral regions (lor). The small labrum (lm) fits over the median groove of the short, compact labium (lb). Dorsally the postclypeus merges with the frons to form a frontoclypeal region (fclp, Fig. 39). Although it is not possible to deter-

mine the exact extent of the frons, it should be noticed that the anterior dilator muscle of the pharynx ( $phym_1$ , Fig. 40) originates just ventrad of the dorsal surface so that the postclypeus probably does not extend beyond this point. The posterior limits of the frons may possibly be marked by the prominent lateral indentations. The vertex ( $vx$ ) bears a pair of ocelli ( $oc$ ). The antenna consists of a basal scape and pedicel and a long threadlike flagellum which shows marks of segmentation basally.

The musculature of the mandibular stylet ( $mds$ , Fig. 46) is uniquely different from that of the preceding forms. In addition to the protractor muscle ( $pmds$ ) running from the lever ( $lvr_1$ ) to the lorum and the retractor muscle ( $rmds_1$ ) going from the base of the stylet to the vertex, there is a second retractor muscle ( $rmds_2$ ) which goes to the anterior tentorial arm ( $at$ ).

The base of the maxillary stylet ( $mxs$ , Fig. 42) has one large retractor muscle ( $rmxs$ ) which originates on the vertex and a pair of protractor muscles originating on the maxillary plate. One protractor muscle ( $pmxs$ ) is inserted near the base of the stylet, the other ( $pmxl$ ) is inserted on the lever ( $lvr_2$ ). The lever is broadly articulated to the apodemal plate of the maxillary ( $mxap$ ).

The short, compact labium (Fig. 43) consists of three segments. Two pairs of small triangular plates are present posteriorly on the terminal segment, one pair located basally, one pair apically. Evans (1937) has suggested that these paired plates may represent the glossae and that the surrounding terminal segment is derived from the paraglossae. Likewise, the basal and middle segments may represent the "mentum" and "prementum." These latter terms are of little value, however, for it has so long been the custom to give names indiscriminately to various divisions of the labium that the actual homology of the parts to which such terms are assigned is doubtful. The usual pair of protractor ( $plb$ ) and retractor muscles ( $rlb$ ) originating on the hypopharyngeal plates are inserted on the apodemal process and base of the labium. A median section of the labium (Fig. 44) reveals six pairs of transverse muscles.

The parts of the hypopharynx and the sucking pump mechanism are very similar to those parts already described in previous forms. It should be noted, however, that the sucking pump cavity when fully distended is unusually large, and together with the well developed dilator muscles ( $dldlp$ ) indicates that this form possesses a powerful sucking apparatus.

The tentorium consists of a posterior tentorial bridge ( $tb$ , Fig. 41) and a pair of anterior tentorial invaginations ( $at$ , Fig. 46) to which the dorsal tentorial arms ( $dt$ ) are attached. The pair of anterior tentorial arms usually running to the posterior bridge is absent. Instead, where the anterior tentorial arm might be expected there is found the tendon from

which arises the retractor muscle of the maxillary stylet. This tendon may in part be a vestige of the anterior tentorial arm. The dorsal tentorial arm can be identified by the antennal muscles (mant) which have their origin on the apex of this part.

*Ceresa bubalus* (Fabr.)  
(Membracidae)

The head and mouthparts of the Membracidae have been treated in the earlier comprehensive works on the taxonomy, biology, and morphology of this group by Branch (1914), Funkhauser (1917), and Lawson (1922). These have provided very desirable and basic information concerning the Membracidae, but certain inaccuracies exist in these studies because the homologies of the head and mouthparts were not as well understood then as they are now. These works have not provided any consideration of the musculature.

The head of *Ceresa bubalus* is considerably flattened anteroposteriorly. Seen in ventral aspect (Fig. 47) the conspicuous median area is the postclypeus (pclp), beneath which is the anteclypeus (aclp). The labrum (lm), suspended from the anteclypeus, fits over the median groove of the three-segmented labium (lb). The lorae (lor) are located on the sides of the clypeal areas. The postclypeus is continuous on the conspicuous median protuberance of the anterior surface of the head (Fig. 48). At least a small dorsal portion of this protuberance representing the frontal region of the head combines with the postclypeus to form a frontoclypeus (fclp), since the anterior dilator muscles of the pharynx (phym<sub>1</sub>, Fig. 49) have their origin here. The vertex (vx), divided by a median ridge, possesses a pair of ocelli (oc). The vertex, which lies dorsally in the previous forms discussed, is anterior in position in a line with the metopidium of the pronotum, while most of the clypeal region, normally anterior, lies ventrally.

The mandibular stylet (Fig. 54) has a large group of protractor muscles (pmds) inserted on the lever (lvr<sub>1</sub>) going to the lorum, and three retractor muscles. The first of these muscles (rmds<sub>1</sub>) originates on the dorsal region of the head capsule, the second (rmds<sub>2</sub>) on the dorsal arm of the tentorium and the third (rmds<sub>3</sub>) originates on a lateral internal edge of the hypopharyngeal wing plate where it meets the margin of the head capsule. All three are inserted on the basal portion of the mandibular stylet.

The maxillary stylet (Fig. 53) is greatly elongated and its pouch has been invaginated beyond the tips of the hypopharyngeal wing plates (Fig. 50), so that it is separated from the vertex of the head by a pair of short retractor muscles. There are two protractor muscles originating on



the maxillary plate (mxp), one (pmxs) inserted at the base of the stylet, the other (pmxl) inserted on the lever (lvr<sub>2</sub>). The lever itself apparently articulates with the lateral edge of the hypopharyngeal wing plate (hwp). It should be noted, however, that the hypopharyngeal wing plate has merged with the apodemal plate of the maxillary (mxap). This makes it appear that in this membracid the wing plate is formed from both the lateral elongation of the posterior of the hypopharynx and an invagination of the maxillary plate.

The three-segmented labrum (Fig. 51) resembles that of the leafhopper *Aulacizes*, in that the posterior surface of the terminal segment bears a pair of almost triangular plates basally. Paired protractor muscles (plb) and retractors (rlb) originating on the hypopharyngeal wing plate are inserted on the apex of the apodemal process and the basal segment, respectively. A median section of the labium (Fig. 52) indicates that four pairs of muscles are present within its three segments.

The hypopharynx (hph, Fig. 49) contains a small salivary syringe (syr), the dilator muscles of which (dsyr, Fig. 50) are attached to the hypopharyngeal wing plates. The sucking pump (pmp) is very similar to those of the previous forms. The epipharyngeal wall upon which the dilator muscles (dlclp) are inserted forms the anterior wall of the pump, while the anterior wall of the hypopharynx forms its posterior wall. The pump leads into the pharynx. It should be noted that the frontal connective nerve from the brain runs anterior to the anterior dorsal dilator muscles of the pharynx. As Snodgrass (1947) has shown, this nerve and its ganglion separates the preoral muscles, which include the dilator muscles of the sucking pump (dlclp), from the postoral muscles, which include the hypopharyngeal muscles and pharyngeal dilator muscles. Behind the brain there are two pairs of dorsal dilator muscles of the pharynx (phym<sub>2</sub>, phym<sub>3</sub>) going to the top of the head capsule and a lateral group (phym<sub>1</sub>) going to the tentorium.

The tentorium consists of a posterior tentorial bar, or bridge (tb), and the short dorsal arm of the tentorium (dt, Fig. 54) which arises from the anterior invagination of the tentorium. The antennal muscles (mant), as usual, have their origin on the dorsal arm of the tentorium. The anterior arm of the tentorium, partly incorporated into the base of the dorsal arm, has otherwise disappeared. The antenna consists of two basal segments, the scape (scp) and pedicel (pdc), and a terminal flagellum (fl).

## THE THORACIC SCLERITES, WINGS, AND LEGS OF AUCHENORHYNCHA

The thoracic sclerites of the Auchenorhyncha, and the Homoptera generally, have received relatively little study. Aside from the general studies of Crampton (1926) and Snodgrass (1927) which contain references to individual Homoptera, the most extensive comparative studies of the thoraces of the Homoptera is that of Taylor (1918). The wings, however, have received better treatment and there exist good comparative studies of the wings of the Fulgoroidea, Cicadellidae, and Cercopidae by Metcalf (1913, 1917a, 1917b) and of the Membracidae by Funkhauser (1913). Myers (1928) has discussed the thorax and wings of the Cicadidae in his comparative study on the morphology of this family.

### *Scolops pungens*

*Prothorax.* The head is closely joined to the prothorax by the cervical membrane. There are no distinct cervical sclerites present. The prothorax (Fig. 55) consists mainly of a saddle-shaped pronotum which covers the dorsum and extends down over most of the pleural region. The pleural region is considerably reduced. A portion of the episternum ( $es_1$ ) extends beyond the ventral margin of the lateral lobe of the pronotum, but the epimeron ( $epm_1$ ) is completely covered. Between these pleural sclerites is the pleural suture ( $pls_1$ ) which extends into the coxal process ( $cxp_1$ ), a pleural articulation for the coxa of the leg.

The prosternum ( $st_1$ , Fig. 60) consists of a small sclerite connected to the episternum on each side by a narrow, elongated precoxal bridge or precoxale ( $pcx_1$ ). The trochantin ( $tn$ ) is a small sclerite which forms a point of articulation for the leg between the episternum and precoxale and the coxa.

A pair of invaginations or furcal pits ( $fp_1$ ) give rise to a pair of sternal apodemes or furcae ( $fu$ , Fig. 63). Each furcal apodeme unites with a pleural apodeme ( $plap_1$ ) represented externally by the pleural suture. Together, these sternal and pleural invaginations represent the prothoracic endoskeleton.

*Mesothorax.* The tergum of this wing-bearing segment (Fig. 56) is composed of several distinct regions, the most conspicuous of which is the large scutum ( $sc_2$ ). Anteriorly a narrow ridge represents the precosta or pretergite ( $pc_2$ ). Behind the scutum is a small scutellum ( $scl_2$ ), the posterior margin of which forms a fold or reduplication ( $rd_2$ ). This posterior fold of the scutellum continues into the axillary cord ( $axc_2$ ), forming a

connection with the posterior margin of the wing. The postnotum ( $pnt_2$ ) although morphologically a part of the mesothorax is more closely associated with the metathoracic tergum. Laterally it unites with the mesothoracic epimeron ( $epm_2$ ) by means of the postalar bridge ( $pw_2$ ). Anteriorly the prealar bridge ( $aw_2$ ) unites with the episternum.

The dorsal region of the forewing is articulated to the metathoracic tergum by means of a basal membranous area within which are a number of articular sclerites, collectively termed the pteralia. The first of these sclerites, the first axillary ( $1ax_2$ , Fig. 56) articulates mesally with the anterior notal wing process ( $anp_2$ ) and laterally with the second axillary ( $2ax_2$ ). The second axillary in turn articulates with the common base of the subcosta and radius of the wing veins and with the third axillary ( $3ax_2$ ), while the latter axillary is united with the base of the vannal region of the wing. The basal margin of the vannal region forms a sclerotized fold or lip which fits into a groove formed in the scutellar region of the tergum, locking the wings in place when they are folded at rest.

The pleuron (Fig. 55) is composed of the episternum ( $es_2$ ) and the epimeron, separated by the pleural suture ( $pls_2$ ). Dorsally these areas continue along the pleural suture to form the pleural wing process or articulation for the wing ( $pw_2$ ), while the pleural coxal process ( $exp_2$ ) articulates ventrally with the coxa. The mesothoracic spiracle ( $sp_2$ ) lies in the membranous region below the prealar bridge.

The membranous ventral area of the wing which unites the wing to the pleuron contains several small sclerites, which serve for the insertion of important wing muscles. These are termed the alaria by Crampton and the epipleurites by Snodgrass. Anterior to the pleural wing process is the basalar sclerite ( $ba_2$ ) united to the episternum. Behind the pleural wing process is a narrow elongate subalar sclerite ( $sa_2$ ) which apparently unites with the postalar bridge.

On the ventral side, the sternum ( $st_2$ ) is broadly joined to the episternum by means of the precoxale ( $pcx_2$ ). The trochantin ( $tn_2$ ) lies between the precoxale and the coxal cavity. A pair of furcal pits ( $fp_2$ ) form invaginations of the sternum which give rise to branched furcal apodemes internally. The lateral branches of these apodemes unite with the pleural apodemes as in the prothorax. The mesothoracic pleural apodeme is considerably developed dorsally and extends into the body cavity just below the tergum.

*Metathorax.* The mesothoracic scutellum overlies a considerable portion of the metathoracic tergum, and the normal position of the two wing-bearing segments has been displaced in figure 56 to reveal the divisions of the metatergum. As already noted the postnotum ( $pnt_2$ ) belonging to the mesothoracic segment, is closely joined to the prescutum ( $psc_3$ ) of

the metathorax. The antecostal suture ( $acs_3$ ) which separates the postnotum from the prescutum is the external demarcation of the poorly developed metathoracic phragma. The prescutum is separated from the scutum ( $sc_3$ ) by elongate membranous areas on each side. The scutellum ( $scl_3$ ) is poorly developed. Its posterior margin folds over to form a reduplication and continues into the posterior margin of the wing by means of the axillary cord ( $axc_3$ ). A broad postnotal region ( $pnt_3$ ) is closely united to the scutellum. The postnotum gives off a pair of narrow arms laterally along the posterior margin of the pleuron to meet on the venter, forming a postcoxal bridge ( $pocx_3$ ). The postcoxal bridge on each side unites with a median triangular sclerite. The apex of this triangle sends an elongate sclerotized process anteriorly between the large membranous area of the coxae, which bifurcates into the body cavity.

The dorsal basal membranous area of the hind wing has a number of articular sclerites. A small first axillary ( $lax_3$ ) lies between the anterior notal process ( $anp_3$ ) and the larger second axillary ( $2ax_3$ ). Posteriorly the third axillary ( $3ax_3$ ) articulates with a prominent posterior notal process ( $pnp_3$ ).

The metathoracic pleuron (Fig. 55) presents a specialized structure, apparently correlated with the development of jumping hind legs. The episternum ( $es_3$ ), demarked from the epimeron ( $epm_3$ ) by the plural suture ( $pls_3$ ), is cleft ventrally by membrane. Both the episternum and the epimeron have been shifted in position so that these sclerites lie almost horizontally, rather than vertically. Consequently the pleural wing process ( $pwp_3$ ) has been pushed to the extreme anterior point of the pleuron. The coxa has become rigidly united with the pleuron and although the coxa ( $cx_3$ ) and meron ( $mr_3$ ) may be broadly distinguished from the episternum and epimeron, considerable comparative study of this region among the fulgorids would be required to determine the exact boundaries of these sclerites. Taylor (1918) has indicated, however, that in species of *Ormenis* and *Fulgora*, a comparable region bears muscles extending to the subalar region, and since such muscles connect the subalar sclerite and meron in other insects he concluded that the region in question is a part of the coxa, and not of the pleuron.

The ventral basal membrane of the wing does not possess an externally visible basalar sclerite anterior to the pleural wing process as does the mesothoracic segment. Posteriorly, however, there is an elongate subalar sclerite ( $sa_3$ ).

On the venter the sternum is united both to the mesothoracic sternum anteriorly and to the episternum laterally through a precoxal bridge ( $pcox_3$ , Fig. 60). A wide membranous area separates the precoxal bridge from the coxae. The origin of the small sclerotized areas within this mem-

branous region is uncertain, but may have been derived from the trochantin.

*Wings.* The forewing is elongate-oval in outline and is somewhat thickened, forming a tegmen-like covering for the membranous hind wing. A vannal fold (vf) divides the hind wing into an anterior remigium and a posterior vannus. The basic wing venation is noted in figures 79 and 80.

*Legs.* The mesothoracic leg (Fig. 80) consists of a basal coxal segment ( $cx_2$ ), a short trochanter (tr), the femur (fe), tibia (ti), and a three-segmented tarsus. The tarsus (Fig. 92) bears a pair of ungues or claws (cl), between which is a membranous pad or pulvillus (pu). The basal rim of the coxa is demarked at the basicoxa (bcx) and a small lateral portion forms the meron (mr). The prothoracic leg (Fig. 89) is almost identical to the mesothoracic leg in structure, except that the meron ( $mr_2$ ) is less developed. The larger metathoracic leg (Fig. 91) is modified for jumping and consists of a coxal segment (cx), the meron ( $mr_3$ ) of which is rigidly joined to the pleuron. There is a small trochanter, a femur, and a tibia with a posterior row of toothlike spines, and a border of spines apically. The apical ends of the first two tarsal segments are similarly spined.

### *Tibicina septendecim*

*Prothorax.* The cervical region of the cicada, *Tibicina septendecim*, contains a pair of median dorsal cervicals (dc, Fig. 57) and a pair of lateral cervical sclerites (lc).

Like the fulgorid, the principal sclerite of the prothorax of the cicada consists of a saddle-shaped pronotum which covers most of the pleural region. In other respects, too, it is quite similar, except that there is a postcoxal bridge ( $pocx_1$ , Fig. 61) ventrally as well as a precoxal bridge (pcx). In addition, the median sternal region ( $st_1$ ) is modified into a troughlike structure in which the labium of the head lies in repose.

*Mesothorax.* The main feature of this segment is that it bears the principal burden of flight of the cicada. As a consequence this segment is greatly enlarged and presents a number of modifications primarily correlated with the flight mechanism. The tergum consists of an anterior prescutum ( $psc_2$ , Fig. 57) with the scutum ( $sc_2$ ) lying posteriorly and laterally. There is a narrow precostal region ( $pc_1$ ) present anteriorly, which is bent back over the prescutum, and this relationship can best be seen in longitudinal section shown in figure 59. The phragma ( $ph_2$ ) which is fairly well developed is not suspended vertically, but is directed anteriorly in a horizontal direction and can be seen dorsally beneath the prothoracic intrasegmental membrane.

The postnotum ( $pnt_2$ ), although closely united with the metathoracic tergum medially, is also joined to the reduplication ( $rd_2$ ), or posterior fold of the scutellum ( $scl_2$ ), laterally. The invaginated plate arising from the posterior margin of the postnotum gives rise to a large, well developed phragma ( $ph_2$ , Fig. 62) upon which arise the powerful oblique dorsal muscles of the mesothoracic tergum. The phragma is thus anchored both to the mesothorax laterally and to the metathoracic segment medially. Four axillary segments, in the basal membranous region of the dorsal surface of the forewing, provide a part of the tergal articulating mechanism.

Laterally (Fig. 58), the episternum and epimeron are respectively divided into upper anepisternal ( $aes_2$ ) and anepimeral ( $aepm_2$ ) regions and below into katepisternal ( $kes_2$ ) and katepimeral ( $kemp_2$ ) regions. Connected to the episternum in the basal membranous area of the ventral surface of the wing is the basalar sclerite ( $ba_2$ ) while the subalar sclerite ( $sa_2$ ) is behind the pleural wing process ( $pwp_2$ ).

The mesosternum consists of a broad basisternum ( $bst_2$ , Fig. 61) separated from the prosternum by a membranous region, but joined laterally to the katepisterna by precoxal bridges ( $pcx_2$ ). The medioposterior furcasternum ( $fst_2$ ) contains a pair of furcal pits ( $fp$ ) which invaginate to form the furcal apodemes internally. Postcoxal bridges ( $pocx_2$ ) join the furcasternum to the katepimera.

*Metathorax.* This segment is considerably reduced in comparison to the mesothorax, and although the hindwing which it bears apparently plays a lesser role in the flight of this insect, it does nevertheless actively enter into the flight mechanism. The scutellum of the mesothorax overlies half of the metathoracic tergum, but the latter has been withdrawn in figure 57 to reveal its parts. To be noted is the fact that medially the scutum ( $sc_3$ ) is separated from the scutellum ( $scl_3$ ) by a membranous cleft. A small postnotum ( $pnt_2$ ) is present behind the scutellum. The basal membranous region of the dorsal surface of the wing contains four axillary sclerites.

Ventrally the basisternum ( $bst_3$ ) is rigidly united with the mesosternum anteriorly and joined to the pleuron by precoxal ( $pcx_3$ ) and postcoxal bridges ( $pocx_3$ ), while the furcasternum ( $fst_3$ ) is posteriorly united with the sternum of the first abdominal segment (I).

*Wings.* The forewing (Fig. 81) is almost twice as large as the hind wing (Fig. 82) and is apparently the principal flight organ, although as has been mentioned the hind wing is undoubtedly an equally active but lesser organ of flight. This is emphasized since the development and sclerotization of the wing-bearing segments is closely correlated with the degree of activity of both the fore and hind wings. Care must be taken

not to mistake structural correlations with the flight mechanism for phylogenetic relationship.

Attention should be called to the nodal line of the fore wing ( $nl$ ) which forms a break in the sclerotization of some of the principal vein branches, previously thought to be present only in the Cicadidae. Evans (1948) has shown that a nodal line is also present in the jassoid family, Hylcidae. The basic venation, noted in figures 81 and 82, is well discussed by Myers (1928) for the Cicadidae as a whole.

*Legs.* The legs of the cicada bear the same segmentation as noted in the fulgorid. The prothoracic leg (Fig. 93) is turned anteriorly and is so drawn. The femur ( $fe$ ) is considerably thickened and bears several spines on its ventral margin. The mesothoracic leg (Fig. 94) shows no particular modification. The meron ( $mr_3$ ) of the metathoracic leg (Fig. 95) is elongate and pointed, forming a projecting spinelike structure. The tibia bears several spinelike, movable setae and a row of spines apically. The distal segment of the tarsus (Fig. 96) bears a pair of claws ( $cl$ ) but no pulvillus.

### *Lepyronia quadrangularis*

*Prothorax.* The pronotum ( $prnt$ , Fig. 67) of the cercopid, *Lepyronia quadrangularis*, is typically saddle-shaped, covering most of the pleuron laterally. Posterodorsally it overlies the anterior part of the mesothoracic tergum, but the pronotum has been displaced anteriorly in figure 66. The epimeron is completely reduced and concealed by the lateral lobe of the pronotum. The sternum ( $st_1$ , Fig. 68) forms a trough for the reception of the labium. In other respects it varies but little from the forms already discussed.

*Mesothorax.* A narrow precosta ( $pc_1$ ) is demarked anteriorly on the tergum, while the prescutum ( $psc_2$ ) behind is separated laterally from the scutum ( $sc_2$ ) by a pair of narrow membranous clefts. The conspicuous scutellum ( $scl_2$ ) is triangular in shape and its posterior half normally overlies the metathoracic tergum (displaced in Fig. 66). As in the fulgorid the posterior lateral margins of the scutellum are grooved to form a locking device ( $twg_2$ ) with the bases of the posterior margin of the tegmina.

Laterally, the episternum is divided into an anepisternum ( $aes_2$ ) and a katepisternum ( $kes_2$ ). The epimeron ( $epm_2$ ) and a part of the metathoracic episternum ( $es_3$ ) is grooved to receive the base of the costal margin of the tegmen. The episternum is broadly united to the sternum. The sternum is differentiated into an anterior prebasisternite ( $pbs_2$ ), the large basisternite ( $bst_2$ ), and a furcasternum ( $fst_2$ ) between the coxal cavities. The furcasternite may possibly be a combination of the furcasternite and the spinasternite found in the orthopteroid orders.

Three axillary sclerites are present dorsally in the basal membrane of the wing, while ventrally there is a well developed subalar sclerite ( $sa_2$ ) and a considerably reduced basalar sclerite. The mesothoracic spiracle ( $sp_2$ , Fig. 67) is located in the membranous region of the pleuron between the pro- and mesothorax.

*Metathorax.* This segment is well developed and apparently plays an important role in the flight mechanism. In this connection it should be noted that the well developed phragma is an invagination of the anterior margin of the prescutum ( $psc_3$ ) and is primarily a functional part of the metathorax, in contrast to the cicada in which the well developed phragma is functionally a part of the mesothorax. Further, there is no pronounced development of a postnotum between the mesothoracic and metathoracic terga. The scutum ( $sc_3$ ) is large and contains a median suture. This median suture ( $ms_3$ ) is the external demarcation of a well developed median tergal apodeme which unites anteriorly with the phragma. The scutellum ( $scl_3$ ) forms a narrow posterior margin of the tergum.

Laterally the anterior margin of the tergum gives off two branches. The anterior of these is the postalar bridge ( $pw_2$ ) of the mesothoracic segment and unites with the mesothoracic epimeron, while the posterior branch forms the prealar bridge ( $aw_3$ ) of the metathoracic segment and unites with the metathoracic episternum ( $es_3$ ). The epimeron ( $epm_3$ ) is united to the postnotum ( $pnt_3$ ) by a postalar bridge ( $pw_3$ ). The metathoracic spiracular opening is concealed in the dorsal angle between the mesothoracic postalare and the metathoracic prealare.

The sternum ( $st_3$ ) is rigidly joined to the mesothoracic furcasternite anteriorly and united with the episternum by a narrow bridge. Although a pair of membranous clefts demark the central region, there is no distinct demarcation of the lateral limits of the sternum.

The basal region of the wing contains three axillary sclerites dorsally, the first axillary sclerite being considerably reduced. Ventrally there is present a subalar sclerite ( $sa_3$ ) but there is no external evidence of a basalar sclerite. The metathoracic spiracle, although not readily visible, is present in the grooved area formed between the mesothoracic epimeron and the metathoracic episternum in the upper region of the pleuron.

*Wings.* (Figs. 83 and 84). The fore wing or tegmen is opaque and reticulated, so that some of its venation is obscured. Doering (1922) has been able to delineate the forewing venation by clearing and the venation which she has obtained through this procedure is shown in broken line. A projecting ridge or keel on the underside of the subcosta of the tegmen latches on to a sharp crest of the metathoracic epimeron and helps to lock



the tegmen in place when at repose. The membranous hindwing bears a row of spines or hooks on the costal margin. The basic venation of both fore- and hindwings is indicated in figures 83 and 84.

*Legs.* The prothoracic (Fig. 97) and mesothoracic legs (Fig. 98) are generally similar, except that the meron ( $mr_2$ ) of the middle leg is produced into a flat spinelike structure. The hind legs (Fig. 99) are considerably modified. The meron ( $mr_3$ ) forms a ball-like structure which fits into a socket formed by the epimeron, so that although not united to the epimeron, it is closely associated with it. The tibia ( $ti_3$ ) has two large spines along its outer edge and a double row of spines at its apex. It is this character of the tibia which is used to distinguish the Cercopidae from the Cicadellidae. The first two tarsal segments also bear an apical row of spines. The last tarsal segment of all the legs bears a pair of claws (cl) and a notched, but single lobed pulvillus (pu), as shown in the tarsus of the mesothoracic leg (Fig. 100). The hind leg of the cercopid bears a considerable resemblance to that of the fulgorid in these respects.

### *Aulacizes irrorata*

*Prothorax.* The prothoracic tergum takes the shape of a saddle-shaped pronotum as in the previous forms described. It is shown in figure 65 in dotted outline in its normal position covering the mesothoracic tergum. The lateral and ventral aspects (Figs. 64 and 69) of this segment do not vary significantly from that of *Lepyronia quadrangularis* above, except that there is no development of a troughlike structure on the sternum as in the cercopid.

*Mesothorax.* The mesothoracic precosta ( $pc_1$ , Fig. 65) consists of a narrow sclerite, separated from the prescutum ( $psc_2$ ) by the antecostal suture ( $acs_2$ ). The antecostal suture is represented internally by a ridge, not by the development of a phragma. The major portion of the tergum is occupied by the scutum ( $sc_2$ ). The posterior tergum consists of the scutellum ( $scl_2$ ), bearing a V-shaped groove ( $twg_2$ ) for the reception of the basal lip of the posterior margin of the tegmen. The postnotum ( $pnt_2$ ), completely covered by the scutellar region of the tergum, gives off a postalar arm ( $pw_2$ ) laterally to the epimeron, whereas the anterior portion of the tergum is united to the episternum by the prealar bridge ( $aw_2$ ). The membranous base of the wing contains three axillary sclerites dorsally and both a basalar ( $ba_2$ ) and subalar sclerite ( $sa_2$ ) ventrally.

The episternum of the pleuron is divided into an anepisternum ( $aes_2$ , Fig. 64) and a katepisternum ( $kes_2$ ). The diagonal line ( $pwg$ ), dividing the epimeron ( $epm_3$ ) into two triangular areas, represents a groove into which fits the basal lip of the costal margin of the tegmen, similar to the arrangement found in the cercopid. The mesothoracic spiracle ( $sp_2$ ) is

located in the upper pleural membranous region between the pro- and mesothorax.

The mesothoracic sternum is also similar to that of the cercopid, there being an anterior prebasisternite ( $pbs_2$ , Fig. 69), a large basisternite ( $bst_2$ ) and a posterior furcasternite ( $fst_2$ ) between the coxal cavities. The basisternite is divided into two by a median suture, and its posterior margin is demarked by another suture. The furcasternite bears the furcal pits ( $fp_2$ ) which form an internal furcal apodeme. Laterally the sternum is broadly joined with the pleuron.

*Metathorax.* The mesothoracic postnotum ( $pnt_2$ , Fig. 65) lies beneath the posterior fold of the mesothoracic scutellum. Morphologically the postnotum is a part of the mesothorax, but as in the cicada it is medially united with the metathorax and laterally with the mesothorax. The large phragma to which the postnotum gives rise through an invagination of its posterior margin is more closely allied with the mesothorax functionally. In this respect it differs from the intersegmental phragma between the meso- and metathoracic segments of the cercopid, which phragma is intimately associated with the metathorax.

The metathorax has no definite prescutal area. The tergum is composed of a large scutum ( $sc_3$ ) and a smaller scutellum ( $scl_3$ ). The metathoracic postnotum ( $pnt_3$ ) behind the scutellum is only sclerotized laterally. A postalar bridge connects the postnotum to the epimeron. Anteriorly, however, there is no distinct prealar bridge to connect the metathoracic tergum to the episternum.

The pleuron consists of a distinct episternum ( $es_3$ , Fig. 64) and epimeron ( $epm_3$ ) separated by the plural suture ( $pls_3$ ). The metathoracic spiracle ( $sp_3$ ) is located in the membranous region of the pleuron, between the meso- and metathorax. The mesothoracic sternum ( $bst_3$ , Fig. 69) has a precoxal connection laterally with the episternum. It sends a median process posteriorly between the coxae, where it unites with a postcoxal bridge given off by the epimeron. The trochantin ( $tn_3$ ) of the coxa is quite large and apparently united with the episternum.

*Wings.* The forewing, or tegmen, is reticulated and thickened. Like the tegmen of the cercopid it is divided by the vannal fold ( $vf$ , Fig. 85) into an anterior remigial portion and a smaller posterior vannus. The hindwing (Fig. 86) is membranous, and quite similar, in venation and the presence of a series of hooks on the costal margin, to that of the cercopid. In addition to the vannal fold ( $vf$ ) it has a jugal fold ( $jf$ ) which demarks the jugum of the wing. The basic wing venation is indicated in figures 85 and 86.

*Legs.* The pro- (Fig. 101) and mesothoracic legs (Fig. 102) are comparatively small and similar in appearance. The metathoracic leg (Fig.

103) is several times larger. Its tibia (ti) is square in cross-section, possesses a row of spines along each of four edges, and is fringed with a double row of spines apically. As with the cercopid and fulgorid, the first two tarsal segments are fringed with spines apically. The claws (cl, Fig. 105) borne apically by the third tarsal segment are adherent laterally to the bilobed pulvillus (pu, Fig. 104) in all three legs.

### *Ceresa bubalus*

*Prothorax.* The membranous cervical region of *Ceresa bubalus* does not contain any cervical sclerites. There are present, however, the paired, triangular, occipital condyles (occ, Fig. 50) borne laterally by the occipital margin of the head.

The unusual development of the pronotum is characteristic of the Membracidae. This structure, important taxonomically, takes on a remarkable variety of shapes throughout the family, developing spines, horns, crests, bulbous structures, and other developments, posteriorly, anteriorly, dorsally and at the humeral angles. Unusual developments of the pronotum are particularly evident in many of the tropical and subtropical forms of this group. According to Funkhauser, the anterior, dorsal, and humeral structures vary haphazardly among the species, and although of almost no value in the differentiation of the higher taxonomic categories, are of considerable value in the delineation of species. The posterior structures, on the other hand, are of a more constant nature and are frequently used for the differentiation of genera.

The cephalic portion of the pronotum, or metopidium (mtp, Fig. 72), of the pronotum, of *Ceresa bubalus* is on a plane continuous with the vertex of the head, and though marked with impunctations, does not possess any special structures. The slightly protruding areas on the lateral margins of the prothorax just above the bases of the forewings are termed the humeral angles (ha), and just above the humeral angles are the lateral projections of the metopidium known as the suprahumeral horns (sh). Obliquely posterior from the suprahumeral horns, a pair of folds meet mesally to form a sharp median edge or carina. The posterior-most portion of the median carina projects as a spinelike posterior process.

The pleural region (Fig. 75) consists of a definite episternal region ( $es_1$ ) bounded laterally by the pleural suture ( $pls_1$ ). A well defined epimeron does not exist, although the lateral lobe of the pronotum just behind the pleural suture may include a portion of the epimeral region. The episternum is turned inwardly immediately behind the head capsule against which it lies. It is joined to the sternum by the precoxal ( $pcx_1$ ).

A posterior view of the prothorax (Fig. 72) reveals a pair of furcal pits ( $fp_1$ ) in the small rectangular sternal plate ( $st_1$ ). The furcal pits

mark the invaginations of the furcal apodemes ( $fu_1$ ) which possess two branches. One branch runs dorsally, and the other curves laterally and abuts against the pleural apodeme ( $plap_1$ ). The triangular trochantin ( $tn_1$ , Fig. 75) lies between the episternum and the coxa.

*Mesothorax.* This segment is large and well developed. The tergum (Fig. 70) is primarily composed of a large anterior scutum ( $sc_2$ ) and a posterior scutellum ( $scl_2$ ). The scutum possesses two pairs of lateral sutures or internal ridges. One pair of such sutures or notaulices ( $no_2$ ) arises anterolaterally and converges toward the median line, while the second pair runs posteromedially from the anterior notal wing process ( $anp_2$ ). A narrow precosts or pretergite ( $pc_1$ , Fig. 78) is set off from the anterior margin of the scutum by the antecostal suture ( $acs_2$ ). Posteriorly, the scutellum covers the narrow postnotum ( $pnt_2$ ) which is united with the metathoracic tergum. The bases of the wings are shown in figure 70, slightly displaced from their normal position at rest. There are three axillary sclerites ( $1ax_2, 2ax_2, 3ax_2$ ) in the basal membranous area of the forewing.

The pleuron (Fig. 71) consists of an episternum ( $es_2$ ) and epimeron ( $epm_2$ ) separated by the pleural suture ( $pls_2$ ). The extensions of these sclerites dorsally along the pleural suture form the pleural wing process, or articulation for the wing ( $pwp_2$ ), while the pleural coxal process, or articulation for the coxa ( $cxp_2$ ) is formed by the extension of the episternum and epimeron at the ventral extremity of the pleural suture. As in the cercopid and cicadellid previously described, the epimeron possesses a diagonal groove into which the basal costal lip of the fore wing fits when the wings are at rest. A distinct basal region ( $ba_2$ ) is united to the episternum dorsally, but a corresponding subalar region is not demarked from the upper region of the epimeron. The pleuron is united to the tergum by the prealar bridge ( $aw_2$ ) joining the episternum to the scutum, and by the postalar bridge ( $pw_2$ ) joining the epimeron to the postnotum. The mesothoracic spiracle ( $sp_2$ , Fig. 71) is in the membranous area just anterior to the prealar bridge.

The sternum (Fig. 74) consists of a central prebasisternite ( $pbs_2$ ) flanked by the basisternal regions ( $bst_2$ ). (Compare with the sternum of *Aulacizes irrorata*.) Even if these areas have a homologous value, it is difficult to define their exact limits due to the broad fusion of the sternum with the pleura and the consequent modifications of structure. Detailed comparative studies of intrafamily modifications and relationships are required to clarify the interpretation of these sternal structures. Posterior to the precoxal bridge, a suture demarks a narrow marginal area which Crampton (1915) has designated as the antecoxale ( $acx_2$ ), similar to such a modification in *Aulacizes irrorata* ( $acx_2$ , Fig. 69). Here again it

appears that the median part of this marginal antecoxale is a part of the basisternal region. The furcasternite ( $fst_2$ ) bearing the furcal pits ( $fp_2$ ), lies between the coxal cavities. These pits invaginate to form the well developed furcal apodemes ( $fu_2$ , Fig. 77), almost reaching to the pleural apodemes ( $plap_2$ ). The remainder of the mesothoracic endoskeleton is formed by a platelike phragma ( $ph_2$ , Fig. 76), bearing a deep median notch. The mesothoracic phragma is formed by the invaginated folds between the postnotum and the metathoracic scutum. A narrow post-coxal bridge ( $pocx_2$ , Fig. 77) unites the furcasternite with the epimeron, behind the coxal cavity. The trochantin ( $tn_2$ , Fig. 78) is a small sclerite lying in the membranous area between the antecoxale and the coxa.

*Metathorax.* This segment is considerably smaller than the mesothoracic segment. The major area of the tergum is occupied by the scutum ( $sc_3$ , Fig. 70), divided medially by a suture ( $ms_3$ ). The median suture is represented internally by a median plate which unites anteriorly with the mesothoracic phragma. The narrow posterior margin of the tergum forms the scutellum ( $scl_3$ ), the lateral extensions of which articulate with the posterior margin of the hind wing by means of the axillary cord ( $axc_3$ ). Three axillary sclerites ( $1ax_3$ ,  $2ax_3$ ,  $3ax_3$ ) are present in the basal membranous area of the wing adjacent to the anterolateral margin of the scutum.

The pleuron of the metathorax consists of an episternum ( $es_3$ , Fig. 71) and epimeron, the latter divided into a large anepimeron ( $aepm_3$ ) and a smaller katepimeron ( $kepm_3$ ). The posterior portion of the mesothoracic epimeron overlies the metathoracic episternum and the metathoracic spiracle ( $sp_3$ ) is concealed in a small dorsal membranous area between these segments. The pleural wing articulation ( $pwp_3$ ) and the pleural coxal articulation ( $exp_2$ ) are found at the respective dorsal and ventral extremities of the pleural suture ( $pls_3$ ). A prealar bridge ( $aw_3$ ), joined to the postalar bridge of the mesothorax, unites the epimeron to the lateral remnant of the postnotum ( $pnt_3$ ). No distinct basalar or subalar sclerites are present in the articulating membranous area of the wing and pleuron.

The sternum (Fig. 74) is composed of an anterior basisternite ( $bs_3$ ), and a posterior furcasternite ( $fst_3$ ) which lie between the coxal cavities. The basisternite is joined to the episternum by a precoxal bridge ( $pcx_3$ ), while the furcasternite is joined to the katepimeron by a postcoxal bridge ( $pocx_3$ ). The furcasternite bears a median pair of furcal pits which form a small furcal apodeme ( $fu_3$ , Fig. 73) internally. The trochantin ( $tn_3$ , Fig. 76), closely approximated with the episternum, articulates with the coxa. As seen in this posterior view of the metathorax the lateral rem-

nants of the postnotum, the postalar bridges, the postcoxal bridges, and the sternum, are all united to form a ringlike sclerite around the metathorax.

*Wings.* Both the fore- (Fig. 87) and hindwings (Fig. 88) are membranous and apparently both pairs of wings are actively used in flight. Funkhauser (1912) has made an excellent comparative study of the wings of the Membracidae, and reference should be made to this study for information concerning the venation. It should, however, be noted that the forewing possesses a vannal fold (vf) along the course of what is probably the second branch of cubitus, which separates the large anterior remigial area from the narrow posterior vannal area, similar to that which occurs in both the cercopid and cicadellid. Funkhauser refers to this vannal fold as the claval suture. The venation\* of the wings of *Ceresa bubalus* is noted in figures 87 and 88.

*Legs.* The prothoracic (Fig. 111) and mesothoracic legs (Fig. 112) are very similar. The coxae, trochanters, femora, tibiae, and three-segmented tarsi of the first two pairs of legs possess no unusual features. The coxae of the jumping metathoracic legs (Fig. 113) are considerably enlarged and their mesal margins each possess an angular, toothed projection which enables the coxae to lock in position against the sternum and each other. The tibia of the hind leg is further modified by the possession of four rows of spines along its length and an apical border of spines. The first tarsal segment is about twice the length of the second tarsal segment, whereas in the pro- and mesothoracic legs the second tarsal segment exceeds the first segment in length. The claws (cl, Fig. 116) adhere to the bilobed, membranous pulvilli (pu) or pads.

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\*The interpretation of the wing venation is largely based on the studies of Metcalf (1913a, 1913b, 1917) and Funkhauser (1913). Evans' interpretation (1946a, 1948), in which  $R_1=R_{1a}$ ,  $R_{2+3}=R_{1b}$ , and  $R_{4+5}=R_5$ , may be the more probable one if the position of the cross-vein  $r$  is accurately traced.

## THE THORACIC MUSCULATURE OF *CERESA BUBALUS*

*The Cervical Muscles.* The movement of the head is controlled by four pairs of muscles (Fig. 50) as follows:

1. A pair of dorsal longitudinal muscles (21) running from the dorsal occipital margin of the head to the lateral pretergal margin of the mesothoracic tergum.

2. A vertical muscle (22) from the dorsolateral occipital margin of the head to the precoxa of the prothorax.

3. A muscle (23) from the occipital condyle to the dorsal, anterior margin of the pronotum.

4. A short, thick muscle (24) from the lateral posterior margin of the hypopharyngeal wing plate to the prothoracic furcal apodeme.

*The Prothoracic Muscles.* These muscles (Fig. 110) are roughly divided into two groups, one with insertions on the furcal apodeme, the other with insertions on the leg and origins on the pronotum. Besides the muscle going from the furcal apodeme to the hypopharyngeal wing plate, mentioned above, there are two other muscles connected to the furcal apodeme.

1. An anterior muscle (31) from the apex of the furcal apodeme running dorsally to the lower region of the metopidium of the pronotum.

2. A posterior muscle (32) from the apex of the furcal apodeme running dorsally to the lateral margin of the mesothoracic pretergite.

Five prominent muscles, with origins on the lower region of the metopidium of the pronotum are inserted on the trochantin, meron, coxa, and trochanter. Posteriorly these are covered or enclosed by a sclerotized partition (mp) shown in part in figure 72. The muscles (Fig. 110) are as follows:

1. A large muscle (34) originating just beneath the ridge demarking the lower region of the metopidium and inserted on the meron.

2. A muscle (35) originating just below the above one on the metopidium and inserted on the mesal tip of the trochantin.

3. A muscle (36) from the upper lateral corner of the lower region of the metopidium, inserted on the basal rim of the coxa just anterior to the pleural articulation.

4. Similar to the above, but inserted on the basal rim of the coxa, just posterior to the pleural articulation (37).

5. This muscle (38) is inserted mesally on the basal rim of the trochanter. Its origin is near the above two muscles in the lateral corner of the metopidium.

The mesothoracic leg will be used to demonstrate the leg musculature. Since the musculature of the leg segments of the pro-, meso-, and meta-thorax shows a general similarity, further description of the prothoracic leg muscles, not originating on the pronotum, will be omitted at this point.

*The Mesothoracic Muscles.* An examination of the musculature of this segment at once indicates that of the two wing-bearing segments, the function of flight is chiefly centered in the mesothoracic segment. Previous studies of the flight mechanism of insects have indicated that the flight movements of the wings are performed by two groups of muscles, the indirect wing muscles and the direct wing muscles. The indirect wing muscles, by causing alternating changes in the shape of the thoracic segment, are primarily responsible for the elevation and depression of the wings. These are as follows:

1. Dorsal longitudinal muscles (41, Fig. 106). A broad pair of median muscles stretched between the mesothoracic phragma and the arched, anterior region of the scutum. These are the chief depressor muscles of the wings.

2. Oblique dorsal muscle (42, Fig. 107). Laterad of the dorsal longitudinal muscles, this muscle extends from the mesothoracic phragma to the lateral region of the scutum. This muscle acts as a depressor in *Ceresa*, but in other insects, where it becomes nearly vertical in position, it may act as an elevator of the wing.

3. Tergosternal muscle (43, Fig. 107). This muscle, extending from the anterolateral region of the scutum to the lateral region of the sternum and the precoxal bridge, is the elevator muscle of the wing. (Figures 106, 107, and 108 have been drawn to reveal the muscles as they are dissected from the median line to the lateral wall of the thoracic segments.)

4. This muscle (47a) extends from the dorsal surface of the projecting pleural apodeme to the anterior region of the posterior notal process.

5. This short, thick muscle (47b) unites the lateral arm of the furca with the pleural apodeme.

The direct wing muscles act as extensors and flexors of the wing. It is these muscles which are primarily responsible for extending the wings into flight position, and in combination with the natural flexibility of portions of the wing, are responsible for bringing the wings back to rest. Although the function of some of these muscles in this capacity is quite apparent or easy to demonstrate, the exact function of others cannot always be shown, for it is a complex integration of a number of these muscles which is responsible for the various kinds of wing motion. Some



of the indirect wing muscles are inserted upon the coxa and probably play a role in the movement of the leg as well.

1. Basalar muscles. Two muscles are inserted upon the upper portion of the episternum, or basalar sclerite, which invaginates into the body cavity. The first of these (44, Fig. 109) arise from a lateral process of the antecoxal sclerite, while the other (45a) arises from a tendon attached to the basal rim of the coxa just anterior to the pleural articulation. A branch of this latter muscle (45b) goes to the anterior margin of the episternum.

2. Subalar muscle. As has been previously noted there is no distinct subalar sclerite. The muscle which arises from the basal rim of the coxa just posterior to the pleural articulation is the one which usually is inserted on the subalar sclerite in other insects where such a sclerite is present. In this instance the muscle (46, Fig. 112) is inserted upon a small invaginated process on the dorsal margin of the epimeron.

3. Muscle of the 2nd axillary. This muscle (49) arises broadly from the anteroventral margin of the episternum and narrows to a tendon which is inserted upon the 2nd axillary sclerite of the fore wing.

*The Ventral Longitudinal Muscles.* The ventral longitudinal muscles (50, Fig. 106) of the mesothorax consist of a pair of small muscles extending from the anterior margin of the mesothoracic furca to the posterior faces of the paired sternal apophyses of the prothorax. In addition there is present a pair of short, thick muscles (51) which extend from the raised posterior region of the furca to the lower posterior wall of the phragma.

*The Muscles of the Leg.* Aside from the muscles mentioned above, which arise on the coxa and are connected with the flight mechanism, there are present a number of leg muscles originating on the thoracic sclerites or their apodemes which are apparently connected with the movements of the leg alone. These muscles are inserted on the coxal and trochanteral segments of the leg and have their origins either on the tergum or on the furcal arms of the sternum. Additional leg muscles are concerned with the movement of the individual leg segments.

#### COXAL MUSCLES (Fig. 112).

1. Tergal promoter of the leg (52, Figs. 107 and 112). This muscle arises on the scutum and is inserted on the ventral end of the trochantin by means of an elongated tendon.

2. Sternal remoter of the leg (53). This muscle arises on the furcal arm of the sternum and is inserted on the posterior basal margin of the coxa.

3. Pleurocoxal muscle (45b). This muscle has already been mentioned in connection with the basalar muscle (45a) of which it is a

branch. Since it arises on the anterior margin of the episternum and is inserted on the basal margin of the coxa just anterior to the pleural articulation, it is in all likelihood directly connected with the movement of the leg.

4. Tergal remoter of the leg (48). This muscle, arising from the posterior corner of the posterior notal process is inserted by means of a tendon on the posterior basal margin of the coxa.

The remaining muscle with a coxal insertion is the subalar muscle (46), inserted on the basal rim of the coxa just behind the pleural articulation.

#### TROCHANTERAL MUSCLES (Fig. 114).

Two groups of muscles are inserted on the basal margin of the trochanter. The mesal articulation of the trochanter with the coxa bears a long tendon upon which are inserted three muscles. The longest of these muscles (54a) arises on the scutum; the second (54b) originates on the furcal arm, while the third (54c) arises on the wall of the coxa. This group of muscles acts as a depressor of the leg. The second group (55), or extensors of the leg, consisting of several muscle bundles, all arise on the outer wall of the coxa and are inserted on the lateral basal rim of the trochanter.

#### FEMORAL MUSCLE (56, Fig. 114).

A single small muscle, inserted on the basal rim of the femoral segment, has its origin on the wall of the distal portion of the trochanter.

#### TIBIAL MUSCLES (Fig. 115).

1. Extensor muscle. This muscle is inserted on the outer basal margin of the tibia by means of a tendon. The tendon bears two groups of muscles, one originating on the wall of the distal portion of the trochanter (57a), the other originating on the wall of the femur (57b).

2. Depressor muscles (58). A pair of short muscles inserted on opposite sides of the inner basal margin of the tibia, arising on the distal portion of the femur.

#### TARSAL MUSCLES (59, 60, Fig. 116).

These consist of two short bundles inserted on opposite sides of the basal rim of the proximal segment of the tarsus, arising on the wall of the distal end of the tibia.

#### POSTTARSAL MUSCLE (61a, Fig. 116).

The unguitractor (unp) of the posttarsus continues into the tarsus and tibia in the form of a long unguitractoral tendon (unt) upon which are inserted two muscle branches, one arising on the wall of the middle portion of the tibia (61a), the other arising on the wall of the proximal portion of the tibia (not shown).

*The Metathoracic Muscles.* The muscles of the metathorax bear very little resemblance to those of the mesothoracic segment. The most striking feature is the complete absence of those muscles termed the indirect wing muscles, the dorsal longitudinals, the oblique dorsals and the tergosternal muscles. The absence of these muscles precludes the possibility that the flight mechanism of the hind wings is in any way similar to that of the fore wings.

The most conspicuous muscles are those associated with the legs. The leg, wing, and other muscles of the metathorax are listed as they are seen in a median section of the thorax and dissected away toward the lateral wall, as follows:

1. Trochanteral extensor of the leg (62a, Fig. 106). This is a large, conspicuous muscle with a tendonal insertion upon the mesal, basal margin of the trochanter, and originating partly on the posterior wall of the mesothoracic phragma and partly on the scutum. A branch of this muscle (62b) inserted upon the same tendon extends to the posterior face of the mesothoracic furca. Another branch (not shown) originates on the wall of the coxa.

2. Adductor of the coxa (63). A small muscle arising on the posterior of the metasternal furca and extending, posteriorly and ventrally, to the inner, posterior margin of the base of the coxa.

3. Ventral muscle (64). This is a short muscle extending from the posterior surface of the metasternal furca to the postcoxal bridge.

4. Tergal remoter of the coxa (65, Fig. 107). A muscle arising on the anterolateral corner of the scutum, inserted by means of a tendon on the lateral rim of the base of the coxa just behind the pleural articulation.

5. A broad, flat muscle (66) inserted on the anterior rim of the base of the coxa; origin on the anterior margin of the episternum.

6. A muscle (67) extending from the trochantin, attached by a tendon to the anterolateral corner of the scutum.

7. A muscle (68) extending from the precoxal bridge to the anterolateral corner of the scutum.

8. A short, narrow muscle (69, Fig. 108) extending from the pleural apodeme to the anterior notal wing process.

The following muscles have their insertion upon the axillary sclerites of the wing.

1. A muscle (70) extending from the lateral shelf of the base of the coxa just behind the pleural articulation to a tendon inserted on the second axillary sclerite.

2. A muscle (71, Fig. 117) extending from the rim of the base of the coxa just behind the pleural articulation to the posterior lever of the third axillary sclerite.

3. A muscle (72) arising on the ventral margin of the anepimeron and inserted on the anterior lever of the third axillary.

## ABDOMINAL SEGMENTS OF AUCHENORHYNCHA

The abdomen of auchenorhynchous Homoptera consists of eleven distinct segments, and the first eight abdominal segments bear spiracular openings. In the past, the proper enumeration of the abdominal segments has sometimes caused confusion, due in large part to the modifications of structure of the two basal segments which form the articulation between the thorax and the remainder of the abdomen. A reduced sclerotization of the terga and sterna of these two segments, and the development of extensive intrasegmental areas of membranization have been largely responsible for the difficulty of delineating the true segmental limits. The picture has been further complicated by the fact that the metathoracic postnotum, usually separated from the thorax by a well defined membranous area in other paurometabolous insects, frequently forms a complete ring with the metathoracic postcoxal bridges which is firmly united with the thorax.

The true segmental limits of the abdomen are marked internally by the intersegmental ridges upon which the dorsal and ventral longitudinal muscles are attached. Externally these intersegmental ridges may be marked by lines or sutures, termed the antecostal sutures, which indicate the primary segmentation. The flexibility of the primary segments has been brought about by a comparatively narrow intrasegmental membranization of the posterior portion of the primary segment, which has resulted in a functional or secondary segmentation. Normally the primary segment between two antecostal sutures, or intersegmental ridges, consists of a wide, anteriorly-sclerotized plate followed by a comparatively narrow, posterior membrane, which is in turn followed by a very narrow rim of sclerite, sometimes absent, just before the succeeding intersegmental ridge. It will be seen that in the basal segment of the representatives of the Auchenorrhyncha under discussion, the primary segment sometimes consists of a narrow anterior rim of sclerite, followed by a wide intrasegmental membrane, and a narrow or wide posterior sclerite. Other modifications of the first and second segments will be discussed in the descriptions of structure which follow. In general, it may be pointed out that where the enumeration of abdominal segments presents difficulty, it is possible to get one's bearings by locating the eighth abdominal segment which bears the last pair of abdominal spiracles.

### *Scolops pungens*

*Visceral Abdominal Segments.* The partially distended abdomen of a female is shown in lateral view in figure 119. The postnotum (pnt<sub>3</sub>) is a

broad sclerite stretching across the dorsum, broadly united to the epimeral regions ( $epm_3$ ) on each side. The first tergite (It) consists of a narrow anterior margin of sclerite firmly united with the postnotum, and a larger, bilobed posterior sclerite. These sclerotized regions are separated by a narrow membranous area. The bilobed areas on either side are united dorsomesally by a narrow sclerite, while the anterior of the bilobed sclerites unites with the anterior rim of the first tergite, which is in turn united to the postnotum. The first spiracle ( $sp_1$ ) is located in the membranous tergal region just behind the posterolateral corner of the postnotum. The second tergum (IIt) consists of a broad, anterior sclerite separated from a smaller posterior sclerite by a membranous region. Laterally, a small arm of sclerite unites the anterior and posterior tergites of the second tergum. The second spiracle ( $sp_2$ ) is located in the anterolateral membrane of the second tergum. The narrow posterior sclerotized portion of the second tergum is firmly joined to the broad sclerotized region of the third tergum. The terga of segments three to eight are uniform, each consisting of a broad, anterior sclerite, and a posterior membrane. The spiracles of these segments are located in the membranous area between the lateral margins of the median tergites and the laterotergites (ltg).

The lateral sclerotized regions below the spiracles are regarded as laterotergites in view of the fact that in other fulgorids the spiracles are located in the upper halves of these sclerites. According to the studies of Snodgrass, the dorsopleural line, which demarks the lower limits of the dorsum, or tergal region, is always formed below the spiracles. Since the spiracles do occur in these lateral sclerites in other fulgorids, it would appear that these sclerites belong to the terga, and are consequently here termed laterotergites.

Ventrally the first sternal segment (Is, Fig. 118) consists of a narrow anterior semicircular sclerite which appears to arise from the region where the posterolateral corner of the postnotum meets the epimeron, and a narrow, median, posterior sclerite, separated by a membranous region. The second sternal segment (IIs) likewise consists of narrow anterior and posterior sclerites separated by a membranous region. Laterally this posterior sclerite of the second sternal segment broadens and fuses with the laterotergite. Sternal segments three to seven consist of broad, anterior sternal plates, each followed by a membranous region. It should be mentioned that these definitive sternal plates are evidently composite plates, formed by the union of the primary sterna with the lateral pleural regions. Morphologically then, these definitive sternal plates are coxosterna or pleurosterna.

*The Female Genitalia and Terminal Abdominal Segments.* Examina-

tion of the structural parts of the ovipositor of *Scolops pungens* will indicate that the fulgorids have retained an exceedingly primitive form of this organ. The eighth tergum (VIII<sub>t</sub>, Fig. 131), although reduced in size, possesses the normal structure of the preceding terga. The definitive eighth sternal plate, however, has become modified. It consists of two lateral halves (1<sub>l</sub><sub>vf</sub>, Fig. 132) separated medially by a membranous area. These give rise at their posteromesal angles to the arms or first valvulae (1<sub>v</sub><sub>l</sub>) of the ovipositor. It can be seen that the separate halves of the definitive eighth sternal plate represent the highly modified first valvifers of the more specialized ovipositors of other families of Auchenorrhyncha.

The ninth tergal plate (IX<sub>t</sub>) gives rise at its lateral margin to a pair of elongated sclerites which extend ventrally. The anterior of these lateral branches of the ninth tergum bends posteriorly and unites with the dorsal edge of the sclerotized portion of the first valvula. As will be seen later this lateral branch of the ninth tergum represents the origin of the inner ramus (1<sub>r</sub><sub>i</sub>) of the first valvula. The posterior, lateral branch of the ninth tergum (2<sub>l</sub><sub>vf</sub>) gives rise ventrally to the second valvula (2<sub>v</sub><sub>l</sub>) and to the broad bilobed flaps dorsally which form the third valvula (3<sub>v</sub><sub>l</sub>). It would appear that this posterior lateral arm of the ninth tergum represents the second valvifer of the specialized homopteran ovipositor.

The nature of the terminal abdominal segments in the fulgorids is distinct from that found in the cicadas, cercopids, cicadellids, and membracids. Posteriorly, the ninth tergum forms a narrow ring which runs ventrally beneath the tenth segment. The tenth segment (X) forms a broad flaplike plate which extends over the dorsal margins of the third valvulae. Its dorsal surface contains a hollowed area in which the circular eleventh segment (XI) rests. The eleventh segment bears a single posterior projection which is termed the anal style (as). It has been suggested that the anal style may represent the fused cerci of orthopteroid insects. The anus opens caudally on the eleventh segment between the base of the anal style and the overhanging posterior margin of the eleventh segment.

*The Male Genitalia and Terminal Abdominal Segments.* The ninth segment (IX, Fig. 133) of the male consists of a single sclerotized plate which forms a complete ring around the abdomen. Protruding caudoventrally from the membranous area behind the sclerotic ring of the ninth segment is a pair of large, blunt parameres (pm), each with a hooked projection on the dorsal margin. Above the parameres is the aedeagus (aed). It consists of a basal ring of sclerite from which a pair of lateral, apically bifurcating, arms are given off posteriorly. Above and below these lateral arms, the aedeagus is membranous. The opening of the

aedeagus, or gonopore (gnp), lies in the membranous lobe above. Between the base of the aedeagus and the base of the parameres, there is present a median, inverted Y-shaped sclerite, or basal plate (not shown). The stem of the Y forms an elongate process which extends to the base of the aedeagus, and each short arm of the Y-shaped basal plate articulates with the base of a paramere. It should be noted that the bases of the parameres do not possess apodemal processes which extend into the body cavity as occur in the cercopid, cicadellid, and membracid. Above the aedeagus is the flaplike tenth segment (X). Both the tenth and eleventh (XI) segments are generally similar to the corresponding segments of the female.

An excellent, comprehensive study of the comparative structure of the male genitalia of Rhynchota, including the Auchenorhyncha, has been made by Singh-Pruthi (1924).

### *Tibicina septendecim*

*Visceral Abdominal Segments.* The general structure of the abdomen of the cicada has been adequately covered by other writers, but is included here, for its comparative value, with the other representatives of the Auchenorhyncha which are discussed. The female abdomen of *Tibicina septendecim* is shown in lateral view in figure 121. The postnotum (pnt<sub>3</sub>) is a narrow sclerite extending to the epimera on each side. The first abdominal tergum (It) consists of two sclerotized portions separated by a membranous area. A narrow, anterior sclerotized margin of the first tergum is united to the posterior margin of the postnotum, while the wider posterior sclerite is joined to the anterior edge of the second tergum. These sclerotized portions of the first tergum are joined laterally. The first abdominal spiracle (sp<sub>1</sub>) lies in the anterolateral corner of the first tergum immediately behind the postnotum.

Tergal segments two to eight consist of broad, arched plates of sclerite anteriorly, followed by posterior segmental membranes. The eighth tergal segment is wider than the terga of the preceding visceral segments.

The first abdominal sternum (Is, Fig. 120) consists of a median, pentagonal plate fused with the posterior margins of the metathoracic post-coxal bridges (pocx<sub>3</sub>). It is divided into two parts, the posterior of which folds into the tympanal cavity. The second sternum (IIs) also consists of two parts. An anterior, median rectangular plate, united with the posterior margin of the first sternal plate, likewise folds into the tympanal cavity and sends out a pair of narrow arms laterally. The second pair of abdominal spiracles (sp<sub>2</sub>) is located in the lateral expansions of the distal ends of these arms. Between these lateral arms of the anterior half of the second sternum and the anterior margin of the posterior half



lie the tympana (typ) or so-called "mirrors," of the auditory organ. The auditory capsule (au) which contains an innervated sense organ, or chordotonal organ, is a tubercle-like, rounded swelling with a slit-shaped membrane on the ventrolateral portion of the second abdominal tergite.

The first two abdominal segments of the male are generally similar in structure to those of the female, except for those modifications of structure associated with the presence of the sound-producing organs peculiar to the male. The ventrolateral portions of the first abdominal tergum are modified to form the large, oval membranous areas, or tymbals (tyb, Fig. 58), which bear conspicuous, parallel, riblike markings.

It has been previously mentioned that the metathoracic epimera of the male are produced posteriorly to form the opercula (opc, Fig. 61) which cover the tympanal chambers. The posterior half of the first abdominal sternum is longer, and the membranous area between the lateral arms of the first and second sterna is larger, than the corresponding parts in the female, so that the tympanal cavity of the male is of greater dimensions than that of the female. The V-shaped lateral arms of the anterior portion of the second sternum are wider and stronger than the homologous arms of the female. It should be noted that Myers (1928), in his comparative studies of the Cicadidae, has followed the error of Vogel in considering these arms as "differentiated anterior parts of the first sternite" and the tympana as "differentiated posterior parts of the first sternite." The correct homologies have been pointed out by Snodgrass (1933).

The song of the male is produced by the contractions of the powerful V-shaped tymbal muscles which extend from either side of the median, keeled, endoskeletal structure of the anterior portion of the second sternum to a pair of internal, sclerotized plates just beneath the tymbal membranes. A short tendon extends from the center of each sclerotized plate to the posteromesal sclerotized corner of each tymbal. According to Myers the contraction and release of the tymbal muscles causes the tymbal to produce a clicking sound. It is an extremely rapid series of such clicks, said to be amplified by the large abdominal air sacs which open directly to the exterior through the first abdominal spiracles, that produces the "song" of the cicada. As in the female, there is an auditory capsule present in the ventral portion of the second abdominal tergum. In the female (Fig. 121), it may be seen that the sterna of segments three to six consist of broad, anterior definitive sternal plates, each of which is followed by a narrowed membranous area. Laterally the sternal plates are united with the tergal plate, each forming a complete ring around the abdomen. The spiracles of these segments are located in the anterolateral corners of the sterna, just beneath the lateral margin of the

tergal plates. The sternal plate of the seventh segment is deeply and broadly notched along its posterior margin.

Following a preliminary discussion of the nature and composition of the abdominal segments of insects, Myers (1928) concludes that each of the abdominal segments in a cicada consists of "a strongly over-arched tergite meeting an entirely ventral sternite, which bears the spiracles," and apparently considers that the pleural areas are not included in the definitive sternal plate. As has been noted, the first valvulae of the fulgorid ovipositor arise from the first valvifers, or limb base of the eighth segment, which are homologous with the lateral portions of the definitive sternal plates of the preceding segments. There is no question here that the pleural regions are incorporated into the definitive sternal plates of the fulgorid. Unless it can be shown that the cicadas represent a special group among the Auchenorhyncha in which the definitive elements of the abdominal segments differ from those of the other families, there would seem little reason to consider that the segmental elements of the cicadas consist only of tergal and sternal portions.

*The Female Genitalia and Terminal Abdominal Segments.* The terminal abdominal segments of the cicada are shown in lateral view in figure 134, with the sclerites somewhat displaced to show their relationship. The eighth tergal plate (VIIIIt) is generally similar to the preceding tergal plates, except for the fact that it abruptly tapers at its lateroventral margin. In the membranous region beneath the lateroventral margin of the eighth tergal plate lies the eighth abdominal spiracle. Below this is the first valvifer (1vlf), which gives rise at its anteroventral margin to the first, or ventral valvula (1vl) of the ovipositor. Two rami, or sclerotic rods, which run along the ventral and dorsal margins of the first valvula strengthen it, and the dorsal or inner ramus forms a track along which the second or inner valvula (2vl) of the ovipositor moves. The dorsal or inner ramus of the first valvula is given off by the small plate (rp) between the first valvifer and the anteroventral angle of the ninth tergite, which plate is united with the ninth tergal plate. The first valvula is thus united with the ninth tergal plate by means of the inner ramus and ramal plate.

The second valvifer (2vlf) is also joined with the ninth tergal plate. The union, of the ramal plate and the second valvifer, with the ninth tergal plate, is a condition apparently homologous with the union of the corresponding parts of the fulgorid ovipositor with the anterior and posterior lateroventral arms of the ninth tergal plate.

The second or middle valvulae (2vl) are borne by the anterior margins of the second valvifers, while the posterior margins give rise to the third or dorsal pair of valvulae (3vl). The second valvulae, united along

their dorsal edges and grooved ventrally, fit within the first valvulae, and together provide a passage for the eggs. The third valvulae are a pair of flaplike structures into which the terminal portions of the ovipositor are withdrawn when at rest. Snodgrass has pointed out that the genital chamber of the female has two openings, an anterior large opening (gnp, Fig. 134) in the membranous vestibulum behind the seventh sternal plate, and a smaller posterior opening between the bases of the second valvulae (not shown).

The terminal abdominal segments consist of a short annular tenth segment (X, Fig. 137) which bears a ring of sclerite, widening ventrally, and the smaller eleventh segment (XI).

*The Male Genitalia and Terminal Abdominal Segments.* The eighth tergal plate of the male (VIII<sub>t</sub>, Fig. 136) has no special modification. The eighth sternal plate (VIII<sub>s</sub>), however, is a shovel-like structure extending considerably posterior of the eighth tergal plate. Between these plates lies the eighth spiracle (sp<sub>8</sub>). The ninth segment (IX) is represented by a circular ring of sclerite sometimes termed the pygophor, or pygofer. The ninth segment and aedeagus (aed) are shown in caudoventral view in figure 138. The pygophor is seen to be broadly ringed dorsally and narrowed ventrally, with toothed, caudoventral margins. The aedeagus is an elongate, sclerotized tube arising in the caudal membranous region of the pygophor. A basal plate (bp), bearing a pair of divergent arms, is united with the base of the aedeagus. The genital opening or gonopore (gnp) is located apically in the expanded membranous region of the aedeagus. A pair of hooklike sclerotized structures are present in this membranous area, one on either side of the gonopore.

The aedeagus is kept in place by the paired ventral claspers (vc) of the tenth segment. The tenth and eleventh segments are shown laterally in figure 130. The ventral claspers are large, hooked sclerotized appendages, firmly united with the sclerotized ring of the tenth segment. The eleventh segment (XI) is circled by a narrow band of sclerite and bears the anal style (as). If the anal style represents the cercus of the eleventh segment, the small oval sclerotized plate at its base may be the base of the cercus, or basicercus. It should be noted that in the male genitalia of the cicada, both the parameres and subgenital plates are absent, although parameres are present in the primitive cicada *Tettigarcta tomentosa*.

### *Lepyronia quadrangularis*

*Visceral Abdominal Segments.* The sclerotized portion of the first abdominal tergum (It, Fig. 123) of the female cercopid, *Lepyronia quadrangularis*, is mainly confined to the lateral area, in which a small anterior plate united with the posterior margin of the postnotum is bridged with

a large posterior plate. The posterior plates of the first tergum on each side are united by a narrow rim of sclerite across the mid-dorsal line. The small, first abdominal spiracular opening ( $sp_1$ ) located in the membranous area immediately behind the metathoracic postnotum is inconspicuous and sometimes difficult to locate.

The anterolateral margin of the second abdominal tergal plate (II<sub>t</sub>) is united to the first tergal plate, and its posterior border is firmly joined to the third tergal plate, so that no segmental movement is possible between the second and third terga. The second abdominal spiracle ( $sp_2$ ) is located at the anterolateral corner of the second tergal plate. The third tergal segment (III<sub>t</sub>) consists of a sclerotized, broad, anterior plate and a posterior membrane. The third spiracle is located in the anterolateral corner of the definitive sternal plate. In segments four to six there is a partial membranization of the tergal plate laterally to form laterotergites (ltg). The seventh and eighth tergal segments are of normal structure. The fourth to eighth abdominal spiracles are located in membranous folds between their tergal and sternal plates.

The first abdominal sternum (I<sub>s</sub>, Fig. 122), consisting of a sclerotized, anterior, median plate and a posterior, narrow fringe of sclerite, is located between the postcoxal bridges ( $pocx_3$ ) and posterior intersegmental line (is). The lateral areas are membranous. The second abdominal sternum (II<sub>s</sub>) consists of a narrow anterior rim of sclerite which borders the intersegmental line, joined by two lateral arms to a wider, posterior sclerite. The definitive sternal plate of the third segment (III<sub>s</sub>) has a median tubercle-like projection on its posterior margin. Sternal segments four to seven are similar in structure, each consisting of a wide, anterior plate of sclerite followed by a posterior, segmental membrane.

*The Female Genitalia and Terminal Abdominal Segments.* The structural elements of the female genitalia of the cercopid, *Lepyronia quadrangularis*, are similar to those of the cicada. In figure 139, the parts of the ovipositor are shown in almost their normal resting position. In figure 128, these parts have been considerably displaced to show their relationship. The first valvifers (1vlf) give rise ventrally to the paired, first valvulae (1vl). The second valvifers (2vlf), joined to the ninth segment (IX), give rise anteriorly to the second valvulae (2vl), the basal halves of which are united dorsally, and posteriorly to the flaplike third valvulae (2vl). The second valvulae move along a sclerotized track on the inner faces of the first valvulae formed by the inner ramal arms (lri), of the first valvulae. The inner ramal arm of each first valvula is joined to the ramal plate (rp) which is in turn united with the anterior margin of the sclerotized plate of the ninth tergite (IX<sub>t</sub>).

The terminal abdominal segments (Fig. 139) of the cercopid are

short. The tenth segment (X) is evidenced by a narrow ring of sclerite. The eleventh segment (XI), in addition to a complete anterior ring of sclerite bears a saddle-shaped sclerite, and a pair of small plates at the base of the anal styles. The anus (an) lies between the bases of the anal styles (as). Ventrally, between the paired anal styles, there is present a median sclerite. All of these sclerotized portions of the terminal segments of *Lepyronia quadrangularis*, unlike the corresponding parts of some of the other Auchenorhyncha, are well sclerotized and distinct.

*The Male Genitalia and Terminal Abdominal Segments.* The ninth segment (IX, Fig. 140) of the male consists of a complete ring of sclerite to which the ventral subgenital plates (gp) are united. A small posterior sclerite is separated dorsally from the main ring of the ninth segment. Protruding caudally from the membrane above the subgenital plates are the paired parameres, the basal plate and the aedeagus. The relationship of these parts is shown in figure 129. The parameres (pm) are paired structures, on either side of the basal plate (bp), each bearing several hooklike spines or projections. The basal plate is triangular in shape and bears a membranous area apically from which the base of the aedeagus originates. The aedeagus bears a pair of bifurcating processes apically, between the bases of which is the genital opening or gonopore. A slender median membranous process lies between the two sclerotized bifurcating processes.

The ringed, sclerotic plate of the tenth segment (X, Fig. 140) is larger than that of the female, but in other respects the terminal abdominal segments of the male are similar to those of the female.

### *Aulacizes irrorata*

*Visceral Abdominal Segments.* The visceral segments of the abdomen of the cicadellid *Aulacizes irrorata*, except for the two basal segments, are subcylindrical and of an almost uniform width and breadth. The first tergum (It, Fig. 125) consists of an anterior sclerotized region united with the postnotum (pnt<sub>3</sub>) and a posterior sclerotized region united laterally with the anterior plate by an oblique bridge of sclerite. The first spiracle (sp<sub>1</sub>) lies in the membranous region of the anterolateral corner of the first tergal segment just behind the postnotum. The second tergum (IIIt) consists of an anterior sclerotized region and a narrow posterior rim of sclerite separated by a membranous area. The true limits of the first and second tergal segments are marked by the intersegmental lines (is). The second spiracle (sp<sub>2</sub>) is located in the membranous region immediately below the anterolateral corner of the broad anterior sclerite of the second tergum. The terga of segments three to eight are generally uniform in structure, each consisting of a wide, anterior sclerotized plate

and a narrow, posterior segmental membrane. Each tergal plate of these segments is differentiated into a laterotergite (ltg) bearing a spiracle in its anterolateral corner. The laterotergite of the third segment is somewhat enlarged and articulates with the posterior margin of the metathoracic epimeron.

The basal sternal segments are shown in figure 124. The first sternal segment (Is) consists of a median sclerotized area, between the metathoracic postcoxal bridges (poxc<sub>3</sub>) and the anterior bar of sclerite of the second sternal segment, and lateral membranous areas. The anterior bar of the second sternal segment (IIs) is followed by a membranous area and a broad W-shaped sclerite. The anterior and posterior regions of sclerite of the second sternum are united laterally. The third to sixth segments consist of anterior, broad, rectangular plates of sclerite followed by membranes. The seventh segmental plate of the female abdomen, which covers the valvifers and bases of the valvulae of the ovipositor, has a convex posterior margin.

*The Female Genitalia and Terminal Abdominal Segments.* The first valvifers (1vlf, Fig. 141) bear the flat, first valvulae (1vl) of the ovipositor. On the ventral edge of the first valvula is a thickened rod of sclerite, the outer ramus (lro). The inner ramal arm (lri) which connects with the ramal plate (rp) runs along the middle of the inner face of the first valvula and gradually disappears toward the apex. The ramal plate is broadly united with the anterolateral region of the tergal plate of the ninth segment (IXt).

The second valvifers (2vlf) bear the second, or middle valvulae (2vl) from their anterior regions and the third or dorsal valvulae (3vl) from their posterior regions. The second valvulae are membranous basally, flatly compressed, have strong saw-toothed dorsal margins apically, and are separate. An outer ramus (2ro) runs along the ventral edge of each second valvula. The dorsal half of the inner face of each first valvula is closely appressed to the ventral half of the outer surface of each second valvula, and it may be possible that the first and second pairs of valvulae act in unison as one pair of appendages. In their resting position they are sheathed by the third valvulae.

The tenth segment (X) is a short, ringed segment, only partially sclerotized ventrally. The eleventh segment (XI) bears an anterior ring of sclerite, two small sclerites on each side and the apical, paired anal styles (as) which are united along their median edges by a membrane.

*The Male Genitalia and Terminal Abdominal Segments.* The ninth segment (IX, Fig. 142) of the male is completely ringed by sclerite. Posteroventrally the paired subgenital plates are united with the ninth annular sclerite. Exserted from the caudoventral membranous region of

the ninth segment are a pair of short, bluntly rounded parameres (pm). Lying medially between the parameres and extending to the base of the aedeagus (aed) is the single, elongate, basal plate (bp). Proximally this basal plate bears a pair of diverging arms, and in this species, it can be seen that the arms of the basal plates articulate with the inner, basal parts of the parameres. The aedeagus bears a pair of diverging sclerotized, sharply pointed arms dorsally. Anterior to these arms and arising at their base is a median projection, sclerotized anteriorly and laterally, but membranous posteriorly, which bears the opening, or gonopore (gnp), of the aedeagus apically. Between the aedeagus and dorsoposterior margin of the ninth annular sclerite on each side, and apparently differentiated from it, is a pair of knoblike sclerotized plates. The tenth abdominal segment (X) is almost entirely reduced to membrane, while the parts of the eleventh segment are essentially identical to those of the female.

### *Ceresa bubalus*

*Visceral Abdominal Segments.* The abdomen of the female membracid, *Ceresa bubalus*, shown in lateral view in figure 127, is highly arched, somewhat compressed laterally, tapers posteriorly, and is suggestive of the structure and shape of the abdomen of the cicada, *Tibicina septendecim*. The first tergum consists of an anterior rim of sclerite united with the metathoracic postnotum (pnt<sub>3</sub>), and a posterior sclerite united with the anterior margin of the tergal plate of the second segment (II<sub>t</sub>). These sclerotized regions of the first abdominal tergum are joined by an oblique bridge of sclerite laterally. The intervening areas are membranous. The first abdominal spiracle (sp<sub>1</sub>) is located laterally in the anterior rim of sclerite immediately behind the metathoracic postnotum.

The second tergal segment (II<sub>t</sub>) consists of a single plate of sclerite, the anterior half of which rises abruptly upward to meet the posterior half of the plate. The latter half is bent at approximately right angles to the anterior portion. The posterior margin of the second tergal plate is rigidly united to the third tergal plate, there being no intervening segmental membrane. The second abdominal spiracle (sp<sub>2</sub>) lies in the membrane below the anterolateral region of the second tergal plate.

The third to seventh abdominal terga, except for a successive reduction in width, are uniform, each consisting of a highly arched anterior plate of sclerite followed by the posterior segmental membrane. The eighth tergum is wider than the preceding segment, and tapers anteroventrally. A ventrolateral region of each of tergal plates three to eight bends underneath the abdomen, in a plane with the sternal plates, to form the laterotergites (ltg). The spiracle of the third segment is located in the anterodorsal corner of the laterotergite, while the spiracles of the

succeeding four segments are each located in the anteroventral corner of their corresponding laterotergites. The eighth abdominal spiracle is located dorsocentrally in the eighth laterotergite.

The first sternal segment (I<sub>s</sub>, Fig. 126) consists of lateral membranous areas and a median, trapezoid-shaped plate of sclerite. The smaller anterior margin, and the wider posterior margin of this median plate respectively are united with the metathorax and the second sternal plate. The second sternal segment (II<sub>s</sub>) consists of anterior and posterior plates of sclerite separated by a middle region of membrane. The posterior plate of the second sternum is united with the sternal plate of the third segment (III<sub>s</sub>). Each of segments three to six consists of an anterior rectangular plate of sclerite separated by membranous regions from its own laterotergites and the succeeding segment. The seventh definitive sternal plate is longer than those of the preceding segments and its posterior margin is notched medially.

*The Female Genitalia and Terminal Abdominal Segments.* A lateral view of the genital segments and the parts of the ovipositor is shown in figure 149. The seventh sternal plate partly covers the paired first valvifers (1<sub>vlf</sub>). The first valvifer gives rise to an outer, ventral blade, or first valvula (1<sub>vl</sub>) of the ovipositor. The anterior regions of the second valvifers (2<sub>vlf</sub>) bear the inner middle blades, or second valvulae (2<sub>vl</sub>) of the ovipositor. The second valvulae are united dorsally, forming a ventral groove for the passage of the eggs, and have a dorsal, saw-toothed edge apically. The flaplike dorsal, or third valvulae (3<sub>vl</sub>), which sheath the blades of the ovipositor, arise from the posterior region of the second valvifers. The relationship of the second and third valvulae to the second valvifer is shown in figure 147.

Each ventral blade of the ovipositor possesses both an outer and inner ramus, while the middle blade possesses only an outer ramus. The relationship of these rami, the other parts of the ovipositor and the ninth tergite are best seen in internal view shown in figure 148. The outer rami (1<sub>ro</sub>) run along the ventral margin of the first valvulae and form a track by means of which the first valvulae slide upon one another. The inner ramus (1<sub>ri</sub>) which runs along the dorsal edge of the first valvula arises from the ramal plate (rp) which is united with the anterolateral corner of the ninth tergite (IX<sub>t</sub>). The outer ramus (2<sub>ro</sub>) of the second valvula runs along the ventral edge of the latter, and together with the inner ramus of the first valvula forms a track, one on each side, by means of which the inner valvulae slide on the outer valvulae. The second valvifer is connected by a short thick bar of sclerite to the inner margin of the anterolateral corner of the ninth tergite.



In the ventral view of the genitalia shown in figure 144 the seventh sternal plate has been pulled back to expose the valvifers and the bases of the valvulae. The genital opening, or gonopore (gnp) by means of which the eggs pass from the median oviduct to the ovipositor, is shown between, and at the base of, the second valvulae.

The terminal abdominal segments are shown in figure 145. These segments in the female present a rather unusual arrangement. The posterior margins of the ninth tergal plate are bounded by an annular membranous region which invaginates within the ninth segment and gives rise to a sclerotized cylindrical tube which is apparently a part of the tenth abdominal segment (X). Within this outer portion of the tenth segment is another tube, somewhat less strongly chitinized, but its anterior margin is rigidly united with the anterior margin of the outer, tubelike portion. This inner, tubelike segment is apparently a posterior portion of the tenth segment. The posterior portion of the tenth segment is followed by a membranous section, followed in turn by another annular sclerite which is a part of the eleventh segment (XI). The remainder of the eleventh segment consists of the anal styles (as) and small paired, basal sclerites.

*The Male Genitalia and Terminal Abdominal Segments.* The male genitalia are shown in lateral view in figure 151. The ninth tergum (IXt) consists of a saddle-shaped tergal plate, broad dorsally and narrowing laterally. On each side the caudoventral region of the ninth tergal plate is differentiated into a flaplike plate bearing an immovable spine (ts). Ventrally, the ninth segment forms a single subgenital plate (gp), which is notched posteriorly. It is shown in ventral view in figure 154. The subgenital plates of other species of membracids, belonging to the genera *Aconophora*, *Platicotis*, *Campylenchia*, *Enchenopa*, and others, consist of either entirely separate paired genital valves and a separate sternal plate, or show these parts in varying degrees of fusion. It therefore appears that the subgenital plate of *Ceresa bubalus* consists of the fused genital valves and ninth sternal plate.

Above the subgenital plate are the elongate, paired parameres (pm). Between the bases of the parameres and extending to the base of the aedeagus is the median basal plate (bp). The aedeagus (aed) is a median, hollow, rodlike structure with an elongate, vertical membranous region caudally which bears the slit-shaped gonopore (gnp). The aedeagus is shown in figure 155, in caudal view. There is a median sclerotized plate, apparently a part of the basal region of the aedeagus, extending to the anteroventral margin of the tenth segment.

The terminal abdominal segments of the male differ from those of the female. The tenth segment (X, Fig. 151) bears none of the modifications of the female, but consists of an annular sclerite followed by a membranous region. The eleventh segment (XI) also has an anterior annular sclerite and paired anal styles (as). The relationship of the terminal abdominal segments and genitalia is shown in caudal view in figure 150.

## THE ABDOMINAL MUSCULATURE OF *CERESA BUBALUS*

*Muscles of the Visceral Abdominal Segments.* The muscles of the abdominal segments of *Ceresa bubalus* are shown in figure 143 and may be classed in three general groups. These are the dorsal longitudinal muscles, the ventral longitudinal muscles, and the lateral muscles. The dorsal longitudinal muscles are in some segments subdivided as median dorsal longitudinal muscles and lateral dorsal longitudinal muscles. These are as follows:

### DORSAL LONGITUDINAL MUSCLES (d).

These muscles extend between the intersegmental ridges, or antecostae, of successive terga, the intersegmental ridges being present on the anterior margins of the tergal plates. In the middle, visceral abdominal segments these muscles are separated into two groups, the median dorsal longitudinal muscles (dm) found on either side of the mid-dorsal line of the terga, and the lateral dorsal longitudinal muscles (dl) extending across the lateroventral portions of ventral longitudinal muscles (v).

### VENTRAL LONGITUDINAL MUSCLES (v).

These muscles extend from the intersegmental ridges, or antecostae, of the successive sterna, the intersegmental ridges being present on the anterior margins of the definitive sternal plates. The muscles are located in the lateral regions of the sternal plates.

### LATERAL MUSCLES (l).

These muscles extend from the lateral margins of the definitive sternal plates to the tergal plates. The lateral muscles extending from the lateral margins of the definitive sternal plates of the typical abdominal segments consists of two groups, one a short, external, lateral muscle (le), extending to the laterotergite, the other a longer internal muscle (li) extending to the lower region of the tergal plate.

Within the first segment there are two bands of median dorsal longitudinal muscles extending from the intersegmental ridge on the posterior margin of the metathoracic postnotum to the succeeding intersegmental line. A ventral longitudinal muscle (v) extends from the metathoracic furcasternum to the anterior of the intersegmental line between the first and second abdominal sterna. A lateral muscle extends from anterior of the intersegmental ridge dorsally to the posterior margin of sclerite of the first abdominal tergum. Behind this muscle is another smaller lateral

muscle (not shown) extending from the lateral intersegmental ridge of the sternum to the intersegmental ridge of the second tergal plate.

The dorsal longitudinal bands of muscle of the second segment are grouped together and not differentiated as median and lateral dorsal longitudinal muscles. A lateral muscle extends from the anterolateral margin of the second sternal segment to a ridge on the ventral region of the third tergal plate. The dorsal, ventral, and lateral muscles of the remaining visceral abdominal segments are typically as described in the outline above, except that the dorsal longitudinal bands of muscle of the seventh segment are grouped together, and in the eighth segment they are hardly differentiated as separate bands of muscle. The ventral longitudinal muscles of the seventh segment are absent. There are no muscles associated with the spiracles.

*Musculature of the Female Genitalia and Terminal Abdominal Segments.* Two groups of muscles are associated with the first valvifer of the eighth segment. The first (81), probably a modification of the lateral muscles of the visceral segments, originates on the eighth tergal plate and is inserted on a lateral or dorsal apodeme of the first valvifer. The second group (82) consists of short, thick muscles extending from the posterior wall of the first valvifer to the base of the outer ramus of the second valvula and to the anterior wall of the second valvifer. These muscles may be modifications of the ventral longitudinal muscles of the visceral abdominal segments.

Two groups of muscle are associated with the second valvifer, both taking their origin on the ninth tergal plate. The first, a single large muscle (91), is inserted on an anterior apodeme of the lateral, dorsal edge of the second valvifer. The second, consisting of several muscles (92), is inserted on the posterior margin of the second valvifer and the base of the third valvula. In addition there is a short lateral muscle (93) extending from the wall of the apical region of the ninth tergal plate to the caudoventral flap of the ninth tergal plate.

Three small muscles are associated with the tenth segment. These muscles are inserted on the circular margin where the outer, anterior tube and the inner, posterior tube of the tenth segment meet. The first of these (101), inserted mediadorsally on the inner rim of the sclerotized tube of the tenth segment, originates on the dorsal wall of the ninth tergal plate. The second and third muscles (102) are inserted ventrolaterally, and originate on the ventral sides of the ninth tergal plate. These cylindrical sclerites of the tenth segment are apparently incapable of being exerted, telescope fashion, but are limited in their protrusion posteriorly by the membrane between the sclerotized portions of the

ninth and tenth segments. The eleventh segment is probably exerted by the turgidity of the body cavity and the rectum.

*Musculature of the Male Genitalia and Terminal Abdominal Segments.* The muscles of the male genitalia are surprisingly complex and it would therefore seem likely that the copulation of these insects is no mere approximation of the genitalia of the male with those of the female. It would seem, rather, that considerable maneuvering and adroit procedure on the part of the male is required for the achievement of successful mating.

The internal apodemal process of each paramere bears five distinct muscles. These muscles, all of them paired except the last, are shown in figures 152 and 153 and are as follows:

1. A large muscle (94) extending from the dorsal margin of the anterior region of the apodeme to the lateroventral region of the ninth tergal plate.
2. A second muscle (95) from the dorsal margin of the anterior of the apodeme, lying mesad of the one above, extending to the posterior, or dorsal margin of the basal plate.
3. A muscle (96) extending from the ventromesal margin of the anterior of the apodeme to the anterior margin of the subgenital plate.
4. A muscle (97) extending from the underside of the posterior region of the apodeme to the inner face of the base of the subgenital plate.
5. A single transverse muscle (98, Fig. 153) uniting the anterior regions of the apodemes.

The caudal membranous region of the ninth segment which lies between the base of the aedeagus and the base of the subgenital plate encircles the base of the parameres on each side. This circle of membrane which is formed around the base of the paramere gives rise internally to a tendon upon which is inserted a fan-shaped muscle (99, Figs. 152 and 153) which originates on the lateral wall of the ninth tergal plate. In addition, a pair of muscles (100), on either side of the median sclerotized process between the aedeagus and the base of the tenth segment, extend to the caudoventral flaps of the ninth tergal plate.

Two pairs of muscles (104, 105, Fig. 153), inserted laterally on the basal margin of the annular sclerite of the tenth segment, have their origins in the dorsal wall of the ninth tergal plate.

## THE PHYLOGENY OF AUCHENORHYNCHA

### Phylogenetic Considerations of Previous Authors

Concepts of phylogeny, although almost entirely absent in the minds of early nineteenth century insect taxonomists, were nevertheless reflected to some small extent in their systems of classification. Thus, the general relationship of those groups of insects belonging to the Homoptera, and those belonging to the Heteroptera was embodied in Westwood's classification of 1840. Similarly, Dumeril (1806) had indicated the relationship within the Homoptera that existed among the Auchenorhyncha and among those groups later known as the Sternorhyncha. It must be remembered, however, that during the nineteenth century, insect classifications were, like the classifications of other animals, based primarily on one or two key characters, such as the wings and mouthparts. Some success was nevertheless achieved in delineating the ordinal and subordinal relations of insects on this basis, but in attempting to extend the use of one or two key characters into familial and lesser categories the consequent failure to represent phylogenetic relationship was more evident.

Osborn (1895) took issue with the prevailing system of his day of placing the Coccidae as the lowest and presumably the simplest group of the Homoptera. Separating the Homoptera into two subdivisions, Sternorhynchi and Auchenorhynchi, he claimed that there is every reason to consider the Sternorhynchi as the derivative form and the Auchenorhynchi as the basal form of the phylogenetic tree. He wrote that "The position of the rostrum upon the sternum, or, more properly, the coalescence of the rostrum with the sternum, must certainly be considered as a more specialized condition than the free form and, in fact, the derivative form, the consolidation of the rostrum with sternum being the result of the close approximation of beak and sternum resulting from their food habits."

Within the Auchenorhyncha, Osborn considered the Cicadidae to have the most generalized condition of wing venation and body structure, while the Membracidae, "except in the extremely specialized pronotum are easily seen to be related to the Cicadidae, and naturally take their position next to them. The Fulgoridae, while possessing specializations of the head, are in thoracic structure and venation more generalized than the remaining families, and while possessing many highly differentiated subgroups, may very probably be interposed between the preceding families and the jassoid division. The Cercopidae in development of the

scutellum and in texture of elytra, as well as in specialization of the tibiae, show characters of rather high rank, and, if placed as subordinate to the Jassoidea, they must at least be considered as a branch of nearly equal or parallel rank."

Since Osborn utilized such terms as "specializations of the head," "generalized," "characters of rather high rank," "subordinate," "nearly equal or parallel rank," etc. without specific meaning, it is not surprising that his concept of relationships within the Auchenorhyncha, as indicated in Chart 1, was entirely erroneous.

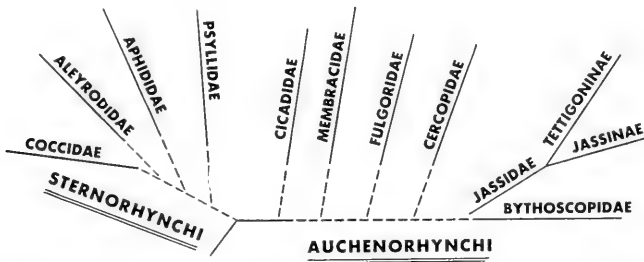


Chart 1. Phylogenetic tree of Homoptera, after Osborn (1895).

Kirkaldy (1910b) pointed out that the interposition of the Fulgoridae between the Cercopidae and the Membracidae is a misconception dating from the earlier studies of Fieber, and was not in the least warranted by the structure or habits of the groups in question. He correctly pointed out that the Fulgoroidea were much more distinct from the rest of the Auchenorhyncha than these latter groups were from each other. In an earlier paper Kirkaldy (1906) concluded that the Fulgoroidea are the "most specialized, highly organized and differentiated" of the Auchenorhyncha, that the Cicadoidea as a whole are of "low estate," and a "slight degree of specialization" is shown by the Tetigonioida (Jassidae, Membracidae and Cercopidae) in almost every point, and that the Membracidae are only Tetigonioida with a highly specialized pronotum. His concept of homopteran relationships is expressed in Chart 2.

As to the paleontological evidence, Handlirsch (1908) pointed out that we can follow the Hemipteroids or Rhynchota up to the Paleozoic; that in the Tertiary all essentially modern families were present and even in the Jurassic the principal groups already appear to be marked out, so that we can assign nearly all Mesozoic forms to the orders Homoptera and Hemiptera (Heteroptera). He writes, "As regards the phylogeny of the groups comprised under the Homoptera, it can in any case be maintained, that the present day forms of fulgorids have retained the most primitive characters. They still have, for example, a simply convoluted

intestine without complicated loops (filter chamber), as occur in the jassids and cercopids, etc. Typical fulgorids are already known to us from the Liassic (Lower Jurassic), indeed in that period are also found forms resembling the jassids\* and a few species which are inclined toward the cercopids and are consequently designated as Procercopidae. Cicadidae first began to be found in the Cretaceous.

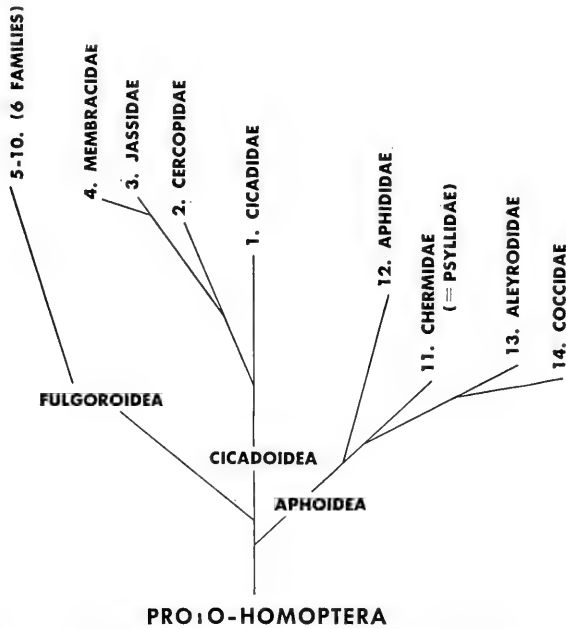


Chart 2. Phylogenetic tree of Homoptera, after Kirkaldy (1910).

“It will not be difficult, to derive the above named families, and the jassids and cercopids as well, from the earlier fulgorids, by the interposition of forms which acquired the characteristic intestinal loops; perhaps these forms were the Procercopidae. The Cicadidae may be derived either from very early cercopids, or also from these Procercopidae, since they too possess the intestinal loops and the characteristic antennae of the families just mentioned. Consequently, I consider the suborder Auchenorrhyncha to be a monophyletic, natural one.”

The complete line of development including the Sternorrhyncha, is, according to Handlirsch, that “From the oldest fulgorids or from the Protohemiptera there developed as early as the Triassic, more specialized

\*Evans (1948) has indicated that “the available evidence would seem to suggest that either true jassoids, or else their immediate ancestors, were in existence during the Permian.”



types (perhaps the Procercopidae), from which presumably the jassids and later the cercopids arose, as did the Psylloidea, and from these latter presumably arose the Coccoidea during the Cretaceous. From cercopid-like forms, may have arisen in the Malm (Middle Jurassic), or soon after, the cicadas, while directly from the fulgorids in the course of the Jurassic arose the Aphidoidea, and presumably the Aleurodoidea in the Cretaceous."

In contrast to the Auchenorrhyncha, Handlirsch maintained that the Sternorrhyncha do not represent a monophyletic group, but a polyphyletic one, and proposed that each of the four families in this group be designated as suborders (though these have superfamily endings), Psylloidea, Aleurodoidea, Aphidoidea, and Coccoidea, of equal rank with the Auchenorrhyncha. His interpretation is expressed in the phylogenetic tree shown in Chart 3.

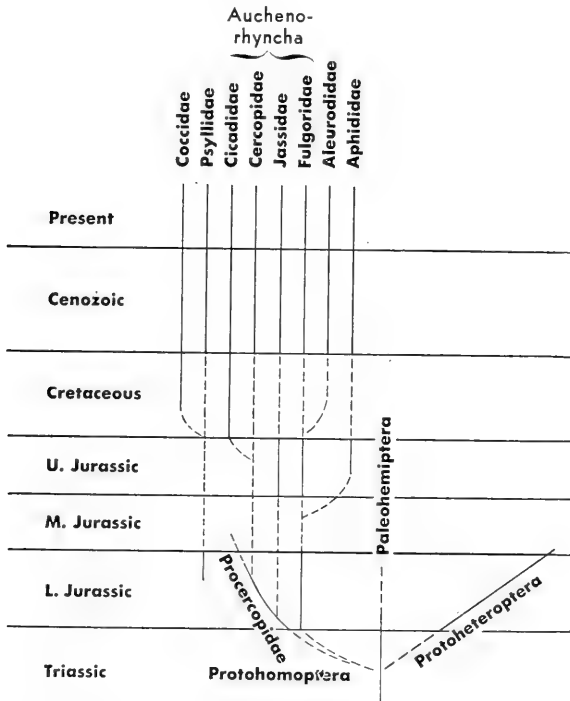


Chart 3. Phylogeny and geological distribution of the Homoptera, after Handlirsch (1908).

Kirkaldy (1910a) took issue with Handlirsch's views on the phylogeny of the Homoptera, particularly as to the derivation of the Aleyrodidae from the Fulgoridae, the placing of both in the same main branch as the

the Aphidae, the separation of all the aforementioned groups from the Psyllidae and the Coccidae, and as to the derivation of the Cicadidae from the Cercopidae, etc. Kirkaldy further disagreed as to the polyphyletic origin of the Sternorrhyncha, maintaining that "if there is any group which is apparently compact, it is the Sternorrhynchous Homoptera."

Taylor (1918) on the basis of a comparative study of the thoracic sclerites of representative Heteroptera-Homoptera, indicated the following relationships of Homoptera, shown by the thorax, without regard to primitiveness:

Cicadidae.....	} Neuropteroid thorax....	} Similar thoracic plan with but few modifications	} Similar general thoracic plan
Jassidae.....			
Aphidae.....			
Psyllidae.....			
Membracidae.....	Specialized prothorax.....		
Cercopidae.....	} Peculiar fusion of metathoracic sclerites and coxae.....		
Fulgoridae.....			
Aleyrodidae.....			

Tillyard (1919), in a paper describing fossil Homoptera, consisting of tegmina from the Upper Triassic of Queensland, concluded that "It would appear proved that the Homoptera became differentiated from a single Palaeo-hemipterous stock, of which *Prosbole* is a representative, in the Middle or Upper Permian. From the same stock the Heteroptera became separated off at a somewhat later period, the oldest true Heteroptera known being the *Dustaniidae* from the Upper Trias of Ipswich. Thus the Homoptera are older than the Heteroptera, as is evident on morphological as well as palaeontological grounds. The separation of the Sternorrhyncha from the Auchenorrhyncha must have taken place before the Upper Trias. The oldest existing family of the Auchenorrhyncha appears to be the Jassidae; the oldest of the Sternorrhyncha are the Psyllidae. Venationally, but not in all other characters, the Jassidae are the older of these two. It may also be pointed out that, after the jassids became differentiated out, the old main stem of the Auchenorrhyncha went on, and continued to be represented by many forms which, *in certain directions*, still preserved archaic characters which the jassids had lost (e.g., the existence of a well developed subcostal vein). Thus there is no difficulty in understanding how the Fulgoroidae and the Cercopidae could have arisen *later in point of time* than the Jassidae, though preserving certain archaic features which the jassids had lost. This is the same problem as that which confronts us in studying the Panorpid orders, in which it is clear, palaeontologically, that the Mecoptera was the first recent order to be differentiated out, though it is, in some

respects, more highly specialized than other orders which arose from the main panorpoid stem *at later dates*, such as the Megaloptera.”

Tillyard’s distinction, between one group of insects that may arise later in point of time, but which preserve certain archaic features which an earlier differentiated group has lost, is a most valuable one—even though I consider his evaluation to be incorrect as applied to the fulgorids, cercopids, and jassids. His ideas on phylogeny are expressed in the diagram in Chart 4.

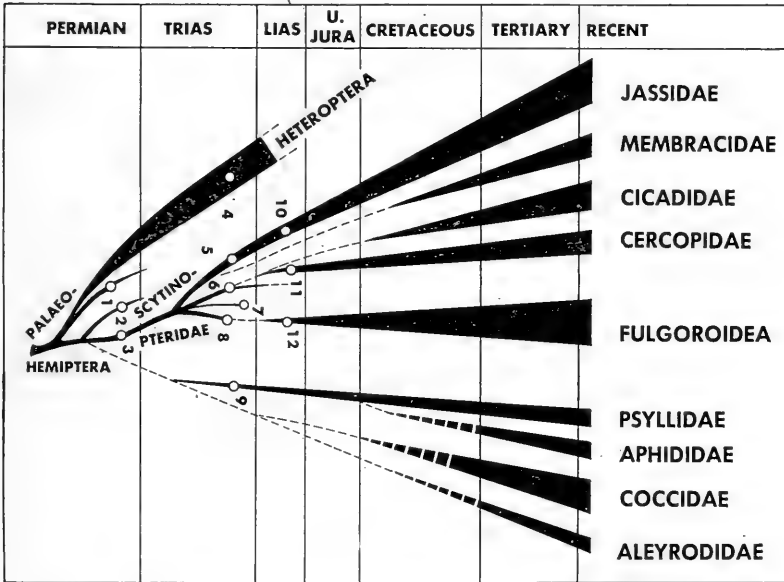


Chart 4. Phylogeny and geological distribution of the Homoptera, after Tillyard (1919). Known fossil types are as follows: 1, *Prosbol*; 2, *Permofulgor*; 3, *Scytinoptera* and *Permoscarta*; 4, *Dunstaniidae*; 5, *Eurymelidium*, *Mesojassus* and *Triassojassus*; 6, *Mesoscytina*, *Mesodiphthera* and *Triassoscarta*; 7, *Ipsvicia*; 8, *Mesocixiinae*; 9, *Triassosylla*; 10, *Archijassus*; 11, *Procercopis*; and 12, *Fulgoridium*.

Singh-Pruthi (1925b), on the basis of an extensive comparative study of the male genitalia of Rhynchota, considered that the “Cicadidae resemble Heteroptera in the form of the VIIIth segment, and in the non-differentiation of the sub-genital plates; the Fulgoroidea also have no sub-genital plates, and moreover, show different grades of aedeagus differentiation parallel to those in Heteroptera. (Still more, most Fulgoroidea, unlike the rest of Homoptera, resemble Heteroptera in not having a complete ovipositor.) But the structure and the position of the basal plates, surrounding the basal foramen or lying on the segmental membrane inside the body cavity, separate the two sub-orders quite dis-

tinctly without any exception. It seems that the heteropterous condition is more primitive, but this cannot be asserted with any certainty unless information about the condition of the basal plates in other orders of insects is available.

“Thus the two sub-orders seem to have a common origin, and are not distinct orders as suggested by some; but they are separated by a good gap, and we must look to palaeontology for some Protohemiptera in which the basal plates are in the intermediate condition.”

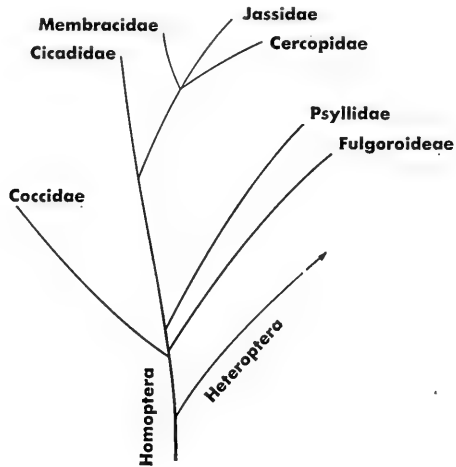


Chart 5. Phylogeny of the Homoptera, after Singh-Pruthi (1925), based on a study of the male genitalia.

Carpenter (1931) described a group of closely related, Lower Permian insects of Kansas, belonging to the fossil family Archescytinidae. He pointed out that the more primitive wing venation of the Sternorhyncha has a reduced anal area and the second anal vein is absent. On the other hand the antennae of Auchenorhyncha, consisting of two short segments plus a bristle or style, are specialized, whereas the antennae of the Sternorhyncha consist of at least three segments and may have as many as twenty-five. As far as the wing venation of the Archescytinidae is concerned, they resemble the Auchenorhyncha, but Carpenter found one species of fossil *Archescytina* which has long antennae consisting of at least twenty-five segments. These insects also have a well developed clavus and three-segmented tarsi, characteristic of Auchenorhyncha. Consequently Carpenter considered that there was hardly justification for placing these Permian insects with the Sternorhyncha, solely on the basis of their antennae. He therefore proposed the erection of a third division, the Paleorhyncha, of equal rank with the Sternorhyncha and

Auchenorrhyncha, "in order to avoid abolishing an outstanding characteristic of the Auchenorrhyncha by expanding the definition of that division to include insects with multisegmented antennae."

Evans (1943) accepted this new division and described a new genus and species, *Austroscytina imperfecta*, belonging to the Archescyntinidae within this division, from the Upper Permian of New South Wales. Later (1948) he pointed out that though it is conceivable that the Archescyntinidae lie close to the line of descent of the Jassoidea, they cannot possibly have been ancestral to the whole superfamily, since the media of the tegmen of the Archescyntinidae is invariably three-branched, and the common ancestor to all the jassoid families must have had a media with four branches. According to him, the Archescyntinidae may possibly have been a jassoid family which had already become specialized in certain directions by Lower Permian times.

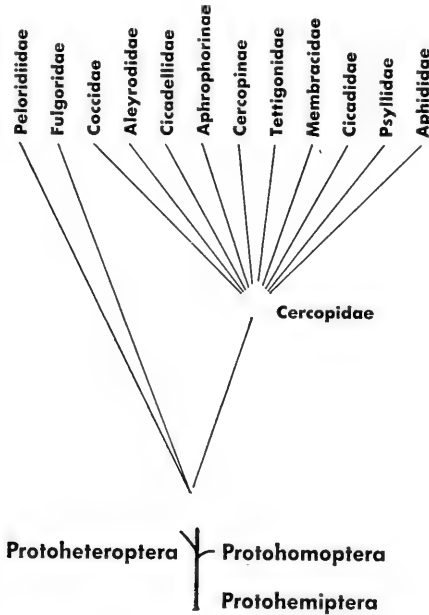


Chart 6. Phylogeny of the Homoptera, after Spooner (1938), based on a study of the head capsule.

Spooner (1938), on the basis of extensive comparative studies of the head capsule of Heteroptera-Homoptera, also recognized the early, distinctly separate origin of the Fulgoridae from that of other families of Auchenorrhyncha, and derived all the remaining families of both Auchenorrhyncha and Sternorrhyncha from the Cercopidae. His conclusions regarding the relationships of the families, arrived at by a study of the head capsule, are shown in Chart 6.

Evans (1940) agreed with Spooner in the separate derivation of the Fulgoridae and Peloridiidae from the Protohomopterous stem, a suggestion which he himself had previously made (1938), but disputed the derivation of the Sternorhyncha from the Cercopidae and the dual origin claimed for the Jassoidea (Spooner's Cicadellidae and Tettigonidae). He indicated that there was no necessity of attempting to derive either the divisions Auchenorhyncha or Sternorhyncha, one from the other. Further, that while it was reasonable to suggest a dual origin of the Jassoidea on the basis of head structure alone, other characters, such as the wing venation of the hind wings, would not support such a dual derivation. Evans' views (1946) on the classification of the Auchenorhyncha are presented in an earlier section of this paper (p. 4).

The above remarks, concerning the phylogeny of the Auchenorhyncha, indicate that there still exists, among students of the Homoptera, considerable contention regarding the relationships within this division. The palaeontological evidence, while it gives some assistance in determining the age of certain fossil Homoptera and the extent to which certain characters were present in these forms, is comparatively meager and does not, at the present time, substantially improve our knowledge of homopteran phylogeny. Although every source of evidence from this line is to be valued, it is doubtful that our ultimate knowledge of relationship will depend upon this source. Insects are fragile, and to date most of our knowledge of fossil Auchenorhyncha and related forms depends to a large extent, on the fossil wings of Homoptera, or parts of such wings. At best, such evidence is one-sided and not conclusive. Tillyard (1919) in describing fossil Homoptera, based on the tegmina, from the Mesozoic of Queensland, noted "the initial difficulty, that the classification of the Homoptera is based for the most part upon characters other than wing venation" and that although "recent studies of the nymphal tracheation in the various families have much improved our knowledge of the venation,—they have not yielded a really satisfactory basis of classification on venational characters alone."\*

### Discussion

The table (p. 64) summarizes the principal similarities and differences found in the representatives of the *Auchenorhyncha* studied herein. It should be noted first that the species selected to represent the family groups were chosen for availability and not for their primitive position within the family. A conclusive picture of phylogeny cannot be drawn

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\*Evans stated his belief (in conversation, 1949), based on his own extensive studies, that for the larger categories (families) the venational characters alone do provide a satisfactory basis of classification.

until one has compared the primitive representatives within the families, but to know what is primitive some such investigation as I have made here must be undertaken. Secondly, a series of representatives within the families should ultimately be compared, but such an investigation is beyond the scope of this study. Many of the characters have been compared, however, with other representatives of the families, and with published descriptions. The subsequent remarks will therefore have some worth, even though limited in extent.

The most striking feature of *Scolops pungens* is the primitive nature of all aspects of the sucking pump mechanism in comparison to those of the other Auchenorhyncha. While acknowledging that the sucking pump and stylets of the Auchenorhyncha are in themselves highly specialized mouthparts, those of *Scolops*, and all other fulgorids as far as I know, have remained in a comparatively primitive state of development. To be noted first in this connection are the small proportions of the preoral clypeal area to the remainder of the head capsule (excluding the cephalic head process) in *Scolops*, compared to the much greater proportions of this area in the cicada, the cercopid, the cicadellid, and the membracid. Figure 8a, representing the lateral view of the head capsule of an undescribed species of *Scudderia* (Orthoptera), has been drawn for comparison with the essentially orthopteroid proportions of the clypeal area to the remaining head capsule in *Scolops pungens* (Compare with Figs. 18, 30, 40, and 49).

In connection with the primitive nature of the sucking pump mechanism in *Scolops pungens*, it should be noted that the mandibular and maxillary stylets both bear single protractor and retractor muscles. In the other forms the musculature is always more complex, there being two or three retractor muscles, and frequently additional protractor and retractor muscles associated with the lever of the maxillary stylet as well as with the stylet itself. There is no evidence, as far as I have been able to ascertain, that the fulgorids have ever developed a sucking pump mechanism comparable to that found in other Auchenorhyncha. It seems sound to assume that the other Auchenorhyncha must have at one time passed through a stage in which the sucking pump mechanism was in a similar, relatively undeveloped state.

The ovipositor of *Scolops pungens* also represents an exceedingly primitive stage of development. Particularly to be noticed is the vertical position and lack of differentiation of the first and second valvifers and the ramal plate (Fig. 131). In contrast, the valvifers and ramal plate of *Tibicina*, *Lepyronia*, *Aulacizes*, and *Ceresa* are considerably modified, their position having shifted in a strongly marked, diagonal, anteroventral direction, and the first and second valvulae are highly specialized. The

	<i>Scolops pungens</i> ( Fulgoridae )	<i>Tibicina septendecim</i> ( Cicadidae )	<i>Lepyronia quadrangularis</i> ( Cercopidae )	<i>Aulacizes irrorata</i> ( Cicadellidae )	<i>Ceresa bubalis</i> ( Membracidae )
Clypeus and sucking pump	Comparatively little developed	Well developed	Well developed	Well developed	Well developed
Lorum	Part of clypeus. Connected to hypopharynx by narrow bridge	Distinct. Connected to hypopharynx by wide bridge	Distinct. Connected to hypopharynx by wide bridge	Distinct. Connected to hypopharynx by wide bridge	Distinct. Connected to hypopharynx by wide bridge
Ocelli	Two	Three	Two	Two	Two
Antennae	Below eyes. Enlarged pedicel	Between eyes. Pedicel not enlarged	Between eyes. Pedicel not enlarged	Between eyes. Pedicel not enlarged	Between eyes. Pedicel not enlarged
Labium	Elongated. Paired posterior plates second of 4 segments	Elongated. Paired posterior plates middle of 3 segments	Short. Paired posterior plates absent	Short. Paired posterior plates* at base of apical segment	Short. Paired posterior plates at base of apical segment
Musculature of stylets	Single protractor and retractor muscles	Multiple protractor and retractor muscles	Multiple protractor and retractor muscles	Multiple protractor and retractor muscles	Multiple protractor and retractor muscles
Tentorium	Posterior tentorial bridge only	Dorsal, anterior arms, and bridge connected	Dorsal, anterior arms, and bridge connected	Anterior arms reduced	Anterior arms absent
Tegula	Present	Absent	Absent	Absent	Absent



Wings	Forewing tegmen-like; hindwing membranous	Both wings membranous	Forewing tegmen-like; hindwing membranous	Both wings membranous	Forewing tegmen-like; hindwing membranous	Both wings membranous
Nodal line	Absent	Present	Absent	Absent	Absent	Absent
Pleural wing groove	Absent	Absent	Present	Present	Present	Present
Meta-thoracic coxa and epimeron	Fused	Distinct	Meron articulates with epimeron	Distinct	Distinct	Distinct
Basal, tarsal segments of hind leg	Apical margins spined	Not modified	Apical margins spined	Not modified	Apical margins spined	Not modified
Pulvillus	Single median lobe	Absent	Notched medially	Absent	Bilobed	Bilobed
Hind tibia	Single row of spines	Four spines	Two large spines	Four spines	Four rows of spines	Four rows of spines
Abdominal spiracles	Between tergites and latero-tergites	Ventral margin of tergites	Ventral margin of latero-tergites	Ventral margin of tergites	Ventral margin of latero-tergites	Ventral margin of latero-tergites
Ovipositor	Primitive	Specialized	Specialized	Specialized	Specialized	Specialized
Male subgenital plates	Absent	Absent	Present	Present	Present	Present
10th & 11th abdominal segments	10th—flat; 11th telescoped	10th & 11th telescoped	10th & 11th telescoped	10th & 11th telescoped	10th and 11th telescoped	10th & 11th telescoped

\*The suggested glossae of Evans (1937).

primitive nature of the ovipositor and the sucking pump, taken together with the simple, unconvoluted condition of the intestinal canal reported for the Fulgoridae by Handlirsch (developed into the specialized "Filter chamber" in the remaining auchenorhynchous families), would indicate to the writer that the Fulgoridae is a group which is distinctly separate from all other Auchenorhyncha, and was the earliest to be differentiated from the common base of the Auchenorhyncha.

Other characters which separate the Fulgoridae from the remaining families are the fusion of the meron of the coxa of the metathoracic leg with the epimeron, and the greatly modified second segment of the antenna. These characters, however, represent specializations rather than primitiveness. The Fulgoridae are also distinct in the possession of a tegula, absent in other Auchenorhyncha, as far as I have been able to ascertain.

Before proceeding further, it would be well to point out that the ovipositor of *Scolops pungens* is considerably more primitive than that found in many representatives of the Orthoptera, which group has mandibulate mouthparts. Thus we can see that within two distinct orders we have a combination of both primitive and specialized characters. The more primitive mandibulate mouthparts are combined with highly specialized ovipositors in many groups of Orthoptera, whereas the fulgorid combines specialized sucking mouthparts (compared to mandibulate mouthparts) with a primitive ovipositor. This should make it clear that insects by themselves are neither primitive nor specialized, and that these terms can only be applied in a true, comparative sense to the individual parts of insects. The fulgorids, for example, have been referred to by some authors as being primitive insects, by others (Kirkaldy, 1906; Funkhouser, 1917) as being specialized. Such terms offer no guide to phylogeny, for it is an evaluation of separate characters which is important in the interpretation of relationships.

There has been considerable controversy concerning the origin of the loral areas. Snodgrass (1938), in supporting his theory that the lorum is derived from the hypopharynx, suggested that the loral areas in the Fulgoridae represent a specialized, rather than a generalized condition. In view of the fact that the clypeal, sucking pump region of the fulgorid is a primitive one, in comparison with other Auchenorhyncha, it would support the contrary concept that the outer part of the lorum is differentiated from the lateral area of the clypeus, rather than from the hypopharynx. Attention is called to the narrow lateral arm of the hypopharynx (1a, Figs. 9 and 10) which connects to the lorum. It seems likely that this narrow arm between the hypopharynx and the lorum has been differentiated from the hypopharynx, and has apparently expanded, in the

other families of Auchenorhyncha, to form the broader connection. Thus it might well be that although the loral areas are derived mainly from the lateral regions of the clypeus, a part of the hypopharynx has formed a bridge with the present structure.

The relationships and origins of the remaining groups of Auchenorhyncha is a much more difficult matter. Much of the difficulty arises from the fact that when we consider the Cicadidae, Cercopidae, Cicadellidae, and Membracidae, we tend to think in terms of the numerous, recent representatives of these groups. These recent representatives have a number of characteristics which, taken together, mark these families off distinctly. Thus, the cercopid, cicadellid, and membracid possess an unmistakable similarity in the general plan of the thoracic sterna which links these three forms together, and differentiates them from the cicada. No doubt this similarity of the thoracic sterna is correlated with another distinguishing feature, the presence of jumping hind legs, which separates the Cercopidae, Cicadellidae, and Membracidae from the Cicadidae. In addition, the head of Cicadidae retains a small fronslike area bearing a median ocellus, absent in Cercopidae, Cicadellidae, and Membracidae. It should be pointed out, too, that the loral areas lie alongside the entire length of the postclypeus in the cicada, clearly the more ancestral condition as indicated in the fulgorids, whereas in the cercopid, cicadellid, and membracid, the upper portions of the lorae are folded into the head capsule or reduced, so that they are seen to lie adjacent to the ventral portion of the postclypeus only. All these characters suggest that the Cicadidae are distinct from the Cercopidae, Cicadellidae, and Membracidae.

In this connection attention is called to the pleural wing grooves, present in *Lepyronia*, *Aulacizes*, and *Ceresa*, which enable the bases of the anterior margin of the tegmina to lock in place when at rest. This device is absent in *Tibicina*. If such structures are consistent within Cercopidae, Cicadellidae, and Membracidae, they may represent another reason for grouping these families apart from the Cicadidae.

Of these remaining three groups, the Cercopidae alone possess a complete tentorium in which the anterior tentorial arms are connected with the posterior arms (as is also the condition in the Cicadidae), whereas in both the Cicadellidae and Membracidae the tentorial structure is reduced; the anterior arms no longer retain a connection with the posterior arms. The hind legs of both Membracidae and Cicadellidae bear spines, which are absent on the hind legs of Cercopidae. Evans (1946a) has recognized these affinities in grouping membracids and cicadellidids in one superfamily, Jassoidea, as distinct from the Cercopoidea. In addition the thoracic sterna of *Aulacizes* and *Ceresa* are exceedingly similar and both

possess a differentiated, mesothoracic antecoxal area ( $acx_2$ , Figs. 69 and 74), absent in *Lepyronia*.

It should be pointed out that a similar tendency toward the reduction of the tentorial structure, already accomplished in the Cicadellidae and Membracidae, is present also in the Fulgoridae. Although most members of the Fulgoridae possess anterior tentorial arms, and in some the dorsal tentorial arms are also present, the tentorial structure is reduced to the posterior tentorial bridge in *Scolops*. The antennal muscles, normally inserted on the dorsal tentorium in many insects, are here inserted on the posterior tentorial bridge. This tendency toward the development or reduction of particular structures within separate phylogenetic lines of the Auchenorrhyncha is a widespread one. We thus find that although the modern representatives of these auchenorhynchous groups are sufficiently distinctive and readily defined, certain more primitive representatives show a remarkable number of features in common, and it is for this reason that any attempt to determine when these familial groups originated in point of time is such a difficult one.

The epistomal suture, lacking in some cercopids, the majority of present-day jassids, and most membracids, is nevertheless present in some representatives of all of these groups as well as in the fulgorids and cicadas. The subgenal, or maxillary, suture, found in some of the fulgorid representatives of this study, is completely present in some jassids (*Ulopinæ* and *Stenocotini*), and is vestigial in the primitive cicada, *Tettigarcta*, some cercopids, and some jassids. It is absent only in membracids. Further, Evans (1948) pointed out that the basic membracid type of tegminal venation,\* as represented by *Xiphistes tuberculatus*, closely resembles the jassid type and differs only in that M is not fused basally with R, and that probably the oldest representatives of the membracids go back to very early times. This basic membracid tegmen closely resembles Evans' (1946a) reconstruction of the hypothetical, ancestral tegmenal venation of the Jassoidea (Evans' families Aetaleonidae, Hylcidae, Eurymelidae, and Jassidae). Only when we consider the more recent groups do we find specializations which are of recent origin. Another character thought to be confined to the family Cicadidae, namely the transverse nodal line of the tegmina, has been found in the jassoid family Hylcidae. Apart from the Hylcidae, no trace of such a line is retained in any other jassoids.

Additional evidence along these lines has recently been brought forth in the interesting studies of Ossiannilsson (1949), who pointed out that

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\*According to Evans the arrangement of the veins of the tegmen offers a more reliable character for the determination of relationships within the Membracidae, than those of the highly variable pronotum (a much more recent specialization), heretofore relied upon.

the tymbal organs of Homoptera, generally considered to be present only in the Cicadidae, are also present in cercopids, membracids (*Centrotus*), some jassoid forms, and the fulgorid, *Ommatidiotus*. In cercopids and certain jassoid genera the female possesses a functional sound-producing organ of the same type as that of the male, though weaker. Moreover, the female of *Paropia* has a distinctly striated tymbal which is, in the male, only represented by traces. In *Doratura* both sexes have a sound-producing organ of the same type and equally well developed. Ossiannilsson suggests that primitively both sexes possessed practically identical tymbal organs, and that the present condition, wherein these organs are usually confined to the males, has been brought about by reduction. He concluded that the possession of a functional tymbal apparatus is general among the Auchenorrhyncha.

Evans (1940b) has called attention to the fact that not only the nymphs of cicadas, but those of many cixiids (Fulgoridae) and certain cercopids are subterranean, and that this may well be a primitive characteristic, possibly associated with severe weather conditions prevailing at some past period of geological history. The study of the habits and behavior patterns of Auchenorrhyncha is an almost unexplored field for the investigator and, if studied from the comparative point of view, could undoubtedly contribute much additional evidence to the solution of problems of relationship.

All of this evidence supports the contention that only the numerous modern representatives of the Cicadidae, Cercopidae, Jassidae, and Membracidae are distinct and well defined; and that there are an impressive number of instances in which primitive, less numerous, and little known representatives of these groups show a variety of characters in common.

It is interesting to note that the meso- and metathoracic segments of *Tibicina septendecim* and *Ceresa bubalus* show certain superficial resemblances of shape and structure, as well as fore- and hindwings which are both membranous. I have already pointed out that the affinity of the membracid thorax lies with that of the cicadellid, and to a somewhat lesser extent with that of the cercopid.

Lawson (1922) suggested that the main branch of the Cercopidae arose a little earlier than that of the Cicadellidae and Membracidae, based on the assumption that spittle-mass production must have required a long time to perfect. Although there is morphological, and perhaps palaeontological, evidence which might support an earlier origin of the Cercopidae, such an earlier origin is not, in my opinion, supported by the development of a specialization such as spittle-mass production. This is

but one example of the difficulties inherent in the attempts to reason out phylogeny.

It is difficult to say whether there have been two "main" divisions of development or three as Evans (1946) has recently suggested. If we are to accept three, I would consider that the Cicadomorpha (Cicadidae) and Jassidomorpha (Cercopidae, Cicadellidae, and Membracidae) are more distinctly separated from the Fulgoromorpha (Fulgoridae) than they are from each other, while acknowledging that the Cicadidae do show distinct differences from the Cercopidae, Cicadellidae, and Membracidae. The Fulgoridae were the earliest group to be differentiated from the base of the auchenorhynchous stem, and are clearly distinct from the remaining Auchenorhyncha. The cercopids, cicadellids, and membracids are closely related, and the latter two groups show very marked affinities. On the basis of this study, and our present knowledge of cicadas on the one hand and the cercopids, cicadellids, and membracids on the other, the writer finds no conclusive evidence to support an earlier origin for one or the other of these groups. Evans, however, has stated (in conversation) that the modern cicadas were probably differentiated earlier than modern jassids, but that the jassoid stem originated at an earlier date than the cicadoid stem. As additional, primitive representatives of these groups come to light, we may be able to make more valid conjectures concerning their probable origin in time.

No attempt has been made to evaluate the taxonomic categories used in this discussion. The family names have been used to indicate broad groups and their general relationship. It is very likely that superfamily and subfamily designations may properly replace certain family groups as various writers have already suggested.

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## LIST OF ABBREVIATIONS

1A	—1st anal	dlclp	—dilator muscles of the clypeus
2A	—2nd anal	dsyr	—dilator muscle of the salivary syringe
3A	—3rd anal	dt	—dorsal arm of the tentorium
aclp	—anteclypeus	e	—compound eye
acs	—antecostal suture	epm	—epimeron
acx	—antecoxal area	eph	—epipharynx
aed	—aedeagus	es	—episternum
aepm	—anepimeron	est	—epistomal suture
aes	—anepisternum	fe	—femur
an	—anus	fl	—flagellum of the antenna
anp	—anterior notal wing process	fp	—furcal pit
ant	—antenna	fr	—frons, or frontal region
as	—anal style	fst	—furcasternite
at	—anterior tentorial arm	fu	—furcal apodeme
atp	—anterior tentorial pit, or invagination	ge	—gena, or genal region
au	—auditory capsule	gnp	—gonopore
aw	—prealar bridge	gp	—subgenital plate
1ax	—first axillary sclerite	ha	—humeral angle of pronotum
2ax	—second axillary sclerite	hph	—hypopharynx
3ax	—third axillary sclerite	hwp	—hypopharyngeal wing plate
ba	—basalare, or basalar sclerite	is	—intersegmental line
bax	—basicoxite	jf	—jugal fold
bp	—basal plate	kepm	—katepimeron
br	—brain	kes	—katepisternum
bst	—basisternite	l	—lateral abdominal muscle
C	—costa	lb	—labium
cl	—claw, or ungue	lc	—lateral cervical sclerite
clr	—clypeal ridge, or apodeme	le	—external lateral abdominal muscle
ex	—coxa	lh	—lateral arm of hypopharynx
exp	—pleural coxal process	li	—internal lateral abdominal muscle
Cu	—cubitus	lm	—labrum
d	—dorsal longitudinal muscle	lor	—lorum
dc	—dorsal cervical sclerite	ltg	—laterotergite
dl	—lateral dorsal longitudinal muscle	lvr <sub>1</sub>	—lever of the mandibular stylet
dm	—median dorsal longitudinal muscle		

lvr <sub>2</sub>	—lever of the maxillary stylet	pw	—postalar bridge
M	—media	R	—radius
mant	—antennal muscle	rd	—reduplication of scutellum
mds	—mandibular stylet	lri	—inner ramus, or sclerotized thickening, of first valvula
mlb	—muscle of the labium	rlb	—retractor muscle of the labium
mm	—muscle maculum, or marking	rmds	—retractor muscle of the mandibular stylet
mp	—muscle partition formed by apodemal wall of pronotum	rmxs	—retractor muscle of the maxillary stylet
mr	—meron of coxa	lro	—outer ramus, or sclerotized thickening, of first valvula
ms	—median suture of metathoracic scutum	2ro	—outer ramus, or sclerotized thickening, of second valvula
mtp	—metopidium of pronotum	rp	—ramal plate
mxp	—maxillary plate	Is, IIs, etc.	—first abdominal sternite, etc.
mxap	—apodemal plate of the maxillary	Sc	—subcosta
nl	—nodal line of wing	sc	—scutum
oc	—ocellus	scl	—scutellum
occ	—occipital condyle	scp	—scape of the antenna
ocn	—ocellar nerve	sgng	—subesophageal ganglion
opc	—operculum	sgs	—subgenal suture
opn	—optic nerve	sh	—suprahumeral horn of pronotum
pc	—precosta, or pretergite	sld	—salivary duct
pclp	—posttelypeus	slg	—salivary glands
pdc	—pedicel of the antenna	sp	—spiracle
ph	—phragma	syr	—salivary syringe
plap	—pleural apodeme	It, IIIt, etc.	—first abdominal tergite, etc.
plb	—protractor muscle of the labium	ta	—tarsus
pls	—pleural suture	tb	—posterior tentorial bridge
pm	—paramere	tg	—tegula
pmds	—protractor muscle of the mandible	thng <sub>1</sub>	—prothoracic ganglion
pmp	—sucking pump	ti	—tibia
pmxs	—protractor muscle of the maxillary stylet	tn	—trochantin
pnp	—posterior notal wing process	tr	—trochanter
pnt	—postnotum	ts	—tergal spine
pocx	—postcoxal bridge	twg	—tergal wing groove
prnt	—pronotum	tyb	—tymbal
pse	—prescutum	typ	—tympanum
ptp	—posterior tentorial invagination	unp	—unguitractor plate
pu	—pulvillus		

v	—ventral longitudinal muscle	1vlf	—first valvifer
vc	—ventral clasper of 10th segment	2vlf	—second valvifer
vf	—vannal fold	vst	—vestibulum
1vl	—first valvula	vx	—vertex
2vl	—second valvula	I, II, etc.	—first abdominal segment, <b>etc.</b>
3vl	—third valvula		

PLATES WITH EXPLANATIONS

PLATE I

1. Lateral view of head of *Acalonia* sp.
2. Frontal view of head of *Acalonia* sp.
3. Frontal view of head of *Ormenis pruinosa* (Say)
4. Lateral view of head of *Ormenis pruinosa*
5. Frontal view of head of *Epitera septentrionalis* Say
6. Frontal view of head of *Oliarus aridus* Ball, with maxillary lobes displaced
7. Frontal view of head of *Scolops pungens*
8. Lateral view of head of *Scolops pungens*
- 8a. Lateral view of head of *Scudderia* sp. (Orthoptera)



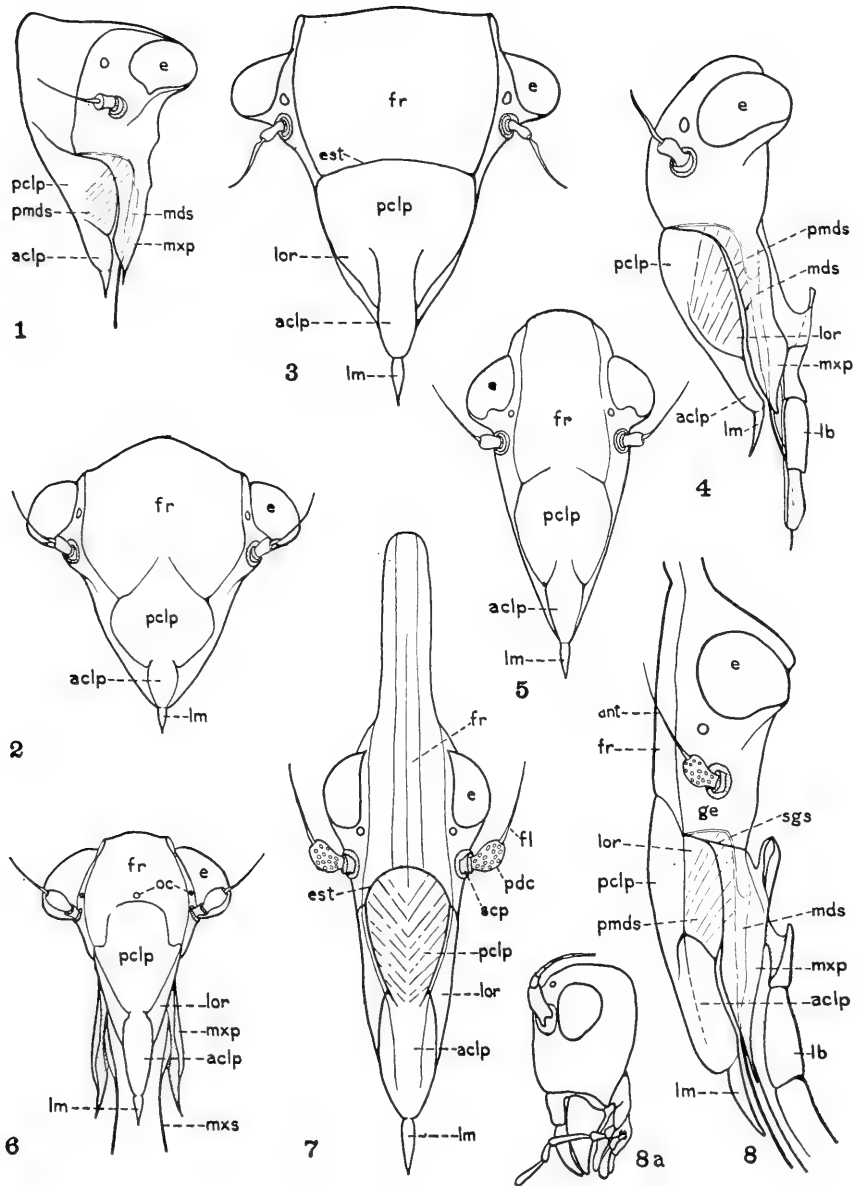


PLATE II

9. Sagittal section of lower part of head of *Scolops pungens*, showing attachment of hypopharynx to the head capsule
10. Anterior views of hypopharynx of *Scolops pungens*
11. Posterior view of hypopharynx, maxillary plate and posterior tentorial bridge of *Oliarus aridus*
12. Muscles and articulation of right mandibular stylet of *Scolops pungens*
13. Sagittal section of the head of *Scolops pungens*
14. Median section of labium of *Scolops pungens*
15. Muscles and articulation of right maxillary stylet of *Scolops pungens*
16. Posterior view of head of *Scolops pungens*, with labium removed
17. Posterior view of labium of *Scolops pungens*

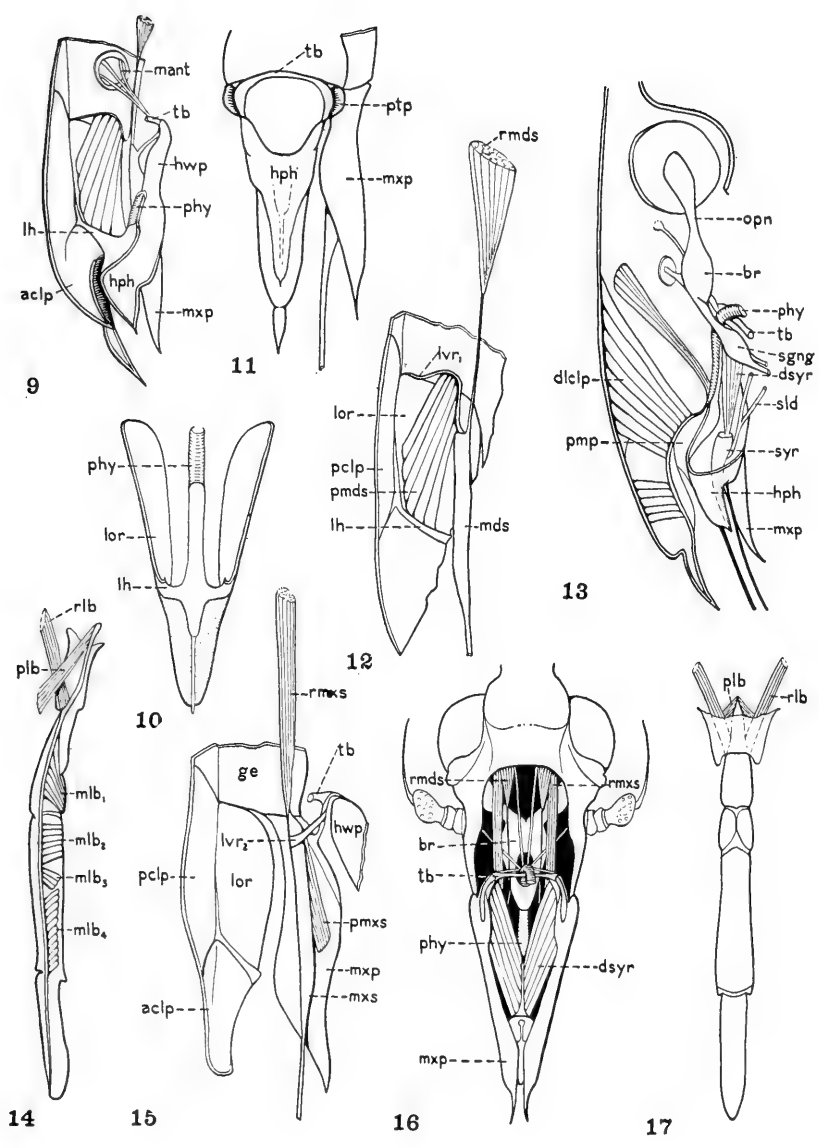
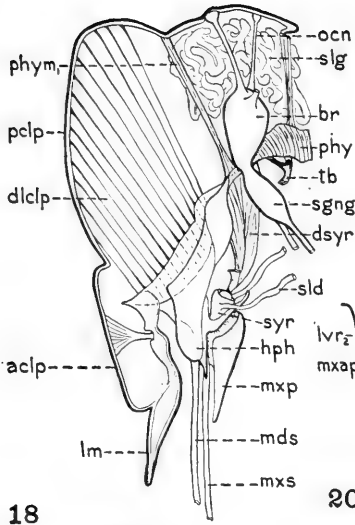


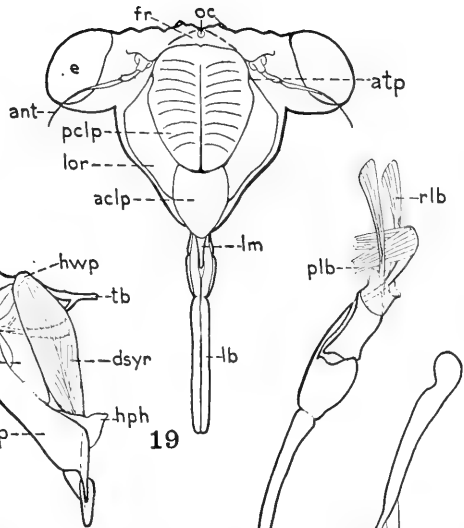
PLATE III

*Tibicina septendecim*

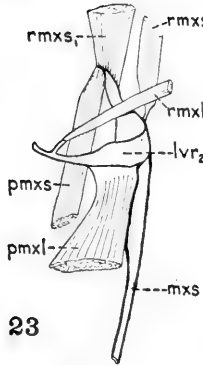
18. Sagittal section of head
19. Anterior view of head
20. Posterior view of hypopharyngeal wing plate
21. Lateral view of labium
22. Median section of basal segments of labium
23. Muscles of the maxillary stylet
24. Cross section of head through hypopharynx, sucking pump, and post-clypeus
25. Posteroventral view of tentorium and hypopharyngeal wing plate of upper right half of head
26. Dorsal view of head
27. Posterior view of head, with labium removed
28. Muscles of the mandibular stylet



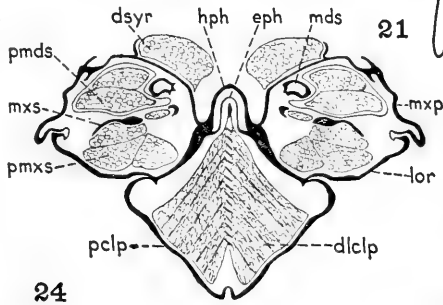
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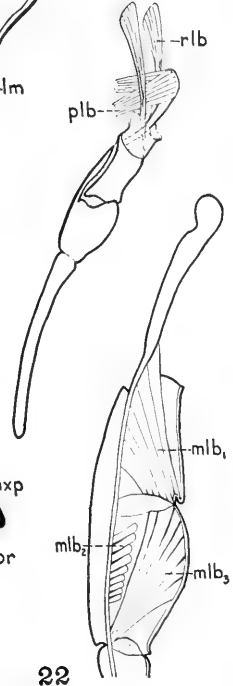
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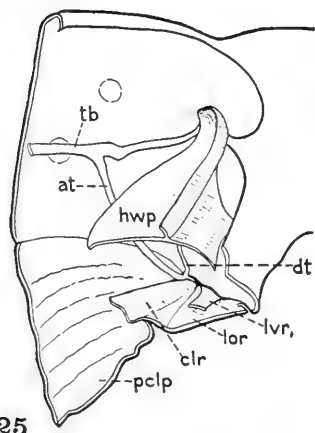
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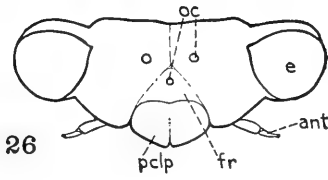
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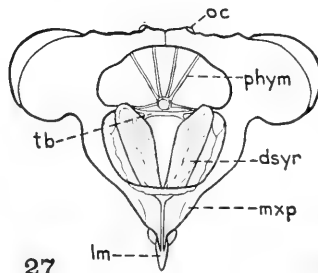
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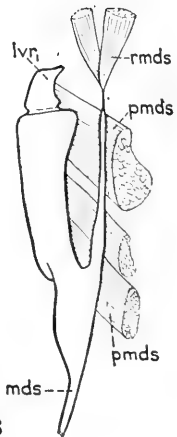
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PLATE IV

*Lepyronia quadrangularis*

29. Anterior view of head
30. Sagittal section of head
31. Dorsal view of head
32. Posterior view of head
33. Basal portion of right maxillary stylet
34. Muscles and articulation of right mandibular stylet
35. Anterior view of left half of head showing the connection of the hypopharynx with the lorum
36. Cross-section of head through the hypopharynx, sucking pump, and postclypeus
37. Median section of the labium

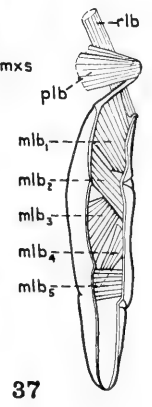
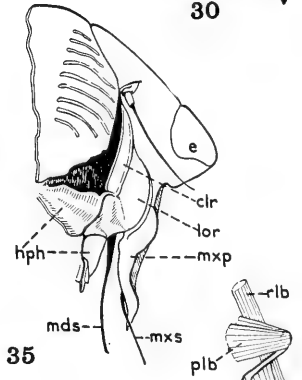
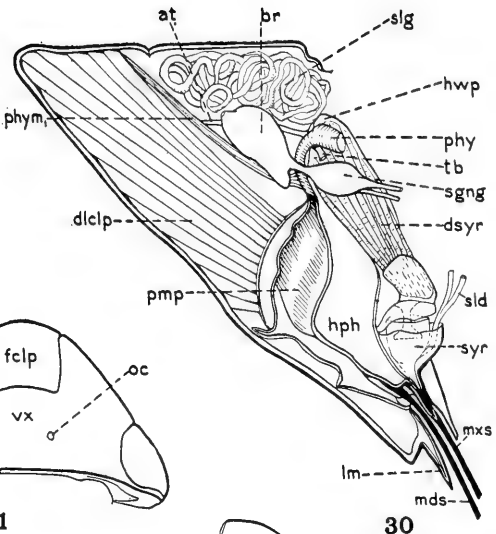
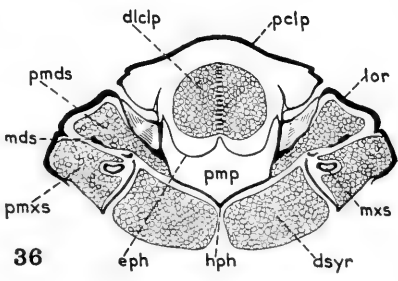
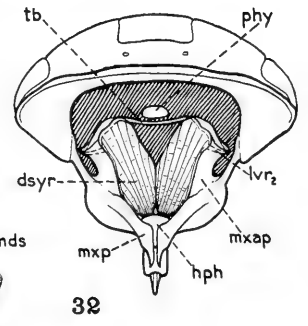
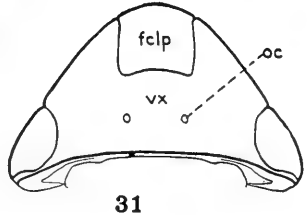
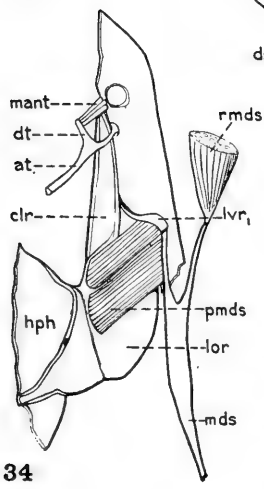
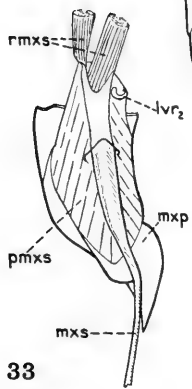
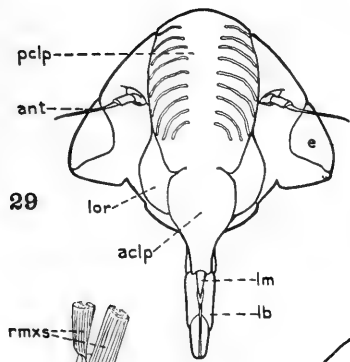
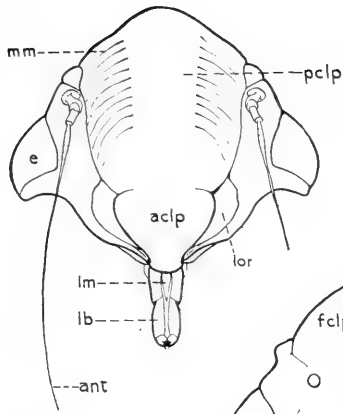


PLATE V

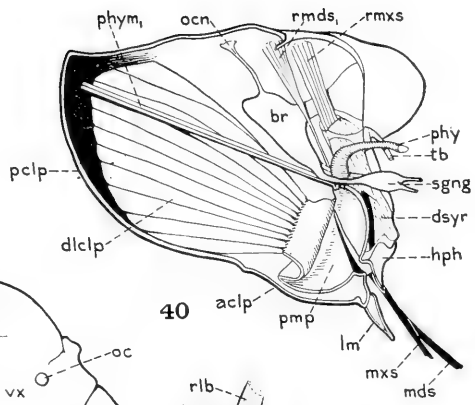
*Aulacizes irrorata*

38. Anterior view of head
39. Dorsal view of head
40. Sagittal section of head
41. Posterior view of head
42. Muscles and articulation of the maxillary stylet
43. Lateral view of labium
44. Median section of labium
45. Cross-section of head through hypopharynx, sucking pump and post-clypeus
46. Posterior view of internal section of head showing the articulation and muscles of the mandibular stylet

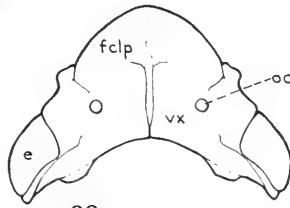




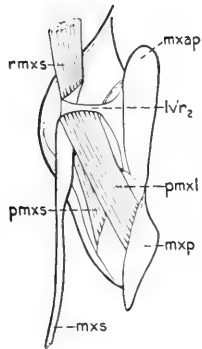
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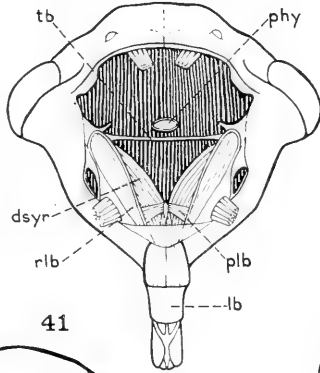
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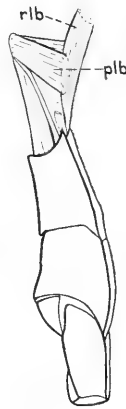
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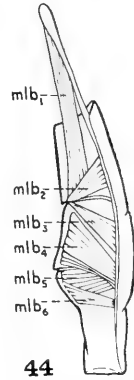
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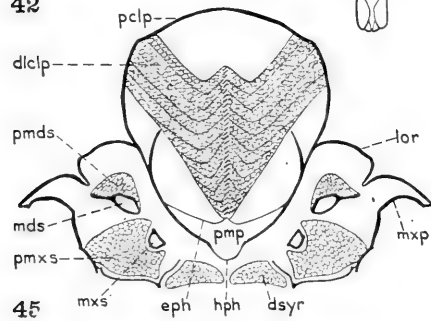
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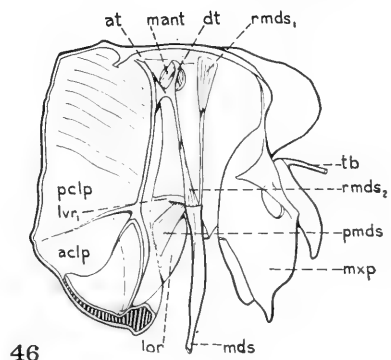
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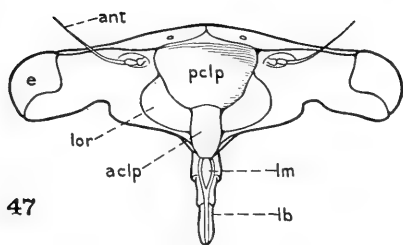


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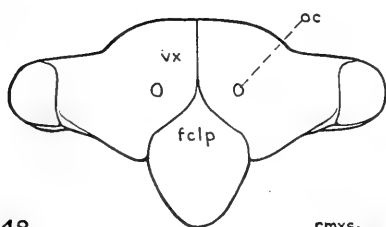
PLATE VI

*Ceresa bubalus*

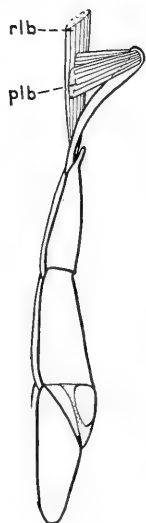
47. Ventral view of head
48. Anterior view of head
49. Sagittal section of head
50. Posterior view of head
51. Lateral view of labium
52. Median section of labium
53. Articulation and muscles of maxillary stylet
54. Sagittal section of head, showing articulation and muscles of mandibular stylet



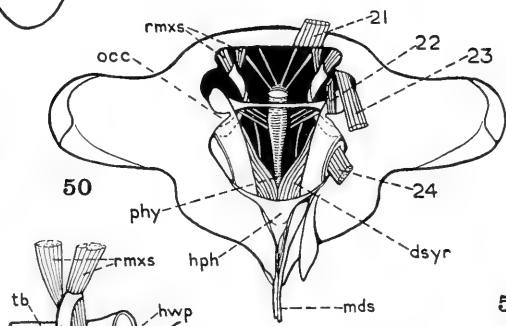
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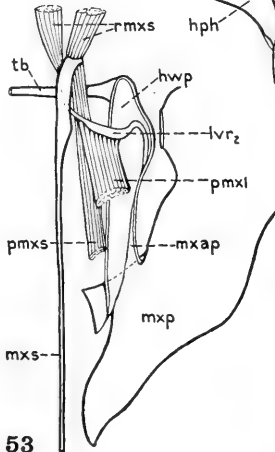
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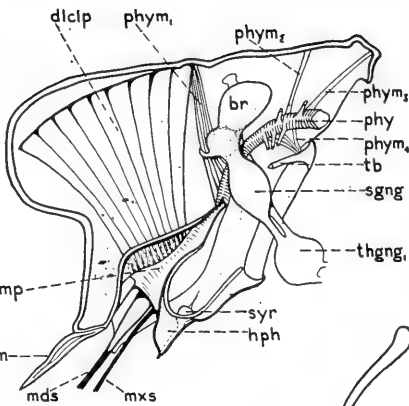
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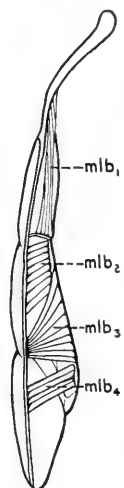
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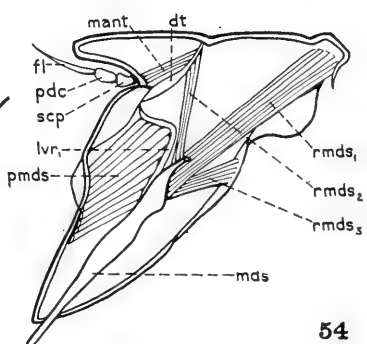
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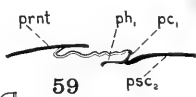
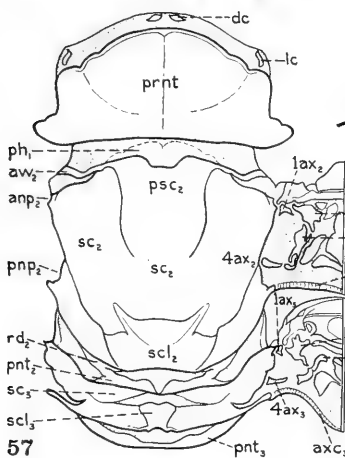
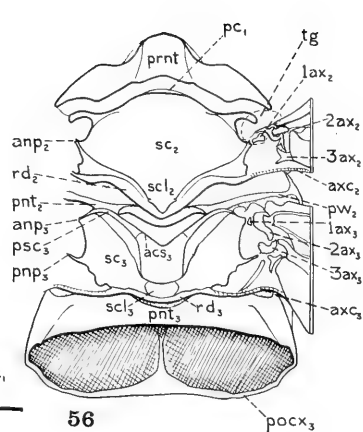
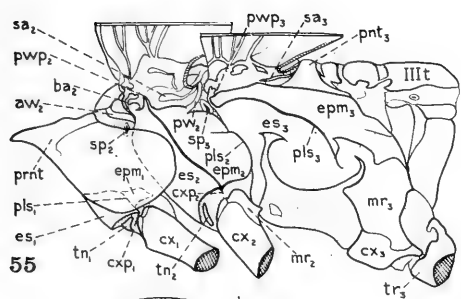
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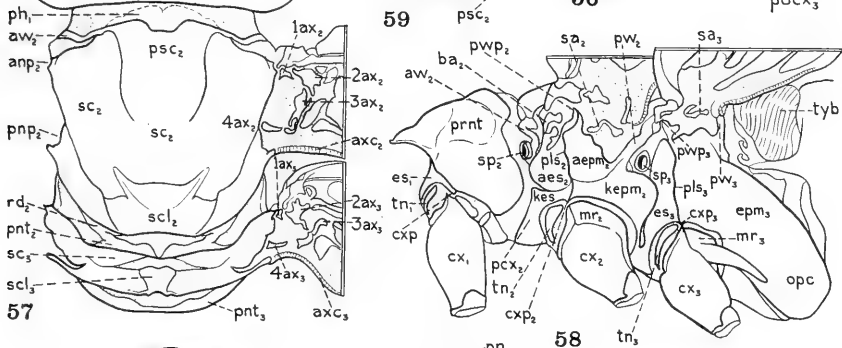
PLATE VII

55. Lateral view of thorax of *Scolops pungens*
56. Dorsal view of thorax of *Scolops pungens*
57. Dorsal view of thorax of *Tibicina septendecim*
58. Lateral view of thorax of *Tibicina septendecim*
59. Dorsal section through intersegmental area of pro- and mesothoracic segments of *Tibicina septendecim*
60. Ventral view of thorax of *Scolops pungens*
61. Ventral view of thorax of *Tibicina septendecim*
62. Posterior view of phragma between meso- and metathoracic segments of *Tibicina septendecim*
63. Posterior view of prothoracic endoskeleton of *Scolops pungens*

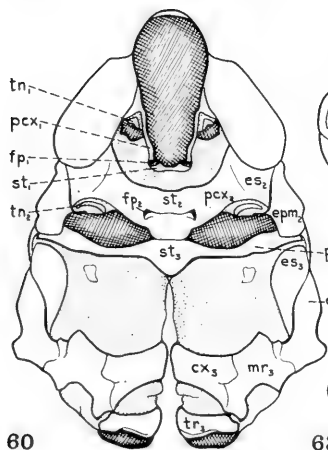


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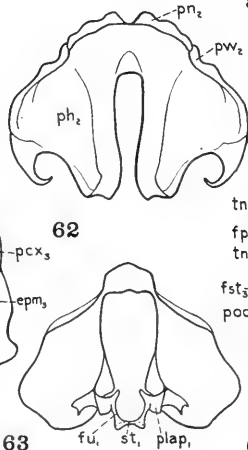
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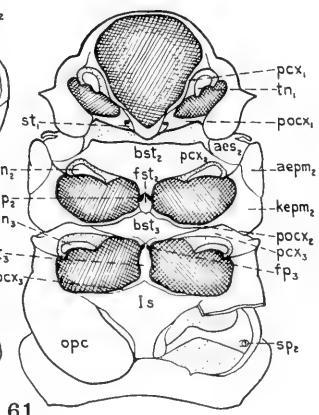
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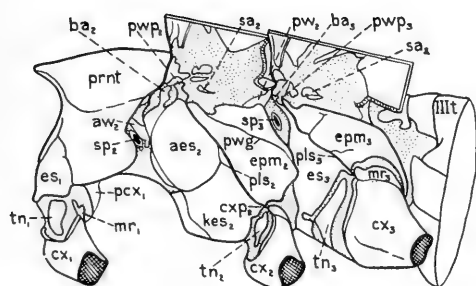
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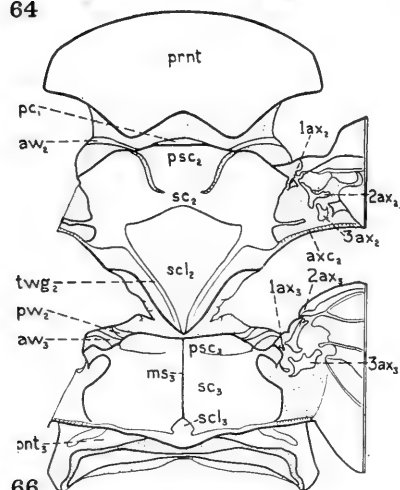
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PLATE VIII

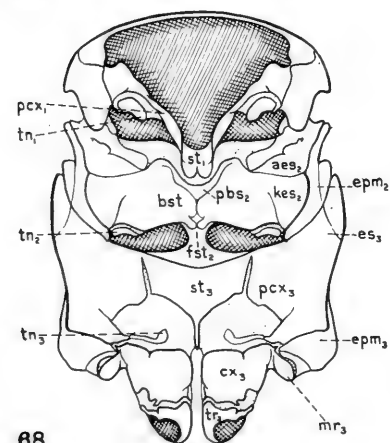
64. Lateral view of thorax of *Aulacizes irrorata*
65. Dorsal view of thorax of *Aulacizes irrorata*
66. Dorsal view of thorax of *Lepyronia quadrangularis*
67. Lateral view of thorax of *Lepyronia quadrangularis*
68. Ventral view of thorax of *Lepyronia quadrangularis*
69. Ventral view of thorax of *Aulacizes irrorata*



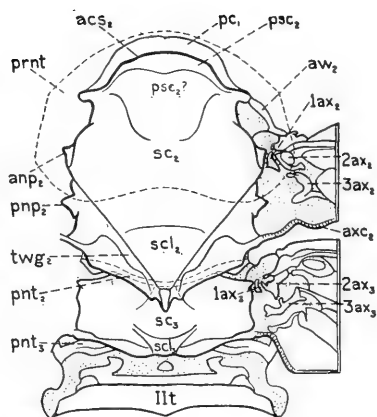
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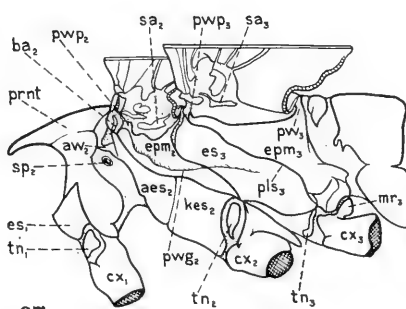
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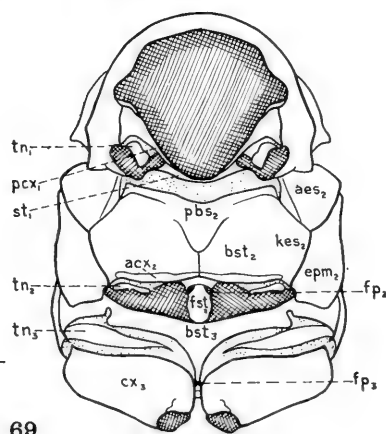
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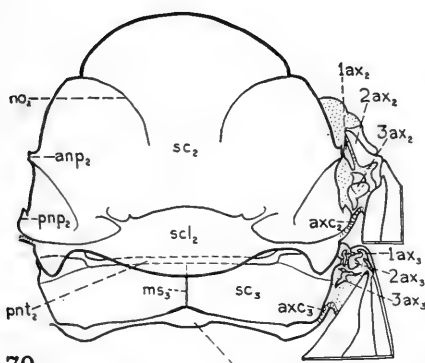
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PLATE IX

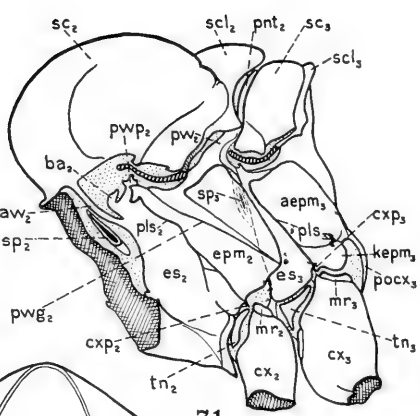
*Ceresa bubalus*

70. Dorsal view of meso- and metathoracic segments
71. Ventral view of meso- and metathoracic segments
72. Posterior view of prothorax
73. Posterior view of metathorax
74. Ventral view of thoracic segments
75. Anterior view of prothorax
76. Anterior view of metathorax
77. Posterior view of endoskeleton of mesothorax
78. Anterior view of mesothorax

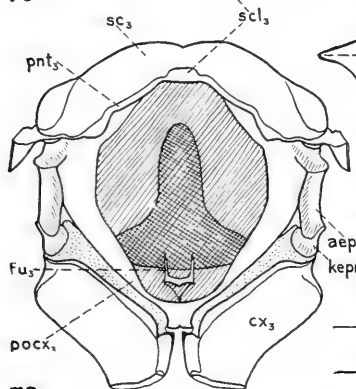




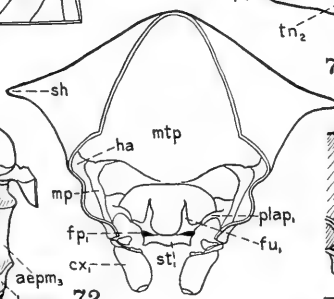
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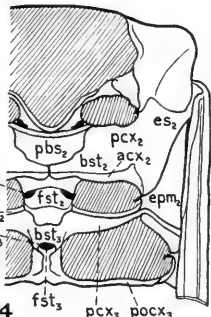
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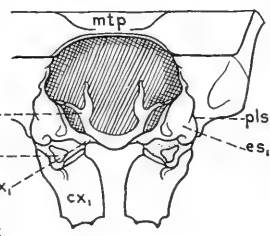
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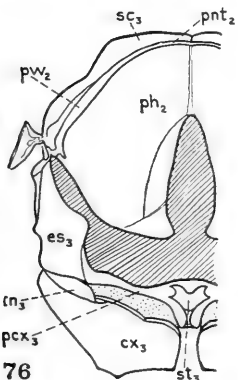
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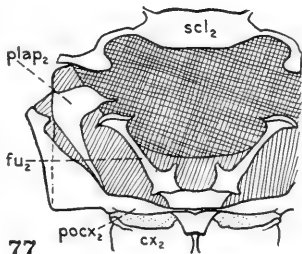
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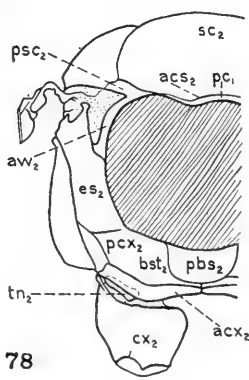
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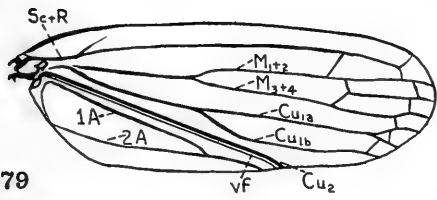
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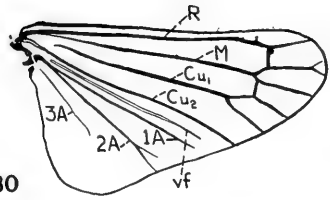
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PLATE X

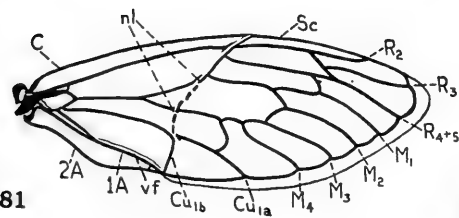
79. Forewing of *Scolops pungens*
80. Hindwing of *Scolops pungens*
81. Forewing of *Tibicina septendecim*
82. Hindwing of *Tibicina septendecim*
83. Forewing of *Lepyronia quadrangularis*
84. Hindwing of *Lepyronia quadrangularis*
85. Forewing of *Aulacizes irrorata*
86. Hindwing of *Aulacizes irrorata*
87. Forewing of *Ceresa bubalus*
88. Hindwing of *Ceresa bubalus*



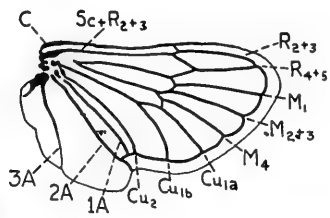
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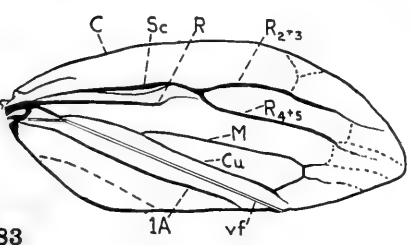
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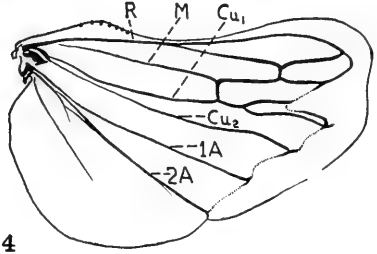
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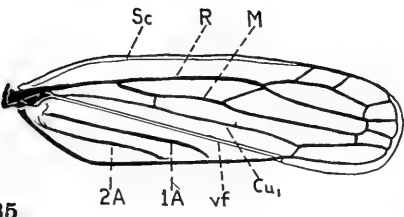
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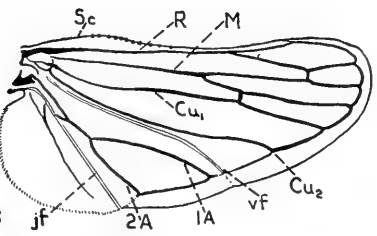
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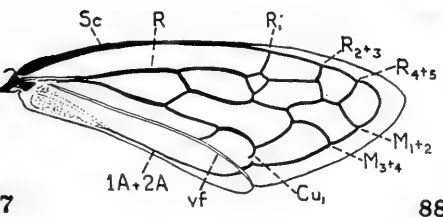
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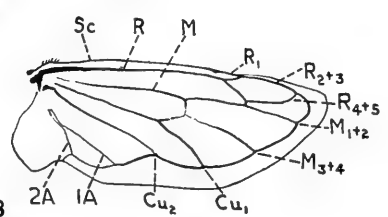
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PLATE XI

89. Prothoracic leg of *Scolops pungens*
90. Mesothoracic leg of *Scolops pungens*
91. Metathoracic leg of *Scolops pungens*
92. Tarsal segments and claws of mesothoracic leg of *Scolops pungens*
93. Prothoracic leg of *Tibicina septendecim*
94. Mesothoracic leg of *Tibicina septendecim*
95. Metathoracic leg of *Tibicina septendecim*
96. Tarsal segments and claws of metathoracic leg of *Tibicina septendecim*
97. Prothoracic leg of *Lepyronia quadrangularis*
98. Mesothoracic of *Lepyronia quadrangularis*
99. Metathoracic leg of *Lepyronia quadrangularis*
100. Tarsal segments and claws of mesothoracic leg of *Lepyronia quadrangularis*
101. Prothoracic leg of *Aulacizes irrorata*
102. Mesothoracic leg of *Aulacizes irrorata*
103. Metathoracic leg of *Aulacizes irrorata*
104. Tarsal segments and claws of prothoracic leg of *Aulacizes irrorata*
105. Lateral view of claw of prothoracic leg of *Aulacizes irrorata*

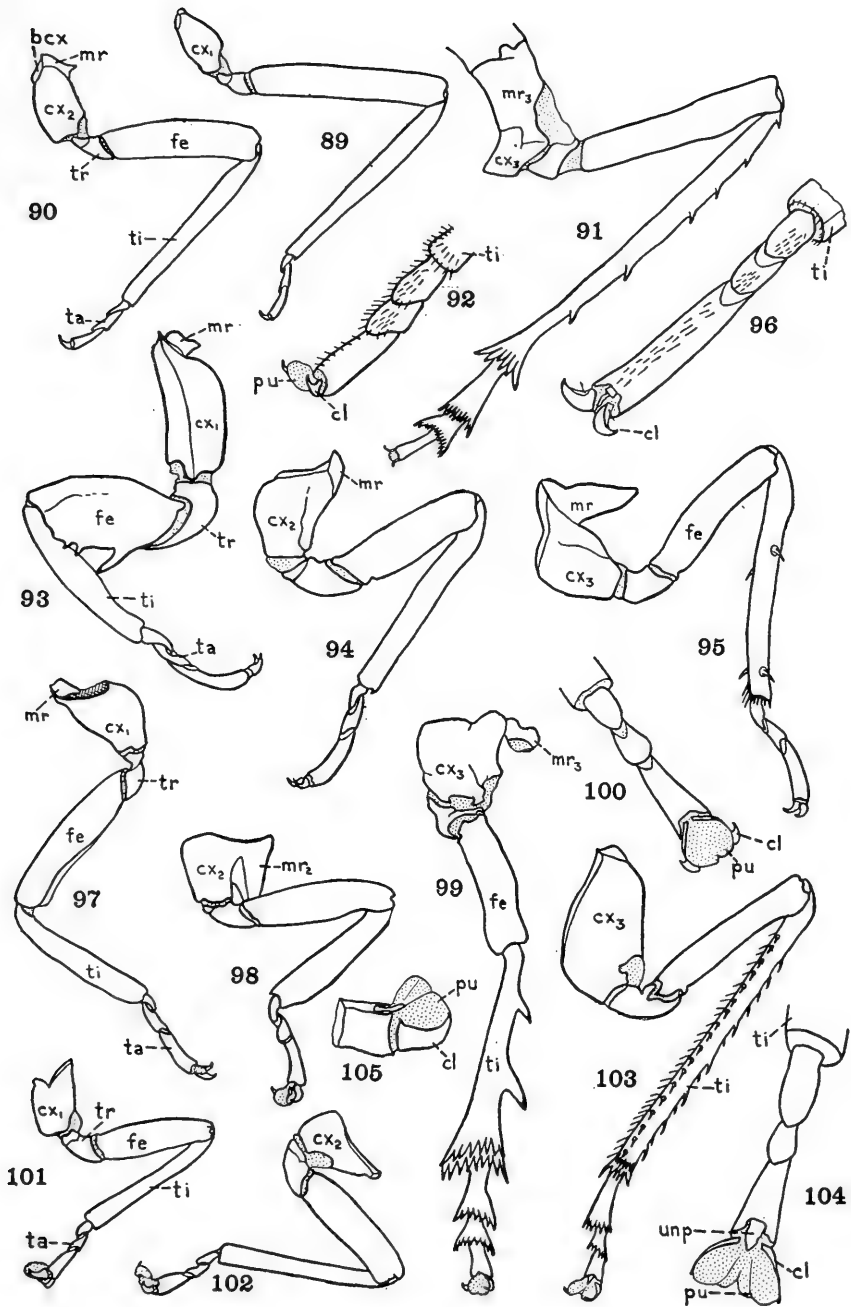


PLATE XII

*Ceresa bubalus*

106. Median sagittal section of head and thorax
107. Lateral sagittal section of meso- and metathoracic segments
108. Lateral sagittal section of meso- and metathoracic segments, showing latermost muscles
109. Lateral sagittal section of mesothoracic segment
110. Posterior view of prothoracic muscles
111. Prothoracic leg
112. Mesothoracic leg, showing coxal muscles
113. Metathoracic leg
114. Trochanteral and femoral muscles of mesothoracic leg
115. Tibial muscles of mesothoracic leg
116. Tarsal and posttarsal muscles of mesothoracic leg
117. Internal view of metathoracic pleuron and muscles

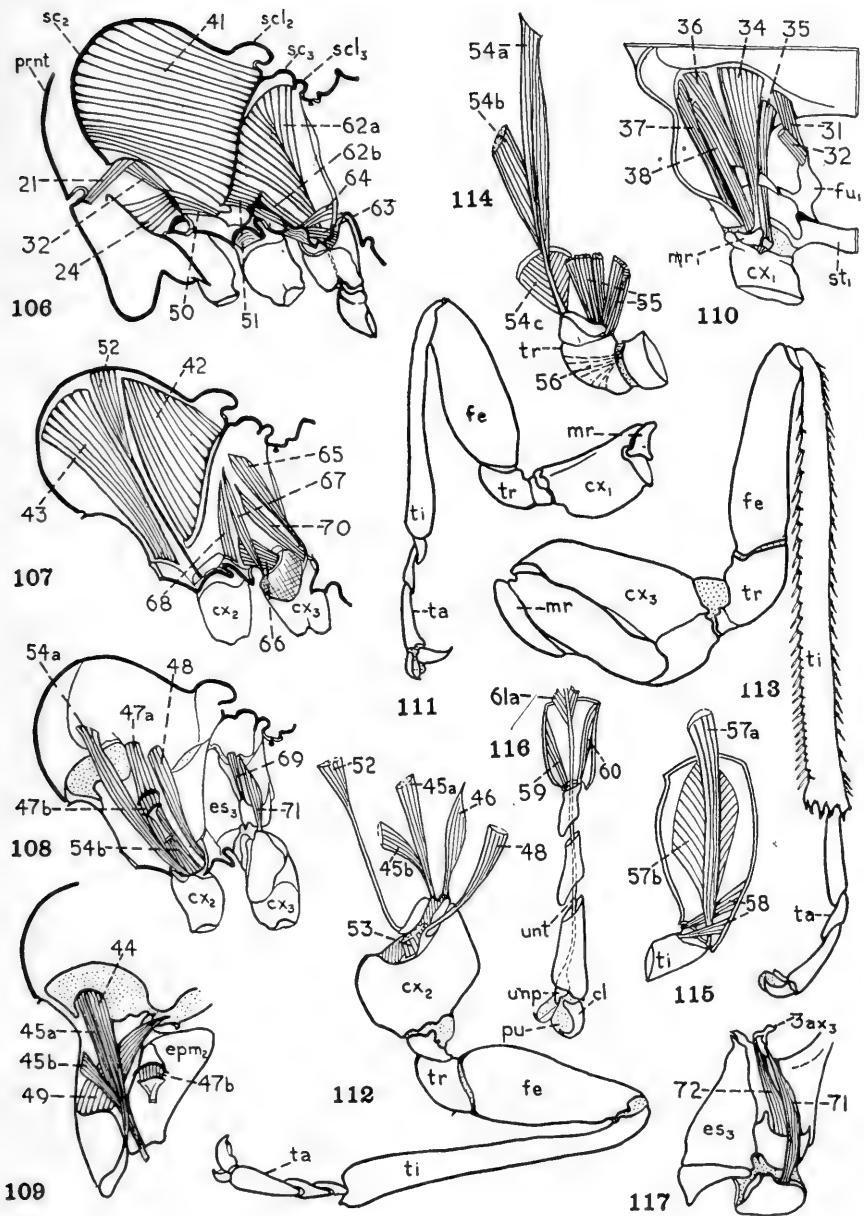


PLATE XIII

118. Ventral view of basal abdominal segments of *Scolops pungens*
119. Lateral view of female abdomen of *Scolops pungens*
120. Ventral view of basal abdominal segments of *Tibicina septendecim*
121. Lateral view of female abdomen of *Tibicina septendecim*
122. Ventral view of basal abdominal segment of *Lepyronia quadrangularis*
123. Lateral view of female abdomen of *Lepyronia quadrangularis*
124. Ventral view of basal abdominal segments of *Aulacizes irrorata*
125. Lateral view of female abdomen of *Aulacizes irrorata*
126. Ventral view of basal abdominal segments of *Ceresa bubalus*
127. Lateral view of female abdomen of *Ceresa bubalus*



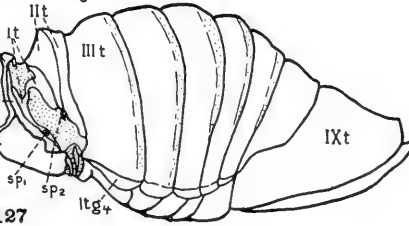
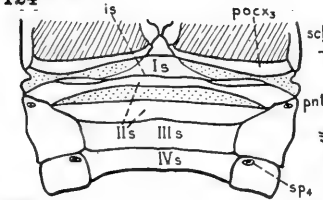
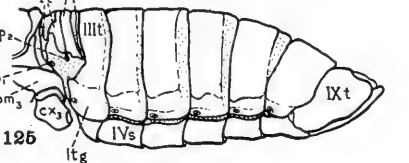
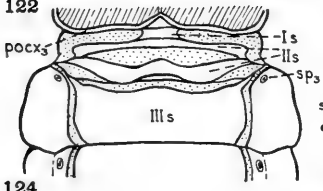
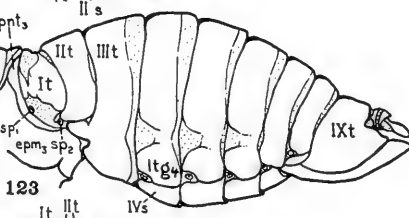
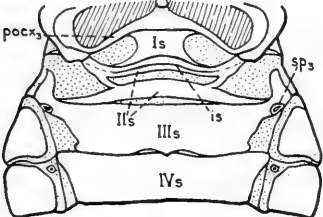
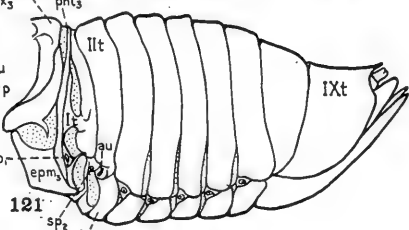
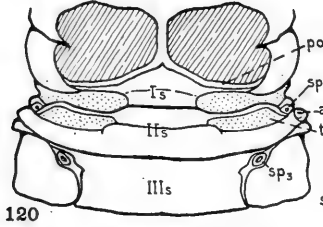
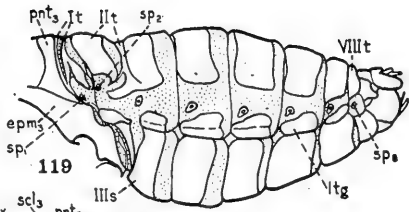
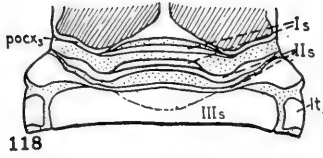


PLATE XIV

128. Lateral view of distended parts of ovipositor of *Lepyronia quadrangularis*
129. Basal plate, aedeagus and paramere of *Lepyronia quadrangularis*
130. Terminal abdominal segments of male, *Tibicina septendecim*
131. Lateral view of genitalia of female, *Scolops pungens*
132. Ventral view of genitalia of female, *Scolops pungens*
133. Lateral view of genitalia of male, *Scolops pungens*
134. Lateral view of genitalia of female, *Tibicina septendecim*
135. Ventral view of genitalia of female, *Tibicina septendecim*
136. Lateral view of male genitalia, *Tibicina septendecim*
137. Lateral view of female terminal abdominal segments, *Tibicina septendecim*
138. Caudoventral view of ninth segment and aedeagus, *Tibicina septendecim*
139. Lateral view of female genitalia, *Lepyronia quadrangularis*
140. Lateral view of male genitalia, *Lepyronia quadrangularis*
141. Lateral view of female genitalia, *Aulacizes irrorata*
142. Lateral view of male genitalia, *Aulacizes irrorata*

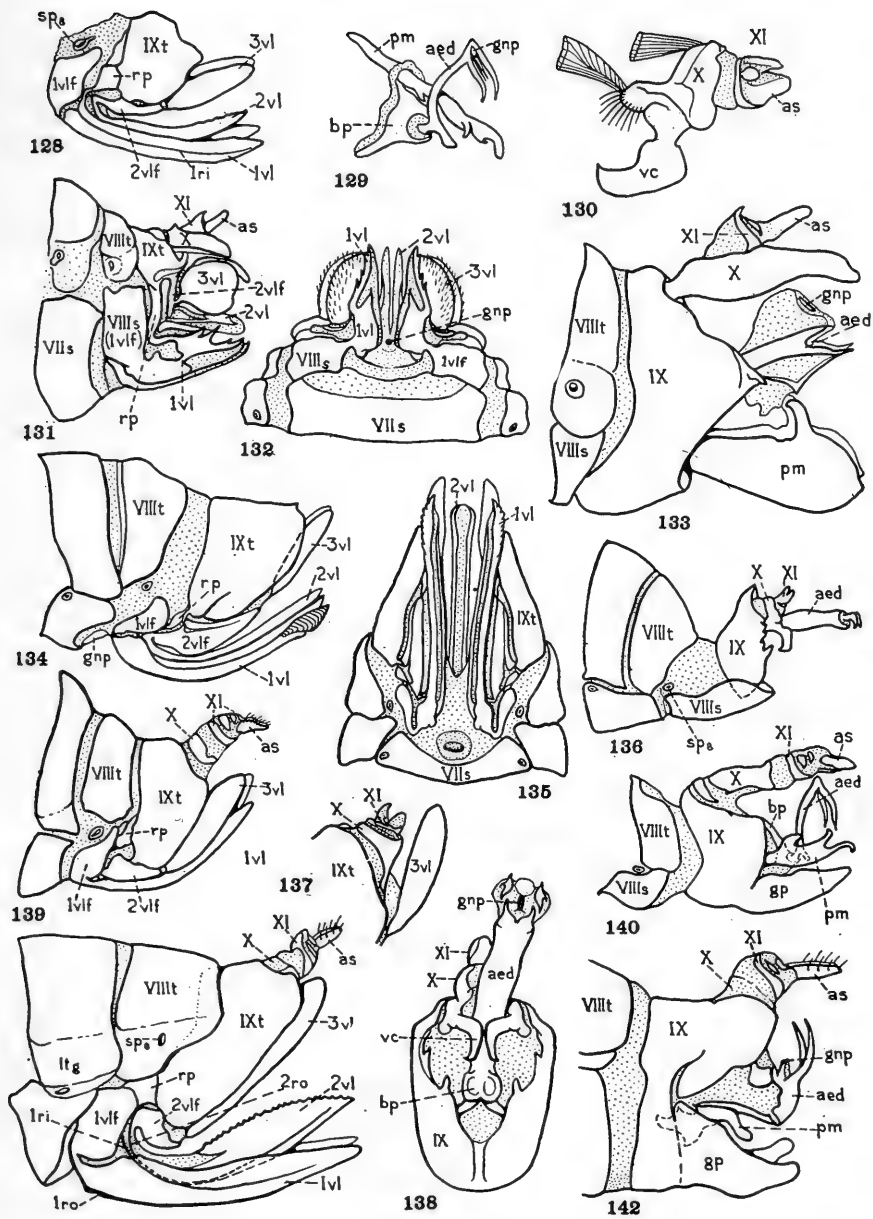
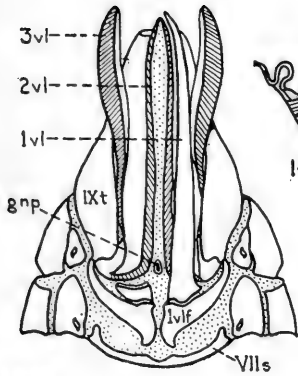


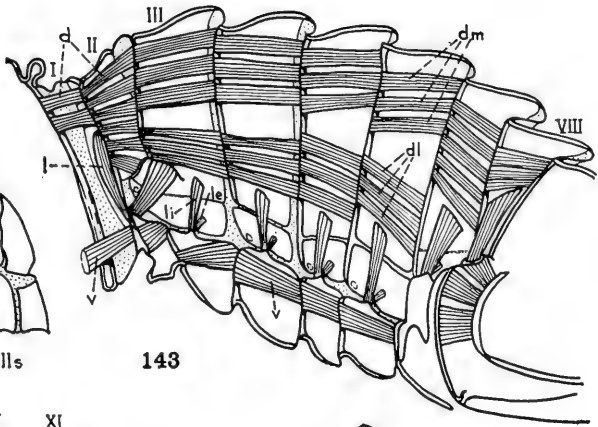
PLATE XV

*Ceresa bubalus*

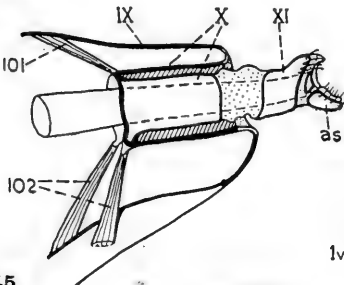
143. Sagittal section of visceral abdominal segments
144. Ventral view of female genitalia
145. Terminal abdominal segments
146. Muscles of the ovipositor
147. Second valvifer with second and third valvulae
148. Internal view of valvifers, valvulae, and rami of ovipositor
149. Lateral view of ovipositor



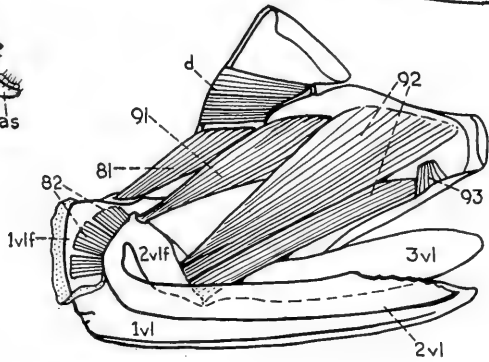
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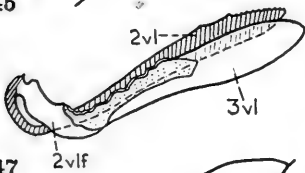
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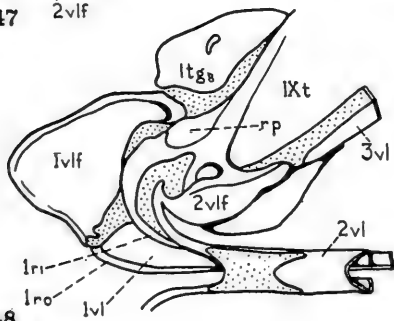
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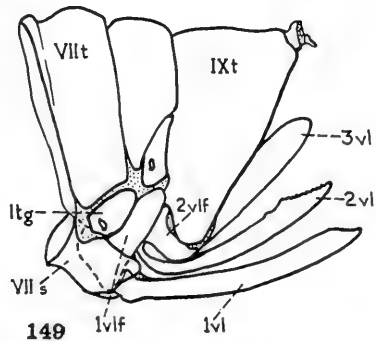
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147



148

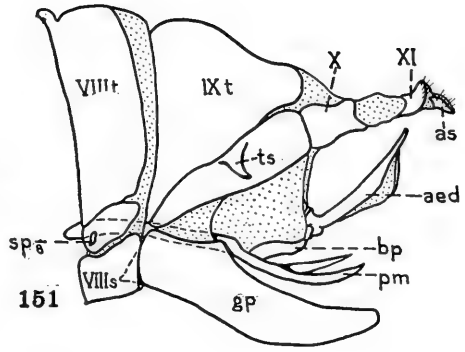
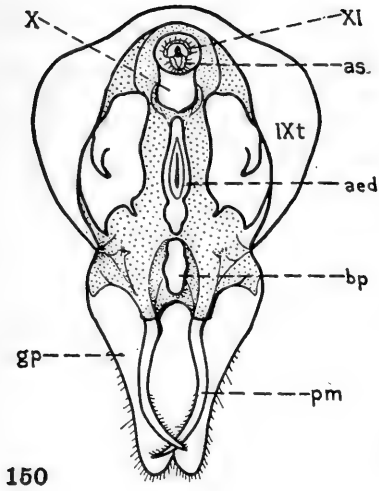


148

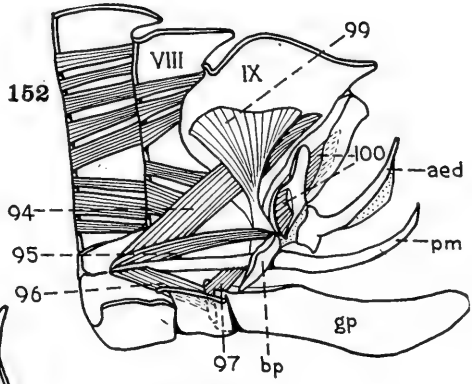
PLATE XVI

*Ceresa bubalus*

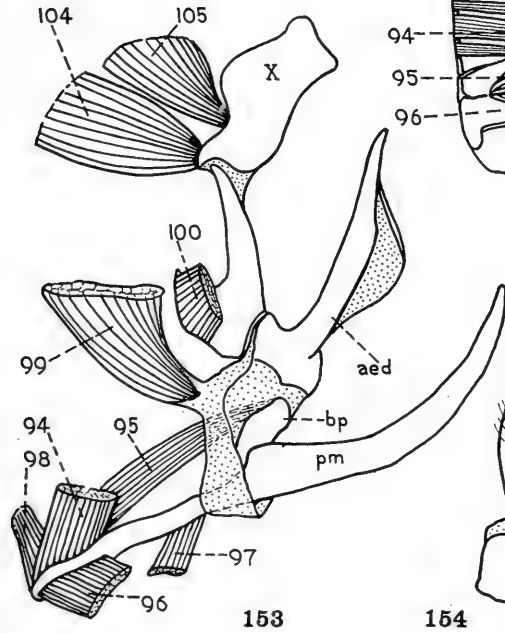
150. Caudal view of male genitalia
151. Lateral view of male genitalia
152. Muscles of the male genitalia, lateral view
153. Dissection showing paramere, basal plate, aedeagus, tenth segment, and musculature
154. Ventral view of subgenital plate
155. Caudal view of aedeagus



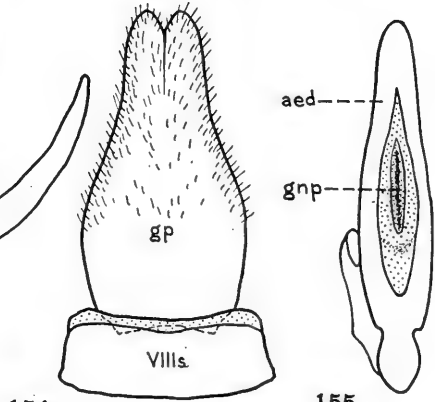
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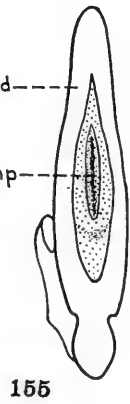
152



153



154



155





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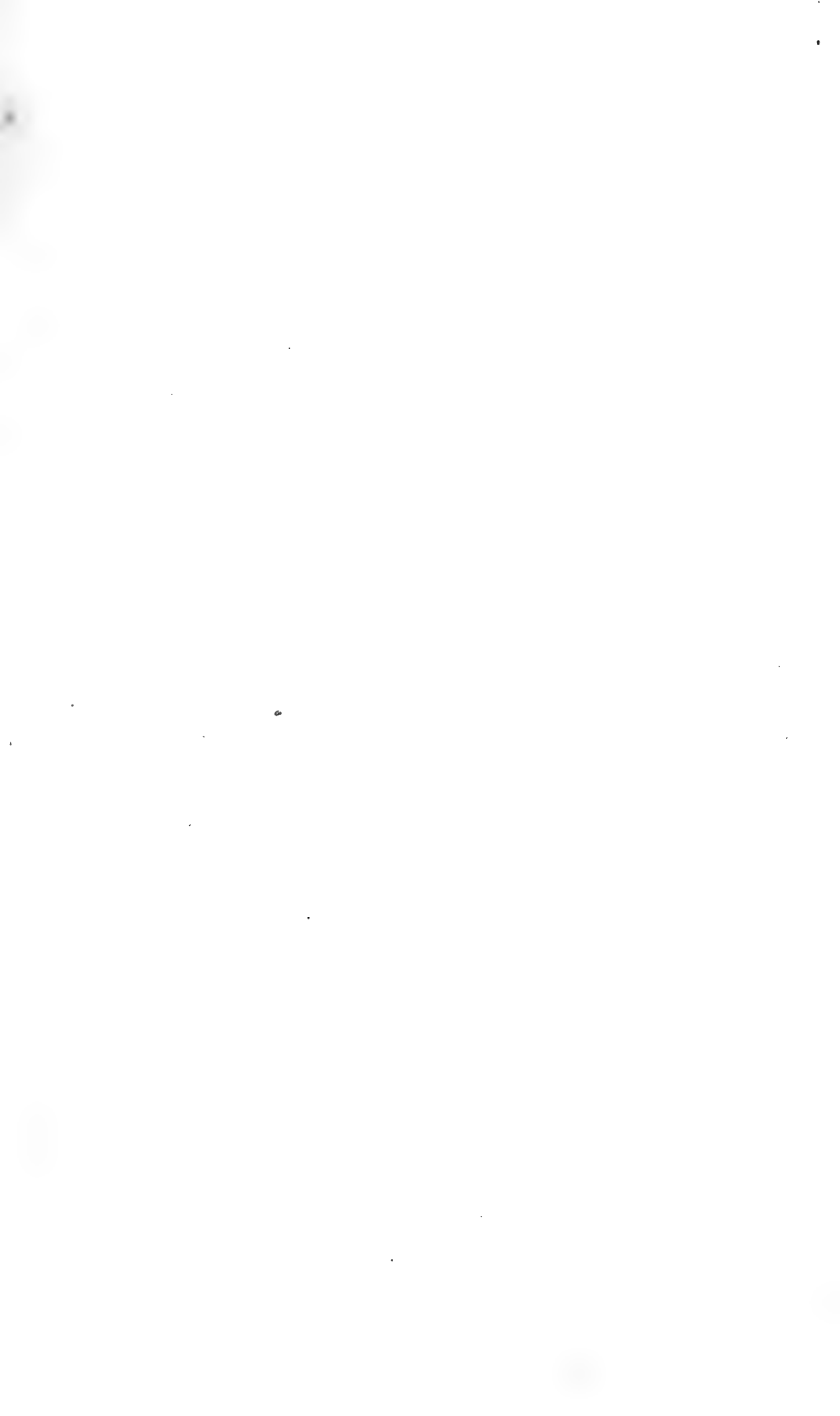
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