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EDITORIAL COMMITTEE

JOHN THEODORE BUCHHOLZ

FRED WILBUR TANNER

HARLEY JONES VAN CLEAVE

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EDITORIAL COMMITTEE

JOHN THEODORE BUCHHOLZ
FRED WILBUR TANNER
HARLEY JONES VAN CLEAVE

THE PHYLOGENY OF THE HEMIPTERA
BASED ON A STUDY OF THE
HEAD CAPSULE

WITH 24 PLATES

BY

CHARLES STOCKMAN SPOONER

CONTRIBUTION FROM THE ENTOMOLOGICAL LABORATORIES OF THE
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INTRODUCTION

The head of the Hemiptera is a highly modified structure. It is not surprising, after comparing it with the head of a generalized, mandibulate insect, to find that there has been considerable controversy regarding the identity of the various sclerites involved. The problem of the homology of these sclerites was practically hopeless until we obtained some direct evidence from embryology. The early work of Heymons (1899) gave us our first clue. This work was later corroborated and extended by Muir and Kershaw (1911, 1912). Further careful studies of the musculature of the various parts by Muir (1926) and Snodgrass (1921, 1928, 1935) have given us a fairly secure foundation upon which to base comparative studies.

Careful and intensive studies of various species have recently been made: *Nepa*, Hamilton (1931); *Naucoris cimicoides*, Becker (1929); *Psylla mali*, Weber (1929). Nevertheless the head in various Hemiptera has quite a variable structure, and in many cases superficially similar parts have been misinterpreted. It was with the hope of indicating some of these misinterpretations and thereby gaining some indication of the phylogeny of the group that this study was undertaken. It was thought that a study of the nymphs would aid in the understanding of some of the adult structures, and an effort was made to obtain and study as many nymphal forms as possible.

The author is fully aware of the impossibility of showing the true phylogeny by a study of a limited group of characters and of the dangers of misinterpretation involved. There is no intention of claiming finality for the suggestions made. Results will be discussed in relation to the findings of other workers using other sets of characters.

The characteristics presented by the head capsule of the Hemiptera appear to be a particularly valuable record for phylogenetic studies because, throughout the order, there has been little modification of function. Hence the structural differences which accompany changes in function are reduced to a minimum. One or two interesting exceptions to this statement will be described later.

Very little attention has been paid to the mouth parts in this work because they are pretty much of the same pattern throughout the order. The mandibles and maxillae are discussed as a means of identifying the fixed parts of the head. The types of mandibular levers have been studied to determine their phylogenetic value.

The terms applied to the various parts are, so far as possible, those which have been in general use. The general nomenclature of MacGillivray (1923b) or Snodgrass (1935) has been followed. New terms or new applications of old ones have been suggested for parts previously

incorrectly named or where systematists have applied different terms for the same structure in the two suborders.

ACKNOWLEDGMENTS

This study was begun under the late Professor A. D. MacGillivray, and the author is greatly indebted to him for help and inspiration. It has been completed under Professor W. P. Hayes, and to him, likewise, the author is indebted for constant help and encouragement.

Some of the specimens used in this study were obtained from the collections of the Illinois State Natural History Survey. I am indebted to the late Professor S. A. Forbes and to Dr. T. H. Frison and Dr. H. H. Ross for these courtesies. Among the most interesting of these materials were nymphs of the enicocephalid, *Systelloderus biceps* (Say) and of the ceratocombid, *Ceratocombus vagans* McA and Mal. These were loaned through the courtesy of Dr. Ross and, so far as I have been able to discover, are the first nymphs of these families on record. The author has since taken two specimens of the nymphs of *Ceratocombus vagans* from the University Woods at Urbana, Illinois.

The author also wishes to thank Professor H. B. Hungerford for gifts of specimens of *Naeogeus burmeisteri* L. and S. and *Ochterus viridifrons* Champ. Mr. H. E. McClure kindly furnished some specimens of *Systelloderus biceps*. Mr. Walter Scruggs has spent many hours in arranging and photographing the plates, for which work the author is very grateful.

MATERIALS AND METHODS

Studies were made of representatives of all of the North American families in which material was available. Nymphs as well as adults were studied in every case in which they were obtainable, and this represents a surprisingly large proportion of the families.

The heads were treated in ten per cent caustic potash until they were fairly clear and were then studied under the binocular microscope. It was found that the details were most readily seen in heads that were preserved and studied in glycerine. This had the further advantage of keeping them soft and flexible.

The mandibular levers were dissected from heads that had been thoroughly treated in the potash. The larger forms were then cleared in carbolxylol and mounted in balsam, while the smaller forms were studied in a drop of glycerine.

The following representatives of the various families were studied. The names are those used in Blatchley's *Heteroptera of Eastern North America* (1926), or Britton's *Hemiptera of Connecticut* (1923), or VanDuzee's *Catalog of the Hemiptera of North America* (1917).

HOMOPTERA

FULGORIDAE

- Otiocerus degerrii* Kby.
Otiocerus wolfii Kby.
Analoptera uhleri VanD.
Lamenia vulgaris (Fitch)
Cyarda melichari VanD.
Acanalonia sp. nymph
Acanalonia latifrons (Walk.)
Ormenis pruinosa (Say)
Pelitropis rotatula VanD.
Oliarus vicarius (Walk.)
Catonia impunctata (Fitch)
Cixius pini Fitch
Epiptera sp. nymph
Cyrpoptus reineckeii VanD.
Liberniella ornata (Stal) nymph
Pentagramma vittatifrons (Uhl.)
 adult and nymph
Dictyophora florens (Stal)
Bruchomorpha sp. adult and nymph

CERCOPIIDAE

- Lepyronia quadrangularis* (Say)
 adult and nymph
Monecophora bicincta (Say)

CICADIDAE

- Tibicen sayi* (Sm. and Grsb.) adult
 and nymph

CICADELLIDAE

- Agallia constricta* VanD.
Oncometopia undata (Fabr.)
Gypona sp. nymph
Jassus olitorius Say adult and nymph
Phlepsius excultus (Uhl.)
Erythronaura comes (Say)
Acinopterus acuminatus VanD.
Euscelis bicolor (VanD.)

APHIDIDAE

- Lachnus* sp.

PSYLLIDAE

- Pachyphsyla celtidis-mamma* Riley
Trioza tripunctata (Fitch)

ALEYRODIDAE

- Trialeyrodes* sp.

HETEROPTERA

BELOSTOMATIDAE

- Belostoma flumineum* Say adult and
 nymph

NEPIDAE

- Ranatra americana* Mont. adult and
 nymph
Nepa apiculata Uhl. adult and nymph

NAUCORIDAE

- Pelocoris femoratus* P. deB. adult and
 nymph

NOTONECTIDAE

- Notonecta* sp. adult and nymph

CORIXIDAE

- Corixa* sp. adult and nymph

GERRIDAE

- Gerris marginatus* Say adult and
 nymph
Gerris remigus Say

VELIIDAE

- Rhagovelia obesa* Uhl. adult and
 nymph

MESOVELIIDAE

- Mesovelia bisignata* Uhl.

HYDROMETRIDAE

- Hydrometra martini* Kirk

NAEOGEIDAE

- Naeogeus burmeisteri* L. and S. adult
 and nymph

OCHTERIDAE

- Ochterus americanus* (Uhler) adult
 and nymph
Ochterus viridifrons Champ.

NERTHRIDAE

- Gelastocoris* sp. adult and nymph

- SALDIDAE
Lamprocanthia sp. adult and nymph
Pentacora sp.
- ANTHOCORIDAE
Triphleps insidiosa (Say) adult and nymph
- CIMICIDAE
Cimex lectularius Linn. adult and nymph
- REDUVIIDAE
Sinea sp. adult and nymph
Emesa brevipennis (Say) adult and nymph
Melanolestes abdominalis H.-S.
- NABIDAE
Nabis subcoloptratus Kirby adult and nymph
- ENICOCEPHALIDAE
Styelloderes biceps (Say) adult and nymph
- CRYPTOSTEMMATIDAE
Ceratocombus vagans McA. and M. adult and nymph
- MIRIDAE
*Miris dolobratu*s (Linn.) adult and nymph
Adelphocoris rapidus (Say)
- LYGAEIDAE
Ichnodemus falicus (Say) adult and nymph
Myodochnus serripes Oliv. adult and nymph
- PYRRHOCORIDAE
Euryophthalmus succinctus (Linn.) adult and nymph
- NEIDIDAE
Neides muticus (Say) adult and nymph
Jalysus spinosus (Say)
- CORIZIDAE
Corizus sp. adult and nymph
Harmoestes reflexulus (Say)
Leptocoris trivittatus Say adult and nymph
- COREIDAE
Anasa tristis (DeG.) adult and nymph
Acanthocephala terminalis Dallas
- ALYDIDAE
Alydus sp. adult and nymph
- PIESMIDAE
Pisma cinerica Say
- TINGITIDAE
Corythuca ciliata Say adult and nymph
- PHYMATIDAE
Phymata sp. adult and nymph
- ARADIDAE
Aneurys sp. adult and nymph
- PENTATOMIDAE
Brochymena sp. adult and nymph
Euschistus servus (Say)
Euschistus servus (Say) variety
Euschistus euschistoides (Vollenhoven)
Euschistus tristigmus (Say)
Euschistus tristigmus luridus Dallas
- CYDNIDAE
Cyrtomenus mirabilis (Perty)
- CORIMELAENIDAE
Corimelaena sp.
- SCUTELLERIDAE
Stethaulax marmoratus (Say)

THE GENERALIZED HEMIPTEROUS HEAD

The generalized head of the Hemiptera would be one which most nearly approaches the head capsule of the mandibulate insects. Since all of the head types of this order are rather far removed from those of any

existing mandibulate insect, the designation of a generalized type of head is rather difficult.

There are extensive differences between the head structures found in the two suborders Homoptera and Heteroptera. There has been, furthermore, some dispute as to which of the suborders is the more primitive. Some workers, who have arranged the orders in an ascending or descending series, assume that the Heteroptera are the more generalized, Comstock (1915). Others have assumed the opposite and have placed the Homoptera first in their ascending series, Kellogg (1905). Tillyard (1918) states that the Homoptera have retained the more primitive wing form and venation, while the Heteroptera have preserved the more primitive form of head and antenna. Muir (1923) believes that the head of Heteroptera is the more primitive.

The earliest fossil forms, however, belong to the Homoptera with the single possible exception of *Eugercon* described by Handlirsch (1908). Considerable discussion has taken place regarding the affinities of this genus. Tillyard (1921) accepts the decision of Handlirsch that it is a heteropteron while Crampton (1927) expresses his doubt about the matter and gives various reasons for deciding that it is not a heteropteron but is perhaps a forerunner of the Diptera. Judging from the figure reproduced by Crampton in his paper, the writer is inclined to agree with him. If this conclusion is sound, then we are left with the fact that all of the earlier fossil forms are homopterous.

The tentorium, as will be shown later, is much more nearly typical in the Homoptera than in the Heteroptera. Certain other features which will be brought out later in this discussion, bear out the fact, that, with one or two exceptions, the head structures of the Homoptera are of a more primitive type than those of the Heteroptera. Only in the form of the labrum in some of the Heteroptera and in the fact that the gular area is not so reduced as in the Homoptera, does the former appear to be the more generalized form.

The fossil record, the form and venation of the wings, the condition of the tentorium and other head structures lead the writer to consider that the Homoptera retain more of the ancestral characteristics than do the Heteroptera. We look, therefore, for the most generalized form of head capsule among the former group.

Most of the workers on the morphology of the Homoptera have used for their studies one of the cicadas. This is perhaps because of their large size and the availability of material as much as the belief that they represent the generalized type. Most of our knowledge of hemipteran morphology has, indeed, been gained from these studies of the cicadan head, and the structure of other forms has been rather haphazardly compared with that of the cicada. Muir and Kershaw (1911a, 1912),

Muir (1926), Snodgrass (1921, 1928, 1935) and Myers (1928) have all made important contributions to the anatomy of this form.

A study of the members of the Fulgoridae, in its broad sense, indicates to the writer that some of the structures of the heads of members of this family show more primitive characteristics than those of any other family of the Homoptera. The author recognizes the fact that this family contains forms which, in many respects, are highly specialized, but he believes, nevertheless, that many of the structures have been retained in rather primitive form. *Otiocerus degeerii* has been selected to indicate the structures from which the above conclusions have been reached. This species (Figs. 1 and 53) shows the presence of an extensive vertex (Fig. 53, *v*), a large frons (*fr*), a distinct postclypeus (*pc*) separated from the frons by the fronto-clypeal suture (the epistomal suture of Snodgrass 1935), a much smaller anteclypeus (*ac*) which bears a small pointed labrum (*lbr*) attached to its posterior margin. The maxillary plate (*mp*) is large and triangular, tapering to a sharp point, the maxillary process. This plate is separated from the clypeus by a deep suture, and it is near the base of this suture that the mandible is attached. This suture is homologous with the genal suture of Muir (1926) and Myers (1928). It marks in reality the lateral limits of the clypeus and, since the maxillary plate is made up in part of the gena, this term may well be retained for it.

The antafossae (*af*) are located on the front just dorsad of the fronto-clypeal suture. The antafossae, then, are also just dorsad of the point of attachment of the mandibles and may serve as landmarks to delimit the postclypeus in those forms in which the fronto-clypeal suture is wanting. This relation between the antafossae and the point of mandibular attachment has been found to be constant in all of the forms examined. Thus a line drawn across the fronto-clypeal area, slightly ventrad of the antafossae will, approximately, separate the two areas.

The lateral margins of the postclypeus are slightly invaginated along the border of the maxillary plate forming the genal suture. The pre-tentorinae occur at the base of these sutures. They are located at the bottom of the infolded area and hence are not visible externally.

The anteclypeus is a rather small area with the lateral margins deeply invaginated and the two invaginations, one from each side, meet within the head and form a hollow cylinder which supports the salivary pump and the setae. A long projection extends from the dorso-ventral margin, extending for a considerable distance dorsad into the region covered by the postclypeus (Fig. 346).

The complete absence in *Otiocerus* of those much discussed sclerites, generally designated as the mandibular plates by morphologists and as lorae by systematists, should be noticed. *Otiocerus* is, in this respect,

more primitive than any of the other Homoptera. The gradual development of these sclerites will be shown later in an interesting series of forms. The mandibular attachment is usually described as being on these sclerites but the evidence here shows that the genal suture is the important feature marking the location of these points. The method of development of these sclerites shows them to be undoubtedly parts of the clypeus and the writer favors the term paraclypeus for them in place of the terms mandibular plates or lorae. This term has been suggested for them by Crampton (1921) and the areas have been referred to as parts of the clypeus by Deshpande (1933).

MODIFICATIONS OF THE PARTS OF THE HEAD IN HOMOPTERA

THE VERTEX.—The vertex is here considered in its morphological concept, that is, as including that portion of the epicranium on each side of the epicranial stem and bounded anteriorly by the epicranial arms. These sutures are termed the coronal and frontal respectively by Snodgrass (1935) but the author sees no reason for changing from the former well known terms. A study of the nymphs gives us an idea of the extent of this area. The epicranial stem and arms are not visible in any adult homopteron known to the author.

The term crown has been suggested by Myers (1928) for the dorsal aspect of the head largely because of the incorrect interpretation of the extent of the vertex in the Fulgoridae. Snodgrass (1935) makes this same error but retains the term vertex and states that this area in the Homoptera, particularly in the Fulgoridae, is a very large area and that these forms, in consequence, have a greatly reduced frons. He further states that the peculiar enlargements of the head, so often found in members of this family, are formed entirely by the enlargement of the vertex. A study of the nymphs of these forms indicates that this conclusion is incorrect. These forms, in general, have the vertex limited largely, if not entirely, to the dorsal aspect of the head, and the cephalic aspect of the head contains an extensive frons (Figs. 11, 40, and 41). The processes on the heads of these insects are then made up of extensions of both vertex and frons. This is true of *Scolops* sp. whose nymphs show a very long epicranial stem extending to the apex of the elongation, then dividing into the two epicranial arms which extend down the cephalic surface of the elongation and mark the position of the frontal carinae in the mature insect. In some families of the Homoptera the vertex is rather extensive and the frons is reduced to a very small area (Fig. 23).

Snodgrass (1935) figures the head of *Occlus borealis* and labels the carinae surrounding the median ocellus as the epicranial arms, and, consequently, the minute area included by them, as the frons. The study of

a cixiid nymph, which the writer succeeded in obtaining only after the plates for this article were made up (and hence it is not figured), shows a rather short epicranial stem with the arms branching out just caudad of the compound eyes, and curving cephalad, paralleling the inner margins of these eyes. Hence the frons is a rather extensive area in these forms. Compare the figure of the nymph of *Epiptera* sp. (Figs. 36 and 63). This is a closely related form.

Reference to figures of the following species will give some idea of the relative extent of the vertex and frons in the various forms. The epicranial stem is comparatively long in such nymphs as the delphacids, *Liburniella ornata* (Fig. 38, *cs*) and *Pentagramma vittatifrons* (Fig. 39), as well as in the cicadid, *Tibicen sayi* (Fig. 44); the membracid, *Ceresa* sp. (Figs. 24 and 25); the cicadellids, *Jassus olitorius* (Fig. 47); *Gypona* sp. (Fig. 48); the aphidid, *Lachnus* sp. (Fig. 50); and in the psyllids, *Pachypsylla celtidis-mamma* (Fig. 51) and *Trioza tripunctata* (Fig. 52). It is only moderately long in the cercopid, *Lepyronia quadrangularis* (Fig. 42) and is very short in such forms as *Bruchomorpha* sp. (Fig. 40) and in *Acanalonia* sp. (Fig. 37).

THE FRONS.—That area of the head capsule bounded dorsally and sometimes laterally by the epicranial arms and ventrally by the fronto-clypeal suture is considered as the frons.

Referring to the remarks made in the discussion of the vertex, we find that this area also varies greatly in size and is not always the greatly reduced sclerite suggested by Snodgrass (1935). As was stated in the description of *Otiocerus degeerii*, the fronto-clypeal suture is wanting in many forms and in these we may use the imaginary line drawn across just ventrad of the antafossae as the ventral limit of the frons.

The frons is very extensive in many of the fulgorids, such as *Otiocerus degeerii* (Fig. 1, *fr*); *Lamenia* sp. (Fig. 2); *Amaloptera uhleri* (Fig. 3); *Cyarda melichari* (Fig. 4); *Ormenis pruinoso* (Fig. 6); *Pelitropis rotatula* (Fig. 7); *Dictyophora florens* (Fig. 15); and *Acanalonia latifrons* (Fig. 18). It is of moderate size in the cercopid, *Lepyronia quadrangularis* (Fig. 20) and the cicadellids, *Oncometopia undata* (Figs. 28 and 49); *Jassus olitorius* (Figs. 29 and 30); *Acinopterus acuminatus* (Fig. 32); and *Erythroneura comes* (Fig. 31). The frons is much reduced in the aphidid, *Lachnus* sp. (Fig. 50) and the psyllids, *Pachypsylla celtidis-mamma* (Figs. 34 and 51) and *Trioza tripunctata* (Fig. 52). In the cicadid, *Tibicen sayi* (Figs. 22, 23, and 44), the membracid, *Ceresa* sp. (Figs. 24 and 25), and the cercopid, *Monocophora bicincta* (Fig. 21), the frons is reduced to an extremely small area.

It is well to call especial attention, here, to the marked difference in the size of the frons in the two cercopids, *Lepyronia quadrangularis* (Fig. 19) and *Monocophora bicincta* (Fig. 21).

THE CLYPEAL REGION.—This region always consists, in the Homoptera, of at least two parts, and in the great majority of forms, of four parts. The statement made by Snodgrass (1935) that in some species of Fulgoridae, the clypeus consists of a single piece is incorrect. He cites *Oecleus borealis* as an example. The division between the anteclypeus and postclypeus is, in this form, obscured by a strongly elevated carina extending vertically down the frons and clypeal region. The lateral aspect of this region, however, shows a clear separation between the two areas and this division is still more readily seen in specimens that have been treated in caustic potash. The paraclypeus is also present in this form.

The anteclypeus and postclypeus are always present in the Homoptera, and in the majority of forms there is a more or less well developed paraclypeus on each side.

This divided condition of the clypeus is commonly found in some of the lower insects, such as the Orthoptera. Crampton (1921) refers to these areas as the postclypeus and the anteclypeus. He also describes the lateral areas of this region as found in the larva of *Corydalis* and applies the term paraclypeus to them. These areas were termed the antecoxal piece of the mandible by Comstock (1925) and the clypealia by MacGillivray (1923b). Crampton (1921) suggests that, in these insects, these areas are formed by the extension of the epicranial arms across the clypeus. This is not the method of their formation in the Hemiptera, and they can therefore not be homologous structures, but the writer has used the term paraclypeus to designate them.

The postclypeus (*pc*) is usually a large and well defined area. It furnishes the attachment plane, internally, for the muscles of the pharyngeal pump. In many forms it is distinctly separated from the frons by the fronto-clypeal suture, as in *Otiocerus degeerii* (Fig. 1); *Catonia impunctata* (Fig. 9) and *Tibicen sayi* (Fig. 23). This suture is wanting in the cercopid, *Lepyronia quadrangularis* (Fig. 20), the membracid, *Carynota mera* (Fig. 26) and in all of the cicadellids (Figs. 27-32). The position of the antafossae (*af*) gives us the clue to the extent of the paraclypeus in these forms. The places of attachment of the pharyngeal muscles also aids in locating its anterior limits.

The greatly reduced frons in the cicada and the enormous enlargement of the postclypeus has resulted in a great deal of discussion as to the homology of these parts. Vickery (1908) called the postclypeus the clypeus, Meek (1903) labelled it the frons, while Berlesi (1909) recognized two areas and called them postfrons and frons. Muir and Kershaw (1911) returned to the term clypeus, Branch (1914) recognized it as the frons as did Snodgrass (1921) and Muir (1926). The latter suggested that it might be a clypeofrons. Snodgrass (1921) demonstrated, by a study of the muscle attachments that it was clearly clypeal in nature and

termed it the postclypeus. Myers (1928), however, still refers to it as the frons.

The postclypeus, in those forms which lack the paraclypeus, is bounded laterally by the genal sutures. These margins are somewhat invaginated and from the ventral portions of these invaginations, wing-like projections extend to the pharyngeal pump which they help to support.

Where the paraclypeus is well developed, the anteclypeus is marked off by a deeply invaginated suture on each side. These are the frontal sutures of Muir (1926), Myers (1928) and Snodgrass (1935). They are not extensions of the epicranial arms, as will be shown later, and hence should hardly be termed the frontal sutures. The invaginations along these sutures form a deep flange about the postclypeus, extending into the head, which serves for muscle attachment and from the ventral margins of which there extend wing-like supports to the pharyngeal pump.

The anteclypeus (*ac*) is a small but well defined area attached to the ventral margin of the postclypeus. The lateral margins are more or less invaginated and sclerotized, ranging from the strongly sclerotized cylinder of *Otiocerus wolfii* (Fig. 346) to the nearly membranous and flattened areas found in cicada. These invaginations serve as supports for the salivary pump and for the mesal margins of the mandibular and maxillary setae.

The paraclypeal regions make up the areas which have occasioned the greatest discussion of any part of the hemipterous head. They have been called the lorae by systematists for many years. Smith (1892), in discussing the morphology of the cicada, stated that they were derived from the mandibular segment and hence referred to them as the mandibular plates. Muir and Kershaw (1911a) described these areas as extensions of the clypeus, and the same authors (1912) stated that they were not formed from the mandibular sclerite and had no relation to the mandibles. They declared them to be homologous with the gena of other orders. Muir (1926) declared them to represent a part of the genal area. He states, in this same work, that there is no embryological evidence that they are parts of the mandibular segments. Snodgrass (1927) agreed with this conclusion but later (1935) again refers to them as the mandibular plates. Myers (1928) homologizes them with the gena and states that they are not lateral clypeal sclerites nor mandibular plates; Weber (1929) calls them the laminae mandibulare, while Deshpande (1933) refers to them as clypeal sclerites.

Examination of the drawings of the head of *Otiocerus degeerii* (Fig. 1) and of *Lamenia* sp. (Fig. 2) shows that the paraclypeal areas are wanting. The anteclypeus is attached, with a very slight indentation, to

the ventral margin of the postclypeus. The drawing of *Amaloptera uhleri* (Fig. 3) shows the anteclypeus included for a considerable distance within the postclypeus, cutting off a small area on each side which may be regarded as the beginning of the paraclypeus (Fig. 3, *pac*). A study of a series of forms such as *Cyrtoda melichari* (Fig. 4), *Acanalonia latifrons* (Fig. 18), *Pelitropis rotatula* (Fig. 7), *Epiptera* sp. (Fig. 11), and *Bruclomorpha* sp. (Fig. 16) shows in the order named progressive steps in the inclusion of the paraclypeus by the postclypeus and hence the increasing size of the paraclypeal areas.

Muir and Kershaw (1912) state that the embryonic development of the Hemiptera shows there is an extension or overgrowth of the areas referred to by them as the genae and the maxillary plates. This satisfactorily explains the conditions found in such forms as the cercopid, *Lcapyronia quadrangularis* (Fig. 20), the membracid, *Carynota mera* (Fig. 26) and others in which the distal ends of these areas extend well beyond the point of union between the postclypeus and the anteclypeus. The paraclypeal areas in some forms have become entirely vertical and are visible only from the lateral aspect, as in *Catonia impunctata* (Figs. 9 and 61).

The study of this series leaves little doubt that the paraclypeal areas are actually portions of the clypeal area cut off by the progressive development of a suture extending from each proximal corner of the anteclypeus. This suture is the one referred to by Muir (1926) as the frontal suture.

THE MAXILLARY PLATES.—The origin of these plates (*mp*) from a part of maxillae in the embryo was first described by Heymons (1899) and corroborated by Muir and Kershaw (1911 and 1912). The terminology of these plates has since been quite uniform. MacGillivray (1923b) refers to them as the hemimaxillae.

These areas, in addition to a portion of the maxillae, undoubtedly include, at least in part, the genae and postgenae. Snodgrass (1921) makes the statement that they are largely postgenae. There are traces of sutures, in some forms, which may indicate the line of fusion of the maxillary area with the postgenae. These sutures have been termed the maxillary sutures by Muir (1926). They are very faint and have been indicated by dotted lines in the drawings of *Euscelis bicolor* (Fig. 82) and of *Monocophora bicincto* (Fig. 71).

Muir (1926) also recognizes a fourth suture, the labial suture, along which the invaginations (metatentorina of MacGillivray 1923b) of the metatentoria occur. The writer has not been able to find these sutures in the forms studied. They may be the line of attachment of the labial membrane to the postgenae or they may represent the postoccipital sutures of Snodgrass (1935).

The maxillary plates form most of the lateral and caudal aspects of the head. They enclose the maxillary and mandibular setae and lend support to them. They become narrower ventrally and end in a sharp point which has been termed the maxillary process. These processes support the labium, especially when the insect is in the act of feeding. The maxillary plates vary greatly in size and shape throughout the group. (Figs. 53-86, *mp*).

THE LABRUM.—This is a small, narrow, triangular sclerite attached to the ventral margin of the anteclypeus. It lies along the base of the groove of the labium, partially covering this groove and lending support to the mandibular and maxillary setae. It varies somewhat in length but is otherwise quite uniform in the Homoptera.

There has been some discussion in regard to the composition of this sclerite. It has frequently been referred to as the epipharynx (Crawford 1914). Muir and Kershaw (1911a) state that "The division between the labrum and the epipharynx is obscure" and suggest the term labrum-epipharynx for it. MacGillivray (1923b) and Myers (1928) follow this terminology. Snodgrass (1935) calls it the labrum.

The epipharynx, in mandibulate insects, is the inner surface of the labrum. In certain sucking insects, as the Diptera, there is evidence of a projecting outgrowth of this inner lining which is visible externally and which may be differentiated from the labrum. There is no such evidence in the Homoptera and, hence, there is no more reason for referring to this sclerite as the labrum-epipharynx in the Homoptera than there is in the mandibulate insect.

THE CAUDAL ASPECT OF THE HEAD.—This area of the head in the Homoptera is almost entirely membranous. The lateral and ventral borders of the large occipital foramen (*oc*) are formed by the occiput which is fused with the vertex without evidence of a suture.

The postoccipital area is membranous, and it is very difficult or impossible to determine the exact division between it and the neck membrane. Odontoidea are seldom distinguishable. Their position is indicated by the occurrence of the metatentorinae (Fig. 91, *mt*). The metatentorinae are externally visible in very few species.

There is no gula or gular area in this suborder. The labium is joined to the maxillary plates by membrane.

THE TENTORIUM.—The tentorium of the Homoptera is very nearly typical. A good deal of discussion has occurred in regard to this structure, and the fact that some secondary structures occur has resulted in some confusion. Muir (1929) states that the anterior arms of the tentorium are invaginated from the hypopharynx and hence cannot be homologized with those of other insects nor should they be used as landmarks of the fronto-clypeal suture. He further states that this is similar

to conditions found in the Myriapoda and the Apterygota and hence indicates a more primitive origin than was previously supposed for the Hemiptera. The author does not understand just what Muir has in mind and does not agree with the conclusions. Snodgrass (1928) points out the homology of the tentorium of all insects with the hypopharyngeal apophyses of the Myriapoda but states that the "final condition is characteristic of all Pterygota except the Ephemera and Odonata." This of course implies the homology of the tentorium of the Hemiptera with that of the mandibulate insects.

The tentorium of the members of the Cercopidae appears to be the most nearly typical of any of the Homoptera. The metatentoria (posterior arms) are invaginated from the membrane, on each side, about at the middle of the occipital foramen (Figs. 100 and 102, *mt*). These metatentorinae supposedly mark the position of the post-occipital suture and of the odontoideae, but neither of these structures are distinguishable in these forms.

The metatentoria extend mesad and unite to form the corpotentorium (body of the tentorium). This appears as a narrow, cylindrical bar, extending across the occipital foramen (Fig. 102, *ct*). A broad, heavily sclerotized plate extends ventrad from each corner of the corpotentorium. The plates merge with the evaginations of the hypopharynx. These wings of the hypopharynx are perhaps the "invagination of the hypopharynx" referred to by Muir (1929). They are clearly secondary in nature and have become united with the tentorium proper during the evolution of the group. They serve as supports for the pharyngeal pump and as guides for the maxillary and mandibular stylets.

Two narrow rods may be observed extending dorsad, one from each side of the meson of the corpotentorium. Near the cephalic ends of these rods each divides into two branches. The branch nearest the meson extends to a point at the base of the genal suture, ventrad of the antafossae where may be found the opening of the invagination which is a pretentorina. The rods in question represent the pretentoria (Fig. 102, *pt*). The lateral branch, extending cephalo-laterad from each pretentorium, probably represents the supratentorium (the dorsal arms) (Fig. 102, *st*). This branch extends forward until it comes in contact with the head capsule where it may become lightly attached. There are no external signs of invagination on the head, for these structures and their position agrees with the account of the supratentorium given by Riley (1904). This author states that the supratentorium in *Blatta* appears as an outgrowth from the pretentorium and that they are not independently invaginated. Nelson (1915) corroborates these findings in the honey bee, *Apis*.

The tentorium in *Lepyronia* (Figs. 101 and 102) and in *Monecophora* (Fig. 100) consists of all of the parts found in the head of generalized

insects and they are formed in the normal manner. There are two pairs of invaginations, the pretentorina and the metatentorina, which occur in relatively the same positions and serve as landmarks for the same sclerites as they do in the mandibulate insects.

The head of the cicadid, *Tibicen sayi* (Figs. 104 and 105), has the same type of tentorium except for the lack of the supratentoria. The Fulgoridae also lack the supratentoria, and there is a great variation in the degree of sclerotization of the pretentoria (Figs. 87-95). Many of these are so lightly sclerotized at the cephalic ends as to be easily pulled free from the head, and one may mistakenly consider them to have been entirely free from the head capsule.

The Membracidae have a somewhat reduced tentorium. There is no evidence of the pretentorial arms in *Cercsa sp.* (Figs. 106 and 107) nor in *Carynota mera* (Fig. 103). In the latter species, the dorsally projecting point at each end of the corpotentorium might be considered a remnant of the pretentorium, but it is not in the normal position and it is difficult to conceive of the structure surviving at the point farthest from the place of invagination. The tentorium of these forms is otherwise similar to that found in the Cicadidae. The loss of the pretentorium may have accompanied the decided deflection of the head, so that the antafossae are located directly beneath the corpotentorium when the head is in its normal position.

Another unusual condition is found in the tentorium of the Cicadellidae. In these forms, the metatentorium and corpotentorium are similar to those described in the preceding families. There are, however, no pretentorial arms attached to the corpotentorium. There does occur, just ventrad of each antafossa, an extensive apodeme which extends dorsad and ends without attachment of the distal end to the head capsule.

These apodemes, in *Jassus olitorius* (Figs. 109 and 110, *ap*) and in *Acinopterus acuminatus* (Fig. 111, *ap*), are long and straight. They are branched in *Euscelis bicolor* (Fig. 112), *Phlepsius excultus* (Fig. 113), and *Oncometopia undata* (Fig. 114). Notice that this branching occurs well toward the distal end of the apodeme in the first two species, while in *Oncometopia* it occurs almost at the point of invagination. The author was unable to find any trace of these apodemes in *Erythroneura comes* (Fig. 115).

The homology of these apodemes is in doubt. One is tempted to refer to them as the pretentoria. They originate at the place at which the pretentorina generally occurs. If they are homologous with the pretentoria then the branches would be the supratentoria. The author has not found any reference to pretentoria which do not connect with the corpotentorium. They have, therefore, been referred to simply as apo-

demes in this work. Embryological studies or the examination of a large range of species might throw some light upon this problem.

The psyllid, *Pachyipsylla celtidis-mamma*, possesses a tentorium which resembles in form that of the cicada. It differs in the fact that the corpotentorium is shorter and that the pretentorial arms are heavier and more firmly united with the head capsule. The aphid, *Lachnus* sp., likewise resembles the cicada in the structure of the tentorium, excepting that the pretentorial arms extend from the corpotentorium at such an angle that they are hidden by the corpotentorium when the head is examined from the caudal aspect.

It is of interest, here, to consider the family Peloridiidae. This is a small family of subantarctic Hemiptera about which there has been much discussion as to its systematic position. It was placed in the Heteroptera originally and Kirkaldy (1906b) included the species in the family Ochteridae. China (1924) suggests that it form a new suborder between the Homoptera and Heteroptera. Myers and China (1929) made a thorough study of the external anatomy of *Hemiodoccus leai* and conclude that the family belongs to the Homoptera and that "it is very near the ancestral stock of the two suborders." A study of their figures shows that the tentorium in this species is typically homopterous and is quite similar to that of some of the Fulgoridae.

THE LABIUM.—Very little attention has been paid to the labium in this study. The pattern, throughout the suborder, is quite uniform. Myers (1928) states that the labium consists of three segments with signs of a fourth. The vast majority of forms possess an apparently three-segmented labium. Oestlund (1918) describes a five-segmented labium for the tribe Lachnini of the Aphididae and considers this condition to be the primitive one for the family. Vickery (1908) figures this type of labium. A six-segmented labium was described for the tropical fulgorid, *Pyrops candelaria*, by Kershaw (1910).

The labium in the Homoptera is attached apparently directly to the neck membrane just behind the ventral corners of the maxillary plates.

THE MANDIBULAR LEVERS.—The mandibular stylets, in the Homoptera, are attached to the head capsule by means of a sclerotized plate which is formed by invagination of the upper end of the genal suture and known as the mandibular lever. One end of this lever is attached to the head near the end of the genal suture, just ventrad of the antafossae. The distal end of the lever is attached to the end of the mandibular stylet. A simple type of this lever is seen in *Otiocerus degeerii* (Fig. 350, 1). The lever in this species joins the mandibular stylet at an acute angle (Fig. 350a, 1). The shape of the head influences the length of the lever and the angle at which it joins the mandibular stylet.

The cicadid, *Tibicen sayi* (Fig. 352), shows a form in which the base of the mandibular stylet is forked. One fork uniting with the lever (1), the second fork extending dorsally into the head and giving attachment to the retractor muscles which arise on the dorsal wall of the head.

This forked condition of the base of the mandibular stylet is also seen in the cercopid, *Lepyronia quadrangularis* (Fig. 351). In this form, the inner fork seems to connect with the base of the maxilla as well as with the retractor muscles. The inner fork is much reduced in *Oncometopia undata* (Fig. 353), being little more than a tendon attaching the retractor muscles. The lever in this species is bent, forming almost a right angle.

The author found no evidence of a mandibular lever in *Pachypsylla celtidis-mamma*. Weber (1929) states that it is absent in *Psylla mali*. The lever, then, may be characteristically wanting in the *Psyllidae*.

THE MAXILLARY LEVER.—The maxillary stylet of the cicada is also attached to the head capsule by means of a lever which is more nearly like the mandibular levers of the Heteroptera than are those of the mandibles of the Homoptera. This structure has not been studied in the other families of the Homoptera. It is lacking in the Heteroptera. The place of attachment of the maxillae varies considerably in the different forms; hence they cannot well be used as landmarks for the head sclerites and, therefore, they have been omitted from this work.

PHYLOGENY OF THE HOMOPTERA

These studies on the head capsule have brought to light a number of points which may be of significance in a study of the phylogeny of the group. A brief summary of the present classification may be of service.

The Homoptera was first divided into the series Auchenorrhyncha and Sternorrhyncha by Amyot and Serville (1843). Duméril (1806) had already proposed the term Auchenorrhyncha. These series were based upon the position of the mouth parts and are still in good standing.

The families recognized as belonging to the Auchenorrhyncha, arranged in a generally accepted ascending order are, the Cicadidae, Cercopidae, Membracidae, Fulgoridae, and Cicadellidae. A few years ago there was a tendency among students of these insects to break up the Fulgoridae and Cicadellidae into a number of families. Recent workers, however, have returned to the older classification and Britton (1923) lists the five families given above. European workers, Muir (1923), still split the Fulgoridae into some fourteen families.

The Sternorrhyncha is composed of the families Psyllidae, Aphididae, Aleyrodidae, and Coccidae. Few changes have been made in this arrangement through the years. Each family forms a distinct and rather homogeneous group.

The author has already stated that he considers the Fulgoridae to have retained some of the most primitive conditions in the structure of the head capsule. It should be emphasized that this family represents quite a varied assortment of insects, many of them highly specialized in certain respects. The splitting of this group into numerous families is probably justified but should await careful morphological studies of representatives of the group from all over the world.

Most workers have considered the Cicadidae as most primitive, while Myers and China (1929) suggest the recently discovered family, Peloriidiidae, as representing the most primitive living forms. The author has not seen specimens of this family and cannot express an opinion upon it. Muir (1923) states that "some writers derive the Psyllidae from a psocid-like ancestor and so we must consider all the other Homoptera and Heteroptera as derived from the Psyllidae. In my opinion this is a reverse of the truth."

The same author in his diagram of the affinities of the Homoptera, derives the Fulgoridae very early from his Protohomoptera—in fact it is the first branch to leave the main homopteran stem.

The developmental series of the paraclypeal areas described in the Fulgoridae indicates a very primitive condition in some of these forms. Certain structural resemblances to the Heteroptera, which will be discussed in detail later, add evidence for this conclusion.

We find, on comparison of the heads of *Tibicen sayi* (Figs. 23 and 72), *Oncometopia undata* (Figs. 28 and 79), and *Moncophora bicincta* (Figs. 21 and 71) a striking similarity in form and structure. All three of these species agree in having a greatly reduced frons and an enormously enlarged postclypeus. *Moncophora* differs markedly in this respect from *Lepyronia quadrangularis* (Figs. 19, 20, 69, and 70). *Oncometopia*, on the other hand, differs in the same degree from the other members of the Cicadellidae studied (Figs. 27, 29, 30, 31, 32, 77, 80, 81, 82, 83, and 84).

These facts indicate that perhaps the group represented by *Oncometopia* was derived from the subfamily Cercopinae of the Cercopidae, which includes *Moncophora*, while the other members of the Cicadellidae arose from the subfamily Aphrophorinae, which includes *Lepyronia*. These forms would then represent two distinct families. *Oncometopia* and its allies has, at times in the past, been separated from the Cicadellidae, placed in a separate family, and known under different names. The name Tettigonidae was applied to this group by Uhler (1875) and Tettigoniellidae by Melichar (1905). Recent writers have reduced this group to subfamily rank.

The adult aleyrodid (Fig. 35) shows closer relationships to some of the Cicadellidae than to the Psyllidae or Aphididae, as far as head

structure is concerned. The latter two groups, characterized by lack of sclerotization of considerable areas of the head capsule, are, thereby, sharply separated from the rest of the Homoptera. Other characters must be considered to obtain any ideas of relationships in the Sternorhyncha. Weber (1929) has discussed these at some length but leaves the question still open.

Kershaw and Muir (1922) studied the genitalia of the Auchenorhyncha and recognized three types of male genitalia: (1) the cercopid type found also in the Membracidae and Cicadellidae, (2) the cicadid type, and (3) the Fulgoroidea type. The last section they further divided into three groups, all developments of the cercopid type. This evidence tends to show the primitive character of the Cercopidae which is also borne out by the present study of the tentorium.

The thoracic sclerites were studied by Taylor (1918). He grouped the Cicadidae and Cicadellidae with the Aphididae and Psyllidae as having similar thoracic structures. The Membracidae stand alone with a specialized prothorax and the Cercopidae, Fulgoridae, and Aleyrodidae are grouped together because of similarly fused metathoracic sclerites.

Two superfamilies of the Auchenorhyncha were recognized by Muir (1923): the Cicadoidea, which possessed antennae with very few sense organs on the flagellum, and the Fulgoroidea, whose antenna possessed many such organs. The structure of the ovipositor, as pointed out in this same paper, overlaps these antennal characters somewhat. He further states that the Cixiidae, considered as a subfamily of the Fulgoridae in this work, possesses the most normal and primitive wing venation of any recent homopteron.

Kirkaldy (1906a) uses the method of oviposition as a basis of dividing the group. He cites the fact that the insects of the Poekillopteridae and Issidae, here recognized as subfamilies of the Fulgoridae, deposit their eggs externally while the Cicadidae, Cercopidae, Cicadellidae, Membracidae, and in part the Fulgoridae deposit them more or less internally. This, perhaps, is further evidence of the primitive position of some of the Fulgoridae.

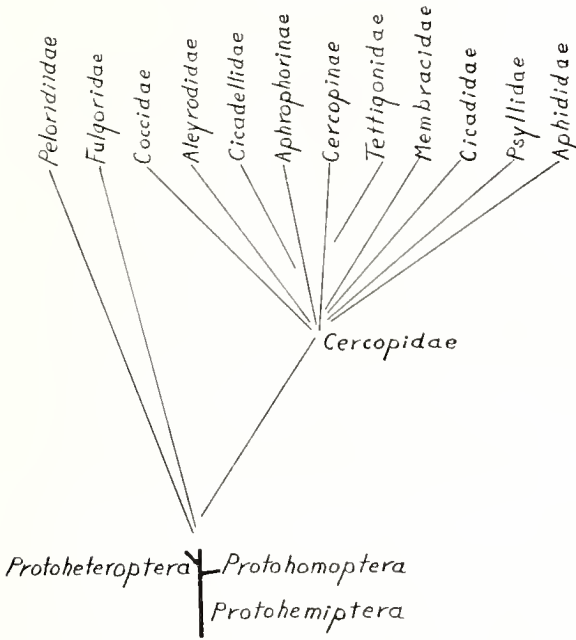
These attempts at unravelling the evolution of the Homoptera are all the writer has been able to find. They show that we are still a long way from the end of the road.

The accompanying diagram (Text-figure 1) gives an idea of the conclusions regarding the relationships of the families arrived at by a study of the head capsule.

THE GENERALIZED HETEROPTEROUS HEAD

The problem of selecting a generalized type of head structure for the Heteroptera is beset with the same difficulties found in the study of the

Homoptera. There is a high degree of specialization in all of the forms, and hence considerable difficulty is experienced in selecting characters which might show progressive development. The outstanding difference in head structure between the Homoptera and the Heteroptera is in the presence of an extensive gular area in the latter group. Students who accept the fossil form *Eugercon* as a primitive heteropteron (Tillyard, 1921) consider that the mouth opening in this group was originally directed cephalad. Consequently the ventral direction of the mouth opening



TEXT-FIGURE 1

becomes a specialized character. No consistent series can be based on this character. It seems to be correlated with feeding habits, the predaceous forms having the more nearly cephalic mouth opening.

Assuming that the Heteroptera originated from a stock common to the Homoptera or as an offshot of the Homoptera, we would expect the size of the gular area to indicate relationships. The shorter the gular area, the more primitive the head structure would be. Here again we find difficulty in arranging the existing forms in any logical series based on this character.

Ekblom (1926) considers the Saldidae as representing the most primitive of living Heteroptera. He bases his conclusions on the short gular area, the ventrally directed mouth, and what he terms the primitive feed-

ing habits, primitive habitat, and methods of egg laying. The writer agrees that the Saldidae are comparatively primitive in head structure and are near the generalized type but he cannot agree with the reasons advanced by Ekblom. Surely the habit of probing the sand for food is not a primitive method of obtaining food nor is the shore line a primitive habitat for insects. Most students consider that insects were originally terrestrial animals and that the present day aquatic and semi-aquatic species are specialized from terrestrial forms and are not generalized forms on the way to a land environment.

A comparative study of the head capsule of the various families of Heteroptera has lead the writer to select two external structures as a guide in selecting the primitive forms and arranging the families in a series. An internal character bears out his conclusions in some cases. Other characters are needed to further subdivide the group. Based upon the study of the Homoptera in which we considered the lack of the paraclypeal areas as a primitive condition, the form of these areas in the Heteroptera is taken as an excellent character which can be used to show successive steps of modification. The second character used in grouping the various families is found in the form of the labrum. This structure, in some species is broad and flap-like (Figs. 152, 155, and 157). It is very similar to that found in most mandibulate insects. This is considered as a generalized form, and the progressive changes to the long slender triangle found in many forms (Figs. 177 and 179) indicates specialization.

Cimex lectularius (Figs. 152, 154, and 237) shows the most primitive combination of these two characters. Objections may be made to the consideration of a parasitic form as a typical or generalized type. However, the writer believes that *Cimex* is a primitive form rather than a degenerate one. Notice the eyes which consist of a scattered group of ocelli. Surely this is a primitive condition. We could consider the loss of the compound eyes as a retrogression accompanying the parasitic habit but we hardly look for a return to the primitive scattered ocelli as such a process. This is certainly the retention of a primitive condition. The writer, however, does not insist too strongly on the acceptance of this form as the most primitive one in the Heteroptera. The members of the family Anthocoridae have equally generalized characteristics, and *Triphleps insidiosa* has been chosen for the description of these primitive characters. (Figs. 158, 239, and 240). The saldid, *Lamprocanthia* sp. also very closely approaches this form in simplicity (Figs. 156 and 238), but for reasons which will be considered later the writer prefers the anthocorid as the most generalized type. Both of these forms show the small paraclypeal areas and the broad, flap-like labrum which have been taken to represent the least specialized condition found in this suborder.

A description of the head capsule of *Triphleps insidiosa* (Figs. 157, 158, 239, and 240) is given as the generalized type. The epicranial stem and arms are distinct in the nymph (Fig. 157, *es, ea*). Each arm extends laterad to the compound eye and parallels the mesal margin of the eye for at least half the length of the eye. These sutures divide the vertex from the frons and mark the caudal limit of the frons as approximately in line with the caudal margins of the compound eyes.

The fronto-clypeal suture is not present, and this fact leaves some doubt as to the exact extent of the frons. The attachments of the mandibular stylets are located, as they are in the Homoptera, near the ends of the genal sutures just below the antafossae. The line between these points, marking the position of the fronto-clypeal suture, must be arched caudad in *Triphleps* so as to miss the anteclypeus. Just how great this arching is is difficult to say, and it is possible that in some forms the postclypeus has been entirely cut into two lateral areas by the retreat of the so-called frontal sutures.

The anteclypeus (*ac*) is a rather narrow area extending cephalad from the postclypeus. Its lateral margins are deeply invaginated. This area is called the tylus by systematists. There is no suture between the postclypeus and the anteclypeus in *Triphleps*.

The paraclypeal areas (*pac*), termed the jugae by systematists, extend, one on each side of the anteclypeus, for about one-half the length of the anteclypeus. The cephalic half of the anteclypeus is bounded on each side by a maxillary plate (*mp*). The labrum (*lbr*) is a broad, flap-like sclerite attached to the cephalic end of the anteclypeus. The lateral and ventral aspects of the head are formed by a solid sclerotized area without sign of sutures. This area is made up of the maxillary plates, the genae, postgenae, and a sclerotized gular area. There are no landmarks present to indicate the extent of any of these parts.

MODIFICATIONS OF THE PARTS OF THE HEAD IN HETEROPTERA

THE VERTEX.—The size of this area varies considerably with the shape of the head. The epicranial arms are visible in all of the nymphs examined. The epicranial stem varies from very long in *Sinea* sp. (Fig. 160) to very short in such forms as *Gerris marginatus* (Fig. 136), *Pelocoris femoratus* (Fig. 125), and *Corixa* sp. (Fig. 133). It is entirely wanting in *Ancurus* sp. (Fig. 206) and *Brochymena* sp. (Fig. 208). The epicranial arms branch out at some point caudad of the cephalic margins of the compound eyes, usually near the posterior margin as in *Sinea* sp. (Fig. 160, *ea*), *Nabis subcoleopratus* (Fig. 165) and *Euryophthalmus succinctus* (Fig. 178). The branching occurs further cephalad in *Emesa*

brevipennis (Fig. 162). The vertex is rather extensive in these forms, but in *Cimex lectularius* (Fig. 153) and *Ischnodemus falicus* (Fig. 175) the arms branch well behind the eyes and the vertex is much reduced. The vertex is limited to the lateral portions of the head capsule in *Aneurus* sp. (Fig. 206) and *Brochymena* sp. (Fig. 208).

The shape of the head seems to control this character, and it varies frequently within the limits of a single family.

THE FRONS.—This area varies inversely with the variation of the vertex described in the preceding section. Those forms with a large vertex have a comparatively short frons. The area also varies with the position of the postclypeus. The fronto-clypeal suture is never present in the Heteroptera. The antafossae serve as landmarks to locate this suture, but due to a pushing back of the clypeal region, accompanied by the curving of the fronto-clypeal line, the anterior limit of the frons is difficult to determine. It is possible that in some cases the clypeal region has been so pushed caudad as to cut the postclypeus completely in two. Pharyngeal muscles are attached in this area, however, which is evidence of its clypeal nature. Weber (1930), in his very excellent book on the Hemiptera, gives figures of the longisections of the heads of an aradid and of the reduviid, *Reduvius personatus*, in which he shows the pharyngeal muscles attached to the head capsule caudad of the anteclypeal area. He also recognizes the presence of the anteclypeus and postclypeus. We cannot recognize any external limits to the cephalic margin of the frons.

The position of the antafossae (*af*) varies greatly within the suborder. This fact has been extensively used as a character to divide the group. The divisions Cryptocerata and Gymnocerata were made on this basis, but, recently, doubt has been expressed as to the phylogenetic value of this character and these subgroups have been abandoned. Reference to the figures will show that they may occur in almost any position. They may be covered by antennal shelves, hidden in pits, or placed on prominent tubercles. The most interesting fact is that with all this migration of the antennae we find that the mandibular levers maintain their point of attachment at the base of the genal suture which somehow arrives at a point near the antafossae in all species. Hence they retain their value as landmarks as they did in the Homoptera.

THE CLYPEAL REGION.—Four areas can be recognized in this region in most forms, and they are homologous with the same areas in the Homoptera. They are the postclypeus, the anteclypeus, and the two paraclypeal areas.

The caudal margin of the postclypeus cannot be determined exteriorly, as was discussed in the previous section. Its cephalic margin is seldom marked by a suture between it and the anteclypeus. Such a suture, however, can be observed in *Myodochus serripes* (Fig. 183) and in *Neides*

muticus (Fig. 185), although it does not appear in the nymphs of these forms (Figs. 181 and 184) and may be a secondary development. It occurs in both nymph and adult of *Phymata* sp. (Figs. 202 and 203). The postclypeus is a very limited area in some forms, and, as was pointed out above, it is perhaps entirely divided in some of the more specialized species. Usually without definite caudal or anterior boundaries it is a rather vague area in this suborder which has led to the frequent statement that it is absent or that the clypeus consists of a single piece (Snodgrass (1935) and MacGillivray (1923)). Muir and Kershaw (1911) describe the early fusion of the frons with the clypeus in the embryo of the reduviid, *Pristhescancus papuensis*. No trace of a suture remains. However, these authors refer to the anteclypeus as the labrum and to the labrum as the epipharynx. This indicates that the clypeus consists of two parts in the embryo and that the postclypeus fuses with the frons.

The anteclypeus, the tylus of systematists, is a well marked area in nearly all of the species of the Heteroptera. Its lateral margins are deeply invaginated along the so-called frontal sutures. The invagination from each side goes deeply into the head and meets the one from the opposite side and fuses with it. This forms a heavily sclerotized cylinder similar to that described for the homopteron *Otiocerus wolffi* (Fig. 346). The mandibular and maxillary stylets pass through this tube, and it also houses the salivary pump. It is found in nearly all of the Heteroptera (Figs. 347 and 348). The anteclypeus of *Corixa* sp. (Figs. 134 and 135) is of interest because of the widening of the distal margin and a turning up of the disto-lateral angles. This gives this sclerite a shape which is quite unique among the Hemiptera. A much less extensive broadening of the distal margin is seen in *Cimex lectularius* (Fig. 154) and in *Lamprocanthia* sp. (Fig. 155).

Four families of the Heteroptera are without a definitely marked anteclypeus. These families are the Naucoridae, *Pelocoris femoratus* (Figs. 125, 126, 127, and 128), Notonectidae, *Notonecta* sp. (Figs. 130 and 131), Ochteridae, *Ochterus americanus* (Figs. 147 and 149), and the Nerthridae, *Gelastocoris* sp. (Figs. 148, 150, 298, and 299). Becker (1929) records the absence of a definite anteclypeus in *Naucoris cimicoides*. There is no indication of any separation of the clypeal area into postclypeus and anteclypeus in these forms, and, furthermore, there are no anteclypeal invaginations supporting the hypopharynx. Heads that have been treated with caustic potash show the pharyngeal structures through the surface, and at first glance these appear to be the anteclypeus. The pharyngeal structures in these forms are developed entirely from the hypopharynx. They consist of the pharyngeal pump and two long wings, one extending from each corner of the hypopharynx dorsad into the head cavity, reaching the occipital border of the head.

The paraclypeal areas are always well developed in the Heteroptera. They extend along each side of the anteclypeus and are bounded laterally by the genal suture. They have been termed the jugae by students of this suborder and have occasionally been referred to as the lorae. They are homologous with the paraclypeal areas of the Homoptera. Their extent varies greatly. They are smallest in *Pelocoris femoratus* (Fig. 220, *pac*) and in *Notonecta* sp. (Fig. 222). Their limits in these forms can be determined only by a study of the internal structure. *Brochymena* sp. (Figs. 208 and 209), *Stethaulax marmoratus* (Fig. 210), *Corimelaena* sp. (Fig. 211) and *Cyrtomenus mirabilis* (Fig. 212) show the greatest development of the paraclypeal areas. They are equal to or exceed the length of the anteclypeus and crowd the maxillary plates to the lateral or ventral aspect of the head. They are also comparatively long in *Corythuca ciliata* (Fig. 199) and *Phymata* sp. (Figs. 202 and 203). Intermediate lengths between these and *Triphleps insidiosa* (Fig. 158) may be observed in such forms as *Nabis subcoleoptratus* (Figs. 166 and 167), *Corizus* sp. (Figs. 188 and 189), and *Neides muticus* (Figs. 186 and 187).

THE MAXILLARY PLATES.—These structures in the Heteroptera are entirely homologous with those of the Homoptera. They are separated from the paraclypeal areas by the genal sutures and lie alongside of the anterior half of the anteclypeus in such forms as *Belostoma flumineum* (Figs. 116 and 117), *Ranatra americana* (Figs. 121 and 122), *Hydrometra martini* (Fig. 145), *Nabis subcoleoptratus* (Fig. 166), and many other forms. Due to the elongation of the paraclypeal areas, the maxillary plates are entirely lateral and ventral in *Phymata* sp. (Figs. 272 and 273), *Brochymena* sp. (Figs. 275 and 276), *Corimelaena* sp. (Fig. 278), *Stethaulax marmoratus* (Fig. 279), and *Cyrtomoenus mirabilis* (Fig. 280).

The maxillary plates are fused with the gena and postgena without trace of sutures. They form most of the lateral and ventral aspects of the head. The maxillary and labial sutures described in the Homoptera (Muir, 1926) are not present in the Heteroptera. It is stated by Muir and Kershaw (1911b) that the basal joint of the labium frequently fuses with the maxillary plates and becomes a part of the head capsule. The author has found no morphological evidence of this in either nymphs or adults.

THE BUCCULAE.—The ventral margins of the maxillary plates are bent at an angle, in many species, forming a pair of projections which have been termed the bucculae (*bu*). They serve as a support to the labium when it is functioning and a protection to it when it is at rest. These structures are modifications of the maxillary plates in the opinion of most workers (MacGillivray, 1923b). Bugnion and Popoff (1911) state that Heymons considers them to represent the rudiments of the

maxillary palps. Many species of the Heteroptera lack these structures and they occur in varying degrees of development in the other species. They are lacking in *Cimex lectularius* (Figs. 235 and 237), *Gelastocoris* sp. (Figs. 234 and 236), and *Systelloderus biceps* (Figs. 248 and 249). Rudimentary bucculae may be seen in *Triphleps insidiosus* (Fig. 240) and *Alydus* sp. (Figs. 263 and 264). They are well developed in *Lamprocanthia* sp. (Fig. 238), *Neides muticus* (Fig. 261), *Brochymena* sp. (Fig. 277), and *Stethaulax marmoratus* (Fig. 279). *Corythuca ciliata* (Figs. 270 and 271) shows the most extensive development of the bucculae. They are projected forward, in the adult, curve around the front of the labium and almost meet.

An effort was made to use this character to show relationships between the various families but no definite results were obtained. They are well developed in such obviously unrelated families as the Belostomatidae (Fig. 214), Saldidae (Fig. 238), Tingitidae (Fig. 271), and Pentatomidae (Fig. 275). They are absent or rudimentary in many equally unrelated families. The bucculae are perhaps more universally well developed in the higher groups, especially in the Pentatomoidea.

THE LABRUM.—This sclerite is attached to the ventral or cephalic margin of the anteclypeus. The Heteroptera may be divided into three groups on the basis of the form of labrum. The first group consists of those forms having a broad, flap-like labrum, and the second contains those species with a long, narrow, triangular labrum. There are a number of intergrading forms in these two groups, and they can be arranged in a fairly regular series. The labrum of the third group consists of a broad, flap-like sclerite with a long, pointed outgrowth from the epipharyngeal area which projects beyond the distal margin of the labrum. This projection has been termed the epipharynx (Fig. 145, *epi*).

The labrum of the first group has been described as the most primitive type found in the suborder Heteroptera and we find it characteristic of the following families: Cimicidae, *Cimex lectularius* (Figs. 152, 153, and 154), Saldidae, *Lamprocanthia* sp. (Figs. 155 and 156), Anthocoridae, *Triphleps insidiosus* (Figs. 157 and 158), Naucoridae, *Pelocoris femoratus* (Figs. 126 and 127), Notonectidae, *Notonecta* sp. (Figs. 130 and 131), and Corixidae, *Corixa* sp. (Figs. 134 and 135).

The families, Reduviidae, *Sinea* sp. (Fig. 159), *Emesa brevipedennis* (Figs. 162 and 163) and *Melanolestes abdominalis* (Fig. 164); and Nabidae, *Nabis subcoleopratus* (Fig. 167), show intermediate stages between the first and second groups. The labrum is rather broad but, nevertheless, longer than broad. *Systelloderus biceps* (Figs. 168 and 169), *Ceratocombus vagans* (Figs. 170 and 171), and *Miris dolobratus* (Fig. 173) possess labra that are narrow but comparatively short. The labrum reaches its greatest length in such forms as *Belostoma flumineum*

(Fig. 118), *Nicides muticus* (Figs. 184 and 185), *Myodochus serripes* (Fig. 183), *Euryophthalmus succinctus* (Fig. 179) and *Harmocstes reflexulus* (Fig. 266).

The third group consisting of those species which possess an epipharyngeal projection, forms a very interesting and distinct unit. A study of *Gerris marginatus* (Fig. 226) and *Nacogeus burmeisteri* (Fig. 229) shows clearly that this projection extends from the under surface of the labrum and hence is purely epipharyngeal in character. It is not always so obvious that it arises from this region alone, as in *Rhagovelia obsca* (Fig. 228), but careful observation proves it to be true in the most obscure cases. This epipharyngeal projection occurs in the following families: Gerridae, *Gerris marginatus* (Fig. 226); Veliidae, *Rhagovelia obsca* (Figs. 141, 142, 227, and 228); Mesoveliidae, *Mesovelia bisignata* (Figs. 143 and 230); Naeogetidae, *Nacogeus burmeisteri* (Figs. 146 and 229); Ochteridae, *Ochterus americanus* (Fig. 149); and Nerthridae, *Gelastocoris* sp. (Fig. 148). The process is very small in the last two families.

The question arises as to whether or not the greatly elongated labrum of the second group is a combination of the labrum and epipharynx of this third group. The ectal surface of the epipharynx might have become sclerotized and joined to the labrum without trace of a suture. That such an occurrence would be possible is suggested in *Myodochus serripes* (Fig. 183), *Alydus* sp. (Fig. 192), and *Leptocoris trivittatus* (Fig. 193). The base of the labrum in these forms is distinctly more sclerotized than the tip and a distinct line of differentiation is observed which has been represented in the figures by dotted lines. This line does not indicate a suture. Is the basal portion labrum and the distal part the epipharynx? The writer prefers to leave the query unanswered until further evidence is at hand. There is no other indication of such an occurrence in other members of the group.

The labrum furnishes us with evidence for one very distinct group of families in the Heteroptera and with a fairly good series showing progressive development of the labrum which may prove of value in determining relationships among the remaining families.

THE CAUDAL AND VENTRAL ASPECTS OF THE HEAD.—The caudal or ventral margins of the maxillary plates are united with each other without trace of a suture, forming a continuous sclerotized plate (*gu*) ventrad or cephalad of the occipital foramen (*of*). This union of the maxillary plates with the accompanying sclerotization forms the outstanding difference between the suborders Heteroptera and Homoptera. This area has been termed the gular area, although a true gula does not occur in this order. MacGillivray (1923) calls the region the genaponta but the author retains the older term for it.

The labium is attached to the cephalo-ventral margin of this plate which, in many species, is notched to receive it: *Triphleps insidiosus* (Fig. 309) and *Ochterus americanus* (Fig. 303). The labrum closes the cephalic side of this notch, as shown in *Ranatra americana* (Fig. 284), *Pelocoris femoratus* (Fig. 288), and *Alydus* sp. (Fig. 330). The labium is attached caudad of the cephalic margin in such forms as *Brochymena* sp. (Fig. 341) and *Stethaulax marmoratus* (Fig. 344). There is a large opening apparent in the head capsule in these forms when the labium is removed. This was described by MacGillivray (1923b) as an artifact which he termed the labiafossa (Figs. 340, 341, and 342, *lf*). A sclerotized bridge extends across the cephalic margin of the labiafossa in some species, *Brochymena* sp. (Figs. 341 and 342, *gy*). This structure was termed the gymnoid by MacGillivray (1923b).

Large projections extend into the head cavity from the margin surrounding the occipital foramen in many species. These structures are termed the occipitalia (*oc*) by MacGillivray (1923b). They are essentially apodemes and may be seen in *Sinea* sp. (Fig. 311), *Melanolestes abdominalis* (Fig. 315), *Phymata* sp. (Fig. 338), and *Pelocoris femoratus* (Fig. 287). They are extremely long, extending through the prothorax in *Belostoma flumincum* (Fig. 282), *Ranatra americana* (Fig. 283), and *Gerris marginatus* (Fig. 293). The figures do not show the entire length of these structures. Two pairs of occipitalia are found in *Pelocoris femoratus* (Fig. 288). The function of these structures is to serve as places of attachment for muscles. The muscles which move the head are attached here as well as the protractor and retractor muscles of the maxillary stylets.

The caudal or ventral aspects of the head in various Heteroptera are shown in the plates (Figs. 281-345). Comparatively few characters of importance in the study of relationships are found in this aspect. The complete lack of sutures renders it impossible to delimit the various areas of which it is composed.

THE TENTORIUM.—There is no trace of a tentorium in the Heteroptera. MacGillivray (1923b) states that only the caudal two-thirds of the metatentoria are to be found in *Bcnacus*. The metatentorinae are wanting, and the remains of the metatentoria are, therefore, far removed from the usual point of invagination, and there is no evidence that any invagination has occurred. Ekblom (1926), Becker (1929), and Hamilton (1931) all describe a tentorium consisting of the body of the tentorium, the anterior arms, and the posterior arms. The structures which they have called the anterior and posterior arms of the tentorium are the hypopharyngeal evaginations similar to those described in the Homoptera. These evaginations project into the head capsule and form places for the attachment of the pharyngeal muscles and guides or supports for the

maxillary stylets. The fusion of these posterior evaginations with the metatentoria was also described in the Homoptera. Hence, the two-thirds of the metatentoria described by MacGillivray are really these hypopharyngeal structures and the metatentoria are entirely wanting. The corpotentorium of the authors mentioned above is apparently the floor of the hypopharynx, as seen in the figures given by Becker (1929).

The structures here described are all present in the Homoptera in addition to a rather typical tentorium. Therefore the structures in the Heteroptera must be homologous with the hypopharyngeal structures of the Homoptera and not with the tentorium. There is no evidence of any part of the tentorium in the Heteroptera.

A peculiar structure is found in the Saldidae. A large, deep apodeme is found along each epicranial arm of the nymph of *Lamprocanthia* sp. (Fig. 155, *ap*). These produce long, slender, heavily sclerotized apodemes in the adult which extend into the head cavity (Fig. 308). At first sight one is apt to homologize them with the pretentoria. They suggest the condition found in the Cicadellidae and described in the section on the tentorium of the Homoptera. They are not invaginated at the same point, however, in the two groups. Those in the Cicadellidae arise in the genal sutures, while in the Saldidae, they occur in the epicranial arms. They are not, therefore, homologous with the pretentoria but are secondary structures with no counterpart in other Heteroptera.

THE LABIUM.—The labium of the Heteroptera was formerly considered to vary in the number of segments it contained, having either three or four segments, and this fact was used in the classification of the group. Recent studies have led to the conclusion that all Heteroptera possess a four-segmented labium. All or part of the basal segment may become attached to the head capsule according to Muir and Kershaw (1911b). This conclusion was based upon embryological evidence, and further evidence must come from this source before we can hope to clarify the situation. We may still use the occurrence of three or four visible segments in the labium to help us in our classification, but we can no longer consider it to be of great phylogenetic importance. No morphological evidence of this fusion was found.

The writer did not include the labium in the present study. It shows some very interesting modifications and would repay extensive study. A few figures have been included in the plates to illustrate some of these variations (Figs. 392-398).

The direction of the mouth opening as evidenced by the place of attachment of the labium is of some interest. Attempts have been made to use this character in the classification of the suborder. These attempts will be discussed later in this paper. The mouth opening is most nearly cephalad in such forms as *Triphleps insidiosus* (Figs. 239 and 240),

Melanolestes abdominalis (Fig. 245), and *Systelloderus biceps* (Figs. 248 and 249). The direction swings considerably ventrad in *Emesa brevipennis* (Figs. 243 and 244), *Nabis subcoleoptratus* (Figs. 246 and 247), and *Sinea* sp. (Figs. 241 and 242). It is definitely ventral in *Neides muticus* (Figs. 260 and 261), *Alydus* sp. (Figs. 263 and 264), and *Piesma cinerea* (Fig. 269). The opening occurs on the ventral surface caudad of the cephalic margin, as shown by the position of the labiafossa in *Phymata* sp. (Figs. 337 and 338), *Brochymena* sp. (Figs. 341 and 342), and *Stethaulax marmoratus* (Fig. 344).

THE MANDIBULAR LEVERS.—The levers which attach the mandibular stylets to the head capsule and which increase the action of the extensor and retractor muscles of the stylets have been described in the Notonectidae by Geise (1883) and in *Nepa* and *Naucoris* by Heymons (1899). The author described them in the Aradidae (Spooners, 1920). It remained for Ekblom (1929) to make an extensive study of these levers and to make use of them in attempting to show the relationships between the families of the Heteroptera. He described four main types of these levers.

The first type has a triangular lever attached to the membrane surrounding the base of the mandibular stylets. The second form is a three-branched lever, one end of which is attached directly to the stylet. The third is a triangular form, attached directly to the stylet which is folded anteriorly, and has a double attachment to the head capsule. The fourth type consists of a quadrangular lever with double walls, closely attached to the base of the mandible but not firmly united with it. The protractor muscle is attached to the center of this type. He uses these four types of mandibular levers as the basis for dividing the Heteroptera into four groups. These groups will be discussed in a later section of this paper.

The writer has studied the mandibular levers of all of the families of the Heteroptera in which material was available and has found them to be of considerable interest. Two of the types described by Ekblom were found to form rather clear-cut groups. These were his third and fourth types. The first and second groups were not easily separated in all cases, and evidence of at least two more types was found.

Type one, the triangular lever attached to the membrane surrounding the base of the mandibular stylet, is found in by far the larger number of the Heteroptera. The large amount of variation within the group may be seen by comparing the figures (369-391). Several other species were examined and the levers were found to come within the range of variation shown in the figures. A tendon of varying length attaches the lever to the membrane about the base of the stylet.

The second type includes, according to Ekblom (1929), *Ranatra* (Fig. 356), *Pelocoris* (Fig. 358), and *Notonecta* (Fig. 359). *Belostoma* (Figs.

354 and 355) should also be included in this group. The great amount of variation is readily observed. A comparison with the lever of *Melanolestes* (Fig. 357) shows that the most consistent difference from the first group lies in the attachment to the mandibular stylets. It is attached directly to the base of the stylets in this second group, while in the first it is attached to the enclosing membrane. Levers of both nymph and adult of *Belostoma* (Figs. 354 and 355) were examined to determine the amount of difference between them. The same thing was done in the aradid, *Aneururus* sp. (Figs. 386 and 387). No essential change occurs between these stages of the insect.

Pelocoris (Fig. 358) and *Notonecta* (Fig. 359) have levers which are sufficiently different to warrant further discussion. The lever of *Pelocoris* is a long, slender loop with one end attached to the head capsule and the other end to the mandibular stylet. The protractor muscle is fastened to the elbow of the loop and a contraction of the muscle brings the ends of the loop toward each other and thus forces the stylet forward. This arrangement is entirely different from that found in any other species. Two pieces make up the lever of *Notonecta* (Fig. 359), a larger triangular piece attached to the head capsule, and a smaller piece attached at an angle just before the apex of the first. The condition of the specimens at hand made it impossible to determine just where the muscles are attached. This is another unique form of lever. The second of Ekblom's groups, then, appears to contain at least three types of levers.

The third group described by Ekblom is found only in the Corixidae, *Corixa* sp. (Fig. 349). This form is triangular and is folded at the outer margin with a rod-like extension extending to the mandible and uniting directly with it.

The fourth type, as was stated, forms a fairly well isolated group. The quadrangular shape of the lever with the rod-like projection fastening to one face and extending directly to the mandibular stylet is found in *Gerris marginatus* (Fig. 360), *Rhagovelia obesa* (Fig. 361), *Mesovelia bisignata* (Fig. 362), *Hydrometra martini* (Fig. 363), and *Naeogeus burmeisteri* (Fig. 364). *Ochterus viridifrons* (Fig. 365) shows a modification of this type in that the rod-like extension is attached to the edge of the plate and that the plate approximates a triangle in form. The lever is attached directly to the mandibular stylet. *Ochterus americanus* (Fig. 366) has the mandibular lever still more triangular in outline, with the arm very slender and tendon-like, while in *Gelastocoris* sp. (Fig. 368) the lever is in the form of a perfect triangle with one corner attached directly to the mandibular stylet.

It is worth calling attention here to the fact that, if we include *Ochterus* and *Gelastocoris*, this group includes all of those forms which possess the epipharyngeal process described in the section on the labrum.

Further discussion of these relationships revealed by the study of the mandibular levers will be made in the section on phylogeny.

A number of species and varieties of *Euschistus* were examined to determine the extent of variation within the genus. *Ochterus viridifrons* (Fig. 365) and *Ochterus americanus* (Fig. 366) show a considerable difference in the shape of the lever. Three species and two varieties of *Euschistus* were examined, but they showed only minor variations in the form of these structures (Figs. 390 and 391).

With the turning in of the direction of the mouth opening from cephalad to ventrad there occurs a bending of the mandibular stylets (Figs. 367, 369, 371, 375, and 376). The levers and the mandibular bases work in the same plane as in those with a cephalic mouth opening, the bend in the stylets accommodating the change in the direction of the mouth opening.

THE MAXILLARY STYLETS.—The maxillary stylets are not attached to the head capsule by means of levers in any heteropteron examined by the writer. Their point of attachment varies so greatly that they cannot serve as landmarks for the head sclerites, and a serious study of them has not been included in this work. It was observed that in the Gerridae, *Gerris remigus*, the maxillae followed the occipitalia back into the mesothorax. Muscles were attached to the occipitalia and to the body wall of the mesothorax.

PHYLOGENY OF THE HETEROPTERA

The Heteroptera is a much larger and more varied group than the Homoptera and consequently the relationships within this group are much more difficult to determine. The present studies have brought to light some characters which are unquestionably of value in deciphering these relationships, and while much remains to be done they are given here in the form of suggestions which may lead to further discoveries.

This suborder appears to be an offshoot of the early Homoptera. Evidence for this statement is, first, the earlier appearance of the Homoptera as fossils and, second, the similarity of the anteclypeal region of some of the Fulgoridae (*Otiocerus wolfii*, Fig. 346) with that of many heteropterons (*Belostoma flumineum*, Fig. 347 and *Euschistus tristigmus*, Fig. 348). The peculiar modification of the alimentary canal known as the filter chamber, in which the caudal part of the intestine loops forward and becomes imbedded in the walls of the ventriculus, is found in most Homoptera. The fact that it is absent in the Fulgoridae and in all of the Heteroptera (Kershaw, 1913) is further indication of the probable ancestral relationship between these two groups.

Reuter (1910) has given a detailed account of the historical develop-

ment of the classification of the Heteroptera to that date and Ekblom (1929) has brought it up to the present time. A detailed account is not necessary here and only a few of the major contributions will be discussed. Reuter (1884-1891) used the classification of Fieber (1851) in which the Heteroptera was divided into two major groups based on the position of the antennae. These two groups were known as the Cryptocerata and the Gymnocerata. Kirkaldy (1908) discarded these two divisions and proposed two groups based on the method of articulation of the metacoxae which he named the Pagiopoda and the Trachalopoda. He regarded the Pentatomidae as containing those forms, which have retained most of the primitive characters of the Heteroptera, and hence reversed the usually accepted arrangement of the families.

The grouping into the Cryptocerata and the Gymnocerata was abandoned by Reuter (1910) who divided the Heteroptera into six series: Hydrobiotica, Trichotolocera, Anonycha, Onychiophala, Polyneura, and Peltoccephala. He based these groups primarily upon the following characters: the presence or absence of ocelli and arolii, the form and structure of the egg, and the condition of the sternal sclerites. His scheme of classification has been largely used since and still forms the basis for most of the present-day work.

Considerable doubt has been expressed recently upon the dependability of the above characters for the separation of the groups. McAtee and Malloch (1924, 1925a, and 1926) point out the modification of the sternal sutures which accompanies the degree of development of the wings. Ekblom (1929) rejects the shape of the egg as a phylogenetic character, and Myers (1924) and Holloway (1935) show that our incomplete knowledge of tarsal structures renders any classification based upon them uncertain.

Ekblom (1929) has given us the most recent scheme of classification of this suborder and his work is by far the most important contribution to the subject in recent times. He bases his classification upon the early scheme of Dufour (1833) and supplies new characters to confirm Dufour's ideas. Dufour divided the Heteroptera into three series, the Geocorises, the Hydrocorises, and the Amphibicorises. Börner (1904) added the Sandaliorrhyncha to include the family Corixidae. These four series are recognized by Ekblom and justified primarily by the types of mandibular levers described in a previous section of this paper.

Evidence obtained in the present study lends support to the validity of this grouping with some minor changes perhaps suggested. The Sandaliorrhyncha, containing the single family Corixidae, is quite evidently valid. The corixids are a very isolated and highly specialized group. The form of the anteclypeus suggests a possible relationship between them and the Saldidae or Cimicidae, but this relationship is extremely remote.

The Hydrocorisae is the least unified group of the four. It contains the families Nepidae, Belostomatidae, Naucoridae, and Notonectidae. As has been pointed out in a previous section of this paper, there are three distinct types of levers in this group, and perhaps the group should be split into three. The Nepidae (Fig. 356) and the Belostomatidae (Fig. 355) would form one group having the three-branched lever described by Ekblom (1929) as typical of the Hydrocorisae. The Naucoridae (Fig. 358) form a group characterized by having the lever in the form of a long, slender loop; while the Notonectidae (Fig. 359) would represent the third group, with a lever consisting of two distinct pieces. The last two families agree in lacking any evidence of the anteclypeus (Figs. 127 and 131).

The third series, the Amphibicorisae, forms a very well defined group. It contains the families Ochteridae, Nerthridae, Naeoegidae, Hydro-metridae, Mesoveliidae, Veliidae, and Gerridae. These forms all possess the epipharyngeal projection from the labrum (Figs. 221 and 226-231), and the mandibular levers (Figs. 360-366) agree in being attached directly to the mandibular stylets. Most of the levers are quadrangular in form, with the Ochteridae showing a gradual shift to the triangular type characteristic of the Geocorisae (Figs. 365 and 366). The Ochteridae and the Nerthridae, on the other hand, agree with the Naucoridae and the Notonectidae in lacking any evidence of the anteclypeus, and thereby bridge the gap between the Amphibicorisae and the Hydrocorisae.

The remaining families of the Heteroptera are included in the series Geocorisae. This forms a very large group, all of the members of which possess a more or less triangular mandibular lever attached to the membrane surrounding the base of the stylet rather than directly to the stylet. The dead structures give very little aid in subdividing this group or in suggesting relationships between the families.

The danger of misinterpreting modifications accompanying similarity of habits is encountered in a group so large as this. A very interesting case of this has been described by China (1931). He states that the coiling of the stylets characteristic of the Aradidae (Figs. 386 and 387) is also found in the European family Termitaphididae and that they are partially coiled in the Plataspidae, another old world family. *Bozius* also has a similar structure. These four otherwise unrelated groups with similar long coiled stylets all have the habit of feeding on fungus.

The predacious forms in the North American families seem to agree in certain characteristics, such as the comparatively wide labrum, the cephalic direction of the mouth opening and in the lack of bucculae. There are, however, many exceptions to these generalities and this may also be a case of morphological parallelism.

The families Cimicidae (Fig. 152), Anthocoridae (Fig. 157), and Saldidae (Fig. 156) form a group characterized by a very wide, flap-like

labrum. The bucculae, on the other hand, are well developed in the Saldidae, rudimentary in the Anthocoridae, and wanting in the Cimicidae. The Reduviidae (Figs. 161, 163, and 165), the Nabidae (Fig. 167), and the Enicocephalidae (Fig. 168) show intermediate stages in regard to the width of the labrum. The Cryptostemmatidae (Fig. 170) and the Miridae (Fig. 173) seem to be related followed, perhaps, by the Lygaeidae (Fig. 176), Pyrrhocoridae (Fig. 180), Corizidae (Fig. 189), and Alydidae (Fig. 192). The last three families show progressive stages in the elongation of the paraclypeal areas and the accompanying lateral or ventral position of the maxillary plates. This is characteristic of the Pentatomoidea, including the families Pentatomidae (Fig. 208), Cydnidae (Fig. 212), and the Corimelaenidae (Fig. 211).

The Aradidae (Fig. 207), the Phymatidae (Fig. 203), the Piesmididae (Fig. 196), and the Tingitidae (Fig. 109) seem to stand rather alone with the great development of the bucculae in common. The Piesmididae (Fig. 196) shows an enormous elongation of the paraclypeal areas. The Neididae (Fig. 185) also possess well developed bucculae but otherwise agree with the Lygaeidae (Fig. 176).

The head structures, on the whole, give comparatively little help in subdividing the Geocorisae. Studies of other structures will be necessary to determine the actual relationships in this group. Some such studies have been made and a brief review of them will be of value.

Taylor (1918) studied the thoracic sclerites and divided the Heteroptera into five groups on the basis of thoracic and coxal characters. Four of these groups he states as being similar in general characteristics. Notonectidae, Corixidae, Belostomatidae, and Nepidae form the first and most distinctive group, all with large metathoracic coxae overlapped by the epipleura and having the meso- and metathoracic pleurae distorted. This group corresponds somewhat with the Sandaliorrhyncha and the Hydrocorisae. The second group includes the Miridae, Nabidae, and Cimicidae which have exposed meso- and metathoracic coxae. The Reduviidae and the Phymatidae form the third group, characterized by the presence of a true coxal cleft in the metathorax. The fourth group, with the mesothoracic scutellum prolonged over the abdomen, includes the Coreidae, Lygaeidae, Tingitidae, Pentatomidae, Scutellaeridae, and Corimelaenidae. The Neididae, Gerridae, and Emesidae form the fifth group, all having the mesothoracic pleurae lengthened horizontally. The last four groups do not agree with the findings in the study of the head structures.

Tullgren (1918) made a very interesting study of the occurrence of Trichobothria in the Heteroptera. These are described by the author as auditory hairs and are apparently the tactile sense organs described by Snodgrass (1935). They have been extensively used in the classification of the spiders. Tullgren found them present in eight families. The

Thyreocoridae, Scutellaeridae, and Pentatomidae had them arranged in the same pattern on the same sternites. The Coreidae, Neididae, and Piesmididae each possessed them and each family had a characteristic arrangement of them. The Pyrrhocoridae and the Lygaeidae agreed in having them arranged in the same pattern but differing from those mentioned above. He found no evidence of these structures in the other families of the Heteroptera nor in the Homoptera.

The genitalia in the Hemiptera were studied by Pruthi (1925). He recognized two main types of genitalia in the Heteroptera which he designated as the pentatomid type and the reduviid type. The pentatomid type included the families Saldidae, Aradidae, Pentatomidae, Coreidae, Neididae, and Lygaeidae. All of the remaining families were included in the group having the reduviid type of genitalia.

The metasternal scent glands were studied by Brindley (1930). He found them present in most of the families. They were absent in the Nepidae and the Hydrometridae. Unfortunately he apparently did not investigate the Naeoegidae, Ochteridae, Nerthridae, Anthocoridae, Veliidae, or Mesoveliidae.

China (1933) bases his classification partially on habits and points out a series originating in the rapidly running and flying, littoral Saldidae and Ochteridae through the more sluggish Nerthridae to the typical aquatic forms Nepidae and Belostomatidae. He points out the structural characters accompanying these changes in habit. He does not give detailed reasons for the remainder of his classification.

This brief review of the important works on the comparative morphology of the Heteroptera indicates that further studies are badly needed, particularly detailed comparative studies of the various parts of the body. Until these are made we cannot hope to arrange the Geocorisae in any satisfactory phylogenetic series.

The accompanying diagram (Text-figure 2) gives a graphic idea of the relationships of the Heteroptera suggested by the study of the head capsule.

SUMMARY

A comparative study of the head capsule of the adults and nymphs of all of the North American families of the Hemiptera in which material was available has been made. This included all of the families of the suborder Homoptera excepting the Coccidae and all of the Heteroptera excepting the families Thaumasticoridae, Microphysidae, and Terna-tophyllidae. Nymphs were available in all of the families studied except the Piesmididae and the Hydrometridae.

Evidence has been advanced to show that the Homoptera represent



TEXT-FIGURE 2

the more primitive suborder and that some members of the Fulgoridae have retained some of the most primitive characteristics found in the group. A series of forms was described showing the gradual development of the paraclypeal areas from the postclypeus by the extension of the so-called frontal sutures. The homologies of these areas have given rise to more discussion than any other part of the hemipterous head.

The structure of the head, particularly of the tentorium, suggests that the other families of the Homoptera have developed from the primitive Cercopidae. The two subfamilies of the Cercopidae differ considerably in head structure. The Cercopinae, characterized by a greatly reduced frons gives rise to the Tettigonidae, Membracidae, Cicadidae, Psyllidae, and Aphididae; while the Aphrophorinae, members of which have retained the large frons characteristic of the Fulgoridae, leads to the Cicadellidae, Aleyrodidae, and Coccidae. The Tettigonidae has alternately been considered as a subfamily of the Cicadellidae and as a separate family. This study indicates that it is a distinct family considerably removed from the Cicadellidae.

Facts are presented to show that the parts of the heteropterous head are homologous with those of the Homoptera, a fact which has often been denied. This removes the objection formerly advanced, against deriving the Heteroptera from the Homoptera.

The Heteroptera were found to lack any trace of a true tentorium. The structures usually described as such originate from the hypopharynx. These hypopharyngeal structures are also found in the Homoptera in addition to a nearly typical tentorium.

The Heteroptera are best grouped into the four series Sandaliorrhyncha, Hydrocorisae, Amphibicorisae, and Geocorisae. The Anthocoridae or Cimicidae are probably the most primitive forms of the Heteroptera and belong to the Geocorisae. The form of the labrum, the type of mandibular lever, the direction of the mouth opening and the development of the bucculae are the most important structures of the head as far as showing the relationships between the families is concerned. The Sandaliorrhyncha is a small and unique series, rather completely isolated from the rest of the Heteroptera. The second series, the Hydrocorisae, is not clearly limited. Three types of mandibular levers are found in these forms which perhaps justifies their separation into three groups. The Amphibicorisae forms a very well defined group characterized by a single type of mandibular lever and also by the development of an epipharyngeal appendage from the labrum. The mandibular lever in the family Ochteridae, of this group, shows a modification in shape toward that found in the most primitive of the Geocorisae, which perhaps indicates the origin of the Amphibicorisae from that group.

Four families, two in the Hydrocorisae, Notonectidae, and Naucoridae,

and two from the Amphibicorisae, Ochteridae, and Nerthridae, agree in lacking all evidence, both external and internal, of an anteclypeal area. This may bridge the gap between these two series.

The Geocorisae is a large and complex series, the relationships of which remain rather obscure. Detailed comparative studies of other body parts are needed to enable us to understand this group. The form of the labrum presents a series of the Cimicidae, Anthocoridae, Saldidae, Reduviidae, Nabidae, Enicocephalidae, and Miridae, in the order named. The Cryptostemmatidae, Miridae, Lygaeidae, Pyrrhocoridae, and Neididae seem to show intermediate stages in several of the head characters. The Aradidae, Phymatidae, and Tingitidae stand more or less isolated, while the Corizidae, Alydidae, Coreidae, Piesmidae, Pentatomidae, Cydnidae, and Corimelaenidae show progressive enlargement of the paraclypeal areas and an accompanying ventral position of the maxillary plates.

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ABBREVIATIONS USED IN THE PLATES

<i>ac</i>	anteclypeus	<i>lf</i>	labiafossa
<i>af</i>	antafossa	<i>m</i>	mandible
<i>ant</i>	antenna	<i>mp</i>	maxillary plate
<i>ap</i>	apodeme	<i>ms</i>	maxillary suture
<i>as</i>	antennal shelf or tubercle	<i>mt</i>	metatentorium
<i>at</i>	attachment of mandibular lever to head capsule	<i>o</i>	ocellus
<i>bu</i>	buccula	<i>oc</i>	occipital parademe of occipitalia
<i>cl</i>	clypeus	<i>of</i>	occipital foramen
<i>ct</i>	corpotentorium	<i>pac</i>	paraclypeus
<i>ea</i>	epicranial arm	<i>pc</i>	postclypeus
<i>epi</i>	epipharynx	<i>pg</i>	postgena
<i>es</i>	epicranial stem	<i>pm</i>	pharyngeal pump muscles
<i>fr</i>	frons	<i>prm</i>	protractor muscles of mandible
<i>g</i>	gena	<i>pt</i>	pretentorium
<i>gu</i>	gula or gular area	<i>rm</i>	retractor muscles
<i>gy</i>	gymnoid	<i>st</i>	supratentorium
<i>l</i>	mandibular lever	<i>v</i>	vertex
<i>lb</i>	labium		
<i>lbr</i>	labrum		

PLATE I

Cephalo-ventral aspect of the head

- FIG. 1.—*Otiocercus dcgeerii*, adult.
FIG. 2.—*Lamenia* sp., adult.
FIG. 3.—*Amaloptera uhleri*, adult.
FIG. 4.—*Cyarda melichari*, adult.
FIG. 5.—*Acanalonia* sp., nymph.
FIG. 6.—*Ormenis pruinosa*, adult.
FIG. 7.—*Pelitropis rotatula*, adult.
FIG. 8.—*Oliarus vicarius*, adult.
FIG. 9.—*Catonia impunctata*, adult.
FIG. 10.—*Cixius pini*, adult.
FIG. 11.—*Epiptera* sp., nymph.
FIG. 12.—*Cyrpoptus reineckeii*, adult.
FIG. 13.—*Pentagramma vittatifrons*, nymph.
FIG. 14.—*Pentagramma vittatifrons*, adult.
FIG. 15.—*Dictyophora florens*, adult.
FIG. 16.—*Bruchomorpha* sp., adult.
FIG. 17.—*Bruchomorpha* sp., nymph.
FIG. 18.—*Acanalonia latifrons*, adult.
FIG. 19.—*Lepyronia quadrangularis*, nymph.
FIG. 20.—*Lepyronia quadrangularis*, adult.

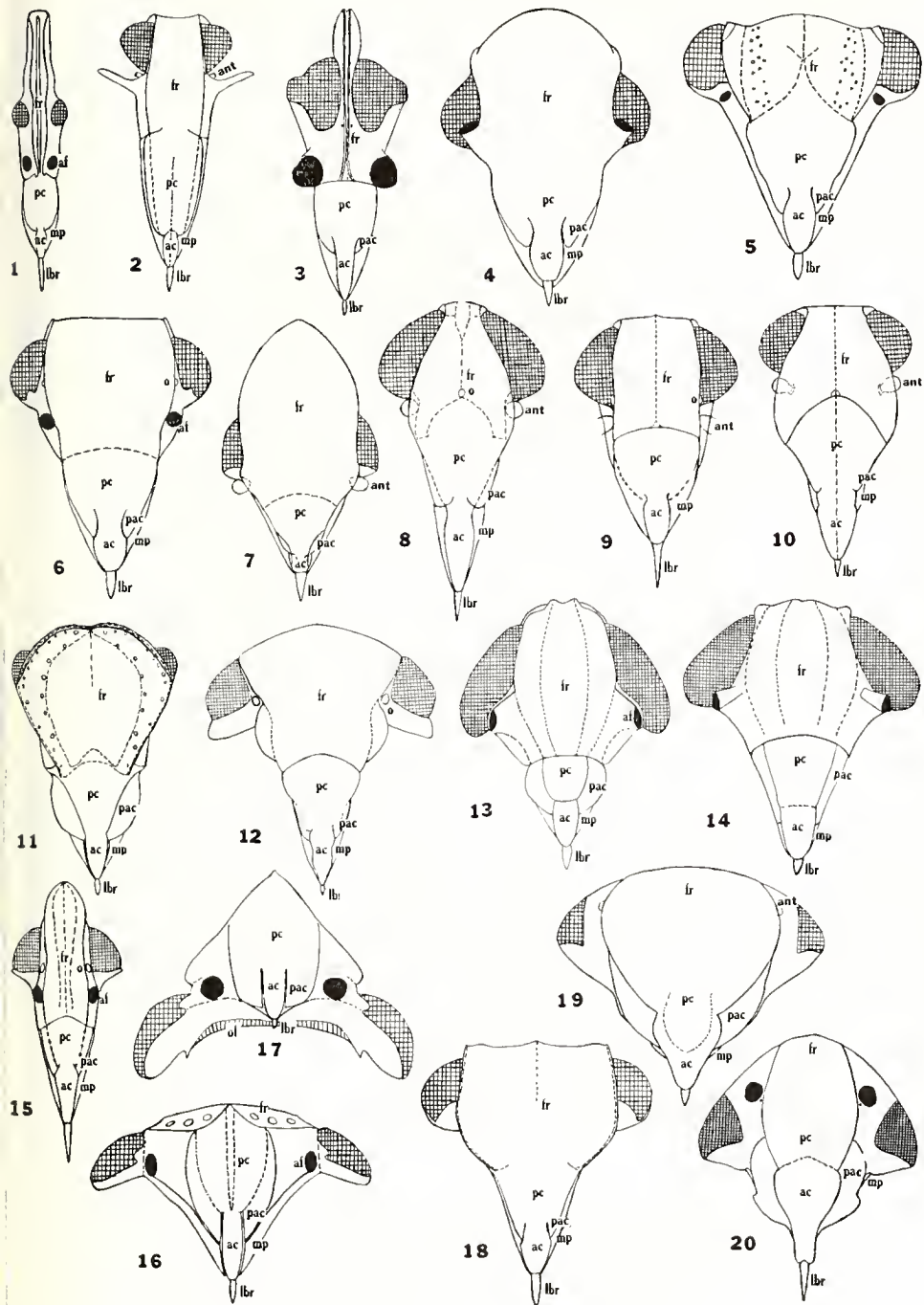


PLATE I

PLATE II

Cephalo-ventral aspect of the head

- FIG. 21.—*Monecophora bicincta*, adult.
FIG. 22.—*Tibicen sayi*, nymph.
FIG. 23.—*Tibicen sayi*, adult.
FIG. 24.—*Ceresa* sp., nymph.
FIG. 25.—*Ceresa* sp., adult.
FIG. 26.—*Carynota mera*, adult.
FIG. 27.—*Agallia constricta*, adult.
FIG. 28.—*Oncometopia undata*, adult.
FIG. 29.—*Jassus olitorius*, nymph.
FIG. 30.—*Jassus olitorius*, adult.
FIG. 31.—*Erythroneura comes*, adult.
FIG. 32.—*Acinopterus acuminatus*, adult.
FIG. 33.—*Lachmus* sp., adult.
FIG. 34.—*Pachypsylla celtidis-mamma*, adult.
FIG. 35.—*Trialeurodes* sp., adult.

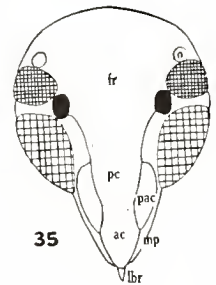
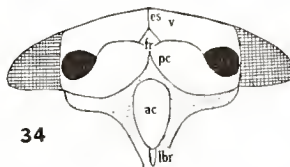
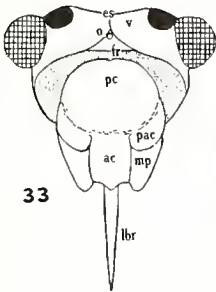
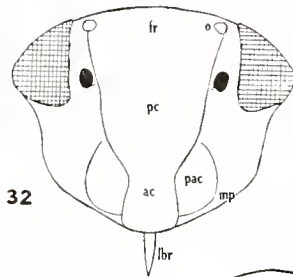
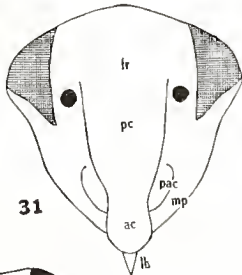
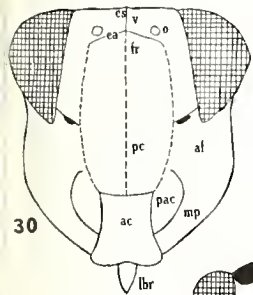
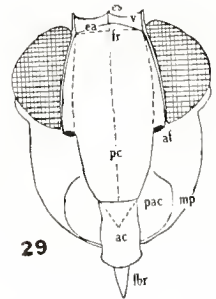
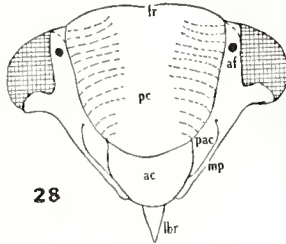
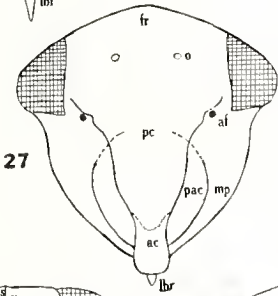
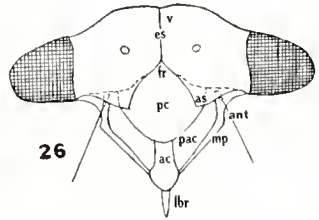
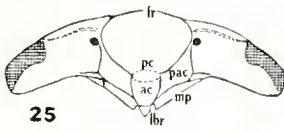
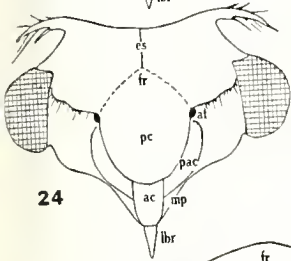
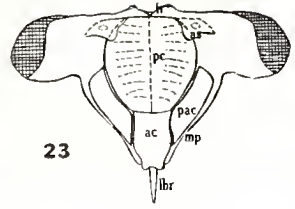
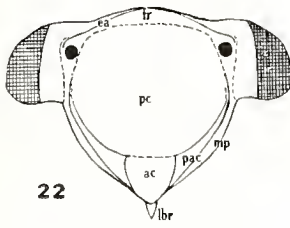
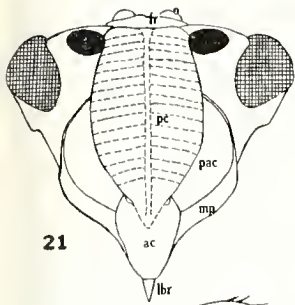


PLATE II

PLATE III

Dorsal aspect of the head

- FIG. 36.—*Unknown fulgorid*, nymph.
FIG. 37.—*Acanalonia* sp., nymph.
FIG. 38.—*Liburniella ornata*, nymph.
FIG. 39.—*Pentagramma vittatifrons*, nymph.
FIG. 40.—*Bruchomorpha* sp., nymph.
FIG. 41.—*Bruchomorpha* sp., adult.
FIG. 42.—*Lepyronia quadrangularis*, nymph.
FIG. 43.—*Lepyronia quadrangularis*, adult.
FIG. 44.—*Tibicen sayi*, nymph.
FIG. 45.—*Ceresa* sp., nymph.
FIG. 46.—*Ceresa* sp., adult.
FIG. 47.—*Jassus olitorius*, nymph.
FIG. 48.—*Gypona* sp., nymph.
FIG. 49.—*Oncometopia undata*, adult.
FIG. 50.—*Lachnus* sp., adult.
FIG. 51.—*Pachypsylla celtidis-mamma*, adult.
FIG. 52.—*Trioza tripunctata*, adult.

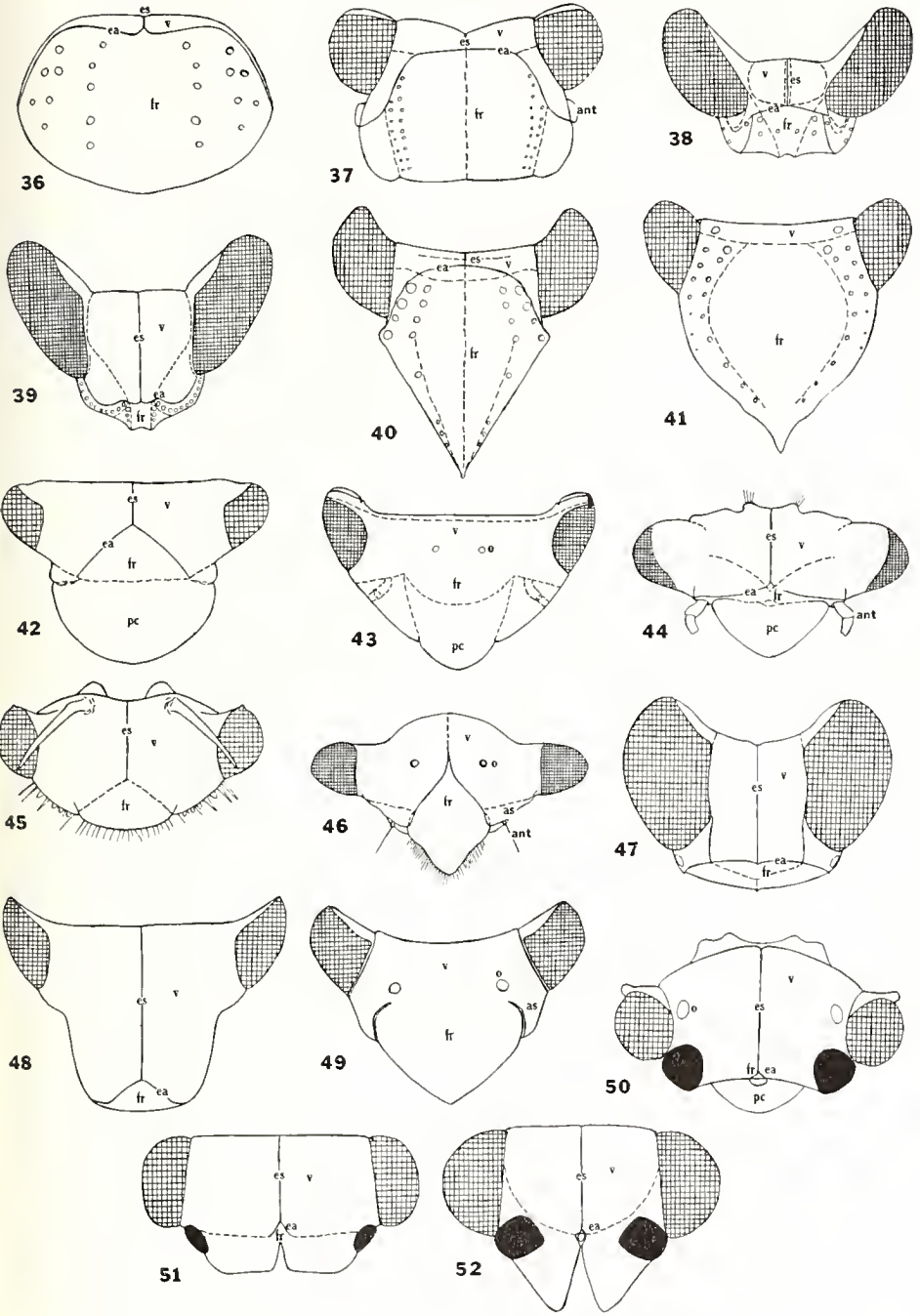
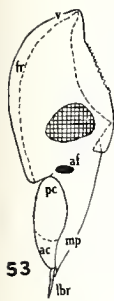


PLATE III

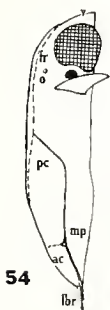
PLATE IV

Lateral aspect of the head

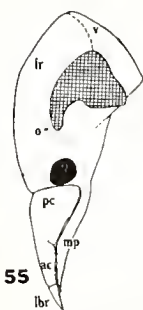
- FIG. 53.—*Otiocerus degeerii*, adult.
FIG. 54.—*Lamenia* sp., adult.
FIG. 55.—*Amaloptera uhleri*, adult.
FIG. 56.—*Acanalonia* sp., nymph.
FIG. 57.—*Acanalonia latifrons*, adult.
FIG. 58.—*Ormenis pruinosus*, adult.
FIG. 59.—*Pelitropis rotatula*, adult.
FIG. 60.—*Oliarus vicarius*, adult.
FIG. 61.—*Catonia impunctata*, adult.
FIG. 62.—*Cixius pini*, adult.
FIG. 63.—*Epiptera* sp., nymph.
FIG. 64.—*Cyrtoptus reineckei*, adult.
FIG. 65.—*Pentagramma vittatifrons*, adult.
FIG. 66.—*Dictyophora florens*, adult.
FIG. 67.—*Bruchomorpha* sp., nymph.
FIG. 68.—*Bruchomorpha* sp., adult.
FIG. 69.—*Lepyronia quadrangularis*, nymph.
FIG. 70.—*Lepyronia quadrangularis*, adult.
FIG. 71.—*Monecophora bicincta*, adult.



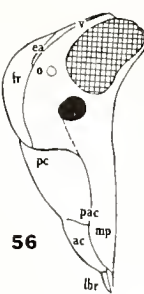
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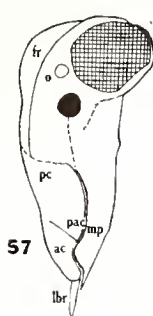
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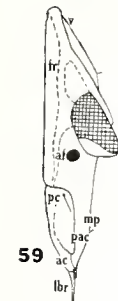
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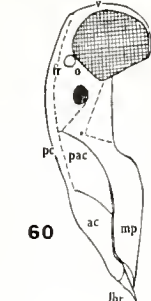
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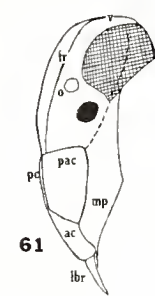
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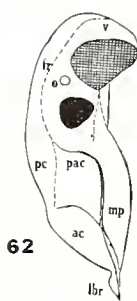
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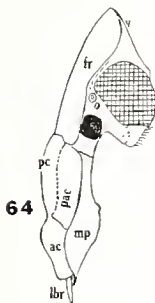
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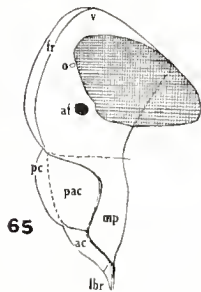
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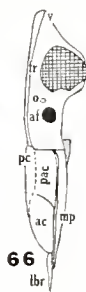
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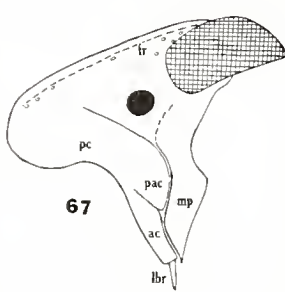
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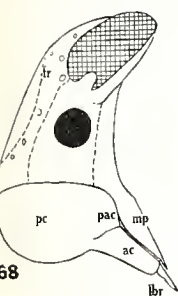
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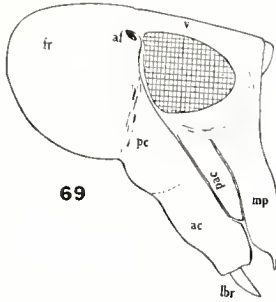
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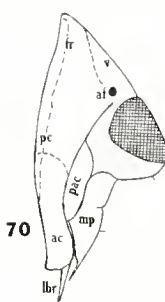
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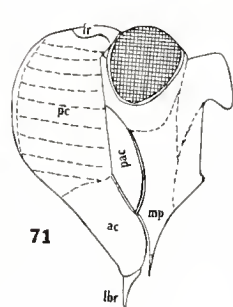
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70



71

PLATE V

Lateral and caudal aspects of the head

- FIG. 72.—*Tibicen sayi*, nymph, lateral.
FIG. 73.—*Tibicen sayi*, adult, lateral.
FIG. 74.—*Ceresa* sp., nymph, lateral.
FIG. 75.—*Ceresa* sp., adult, lateral.
FIG. 76.—*Carynota mcra*, adult, lateral.
FIG. 77.—*Agallia constricta*, adult, lateral.
FIG. 78.—*Gypona* sp., nymph, lateral.
FIG. 79.—*Oncometopia undata*, adult, lateral.
FIG. 80.—*Phlepsius excultus*, adult, lateral.
FIG. 81.—*Acinopterus acuminatus*, adult, lateral.
FIG. 82.—*Euscelis bicolor*, adult, lateral.
FIG. 83.—*Jassus olitorius*, adult, lateral.
FIG. 84.—*Erythroneura comes*, adult, lateral.
FIG. 85.—*Lachnus* sp., adult, lateral.
FIG. 86.—*Trialeurodes* sp., adult, lateral.
FIG. 87.—*Otiocerus degeerii*, adult, caudal.
FIG. 88.—*Lamenia* sp., adult, caudal.
FIG. 89.—*Acanalonia* sp., nymph, caudal.
FIG. 90.—*Acanalonia latifrons*, adult, caudal.

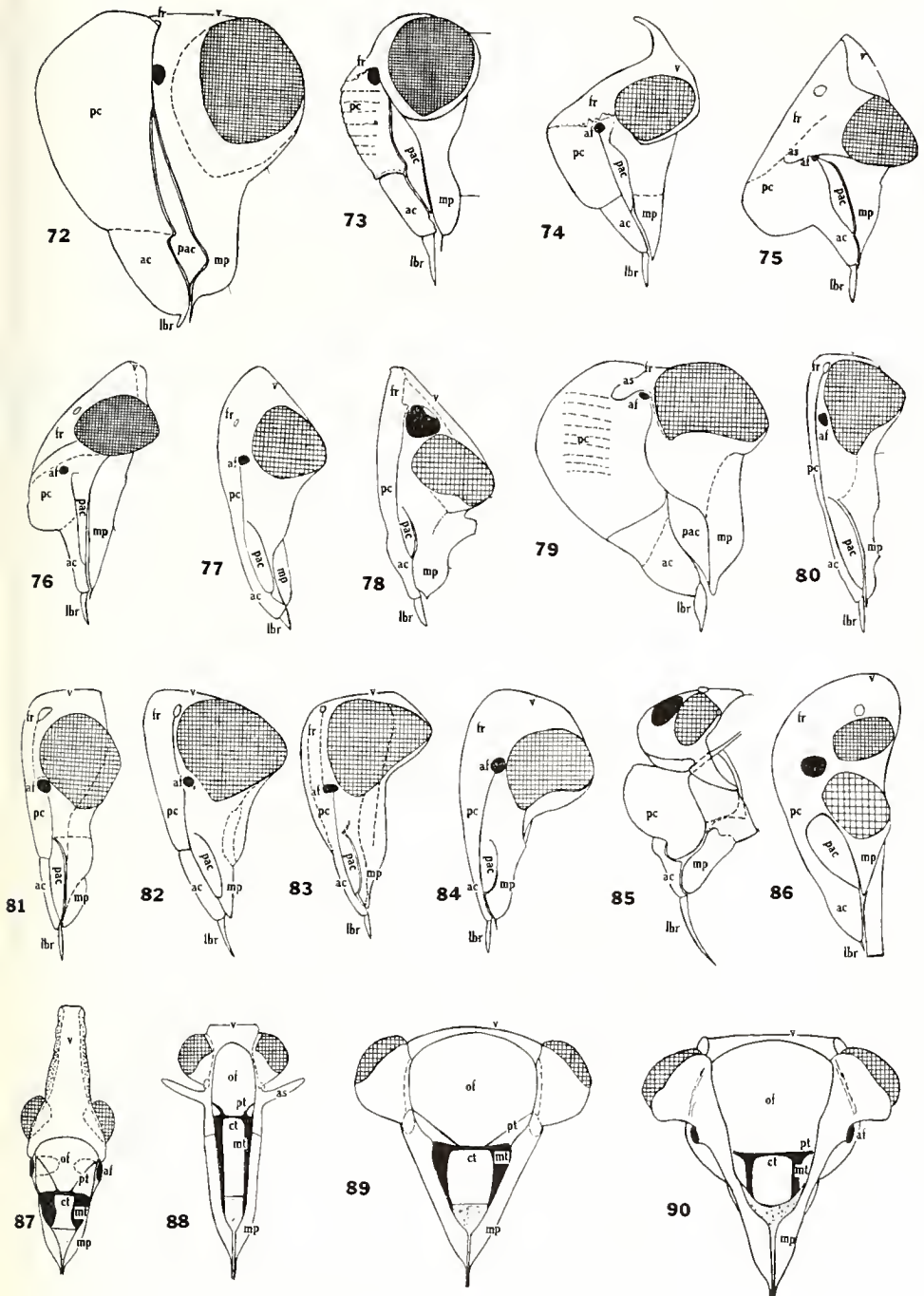


PLATE V

PLATE VI

Caudo-dorsal aspect of the head

- FIG. 91.—*Ormenis pruinosa*, adult.
FIG. 92.—*Pelitropis rotatula*, adult.
FIG. 93.—*Oliarus vicarius*, adult.
FIG. 94.—*Catonia impunctata*, adult.
FIG. 95.—*Epiptera* sp., nymph.
FIG. 96.—*Cyrroptus reineckeii*, adult.
FIG. 97.—*Pentagramma vittatifrons*, adult.
FIG. 98.—*Dictyophora florens*, adult.
FIG. 99.—*Bruchomorpha* sp., adult.
FIG. 100.—*Monocophora bicincta*, adult.
FIG. 101.—*Lepyronia quadrangularis*, nymph.
FIG. 102.—*Lepyronia quadrangularis*, adult.
FIG. 103.—*Carynota mera*, adult.
FIG. 104.—*Tibicen sayi*, nymph.
FIG. 105.—*Tibicen sayi*, adult.
FIG. 106.—*Ceresa* sp., adult.
FIG. 107.—*Ceresa* sp., nymph.
FIG. 108.—*Gyftona* sp., nymph.

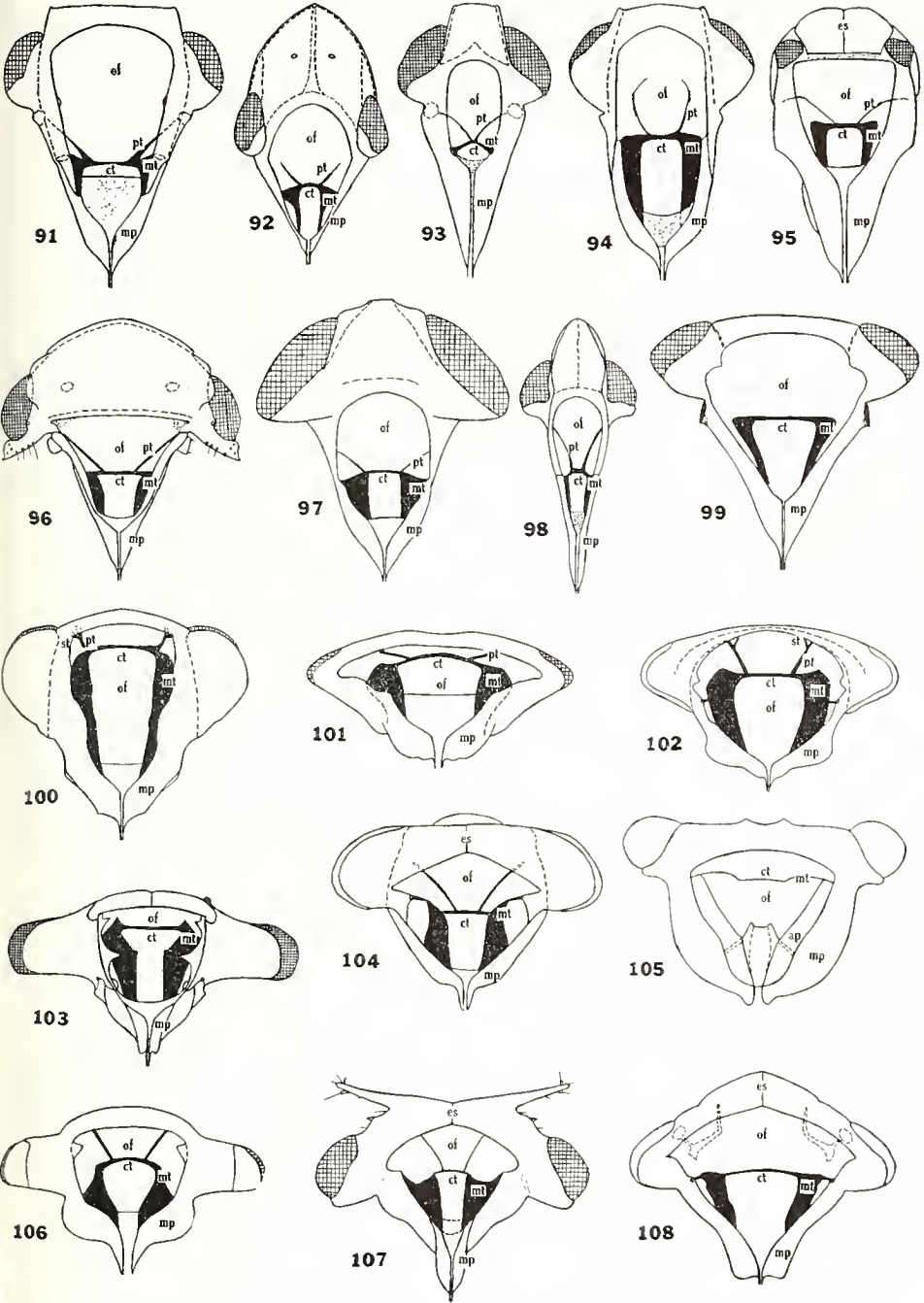
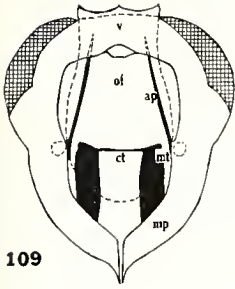


PLATE VI

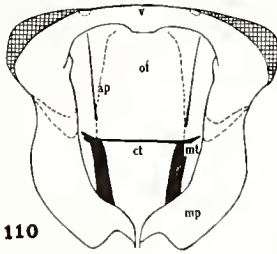
PLATE VII

Caudo-dorsal, dorsal, and cephalic aspect of the head

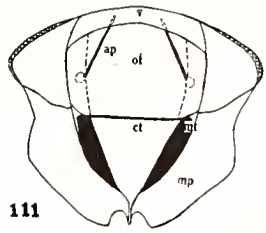
- FIG. 109.—*Jassus olitorius*, nymph, caudo-dorsal.
FIG. 110.—*Jassus olitorius*, adult, caudo-dorsal.
FIG. 111.—*Acinopterus acuminatus*, adult, caudo-dorsal.
FIG. 112.—*Euscelis bicolor*, adult, caudo-dorsal.
FIG. 113.—*Phlepsius excultus*, adult, caudo-dorsal.
FIG. 114.—*Oncometopia undata*, adult, caudo-dorsal.
FIG. 115.—*Erythroneura comes*, adult, caudo-dorsal.
FIG. 116.—*Belostoma flumineum*, nymph, dorsal.
FIG. 117.—*Belostoma flumineum*, adult, dorsal.
FIG. 118.—*Belostoma flumineum*, adult, cephalic.
FIG. 119.—*Belostoma flumincum*, nymph, cephalic.
FIG. 120.—*Ranatra americana*, adult, cephalic.
FIG. 121.—*Ranatra americana*, adult, dorsal.



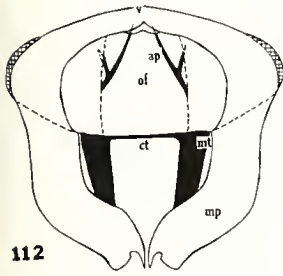
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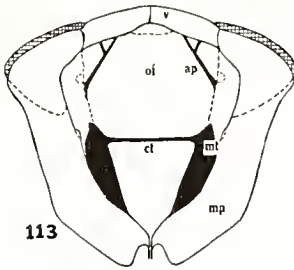
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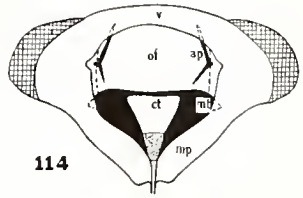
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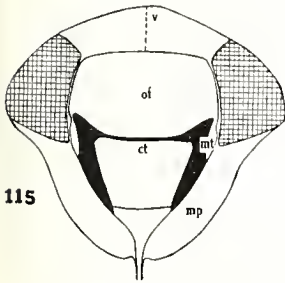
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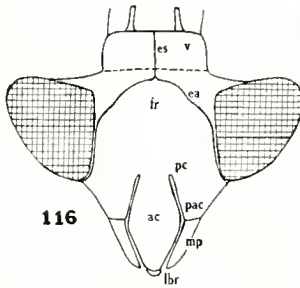
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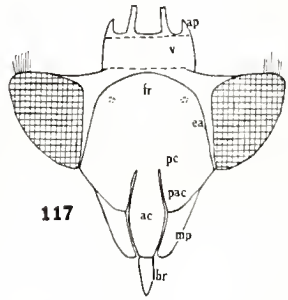
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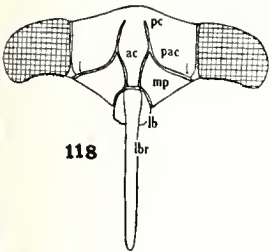
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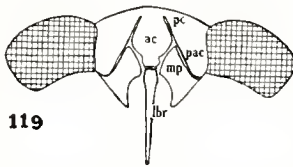
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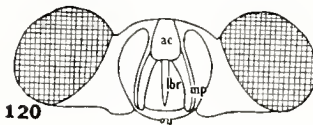
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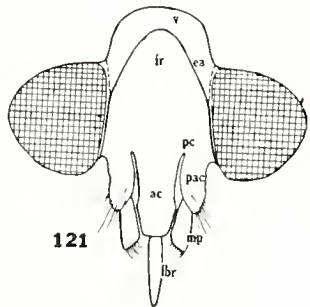
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PLATE VIII

Dorsal, ventral, and cephalic aspects of the head

- FIG. 122.—*Ranatra americana*, nymph, dorsal aspect.
FIG. 123.—*Nepa apiculata*, nymph, dorsal aspect.
FIG. 124.—*Nepa apiculata*, adult, dorsal aspect.
FIG. 125.—*Pelocoris femoratus*, nymph, dorsal aspect.
FIG. 126.—*Pelocoris femoratus*, nymph, cephalic aspect.
FIG. 127.—*Pelocoris femoratus*, adult, cephalic aspect.
FIG. 128.—*Pelocoris femoratus*, adult, dorsal aspect.
FIG. 129.—*Notonecta* sp., nymph, dorsal aspect.
FIG. 130.—*Notonecta* sp., nymph, cephalic aspect.
FIG. 131.—*Notonecta* sp., adult, cephalic aspect.
FIG. 132.—*Notonecta* sp., adult, ventral aspect.
FIG. 133.—*Corixa* sp., nymph, dorsal aspect.
FIG. 134.—*Corixa* sp., nymph, cephalic aspect.
FIG. 135.—*Corixa* sp., adult, cephalic aspect.
FIG. 136.—*Gerris marginatus*, nymph, dorsal aspect.

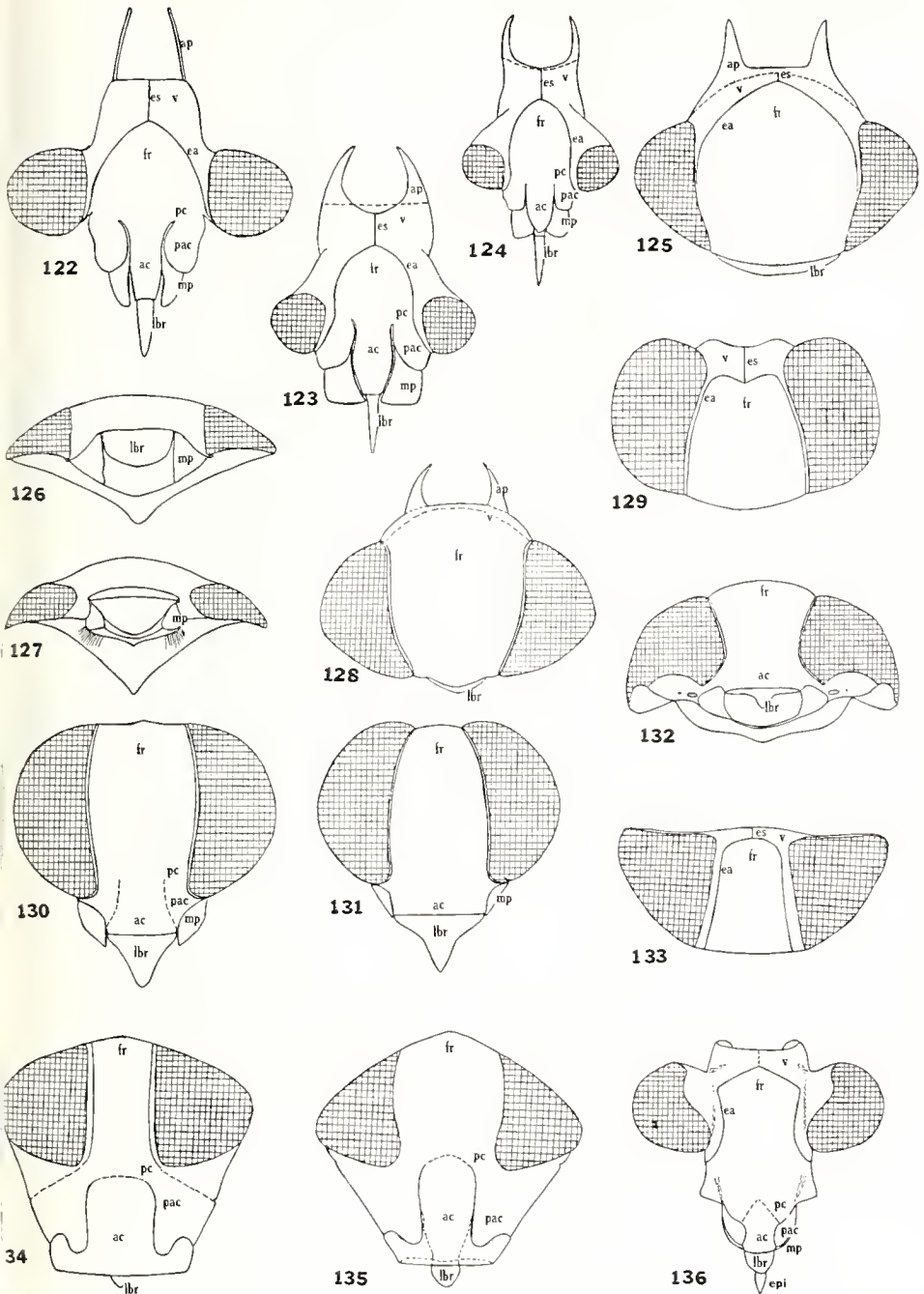
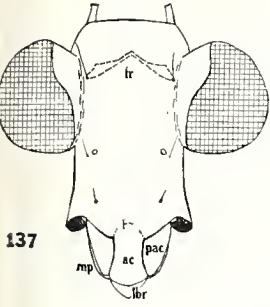


PLATE VIII

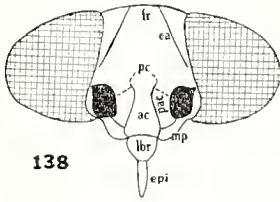
PLATE IX

Dorsal and cephalic aspects of the head

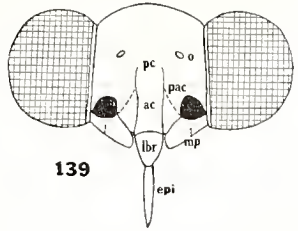
- FIG. 137.—*Gerris marginatus*, adult, dorsal aspect.
FIG. 138.—*Gerris marginatus*, nymph, cephalic aspect.
FIG. 139.—*Gerris marginatus*, adult, cephalic aspect.
FIG. 140.—*Rhagovelia obesa*, nymph, dorsal aspect.
FIG. 141.—*Rhagovelia obesa*, nymph, cephalic aspect.
FIG. 142.—*Rhagovelia obesa*, adult, cephalic aspect.
FIG. 143.—*Mesovelia bisignata*, adult, dorsal aspect.
FIG. 144.—*Hydrometra martini*, adult, dorsal aspect.
FIG. 145.—*Hydrometra martini*, adult, cephalic aspect.
FIG. 146.—*Nacogeus burmeisteri*, adult, cephalic aspect.
FIG. 147.—*Ochterus americanus*, adult, cephalic aspect.
FIG. 148.—*Gelastocoris* sp., nymph, cephalic aspect.
FIG. 149.—*Ochterus americanus*, nymph, cephalic aspect.
FIG. 150.—*Gelastocoris* sp., adult, cephalic aspect.
FIG. 151.—*Cimex lectularius*, nymph, cephalic aspect.



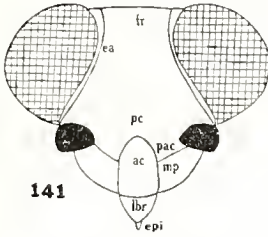
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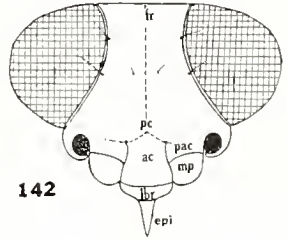
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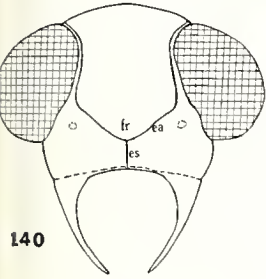
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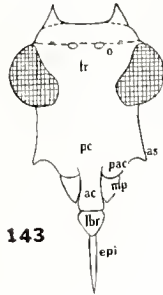
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142



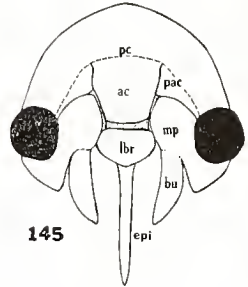
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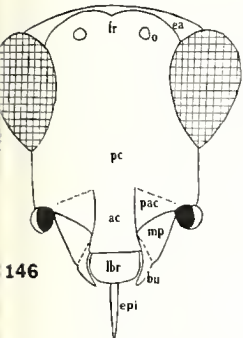
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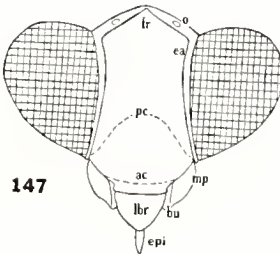
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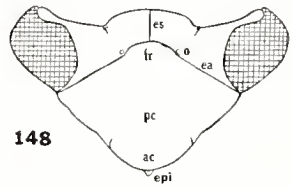
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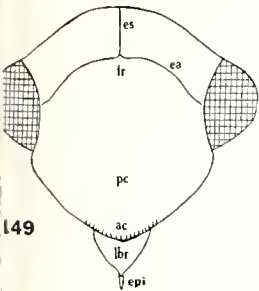
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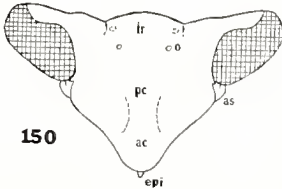
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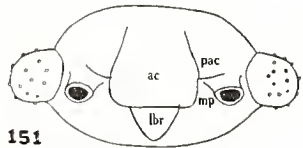
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150

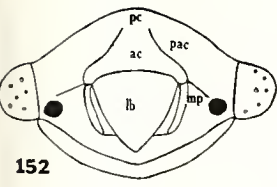


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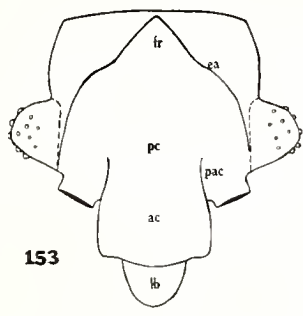
PLATE X

Dorsal and cephalic aspects of the head

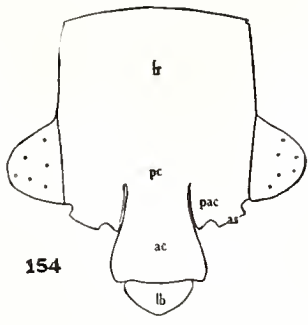
- FIG. 152.—*Cimex lectularius*, adult, cephalic aspect.
FIG. 153.—*Cimex lectularius*, nymph, dorsal aspect.
FIG. 154.—*Cimex lectularius*, adult, dorsal aspect.
FIG. 155.—*Lamprocanthia* sp., nymph, cephalic aspect.
FIG. 156.—*Lamprocanthia* sp., adult, cephalic aspect.
FIG. 157.—*Triphleps insidiosa*, nymph, dorsal aspect.
FIG. 158.—*Triphleps insidiosa*, adult, dorsal aspect.
FIG. 159.—*Sinea* sp., nymph, cephalic aspect.
FIG. 160.—*Sinea* sp., nymph, dorsal aspect.
FIG. 161.—*Sinea* sp., adult, dorsal aspect.
FIG. 162.—*Emesa brevipennis*, nymph, dorsal aspect.
FIG. 163.—*Emesa brevipennis*, adult, dorsal aspect.
FIG. 164.—*Melanolestes abdominalis*, adult, dorsal aspect.
FIG. 165.—*Nabis subcoleoptratus*, nymph, dorsal aspect.
FIG. 166.—*Nabis subcoleoptratus*, adult, dorsal aspect.
FIG. 167.—*Nabis subcoleoptratus*, nymph, cephalic aspect.



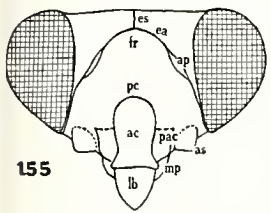
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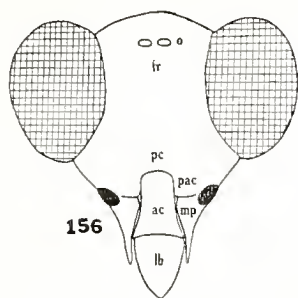
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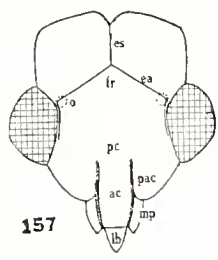
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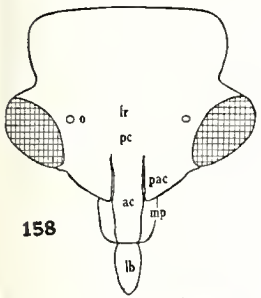
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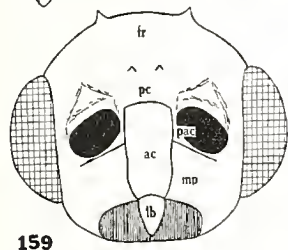
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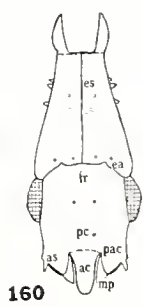
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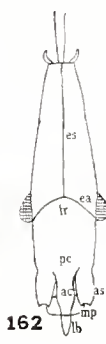
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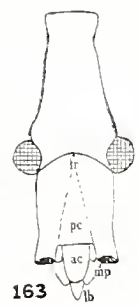
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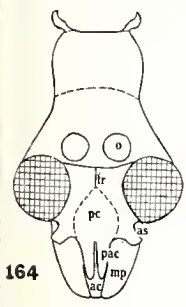
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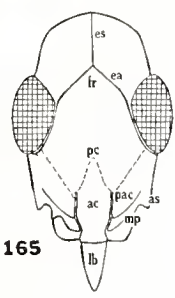
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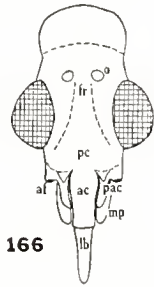
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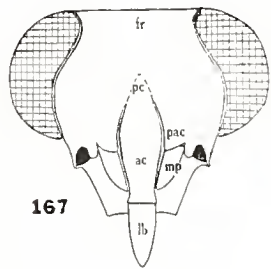
164



165



166



167

PLATE XI

Dorsal and cephalic aspects of the head

- FIG. 168.—*Systelloderus biceps*, nymph, dorsal aspect.
FIG. 169.—*Systelloderus biceps*, adult, dorsal aspect.
FIG. 170.—*Ceratocombus vagans*, nymph, dorsal aspect.
FIG. 171.—*Ceratocombus vagans*, adult, dorsal aspect.
FIG. 172.—*Miris dolobrotus*, nymph, dorsal aspect.
FIG. 173.—*Miris dolobrotus*, adult, cephalic aspect.
FIG. 174.—*Adelphocoris ropidus*, adult, cephalic aspect.
FIG. 175.—*Ischnodemus falicus*, nymph, dorsal aspect.
FIG. 176.—*Ischnodemus falicus*, adult, dorsal aspect.
FIG. 177.—*Ischnodemus falicus*, adult, cephalic aspect.
FIG. 178.—*Euryophthalmus succinctus*, nymph, dorsal aspect.
FIG. 179.—*Euryophthalmus succinctus*, nymph, cephalic aspect.
FIG. 180.—*Euryophthalmus succinctus*, adult, dorsal aspect.
FIG. 181.—*Myodochus scriripes*, nymph, dorsal aspect.
FIG. 182.—*Myodochus scriripes*, adult, dorsal aspect.

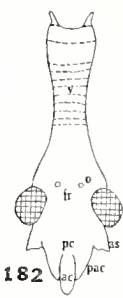
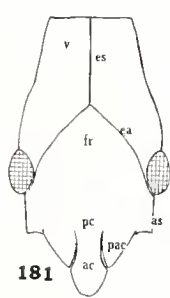
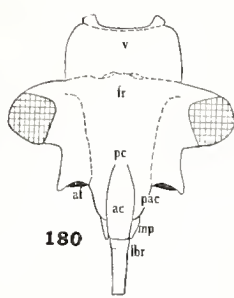
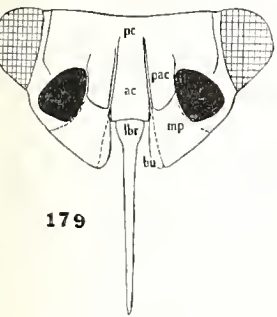
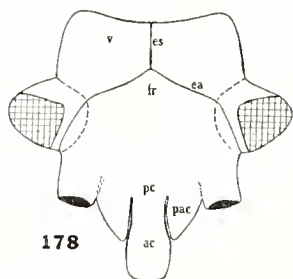
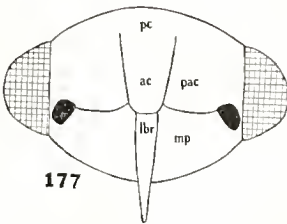
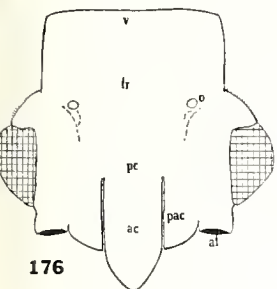
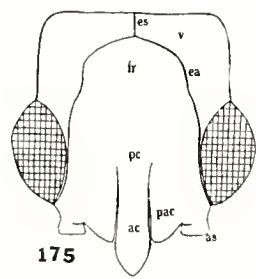
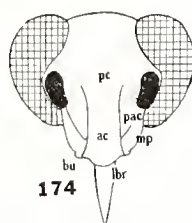
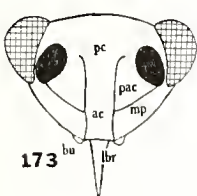
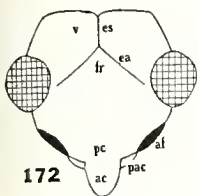
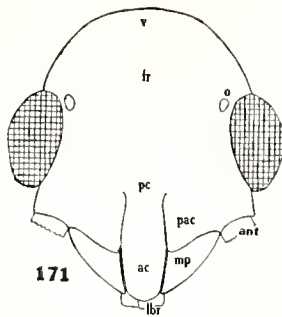
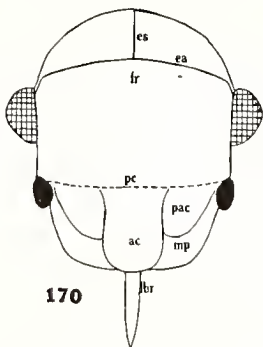
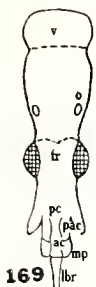
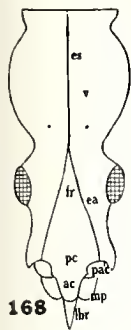


PLATE XI

PLATE XII

Dorsal and cephalic aspects of the head

- FIG. 183.—*Myodochus serripes*, adult, cephalic aspect.
FIG. 184.—*Neides muticus*, nymph, cephalic aspect.
FIG. 185.—*Neides muticus*, adult, cephalic aspect.
FIG. 186.—*Neides muticus*, nymph, dorsal aspect.
FIG. 187.—*Neides muticus*, adult, dorsal aspect.
FIG. 188.—*Corizus* sp., nymph, dorsal aspect.
FIG. 189.—*Corizus* sp., adult, cephalo-dorsal aspect.
FIG. 190.—*Harmoestes reflexulus*, adult, dorsal aspect.
FIG. 191.—*Alydus* sp., nymph, cephalo-dorsal aspect.
FIG. 192.—*Alydus* sp., adult, cephalo-dorsal aspect.
FIG. 193.—*Leptocoris trivittatus*, nymph, dorsal aspect.
FIG. 194.—*Leptocoris trivittatus*, adult, cephalic aspect.
FIG. 195.—*Leptocoris trivittatus*, adult, dorsal aspect.
FIG. 196.—*Piesma cincrea*, adult, dorsal aspect.
FIG. 197.—*Corythuca ciliata*, nymph, dorsal aspect.
FIG. 198.—*Corythuca ciliata*, nymph, cephalic aspect.

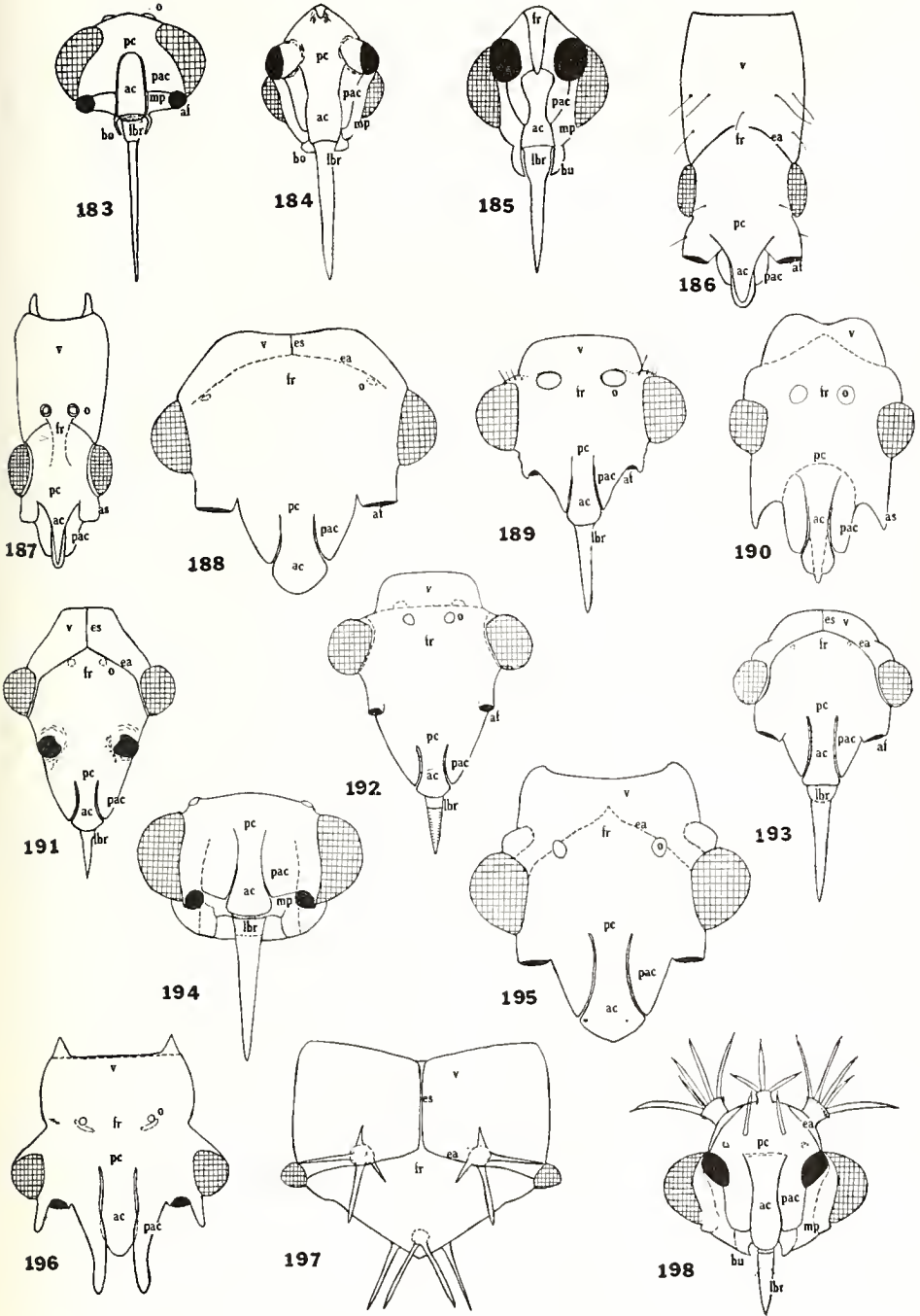
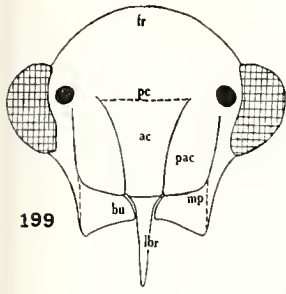


PLATE XII

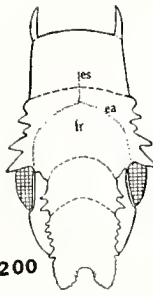
PLATE XIII

Dorsal and cephalic aspects of the head

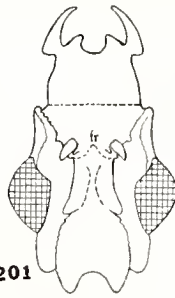
- FIG. 199.—*Corythuca ciliata*, adult, cephalic aspect.
FIG. 200.—*Phymata* sp., nymph, dorsal aspect.
FIG. 201.—*Phymata* sp., adult, dorsal aspect.
FIG. 202.—*Phymata* sp., nymph, cephalic aspect.
FIG. 203.—*Phymata* sp., adult, cephalic aspect.
FIG. 204.—*Aneurus* sp., nymph, cephalic aspect.
FIG. 205.—*Aneurus* sp., adult, cephalic aspect.
FIG. 206.—*Aneurus* sp., nymph, dorsal aspect.
FIG. 207.—*Aneurus* sp., adult, dorsal aspect.
FIG. 208.—*Brochymena* sp., nymph, dorsal aspect.
FIG. 209.—*Brochymena* sp., adult, dorsal aspect.
FIG. 210.—*Stethaulax marmoratus*, adult, dorsal aspect.
FIG. 211.—*Corimelaena* sp., adult, dorsal aspect.
FIG. 212.—*Cyrtomenus mirabilis*, adult, dorsal aspect.



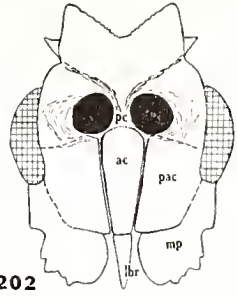
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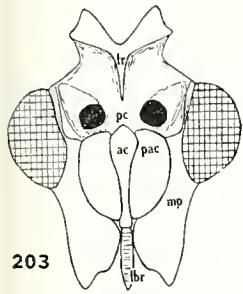
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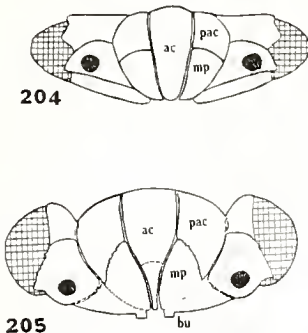
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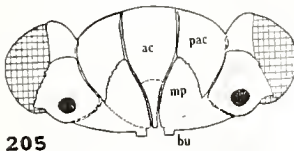
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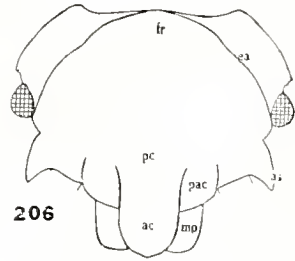
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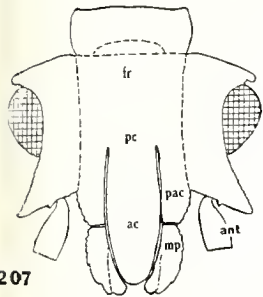
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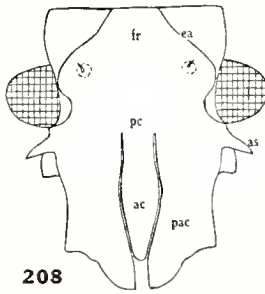
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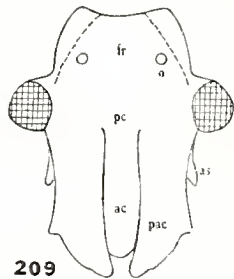
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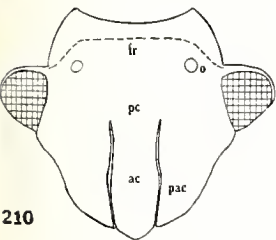
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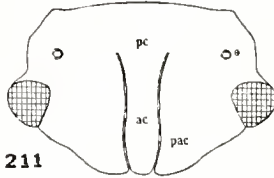
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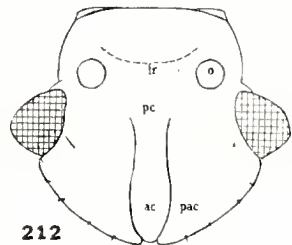
209



210



211



212

PLATE XIV

Lateral aspect of the head

- FIG. 213.—*Belostoma flumineum*, nymph.
FIG. 214.—*Belostoma flumineum*, adult.
FIG. 215.—*Ranatra americana*, adult.
FIG. 216.—*Ranatra americana*, nymph.
FIG. 217.—*Nepa apiculata*, nymph.
FIG. 218.—*Nepa apiculata*, adult.
FIG. 219.—*Pelocoris femoratus*, adult.
FIG. 220.—*Pelocoris femoratus*, nymph.
FIG. 221.—*Gerris marginatus*, nymph.
FIG. 222.—*Notonecta* sp., nymph.
FIG. 223.—*Notonecta* sp., adult.
FIG. 224.—*Corixa* sp., nymph.
FIG. 225.—*Corixa* sp., adult.
FIG. 226.—*Gerris marginatus*, adult.
FIG. 227.—*Rhagovelia obesa*, nymph.
FIG. 228.—*Rhagovelia abesa*, adult.
FIG. 229.—*Nacogeus burmeisteri*, adult.
FIG. 230.—*Mesovelia bisignata*, adult.
FIG. 231.—*Hydrometra martini*, adult.

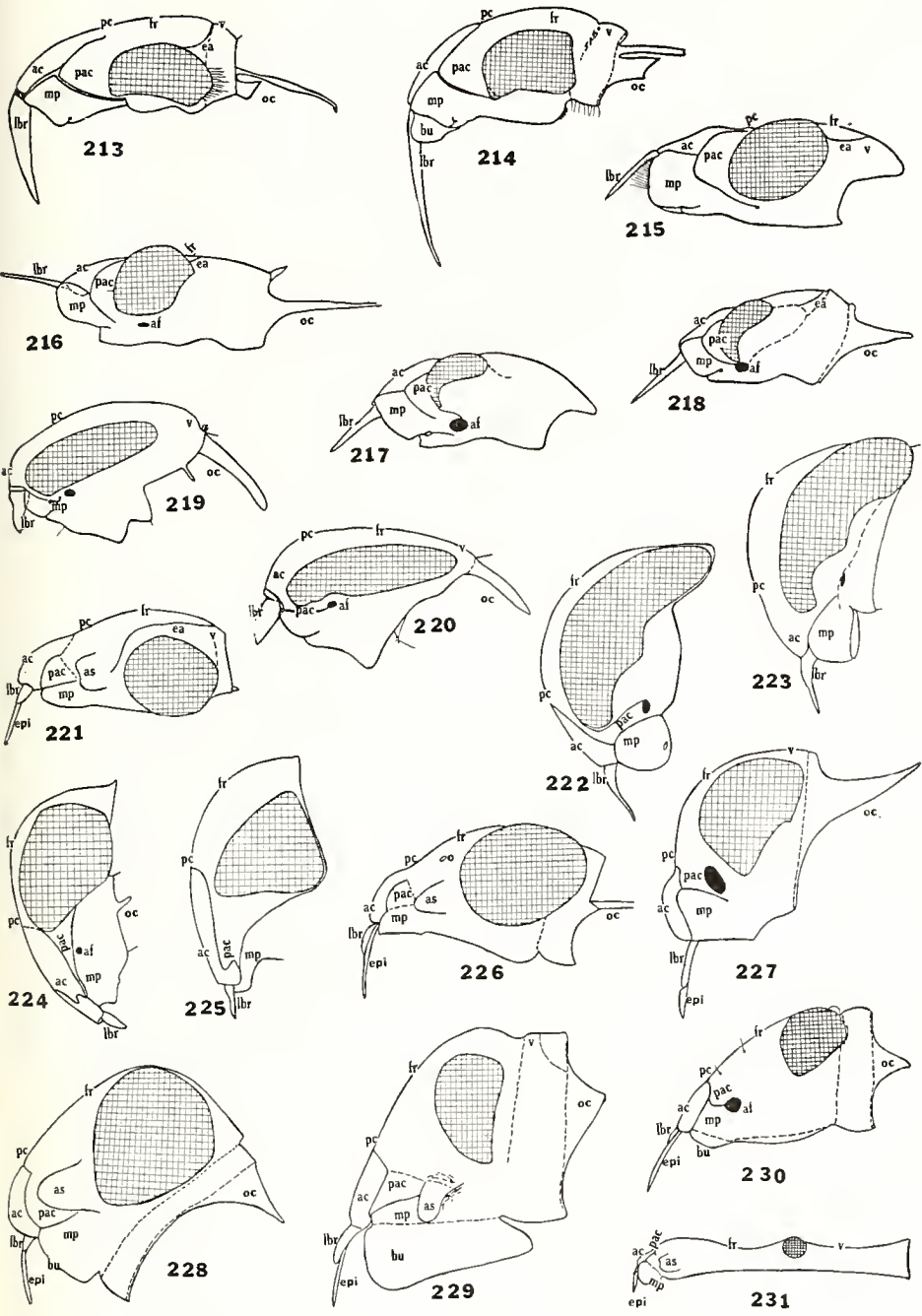


PLATE XIV

PLATE XV

Lateral aspect of the head

- FIG. 232.—*Ochterus americanus*, nymph.
FIG. 233.—*Ochterus americanus*, adult.
FIG. 234.—*Gelastocoris* sp., nymph.
FIG. 235.—*Cimex lectularius*, nymph.
FIG. 236.—*Gelastocoris* sp., adult.
FIG. 237.—*Cimex lectularius*, adult.
FIG. 238.—*Lamprocanthia* sp., adult.
FIG. 239.—*Triphleps insidiosa*, nymph.
FIG. 240.—*Triphleps insidiosa*, adult.
FIG. 241.—*Sinea* sp., nymph.
FIG. 242.—*Sinea* sp., adult.
FIG. 243.—*Emesa brevipennis*, nymph.
FIG. 244.—*Emesa brevipennis*, adult.
FIG. 245.—*Melanolestes abdominalis*, adult.
FIG. 246.—*Nabis subcoleoptratus*, adult.
FIG. 247.—*Nabis subcoleoptratus*, nymph.
FIG. 248.—*Systelloderus biceps*, nymph.
FIG. 249.—*Systelloderus biceps*, adult.
FIG. 250.—*Ceratocombus vagans*, nymph.

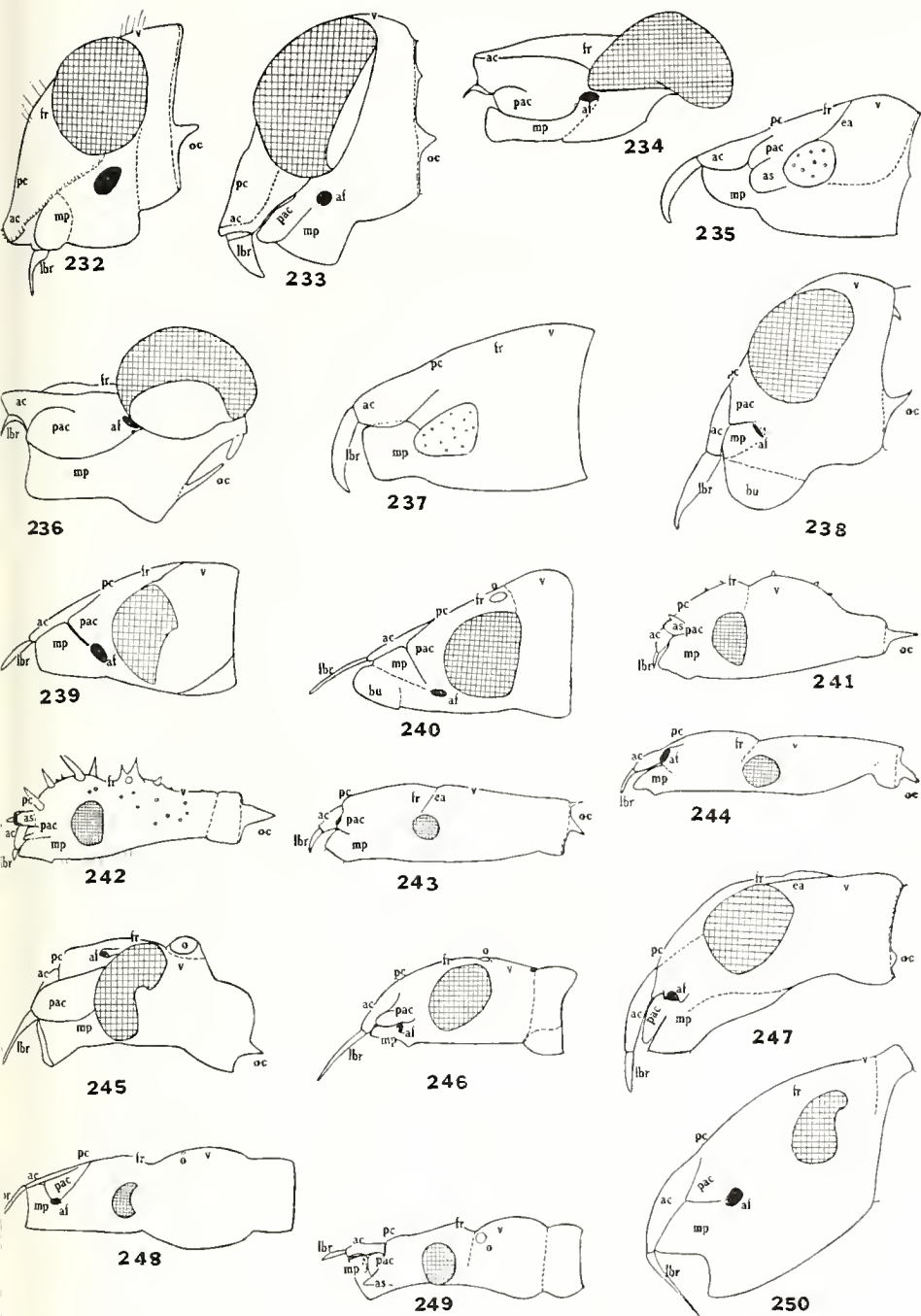
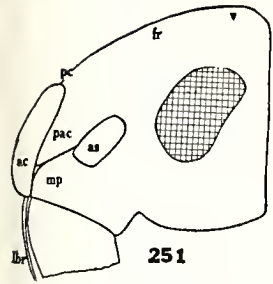


PLATE XV

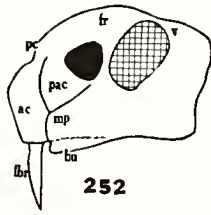
PLATE XVI

Lateral aspect of the head

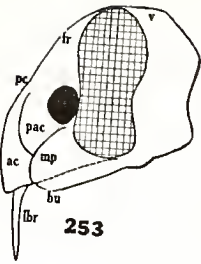
- FIG. 251.—*Ceratocombus vagans*, adult.
FIG. 252.—*Miris dolobrata*, adult.
FIG. 253.—*Adelphocoris rapidus*, adult.
FIG. 254.—*Ischnodemus folicus*, nymph.
FIG. 255.—*Ischnodemus folicus*, adult.
FIG. 256.—*Euryophthalmus succinctus*, nymph.
FIG. 257.—*Euryophthalmus succinctus*, adult.
FIG. 258.—*Myodochus serripes*, nymph.
FIG. 259.—*Myodochus serripes*, adult.
FIG. 260.—*Neides muticus*, nymph.
FIG. 261.—*Neides muticus*, adult.
FIG. 262.—*Corizus* sp., nymph.
FIG. 263.—*Alydus* sp., adult.
FIG. 264.—*Alydus* sp., nymph.
FIG. 265.—*Corizus* sp., adult.



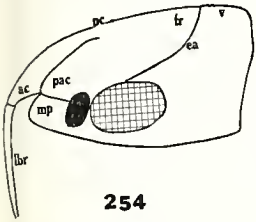
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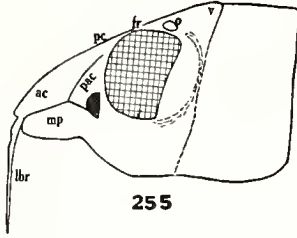
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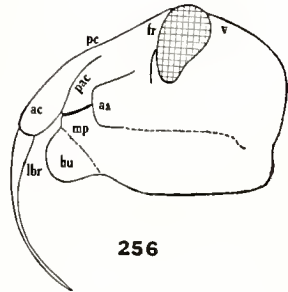
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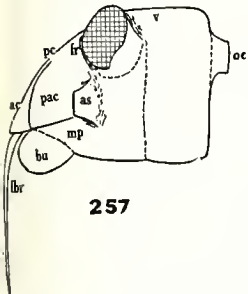
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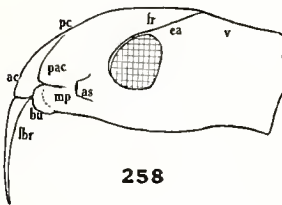
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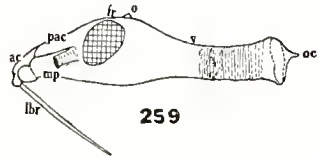
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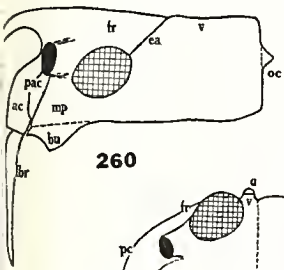
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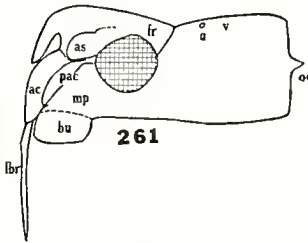
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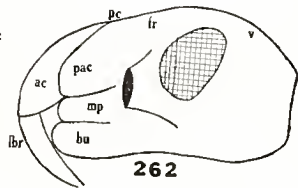
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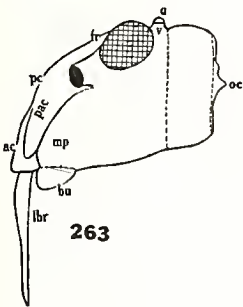
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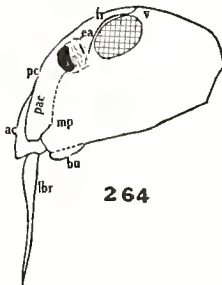
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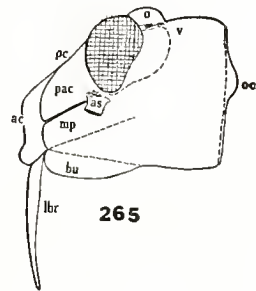
262



263



264



265

PLATE XVII

Lateral aspect of the head

- FIG. 266.—*Harmoestes reflexulus*, adult.
FIG. 267.—*Leptocoris trivittatus*, adult.
FIG. 268.—*Leptocoris trivittatus*, nymph.
FIG. 269.—*Piesma cinerea*, adult.
FIG. 270.—*Corythuca ciliata*, nymph.
FIG. 271.—*Corythuca ciliata*, adult.
FIG. 272.—*Phymata* sp., nymph.
FIG. 273.—*Phymata* sp., adult.
FIG. 274.—*Aneurys* sp., nymph.
FIG. 275.—*Aneurys* sp., adult.
FIG. 276.—*Brochymena* sp., nymph.
FIG. 277.—*Brochymena* sp., adult.
FIG. 278.—*Corimelaena* sp., adult.
FIG. 279.—*Stethaulax marmoratus*, adult.
FIG. 280.—*Cyrtomoenus mirabilis*, adult.

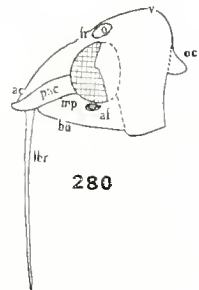
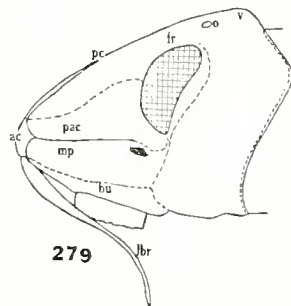
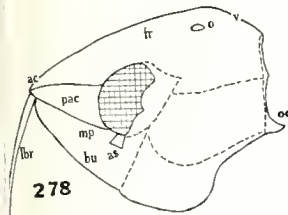
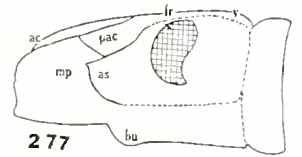
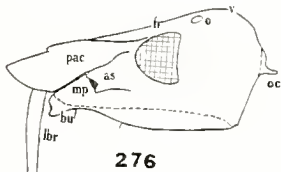
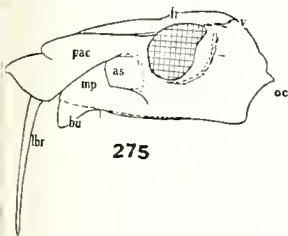
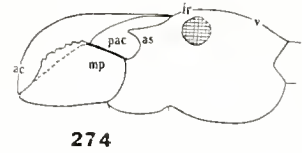
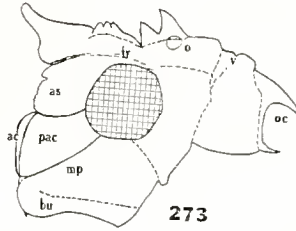
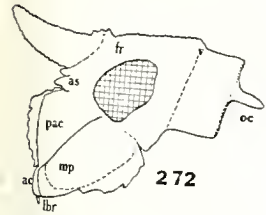
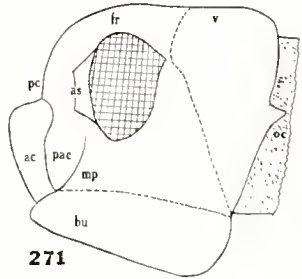
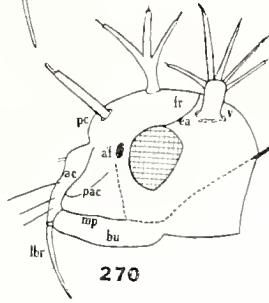
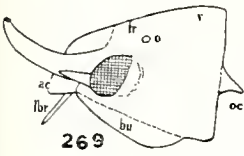
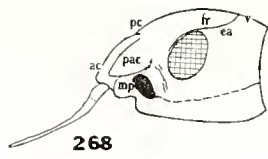
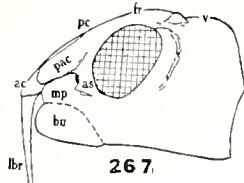
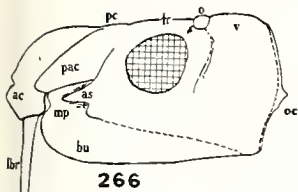
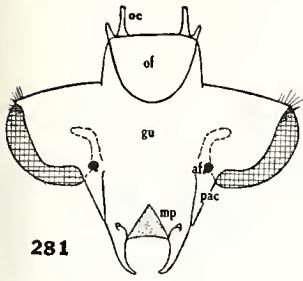


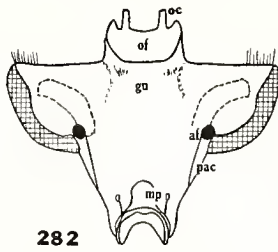
PLATE XVIII

Ventral and caudal aspects of the head

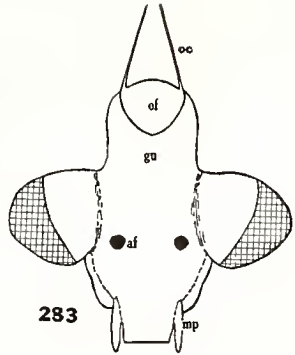
- FIG. 281.—*Belostoma flumineum*, nymph, ventral aspect.
FIG. 282.—*Belostoma flumineum*, adult, ventral aspect.
FIG. 283.—*Ranatra americana*, nymph, ventral aspect.
FIG. 284.—*Ranatra americana*, adult, ventral aspect.
FIG. 285.—*Nepa apiculata*, nymph, ventral aspect.
FIG. 286.—*Nepa apiculata*, adult, ventral aspect.
FIG. 287.—*Pelocoris femoratus*, nymph, ventral aspect.
FIG. 288.—*Pelocoris femoratus*, adult, ventral aspect.
FIG. 289.—*Notonecta* sp., adult, caudal aspect.
FIG. 290.—*Corixa* sp., adult, caudal aspect.
FIG. 291.—*Corixa* sp., nymph, caudal aspect.
FIG. 292.—*Gerris marginatus*, nymph, ventral aspect.
FIG. 293.—*Gerris marginatus*, adult, ventral aspect.



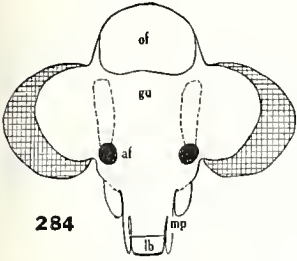
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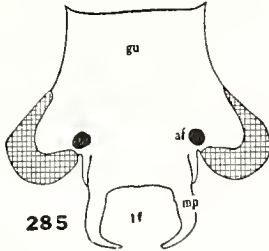
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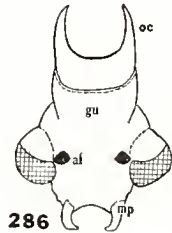
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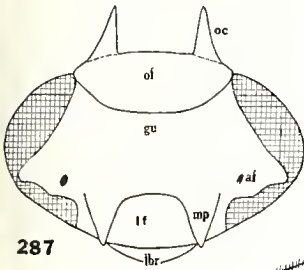
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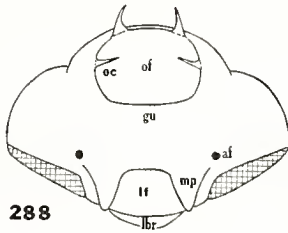
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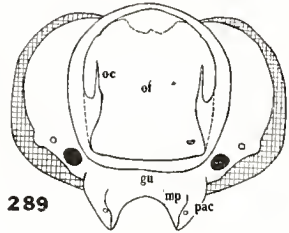
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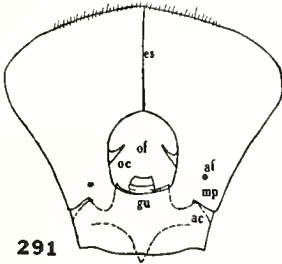
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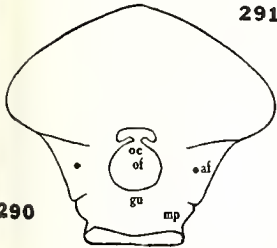
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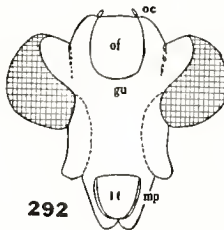
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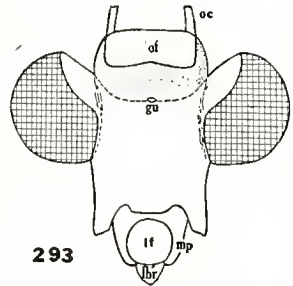
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292



293

PLATE XIX

Ventral and caudal aspects of the head

- FIG. 294.—*Rhagozelia obesa*, adult, ventral aspect.
FIG. 295.—*Mesozelia bisignata*, adult, ventral aspect.
FIG. 296.—*Hydrometra martini*, adult, ventral aspect.
FIG. 297.—*Naeogus burmeisteri*, adult, ventral aspect.
FIG. 298.—*Gelastocoris* sp., nymph, ventral aspect.
FIG. 299.—*Gelastocoris* sp., adult, ventral aspect.
FIG. 300.—*Gelastocoris* sp., nymph, caudal aspect.
FIG. 301.—*Gelastocoris* sp., adult, caudal aspect.
FIG. 302.—*Ochterus americanus*, adult, ventral aspect.
FIG. 303.—*Ochterus americanus*, nymph, caudo-ventral aspect.
FIG. 304.—*Ochterus americanus*, adult, caudal aspect.
FIG. 305.—*Lamprocanthia* sp., nymph, caudal aspect.
FIG. 306.—*Cimex lectularius*, nymph, ventral aspect.
FIG. 307.—*Cimex lectularius*, adult, ventral aspect.
FIG. 308.—*Lampraconthia* sp., adult, caudal aspect.
FIG. 309.—*Triphleps insidiosa*, adult, ventral aspect.
FIG. 310.—*Triphleps insidiosa*, nymph, ventral aspect.

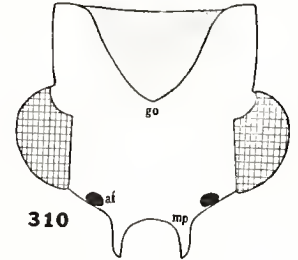
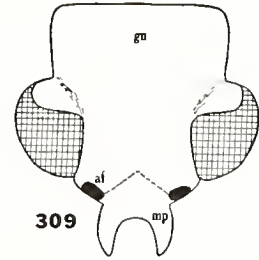
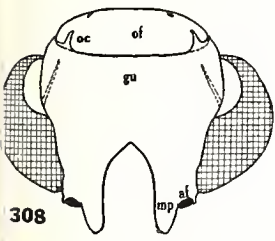
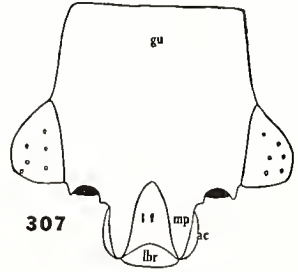
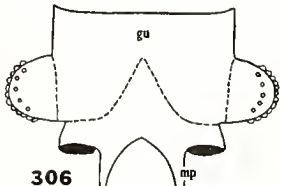
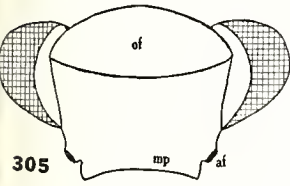
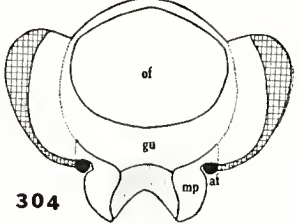
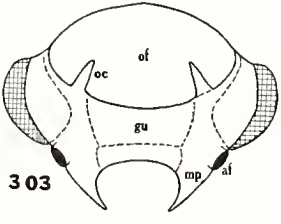
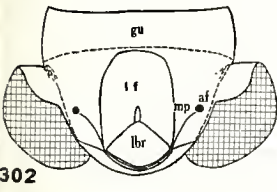
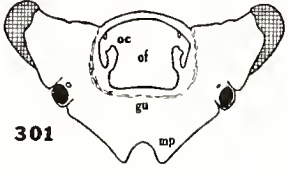
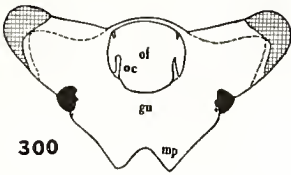
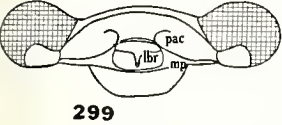
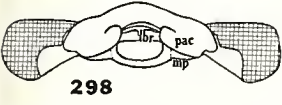
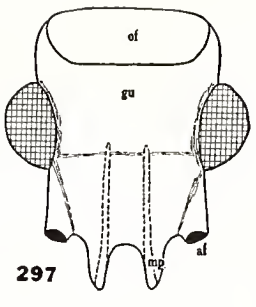
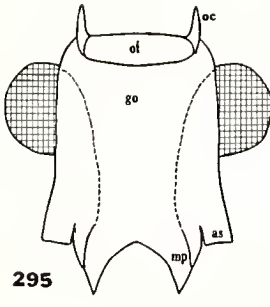
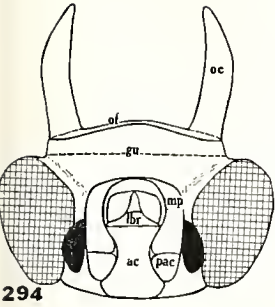


PLATE XIX

PLATE XX

Ventral aspect of the head

- FIG. 311.—*Sinea* sp., nymph.
FIG. 312.—*Sinea* sp., adult.
FIG. 313.—*Emesa brevipennis*, nymph.
FIG. 314.—*Emesa brevipennis*, adult.
FIG. 315.—*Melanolestes abdominalis*, adult.
FIG. 316.—*Nabis subcoleopratus*, nymph.
FIG. 317.—*Nabis subcoleopratus*, adult.
FIG. 318.—*Systelloderus biceps*, adult.
FIG. 319.—*Ischnodemus falicus*, nymph.
FIG. 320.—*Ischnodemus falicus*, adult.
FIG. 321.—*Euryophthalmus succinctus*, nymph.
FIG. 322.—*Euryophthalmus succinctus*, adult.
FIG. 323.—*Myodoclus serripes*, nymph.
FIG. 324.—*Myodoclus serripes*, adult.
FIG. 325.—*Neides muticus*, nymph.
FIG. 326.—*Neides muticus*, adult.
FIG. 327.—*Corizus* sp., nymph.
FIG. 328.—*Corizus* sp., adult.

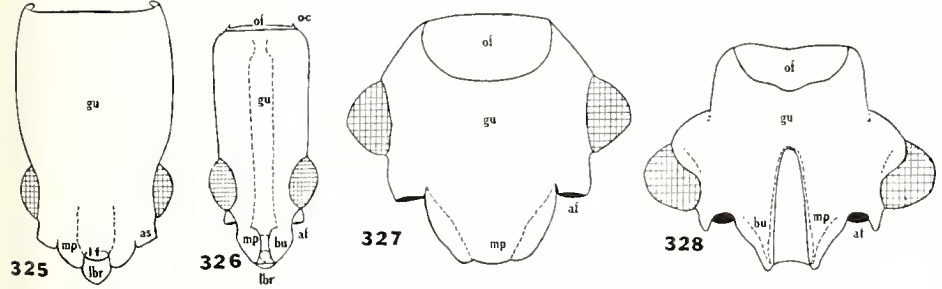
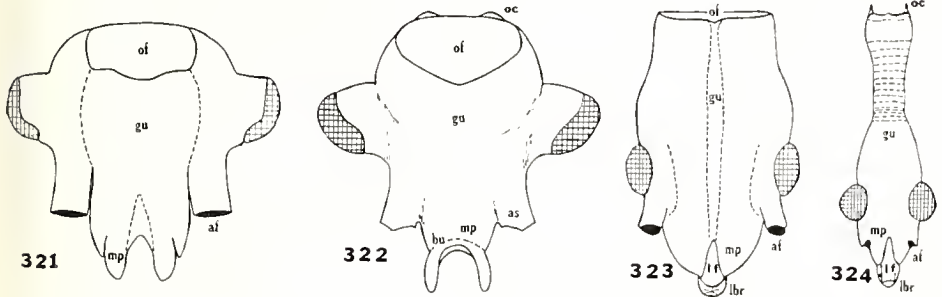
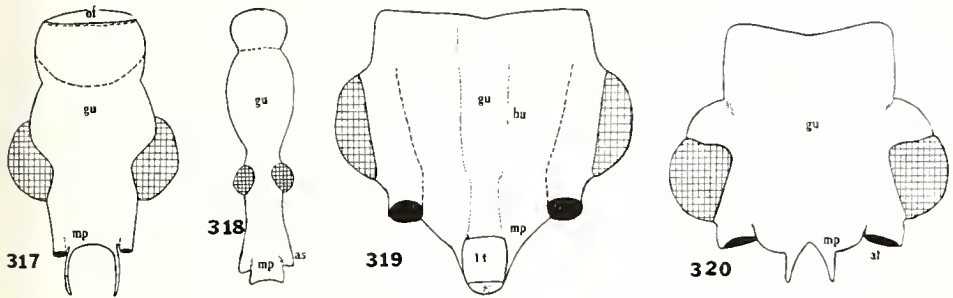
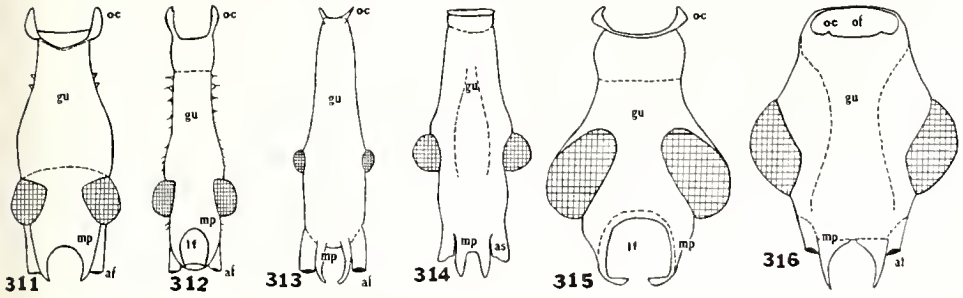


PLATE XX

PLATE XXI

Ventral aspect of the head

- FIG. 329.—*Harmoestes reflexulus*, adult.
FIG. 330.—*Alydus* sp., nymph.
FIG. 331.—*Alydus* sp., adult.
FIG. 332.—*Leptocoris trivittatus*, nymph.
FIG. 333.—*Leptocoris trivittatus*, adult.
FIG. 334.—*Piesma cineria*, adult.
FIG. 335.—*Corythuca ciliata*, nymph.
FIG. 336.—*Corythuca ciliata*, adult.
FIG. 337.—*Phymata* sp., nymph.
FIG. 338.—*Phymata* sp., adult.
FIG. 339.—*Aneururus* sp., nymph.
FIG. 340.—*Aneururus* sp., adult.
FIG. 341.—*Brochymena* sp., nymph.
FIG. 342.—*Brochymena* sp., adult.

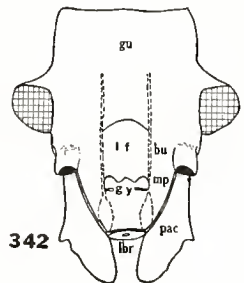
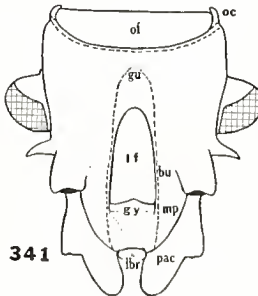
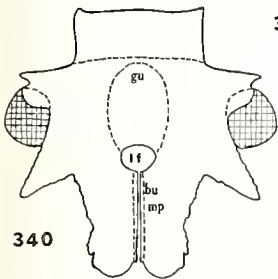
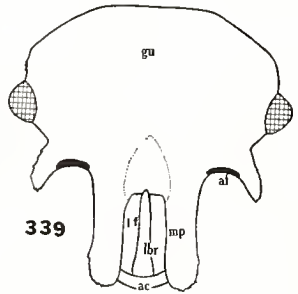
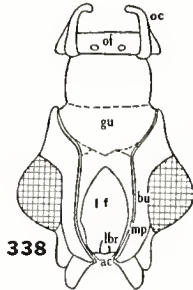
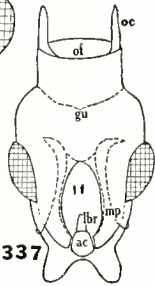
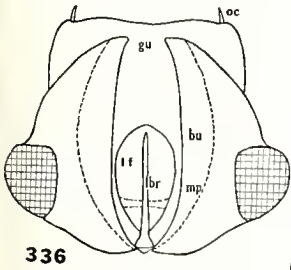
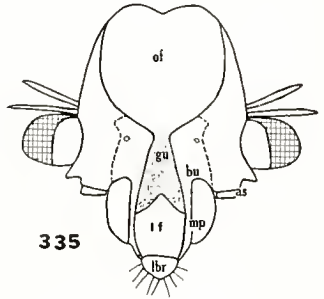
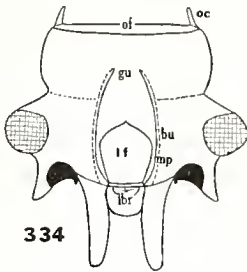
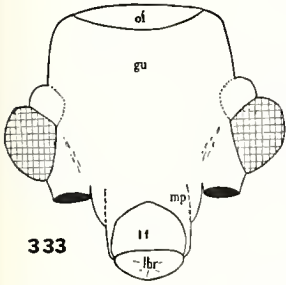
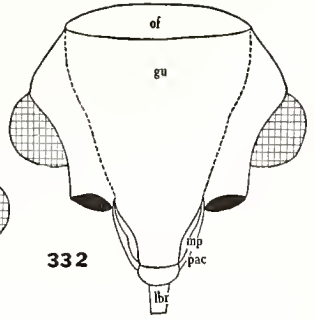
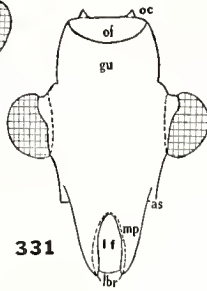
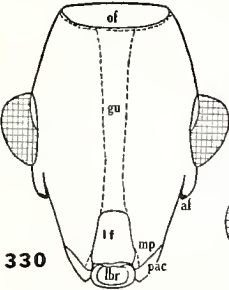
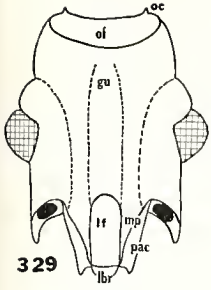


PLATE XXI

PLATE XXII

Ventral aspect of the head

- FIG. 343.—*Cyrtomoenus mirabilis*, adult.
 FIG. 344.—*Stethaulax marmorotus*, adult.
 FIG. 345.—*Corimelaena*, adult.

Anteclypeus and labrum, lateral aspect

- FIG. 346.—*Otiocerus wolffi*, adult.
 FIG. 347.—*Belostoma flumineum*, adult.
 FIG. 348.—*Euschistus tristigma*, adult.

Mandible and lever

- FIG. 349.—*Corixa* sp., adult.
 FIG. 350.—*Otiocerus degeerii*, adult.
 a. Marginal view.
 FIG. 351.—*Lepyronia quadrangularis*, adult.
 a. Marginal view.
 FIG. 352.—*Tibicen sayi*, adult.
 FIG. 353.—*Oncometopia undata*, adult.
 FIG. 354.—*Belostoma flumineum*, nymph.
 FIG. 355.—*Belostoma flumineum*, adult.
 FIG. 356.—*Ranatra americana*, adult.
 FIG. 357.—*Melanolestes abdominalis*, adult.
 FIG. 358.—*Pelocoris femoratus*, adult.
 FIG. 359.—*Notonecta* sp., adult.
 FIG. 360.—*Gerris marginatus*, adult.
 FIG. 361.—*Rhagovelia obesa*, adult.
 FIG. 362.—*Mesovelia bisignata*, adult.
 FIG. 363.—*Hydrometra martini*, adult.
 FIG. 364.—*Nacogeus burmeisteri*, adult.

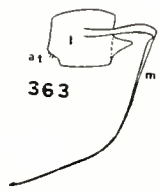
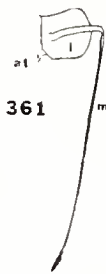
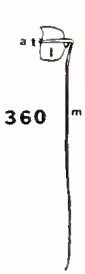
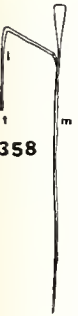
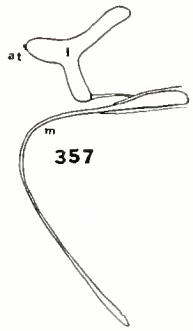
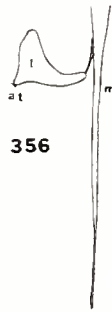
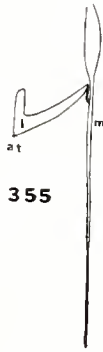
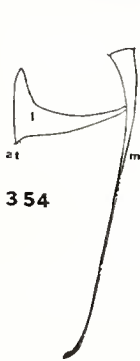
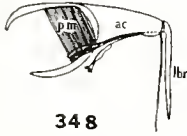
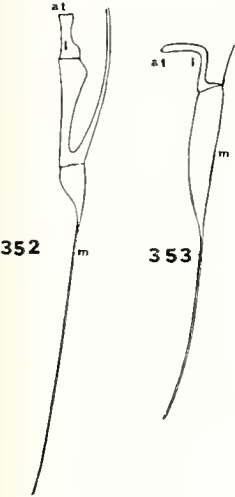
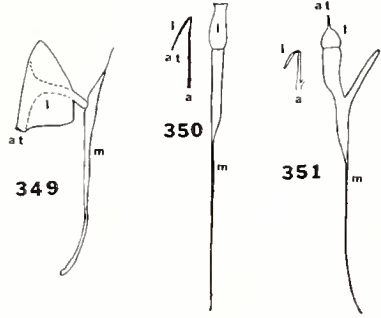
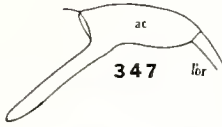
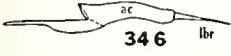
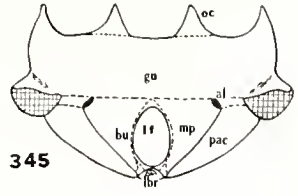
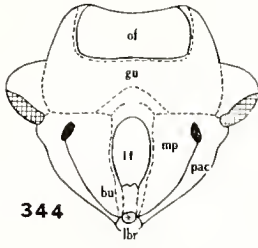
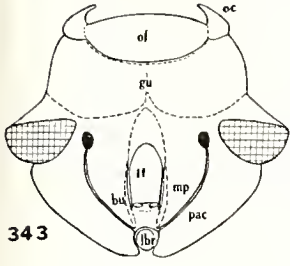


PLATE XXII

PLATE XXIII

Mandible and lever

- FIG. 365.—*Ochterus viridifrons*, adult.
FIG. 366.—*Ochterus americanus*, adult.
FIG. 367.—*Cimex lectularius*, adult.
FIG. 368.—*Gelastocoris* sp., adult.
FIG. 369.—*Pentocora* sp., adult.
FIG. 370.—*Sinea* sp., adult.
FIG. 371.—*Emesa brevipennis*, adult.
FIG. 372.—*Miris dolobratus*, adult.
FIG. 373.—*Adelphocoris rapidus*, adult.
FIG. 374.—*Ischnodemus falicus*, adult.
FIG. 375.—*Euryophthalmus succinctus*, adult.
FIG. 376.—*Myodochus serringes*, adult.
FIG. 377.—*Neides muticus*, adult.
FIG. 378.—*Jalysus spinosus*, adult.
FIG. 379.—*Corizus* sp., adult.
FIG. 380.—*Alydus* sp., adult.
FIG. 381.—*Anasa tristis*, adult.

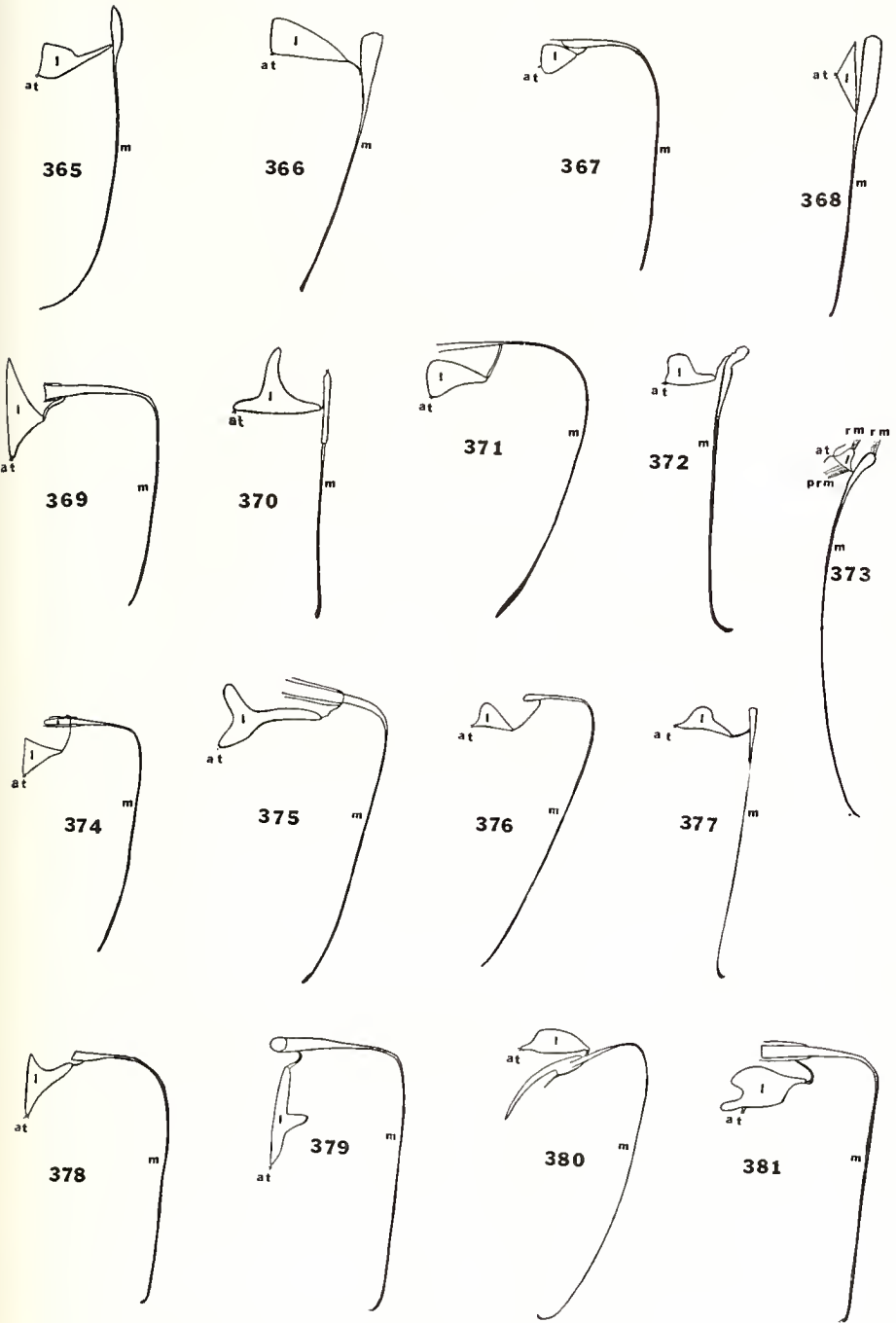


PLATE XXIII

PLATE XXIV

Mandible and lever

- FIG. 382.—*Acanthocephala terminalis*, adult.
 FIG. 383.—*Piesma cinerea*, adult.
 FIG. 384.—*Corythuca ciliata*, adult.
 FIG. 385.—*Phymata* sp., adult.
 FIG. 386.—*Aneuris* sp., nymph.
 FIG. 387.—*Aneuris* sp., adult.
 FIG. 388.—*Cyrtomoenus mirabilis*, adult.
 FIG. 389.—*Stethaulax marmoratus*, adult.
 FIG. 390.—a. *Euschistus servus*, adult, lever.
 b. *Euschistus euschistoides*, adult, lever.
 c. *Euschistus tristigmus*, adult, lever.
 FIG. 391.—a. *Euschistus tristigmus luridus*, adult, lever.
 b. *Euschistus servus* variety, adult, lever.

Labium

- FIG. 392.—*Gerris remigera*, adult, lateral aspect.
 FIG. 393.—*Ochterus americanus*, adult, lateral aspect.
 FIG. 394.—*Gelastocoris* sp., adult, lateral aspect.
 FIG. 395.—*Ceratocombus vagans*, adult, lateral aspect.
 FIG. 396.—*Pentacora* sp., adult, lateral aspect.
 FIG. 397.—*Miris dolobratius*, adult, lateral aspect.
 FIG. 398.—*Adelphocoris rapidus*, adult, lateral aspect.

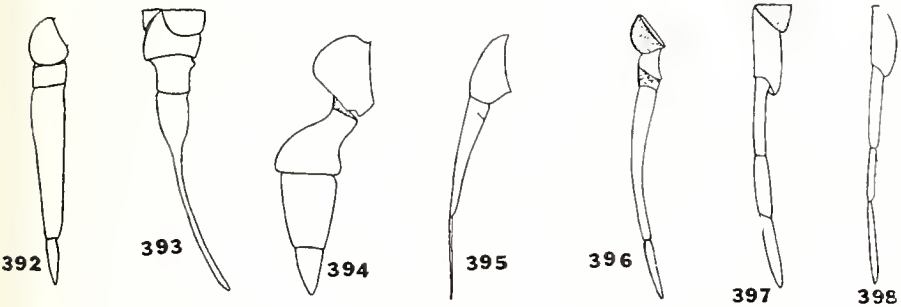
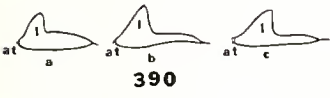
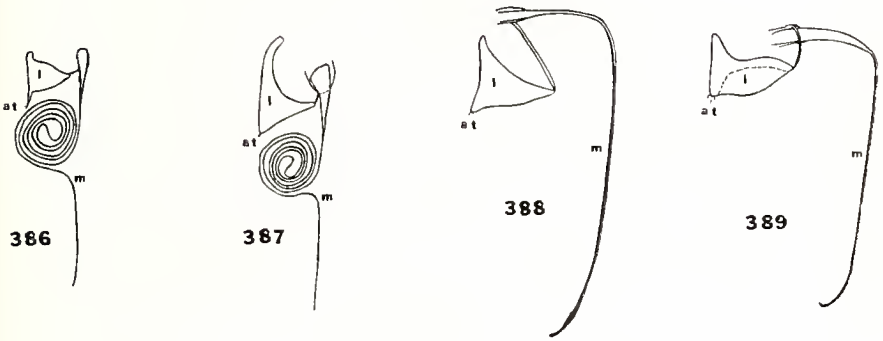
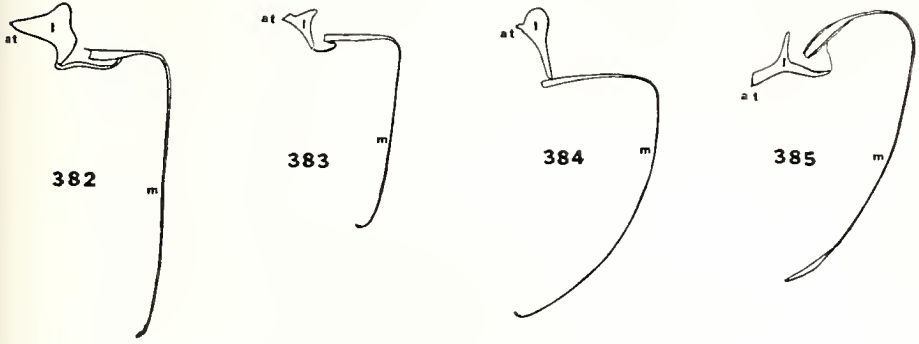


PLATE XXIV

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