THE COMPARATIVE MORPHOLOGY OF THE MALE GENITALIA OF THE PRIMITIVE LEPIDOPTERA

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INTRODUCTION.

The primitive Lepidoptera discussed in this paper include the Jugate Lepidoptera, (Hepialidae and Prototheoridae), the Jugo-frenate Lepidoptera, (Mnesarchaeidae, Micropterygidae, and Eriocraniidae), and the Frenate superfamilies Tineoidea, Eucleoidea, and Bombycoidea. The object in this discussion is to compare the male genitalia of these groups of Lepidoptera with each other and with those of nearly related orders of insects, and to ascertain from this comparison the value of these organs in gaining a more complete knowledge of the natural relationships of the insects treated.

HISTORICAL SURVEY

References to the male genitalia of Lepidoptera are to be found in the works of such early writers as Malpighi, Swammerdam, and Reamur. Malpighi, (1669), briefly described the male genitalia of Bombyx mori in connection with his discussion of the reproductive system in this insect. Swammerdam, (1737), in much the same manner outlined the gross structure of the genitalia in the European butter-fly, Vanessa urticae. Reamur, (1742), described the physiology of the reproductive system in male Lepidoptera but made little effort to describe the genitalia. The works of these authors are characterized by a tendency to emphasize the physiology of the reproductive system with little or no description of the external

armature which comprises the genitalia.

The first detailed description of the reproductive organs in the microlepidoptera was by Suckow in 1828. This author described these organs in Tinea pellionella but contributed practically nothing toward the morphology of the genital appendages.

The works of Burmeister, (1832), Kirby and Spence (1838), and Siebold and Stannius (1848) illustrate the first detailed attempts to describe the external and more visible parts of the genital armature. In these the term valvae or valves was used to denote the two lateral outer appendages. Burmeister (1870, '74) makes further use of this term in describing the genus Euryades and specified that these valves were appendages of the eighth urite, a conclusion arrived at thru his failure to count the first abdominal somite.

De Haan (1842), in describing the genitalia of the Papilionidae used the Dutch term, "kleppen", for the valves and designated the inner lateral appendages as, "zijdelingsche aanhangels".

Scudder and Burgess (1870) called attention to the asymmetry of the male genitalia in certain species of Nisoniades and added a few new terms which described certain parts quite specifically. The term "clasp" was used instead of valve; the process arising from the basal portion of the clasp was called the "basal process", and the dorsal portion of the genital armature was named the "upper organ". The terms "main body" and "dorsal crest" were used rather interchangeably for the proximal portion of the upper organ and the distal half was referred to as the "apical portion". The figures accompanying this paper are clear and leave no doubt as to the identity of the parts described. It is also of interest to note that these authors were among the first to emphasize the usefulness of the genitalia as specific characters expressing their confidence in the reliability of

them for the purpose of distinguishing closely related species.

In 1876 Buchanan-White published the first comprehensive survey of the male genitalia of Lepidoptera under the title, "Of the Male Genital Armature in the European Rhopalocera". In this work the term "harpago" was used for the valve and "tegumen", for the "upper organ" of Scudder and Burgess. This paper and the one by Gosse (1883) had a marked influence in the developing of a comprehensive system of nomenclature for the male genitalia in Lepidoptera and in stimulating future work in this field.

Gosse was influenced by the divided condition of the lateral appendages in the Papilionidae to use the term valve for the entire appendage and to restrict the term harpe to "those portions which project freely into the enclosed space between the valves". The term "uncus" was added to describe the hook like tip of the tegumen and "scaphium" for the "mass of shining white tissue apparently in organic union with the lower surface of the uncus near its origin".

Subsequent to the work of Buchanan-White and Gosse the investigation of the male genitalia of Lepidoptera followed two rather distinct lines of endeavor. In the first of these the authors described the genital appendages in certain genera or groups, using them as characters for the separation of species; in the second, the morphology and ontogeny of these organs were described for the purpose of comparison in more comprehensive, yet related, groups. Of the former, the works of Hoffman (1888, '95), Smith (1889, '98), Pierce (1909, '14, '22), Busck and Heinrich (1921) and Heinrich (1923) are among the most important from the standpoint of the microlepidopterist. Hoffman's descriptions of the genitalia of the Butalidae illustrated the first serious attempt to describe the external genital armature of such small insects. Smith demonstrated the value of the harpes for separating closely related species of Noctuidae and inspired Pierce to make a more comprehensive

study of the genitalia in this family. Pierce's extensive works on the Noctuidae, Geometriidae, and Tortricidae are the most comprehensive accounts of the genitalia in these groups up to the present time and serve as the basis for the work being carried on by present day investigators. Busck and Heinrich have adopted Pierce's system of nomenclature in describing the genitalia in new species of North America Lepidoptera and Heinrich, in his recent revision of the Eucosminae, has effectively applied the genital characters in clearing up many of the difficult problems in the natural relationships of the members of this group.

In the second class of investigators Cholodkovsky (1885), Peytoureau (1895), Stitz (1900), and Zander (1903), and Petersen (1900, '04)* are most worthy of consideration. Cholodkovsky's description of the genitalia in the Adelid moth, Nemotois metallicus Pod., illustrated an early attempt to comprehend the genital system in an insect which because of its minute size and vestiture of scales offered an excellent chance for the development of delicate technique, This work served as the basis for future investigations on the internal genitalia in Lepidoptera and Trichoptera which will be referred to later. Cholodkovsky's treatment of Nematois exhibits a keen and correct insight into the structure of the genitalia. He expresses his regret in being unable to find a system of nomenclature for the genitalia in the literature of his day and proceeds to originate one which admirably serves his purpose. He recognizes the "vinculum" of present day authors as the ninth sternite, and the tegumen as the combined ninth and tenth terga, the latter being rudimentary or "embryonic". For the valves he uses de Haan's term kleppen and suggests that they may represent larval appendages which

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* The works of this author have come to my attention since the writing of this manuscript and are included in the bibliography. In his paper on the significance of the genitalia in the differentiation of species he discusses at length the morphology of the male genitalia and adopts the terminology of Zander (1903), adding the term "fultura penis" to describe the processes associated with the ventral surface of the "ring wall". In the terminology adopted in this paper these are called the "juxta".

were suppressed in the pupa, i.e. the "schwanzlappen" which Tichomiroff (1880), described in the pupa of Bombyx mori. Cholodkovsky describes the penis as a hollow chitinous rod which enters the ninth somite thru a membranous tube, the "praeputium", reenforced ventrally by a flat chitinous plate, i.e. the annellus and juxta of Pierce. He applies the term "eichelposterchen" to the membranous tip of the penis, i.e. vesica of Pierce, and noted that it was eversible.

The work of Peytoureau comprises a number of extensive treatises on the comparative morphology of the genitalia in the more important insect orders. His study of the Lepidoptera includes six species, and while these were all macrolepidoptera, it is of importance because his conception of the morphological units is based on a study of the pupal development and the nervous system of the genital appendages. He regards the tegumen as being composed of the fused ninth and tenth terga which are distinct and unfused in the pupa. He calls attention to the close connection of the valves, the ninth sternum, and the basement membrane, (anellus), in the pupa, and he regards the penis as the chitinized terminal portion of the ejaculatory duct. He describes the formation of the saccus or median process of the anterior margin of the ninth sternite in Bombyx mori and considers it part of the membrane between the eighth and ninth sterna. With regard to the nervous system, he showed that the genitalia were ennervated by the "sixth lateral" and the "post terminal" nerves of the last abdominal ganglion, the former supplying the muscles of the base of the ninth sternum and valvae and the latter the tegumen, the anellus, and the retradtor muscle of the penis.

Stitz, using the nomenclature of Buchanan-White described the genitalia of a series of Lepidoptera in a manner very similar to Cholodkovsky's treatment of Nematois. Of the species included as microlepidoptera, four were Tineoidea.

The work of Zander is probably the most important contribution to the morphology and ontogeny of the male genitalia of the Lepidoptera. He correlated the nomenclature of Buchanan-White and Gosse with the morphological units comprising the genitalia by comparing the adult structures in a large number of moths and butterflies and tracing their development in the larval and pupal stages of a more generalized species. His work on the Lepidoptera was preceeded by investigations of a similar nature on the Hymenoptera (1900), and Trichoptera (1901), and thru his conception of a common plan of structure for the genitalia in these orders he correctly interpreted the various modifications of identical parts without introducing a large and cumbersome nomenclature. In the Tineoidea seventeen species were examined, of which four were Micropterygidae, three Aculeata, and one Tineidae.

His investigation of the ontogeny consisted of a careful examination of the larval, prepupal, and pupal stages of a Tortricid moth, Parapoynx stratiatoria, based on the previous work of Peytoureau, Verson and Bisson (1896), and Klinkhardt (1900). By tracing the development thru each larval instar from the very first he improved upon the results of these investigators and recorded the following observations: The male genitalia are formed and develop in a pouch on the ventral side of the hind margin of the ninth somite formed in the first instar by an invaginating of the ectoderm of that region. This pouch was first observed in Pieris brassicae by Herold (1815) and later in Bombyx mori by Verson and Bisson. These authors regarded this pouch as a part of the intersegmental membrane between the ninth and tenth somites but Zander shows that it is actually a portion of the ninth sternum thru its relation to the underlying muscles. During the third instar this pouch enlarges into a flask shaped pocket and a pair of conical buds develop at the bottom. In the fourth instar these divide giving rise to a dorsal outer pair and a ventral inner pair. In the last instar the latter

unite to form the embryonic penis, and the former migrate to the caudal margin of the ninth sternum. At pupation with the disappearance of the genital pouch these outer buds lie at the surface in close connection with the ninth sternum and form the embryonic valves.

At this stage the penis is invaginated in a second depression which Zander calls the "penis pouch" and thru its deepening and the enlargement of the penis the anellus is formed. This Zander calls the "ring wall". During this stage in the pupal development the tenth somite which was suppressed at pupation by the telescoping of the last two abdominal segments of the larva develops a dorsal and ventral appendage, the uncus and the gnathos. These enlarge to form a hood above and below the anus. The lumen of the penis which was formed when the two inner buds united at the bottom of the genital pouch grows deeper as the penis lengthens, eventually ramifies the entire organ and is joined to the caudal end of the ejaculatory duct.

Shortly before the emergence of the adult the parts of the genitalia are chitinized, the deposit of chitin being most heavy on the tegumen, uncus, gnathos and vinculum. The ventral wall of the anellus is chitinized in some species thus forming the juxta, while in others the entire anellus becomes a chitinous cone. The base of the penis fuses with the portion of the pocket surrounding it and assumes a heavy coat of chitin leaving only the short connection to the ejaculatory duct and the extreme distal end membranous. After this the parts become covered with hair and scales and the genitalia assume the appearance of the definitive structures.

These results of Zander have made clear the significance of the parts of the genitalia and served as the basis for a uniform system of nomenclature suggested by McDunnough in 1911. This author recommended the adoption of a set of terms to be determined by the law of priority for

scientific names, a law which does not apply to morphological nomenclature. Consequently his terminology has not been adopted by all workers on Lepidoptera. It differs little from that of Pierce and in the following description of the parts comprising the genitalia I have included his terms whenever they were equivalent to those of Pierce.

Aside from descriptions of the morphology of the genitalia of the Lepidoptera in the literature on this order many references of value will be found in general literature on insect morphology and particularly in the contributions relating to the genital system. A discussion of such literature would be quite voluminous and aside from the purpose of this paper. However the contributions of Walker (1922), and Crampton (1918, '19, '20, '21, '22) are of particular interest because these authors have compared the male genitalia thruout all the lower insect orders up to and including the lower Lepidoptera. The nomenclature used by them is a compilation of the terms used by Berlese (1882, 1906, '09), Escherisch (1903, '04), Heymons (1895, '96, '99, 1912), Verhoeff (1903), Verson (1904), and others, and is compared with that adopted for the Lepidoptera in a subsequent table. Both of these authors have reached the conclusion of Zander regarding a fundamental plan of genitalia structure common to all insects. They have homologized the genital appendages very thoroly thruout the orthopteroid and neuropteroid insects and their allies and from this have deducted certain conclusions regarding their phylogeny. Such of these orders as show particular relationships to the Lepidoptera are discussed in a subsequent section of this paper.

Nomenclature

Reference has already been made to the contributions of Pierce, Busck, and Heinrich to the nomenclature of the male genitalia of the Lepidoptera. Altho Busck and Heinrich have not adopted all of the terms

which Pierce uses in his more recent descriptions of the Geometriidae and Tortricidae, or those suggested by McDunnough, the system which they have applied to North American Lepidoptera differs so little from those of Pierce and McDunnough that, in view of the fact that they have contributed more than have any other authors to our knowledge of these organs in the native species, it has seemed best to adopt their terms in this paper. In defining these terms in a subsequent section of our discussion we have pointed out the equivalent terms of Pierce and McDunnough.

The works of Walker and Crampton, previously mentioned, form the basis for the most recent comparison of the genitalia or orthopteroid and neuropteroid insects. The system of nomenclature used by them may be readily homologized with that of Busck and Heinrich and is used in the section of our discussion dealing with a comparison of the genitalia of the Orthoptera, Neuroptera and Lepidoptera. To make these terms readily comparable and to show their relation to the morphological units of the genitalia as determined by Zander the systems of Busck and Heinrich, Walker and Crampton, and Zander are tabulated below. The nomenclature originally applied by Walker and Crampton to the Orthoptera has been subjected to many changes by the latter author as his conception of the significance of these structures in the different insect orders became clearer. This has led to the correction of certain terms originally misused and the replacement of others by new ones which the author thought more applicable. There has resulted a cumbersome and poorly organized system from which I have selected only the most reliable terms for use in the comparative table and in the discussion of the orthopteroid and neuropteroid genitalia.

Comparative Table of Systems of Nomenclature used by Busck and Heinrich, Walker and Crampton, and Zander

Busck and Heinrich	Walker and Crampton	Zander
Tegumen	Ninth Tergite or Epiproct	Ninth Tergite (Rückenschuppe)
Uncus	Epiandrium or Epiproct(In part)	Dorsal appendage of the tenth somite; Uncus
Gnathos	Paraprocts?	Ventral appendage of the tenth somite; scaphium.
Socii	Surgonopods (Neuroptera, Mecoptera and Trichoptera·)	Lateral prolongations of the postsegmental margin of the ninth tergite; Anal appendages.
Vinculum	Ninth sternite; Hypandrium (when forming a plate); Coxasternum (in part)	Ninth sternite
Saccus	———	Medio-ventral projection of the ninth sternite; Saccus
Harpes	Gonapophyses, or Gonastyli*(in Orthoptera)	Appendages of the ninth sternite; Valvae
Transtilla	———	———
Anellus	Parameres (in part) Epiphallus?	Portion of penis pouch surrounding the penis where it enters the genitalia; Ring wall
Juxta	Pseudosternite?	Chitinized venter of the Ring Wall
Aedoeagus	Phallus, Penis or Aedeagus	Chitinized outer end of the penis
Penis	Ejaculatory Duct	Ductus Ejaculatorius

*Crampton regards the Harpes as the terminal portion, or Gonostyli, the coxites having fused with ninth sternum.

A Description of the Parts Comprising the Male Genitalia in Lepidoptera.

The following structures ordinarily comprise the male genitalia in Lepidoptera and can be recognized and homologized thruout the different families.

Somites: The abdomen of the Lepidoptera consists of ten distinct segments or somites each of which, with the exception of the tenth, possesses a distinct tergum and sternum. Ordinarily somites 1 - 8 undergo little modification. Occasionally the chitin of the terga and sterna of certain somites is interrupted by circular, membranous orifices, which are referred to as "fossae" in subsequent discussion. Sometimes the seventh and eighth sterna bear prominent hair pencils or tufts (Haartaschen, Poljanec, 1901), which are concealed in membranous pockets of the intersegmental membrane. Similar structures have been described on more anterior segments in the Sphingidae et al. In some Rhopalocera lateral processes arise from the posterior margin of the eighth sternite (Rami, Stickel, 1899), and the Bombycidae usually possess an armature of hooks and processes on this segment. In the Scythrididae, Gelechiidae et al. the eighth sternum and tergum are separated along their lateral margins and form a ventral and dorsal hood over the genitalia. In the Plutellidae the eighth sternum is divided on the median line and the lateral lobes thus formed surround the genitalia.

Genitalia: The genitalia proper include the highly modified ninth and tenth somites and are composed of the following parts:

Tegumen,(Buchanan-White, 1878)*: This term is applied to the tergal portion of the ninth somite which forms the dorsal part of the genitalia.

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* Buchanan-White's use of the term tegumen included both the tergum and sternum; later the sternum was called the saccus by Baker, and the vinculum by Pierce, so the term tegumen is now restricted to the tergum and is equivalent to the upper organ of Scudder and Burgess.

It articulates laterally with the ninth sternum, the suture frequently being solidly fused. The anus opens directly below the caudal margin of the tegumen and is largely concealed by it.

Tenth Somite: This somite is usually membranous and retracted but in the Micropterygidae and Adelidae Zander and Cholodkovsky have described the tergum as a small terminal sclerite separated from the ninth by a distinct suture. In such generalized forms the absence of the uncus allows a normal development of this usually suppressed somite. The anus opens at the terminal end of the somite and in most Lepidoptera where the segment is entirely membranous it is indistinguishable from the distal end of the anal tube.

Uncus, (Gosse, 1883): This and the following two parts constitute the anal armature and belong to the tenth somite; because of its retraction however they assume a superficial attachment to the tegumen. Zander has shown that when these processes are developed the tenth somite remains membranous thruout the entire development of the genitalia serving only as the base for their attachment. In shape the uncus is hook like, spoon shaped, clavate, emarginate, bifed or trifed; it is usually heavily chitinized. In the primative Lepidoptera it is often absent or reduced to a small hook which over arches the anus.

Socii, Pierce, 1914): These are paired organs, normally soft, membranous, and hairy, which arise from the tegumen on each side of the anus. They are absent in most of the primative Lepidoptera but occur almost invariably in the more specialized families.

Gnathos, (Pierce, 1914) = (Scaphium, Gosse, 1882): = (Subscaphium, Pierce 1909). This also is a paired organ which arises from the tegumen near the base of the uncus. When complete it consists of two lateral arms which surround the anus and a median ventral plate situated directly below the anus. It is subject to great modification, the ventral plate often being

reduced or absent. In many of the families treated in this discussion it is entirely missing.

Vinculum, (Pierce, 1909) = (Saccus, in part, Baker, 1891): This term is applied to the ninth sternite which usually takes the form of a ventral chitinous band articulating with the tegumen at its lateral margins. In the Micropterygidae and Eriocraniidae it differs little in width from the tegumen and is often solidly fused with it; in the Aculeate Tineoidea it is much longer than the tegumen, U or V-shaped and more heavily chitinized. The opposite tendency prevails in the higher groups where the vinculum is often reduced to a narrow transverse band which connects the bases of the harpes.

The anterior margin or apex of the vinculum is often produced anteriorly to form a medio-ventral chitinous sack which lies beneath the eighth sternite. The name "Saccus" was applied to this structure by Baker in 1891 and Pierce, 1914, in revising his terminology, applied it to the vinculum and saccus combined. Since Baker's original use of the term "Saccus" applied to the invagination rather than to the entire ninth sternum we prefer to adopt McDunnough's suggestion and apply the term vinculum to the entire ninth sternum whether or not its margin is produced to form a saccus. The saccus occurs in most of the Tineidae and nearly allied microlepidoptera as well as in many Bombycoidea and Rhopalocera.

Harpes, (Smith, 1890) = (Valvae, Burmeister, 1832): These are paired clasping organs which articulate to the posterior margin of the vinculum. Often too their bases are closely associated with the juxta and in many Hepialidae are articulated to it. In most primative Lepidoptera the harpes are symmetrical, altho there are frequent exceptions. They are normally triangular, finger like, or spoon shaped. In many families, especially among the higher Lepidoptera, the harpes are divided into three distinct

lobes or areas, a dorsal, apical and ventral, called by Pierce the costa, valvula or cucullus, and sacculus. In the Noctuidae, et. al. the sacculus and costa frequently develop appendages or processes which become so widely separated from the remainder of the harpe that they have been described as separate structures. The "clasper" of Smith and the "ampulla" of Pierce come under this class but because such modifications occur so rarely in primative forms need not be extensively discussed in this paper. Occasionally the harpes are greatly reduced and fused with the vinculum so closely that they are practically functionless as claspers, e.g. Eriocraniidae.

Reference has already been made to the investigations of Zander on the development of the harpes in which he showed that they are appendages of the ninth sternum which arise from the lateral buds of the genital pouch and during pupal development, migrate to the periphery, and become attached to the ninth sternum.

Transtilla, (Pierce, 1914): In most Lepidoptera this structure occurs in the form of a chitinized band or bridge which connects the inner costal angles of the harpes passing just below the gnathos and behind the aedoeagus. Sometimes it is lobed and ornamented with spines.

The above parts have been called by Pierce the "external part" of the genitalia and constitute the accessory armature. The following structures are called the "internal part" and comprise the intromittant organ and its armature.

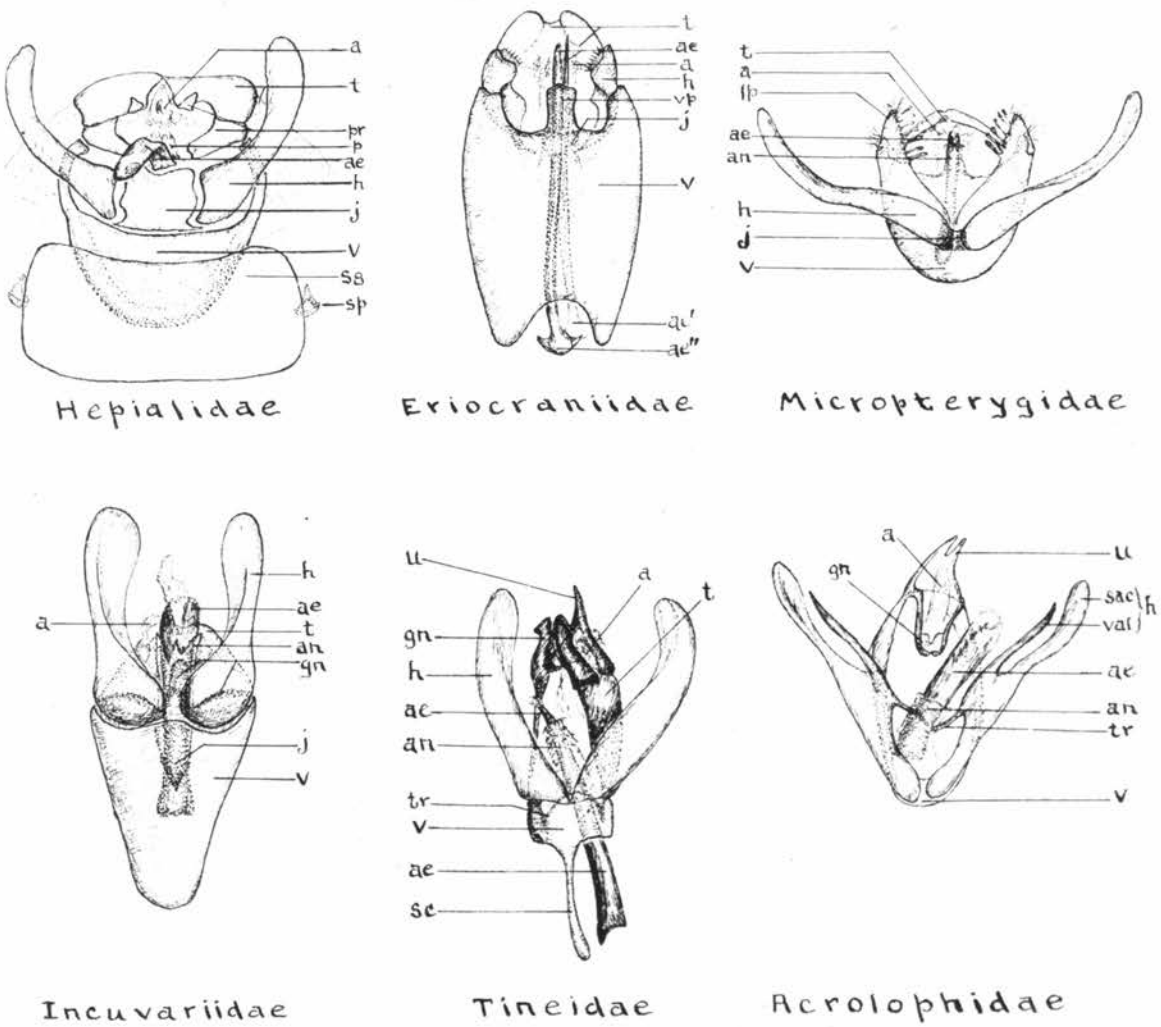
Anellus and Juxta, (Pierce, 1914): The anellus is the cone like tube thru which the penis enters the ninth somite. It is usually membranous, often covered with spines and bears a triangular or quadrate plate, the juxta, on its ventral surface. The lateral margins of the juxta may be produced to form hairy lobes or the central portion elongated into a process which supports the aedoeagus. Occasionally the entire anellus is chitinized forming a funnel or perforated plate thru which the aedoeagus protrudes.

Aedoeagus, (Pierce, 1909): This structure ordinarily consists of a chitinous tube which enters the ninth somite thru the anellus and is supported by it and the juxta. It is heavily chitinized, frequently armed with spines and serrations and has the posterior end inflated to form a blind pouch in which are lodged the retractor muscles of thepenis. Zander has shown that the aedoeagus is the chitinized terminal portion of the penis and its bulbous base is formed from the modification of the penis pouch. In the Hepialidae the aedoeagus occurs as a flat plate and the membranous penis passes behind it and opens at its caudal margin.

Penis, (Busck and Heinrich, 1921) = (Ductus ejaculatorius, (Pierce,1914): This term applies to the terminal portion of the ejaculatory duct which lies within the aedoeagus. It is a soft eversible tube which may be projected by blood pressure beyond the tip of the aedoeagus and serves to introduce the sperms into the bursa copulatrix of the female. This eversible tip is called the "vesica", Pierce, 1914, and is often armed with spines or clusters of spines called "cornuti".

The accompanying text figures illustrate the arrangement of the above described structures in the most common types of genitalia which occur in the primitive Lepidoptera.

Figure I.



Ventral views of the Male Genitalia of Primitive Lepidoptera, illustrating homologies and the arrangement of parts. (semi-diagramatic).

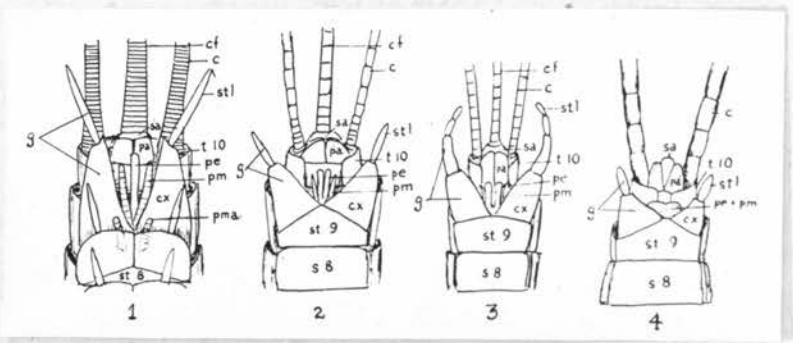
a - anus
ae - aedoegus
ae' - dorsal wall of aedoegus
ae'' - ventral wall of aedoegus
an - anellus
gn - gnathos
h - harpe
j - juxta
lp - lateral process of tegumen
p - penis
pr - caudal process of tegumen
sg - eighth sternum
sac - sacculus
sc - saccus
sp - spiracle
t - tegumen
tr - transtilla
u - uncus
v - vinculum
val - valvula or cucullus
vp - median process of vinculum.

A COMPARISON OF THE LEPIDOPTEROUS TYPE OF MALE GENITALIA WITH THOSE FOUND IN INSECTS OF NEARLY RELATED ORDERS

In this discussion we wish to show that the type of male genitalia which prevails in the Lepidoptera is to be found in a somewhat modified condition in those insects most nearly related to them i.e. the Trichoptera, Neuroptera and Mecoptera. The plan of structure in this type has its origin in the most primative insect forms and has been traced by Walker and Crampton in its various modifications thru the Thysanura, Ephemerida, and Orthoptera. As certain of these forms are in the direct line of development toward the type found in Lepidoptera they will be discussed in detail under the various insect orders in which they occur.

Thysanura and Ephemerida.

Figure II



Ventral views of male genitalia of Thysanura, Ephemerida and Orthoptera (after Walker).

1 - Machilis
2 - Hypothetical primative type
3 - Ephemerid
4 - Gryloblatta nymph.

Abbreviations:

c - cercus
cf - caudal filament or telofilum
cx - coxite of 9th sternite
cx_g - coxite of 8th sternite
g - gonopophysis, which is composed of cx, the coxite and stl, the stylus
pa - paraproct
pe - penis
pm - posterior paramere or its main process
pma - anterior paramere
sa - supra - anal plate
stl - stylus
s_g - 8th sternite
s_9 - 9th sternite
t_9 - 9th tergite
t_{10} - 10th tergite

The genitalia of these two orders may be conveniently discussed together because they possess many points in common and furnish a generalized, basic, type of genitalia from which may be derived the types found in the other insect orders. In the Thysanura as illustrated by Machilis, (Text fig. II, 1) the ninth sternum is quite small and completely hidden by the coxites of the eighth. It bears two large coxites each with a terminal stylus. These are homologous with the coxites and styli of the Ephemerida, (Text fig. II, 3), and with the harpes of the Lepidoptera and the gonopophyses of related orders. In the Ephemerida the coxites possess two or three segmented styli which become clasper-like just as do the gonopophyses of the higher insects, and develop prominent basal muscles for their manipulation.

In certain species of the genus Heptagenia, i.e. flavescens Wlsh., and tripunctata Banks., the ninth sternum is slightly produced between the coxites and suggests a ventral plate or "hypandrium" which is characteristic of many Orthoptera, Neuroptera and Mecoptera.

In both orders the ninth tergum is an unmodified transverse sclerite rounded laterally and articulating with the pleura.

In the Thysanura the tenth somite is well developed and bears three caudal appendages, the two lateral ones, the cerci, and a central one, the telofilum or cerciform appendage. The anus opens beneath these. Crampton, (1921), in homologizing these structures with the terminal appendages of Isopod Crustacea, considers the basal segment of the telofilum as homologous with the eleventh somite, the remaining segments as the telson, and the cerci and their basal plates, the paraprocts, as the vestiges of a pair of biramous limbs in which the protopodite is represented by the paraproct, the endopodite by the cercus, and the exopodite is lost. Wheeler's work on the embryonic development of Xiphidium, (1893), also supports the view that the cerci and their basal plates represent the eleventh somite, and its appendages. The same arrangement of the tenth and eleventh somites

obtains in the Ephemerida. In this order however there is a median shelf-like structure suspended beneath the anus. Walker has homologized this with the subanal vomer of the Phasmidae and it resembles very closely the gnathos of Lepidoptera and similar subanal structures of the Neuroptera and Trichoptera.

The penis of the Thysanura is a single, median, membranous or lightly chitinized, tube reenforced laterally by a pair of chitinous processes, the parameres. In the Ephemerida these parts are fused forming a median, membranous structure which possesses two efferent ducts. Walker considers this type as the more primative of the two and believes that the generalized insect ancestor possessed two penes each with a separate ejaculatory duct just as the females of certain Thysanura still retain double genital apertures.

From this brief survey of the genitalia of these two orders it will be seen that they are constructed along the same general plan and that the Ephemerida, altho retaining a more primative type of penis, tends to develop a large ninth somite provided with forcep-like coxites and styli thus forshadowing the clasping type of genitalia which characterizes the Lepidoptera and its near relatives.

Species examined: Machilis sp.
Heptagenia flavescens Wlsh.
Heptagenia tripunctata Banks.
Heptagenia interpunctata Say.
Callibaetis ferruginea Wlsh.
Hexagenia bilineata Say.
Blasturus cupidus Say.

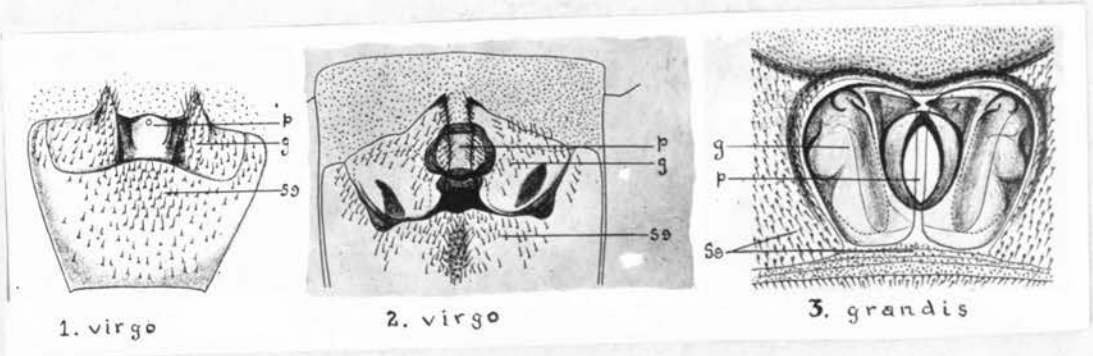
Orthoptera

Close resemblances to the type of genitalia just described for the Ephemerida are found only in a very generalized Orthoptera. Walker (1914 and '19), has described such a form in Grylloblatta campodeiformis Walk.

(Text fig. I, 4) from Australia and has given the development of the male genitalia particular attention. It resembles the clasping type of genitalia as described for the Ephemerida in the following respects. The ninth sternum bears on its posterior margin a pair of coxites each with a terminal stylus. Altho unsymmetrical in the adult, these are almost alike in the nymph and are movably articulated to the sternum. They possess prominent basal muscles which Walker believes enables them to function as claspers, thus resembling gonopophyses. The tenth somite and the penis are much the same as in the Ephemerida and need not be discussed except to state that the latter is composed of two papillae with a single, central, ejaculatory duct. In the remainder of the Orthoptera the coxites are suppressed or fused with the ninth sternum, the penis is complicated and unsymmetrical and the entire genitalia depart greatly from the simple type of Grylloblatta.

Plecoptera and Odonata

Figure III.



Ventral views of the male genitalia of Odonata (after Van der Weele)
1 - Colopteryx virgo L., nymph. 3. Aeschna grandis L., adult
2 - Colopteryx virgo L., adult.

Abbreviations:
g - gonopophysis
p - opening of the ejaculatory duct or homologue of penis in other insects.
s_9 - 9th sternite.

The adults of these orders bear little resemblance to the generalized genitalia just described because the ninth and tenth somites retain the ring-like structure of the preceeding somites and coxites and styli are not developed. The nymphs of the Odonata (Text fig. III, 1) however, bear small appendages on the caudal margin of the ninth somite which Van der Weel, (1906), has homologized with the gonopophyses of the higher insects. In the adult (Text fig. III, 2 and 3) these are greatly reduced and form small plates on each side of the opening of the ejaculatory duct, and the large appendages developed on the tenth somite which are usually called gonopophyses in the taxonomic literature are not in any sense homologous with the true gonopods of higher insects.

Neuroptera

The male genitalia of this group show such a wide diversity of structure that it is difficult to select a series of forms which will illustrate the transition from the generalized genitalia of the Ephemerida and Grylloblattoidea to the more specialized types which are characteristic of the Mecoptera, Trichoptera and Lepidoptera. By selecting the more generalized representatives of each of the natural subdivisions of the order and discussing in detail each structure comprising the genitalia, rather than the complex, some idea can be obtained of the extremely synthetic nature of the genitalia in this order and of the generalized type from which so large a number of diverse forms has been derived.

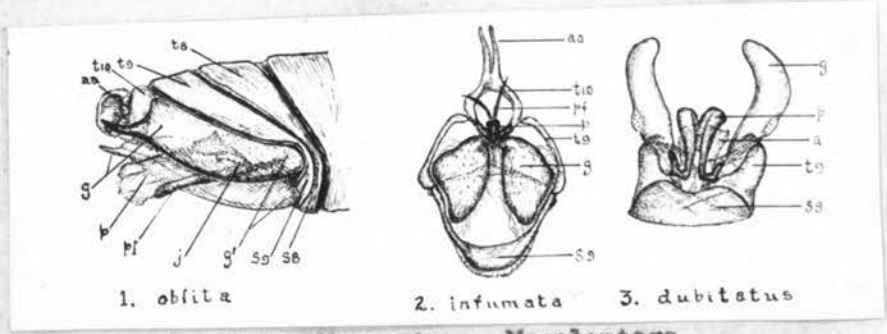
Crampton has discussed in detail the morphology of the genitalia of the Neuroptera and homologized the parts with those of the Mecoptera, Trichoptera, and Lepidoptera. His conclusions regarding the homologies are in the main correct but unfortunately he has not examined the more primative members of many of the groups and has failed to gain a conception of the

true significance of many of the structures which he figures. He has also apparently ignored the excellent figures which Van der Weele, (1910), and Ebsen-Peterson,(1913, '21), give in their revisions of the Megaloptera and Mecoptera which furnish the various steps in the lines of genitalia specialization occuring in these groups.

For convenience the general characters of the genitalia of the Neuroptera are outlined below while their special morphology is discussed under the various families into which the order is divided.

General characters: Ninth sternum enlarged and produced to form a ventral plate or so called hypandrium beneath the genitalia, thus crowding the gonopophyses dorsad so that they are often closely associated with the anus. The penis is either a membranous papilla thru which the ejaculatory duct opens, a pair of papillae with the opening between them, or a chitinous plate or process with the duct opening at its base. The simple papilla type resembles that in the Ephemerida and Grylloblatoidea, while the plate and process types are closely analogous to that of the Jugate Lepidoptera except that in the latter the duct opens at the posterior margin of the plate. In none of the Neuroptera do we find a hollow, tube-like penis such as is characteristic of the Trichoptera and most Lepidoptera. In the following discussion of the special morphology the family divisions of Van der Weele are used for the Megaloptera, and those of Ebsen-Peterson (1906), for the Neuroptera Planipennia.

Figure IV.



Male genitalia of the Neuroptera, Megaloptera.
1- Raphidia oblita Hag., right side. 3- Archichauliodes.
2- Sialis infumata Newm., venter.

Abbreviations:
a - anus
aa - anal appendages
g'- base of gonopophysis
g - gonopophyses
j - armature of base of penis
p - penis
pf - filamentous process of penis
pl - ventral plate of penis
sg - 8th sternite
s9 - 9th sternite
t9 - 9th tergite
t_{10}- 10th tergite

Megaloptera: There is no clear cut series of genitalia characters which will distinguish this group from the Planipennia. The more generalized tendencies seem confined to the Sialidae and Raphididae of the Megaloptera, while the specialized ones occurring in the other families simply are carried further in the Planipennia.

Raphididae: (Text fig. IV, 1). The genitalia of this family are the most generalized of the Neuroptera and forshadow many of the characters occuring in the Trichoptera and Lepidoptera. The ninth sternum is not produced to form a hypandrium but is emarginate and bears a pair of large gonopophyses on its posterior margin; these are ventral in position thus differing from the gonopods of most Neuroptera which tend to become dorsal. The gonopophyses are entire, (R. oblita Hag.), or emarginate or deeply cleft, (R. xanthostigma Rostock). The penis is either an elongate, membranous papilla chitinized on the venter,(R. oblita), or an irregular papilla with several fleshy protuberances, (R. xanthostigma). The ventral chitinization in R. oblita is basally connected with the gonopophyses and suggests the juxta of Lepidoptera. This type of penis is the closest approach in the Neuroptera to the chitinized tube of the Trichoptera and Lepidoptera. The tergum of the ninth somite is transverse and unmodified; the tenth and eleventh somites are represented by a dorsal plate which over arches the anus and bears a pair of short unsegmented processes, possibly the rudimentary cerci. Species examined: R. xanthostigma Rostock, R. oblita Hag.

Sialidae: (Text fig. IV, 2). The genitalia of this family are less generalized than those of the preceding but several features suggest close homology with the Raphididae and with the Lepidoptera. The ninth sternum is slightly produced and forms a short hypandrium thus forcing the gonopophyses dorsad so that they are lateral in position and articulate with the pleural region of the somite. They are triangular or quadrate in shape and suggest the harpes of the Aculeate Lepidoptera, i.e. Adela or Nepticula. The penis

consists of a pair of fused chitinous plates often bearing terminal spines, or a pair of papillae. The tenth and eleventh terga are indistinguishably fused and terminate in a pair of processes. In the European species of Sialis these are short, recurved, and heavily chitinized and resemble a bifed uncus.

Species examined: Sialis infumata Newm.
Sialis lutaria L.

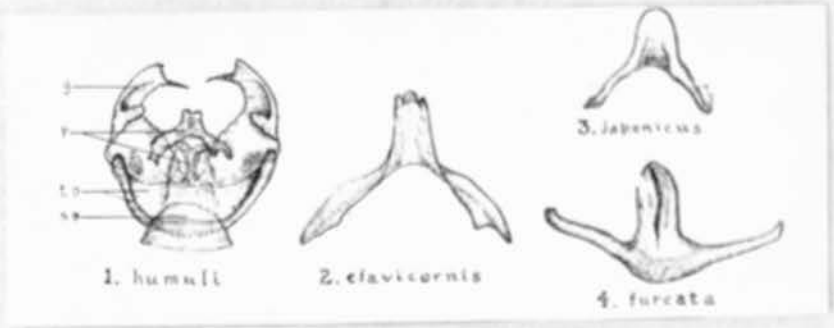
Corydalidae: The remaining Megaloptera are grouped in this family under two tribes, the Neurotomini and the Chauliodini, the first characterized by a longitudinal dividing of the gonopophyses into a dorsal and ventral portion which gives them the appearance of two separate pairs of gonopophyses and the second by the reduction and dorsal migration of the gonopophyses so that they appear as small plates closely associated with the anus. Most of the species of this family have been figured by Van der Weele and Crampton and need not be described. Archichauliodes, (Text fig. IV, 3), is the most generalized member of the family having undivided gonopophyses which are large and clasper-like, a small ninth sternum, and a penis consisting of two chitinized processes with a single ejaculatory opening between them.

Species examined: Archichauliodes dubitatus Walk.
Parachauliodes japonicus McLach.
Chauliodes pectinicornis L.
Nigronia serricornis Say.
Hermes maculipennis Gray.
Chloronia hieroglyphica Rambur.
Corydalus cornutus L.

Neuroptera Planipennia: The male genitalia of this group closely resemble the types found in the Neurotomini and the Chauliodini. The Mantispidae, Ascalaphidae and Myrmeleonidae are further specializations of the type found in Corydalis of the Neurotomini, the Hemerobiidae may be derived from Archichauliodes, the Nemopteridae are modified Hemerobiids with Drepanepteryx as an intermediate form, and the Coniopterygidae are also close Hemerobiid relatives from the viewpoint of genitalia structure. Of

these families the Hemerobiidae (Text fig. V, 1), represent the most generalized type. The penis of all the Planipennia and some Megaloptera (Parachauliodes) superficially resembles that of the Hepialid Lepidoptera and a series of these are figured for comparison. (Text fig. V, 2,3,and 4).

Figure V.



Male genitalia and penis of Neuroptera, Planipennia and Megaloptera.
1 - Hemerobius humuli Linn., venter. 3 - Parachauliodes japonicus, McLach, penis.
2 - Tomatares clavicornis Hag. penis. 4 - Albardia furcata Van der Weele, penis.

Abbreviations:
g - gonopophysis
p - penis
sg - 9th sternite
tg - 9th tergite.

Species examined:

Mantispidae
(Mantispa interrupta Say
(Mantispa formosana
(Climaciela brunnea Say

Ascalophidae
(Albardia furcata Weele
(Caloboterus versicolor Burm.
(Acheron trux Wlk
(Hybris javana Burm.
(Hybris subjacens Wlk.
(Deleproctophylla australis Fab.

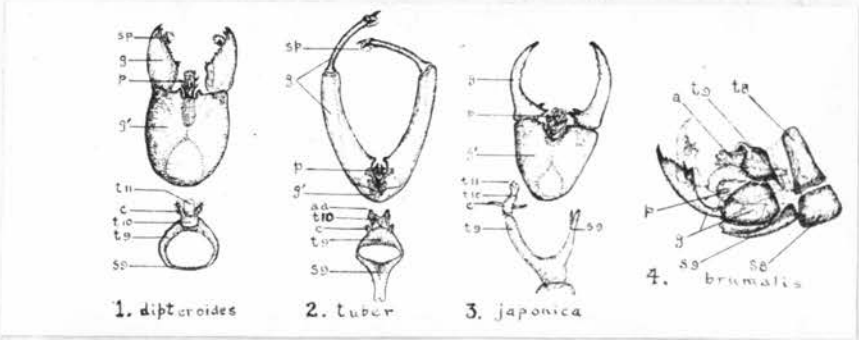
Myrmeleonidae
(Tomatares clavicornis
(Ochanthachsis distincta
(Palpares caffer Burm.
(Myrmelon sp.

Hemerobiidae
(Micromus timidus Hag.
(Micromus angulatus Stph.
(Micromus posticus Wlk.
(Boriomyia concinnus
(Boriomyia subnebulosus Stph.
(Hemerobius humuli L.
(Hemerobius micans Ol.
(Hemerobius strigosus Zh.
(Hemerobius stigmaticus Fh.
(Polystoechotes punctatus Fab.
(Drepanopteryx phalaenoides L.

Osmylidae	(Climacia areolaris Hag.
	(Sisyra vicaria Wlk.
	(Sisyra fuscata F.
	(Osmylus maculatus F.
	multipunctatus Ml.
	tuberculatus
Chrysopidae	(Leucochrysa vania Schd.
	(Ankylopteryx 8-punctata F.
	(Ankylopteryx borneensis Weele.
Coniopterygidae	(Coniopteryx psociformis

Mecoptera

Figure VI.



Male genitalia of the Mecoptera (views ventral unless otherwise specified)
1 - Nannochorista dipteroides Till.
2 - Merope tuber Newm.
3 - Panorpa japonica Thunb.
4 - Boreus brumalis Ftch. right side.

Abbreviations:

a - anus	t_8 - 8th sterna
aa - anal appendages	s_9 - 9th sterna
c - cercus	t_8 - 8th terga
g - gonopophysis	t_9 - 9th terga
g' - fused bases of gonophyses	t_{10} - 10th terga
p - penis	t_{11} - 11th terga
sp - sense organ	

With the exception of one family, the Bittacidae, the male genitalia of the members of this order present many interesting structural characters in common with the Trichoptera and primative Lepidoptera and form a connecting series between them and the Ephemerida and lower Neuroptera. The general characteristics of the genitalia of the order are as follows: Abdomen with ten well developed somites, the tenth bearing a pair of cerci; ninth sternum usually produced caudad to form a hypandrium; gonophyses two jointed, the basal joints resembling the coxites of the

Ephemerida and Grylloblattoidea and the unsegmented distal joint, the styli. The ninth sternum and the coxites are often fused to form a vinculum-like structure which surrounds the penis which is a chitinized or membranous tube often armed with spines or processes. The special morphology will be discussed under the various families which Ebsen-Peterson, (1921), uses in his revision of the order, with the addition of the Nannachoristidae which, following Tillyard's (1919) suggestion is elevated to family rank.

Meropidae: (Text fig. VI, 2). The genitalia of this family are the most generalized of the order. The ninth sternum is slightly produced forming a small hypandrium; the tergum is large and transverse and bears a pair of small processes called the dorsivalvae. The tenth tergum is folded under these and bears the one jointed cerci. The gonopophyses are very long and the terminal joint is toothed at the apex and bears a small sense organ in the notch. These joints articulate with the basal joints so that their movement is toward the meson and at right angles to them. The basal joints are fused proximally on the ventral line forming a small U-shaped structure beneath the penis. The penis is short, heavily chitinized, and consists of a pair of basal processes which are fused with the gonopophyses and four distal processes or spines which project caudally between the gonopods. Species examined: Merope tuber, Newm.

Boreidae: (Text fig. VI, 4). The genitalia of this family differ from those of the preceding in the following respects: the hypandrium is larger; the dorsa-valvae are absent; the tenth somite is represented by the anus and the cerci by small tubercles associated with it; the gonopophyses are shorter with the basal joint heavier and the distal joints fold dorsad so that they lie above the basal ones. Their apices are serrate and the sense organ is rudimentary. Their fused bases are narrow and U-shaped. The penis is membranous and hangs free between the gonopophyses.

Species examined: Boreus brumalis L.

Nannochoristidae: The genitalia of this family are a modification of the type described in Merope and resemble in many respects the genitalia of the Jugofrenate and Aculeate Lepidoptera. The ninth sternum is narrow, transverse, and is not produced into a hypandrium. The tenth and eleventh terga are small rectangular sclerites, the latter of which bears a pair of two jointed cerci. The gonopophyses are very large and the basal joints are entirely fused and form a U-shaped structure very similar to but obviously not homologous with the vinculum in the Aculeate Tineoidea. The distal joints are short, triangular, with a serrate inner margin which bears a sense organ composed of a cup-shaped base and a membranous bulb-like apex. In shape, these closely resemble the harpes of the Aculeate Tineoidea. The penis consists of a short, heavily chitinized aedoeagus, terminated with spines and a membranous eversible tip, and is fused with the basal joints of the gonopophyses.

Species examined: Nannochorista dipteroides Till.

Panorpidae: The genitalia of this family (Text fig. VI, 3), so closely resemble those of the Nannochoristidae that it is unnecessary to describe them in detail. The figure of Panorpa japonica Thunb. will serve to bring out the morphological features of the group.

Species examined: Panorpa japonica Thunb.
Panorpodes carolinensis
Panorpa sp. (N.A.)

Bittacidae: The genitalia of this family resemble those of the Nematocerous Diptera more closely than any of the Lepidoptera and need not be discussed in this paper.

Trichoptera

Altho the male genitalia of the various families comprising this order are quite diverse, the more generalized families show close structural affinity with those of the Mecoptera and Lepidoptera. In their resemblance to the Lepidoptera it is often difficult to distinguish between superficial

similiarities and those which are of actual phylogenetic value. Consequently only the more generalized members have been selected for detailed comparison with the primitive Lepidoptera and only brief reference is made to the specialized tendencies of the higher families.

The comparative morphology within the order has been exhaustively treated by Zander, (1901), and Klapalek,(1904), and the anatomy of the internal genital system of the male by Stitz, (1904), and Cholodkovsky (1913). The contribution of Zander and Cholodkovsky are of especial interest because they have included in their comparisons references to similarities between the Trichoptera and Lepidoptera.

Zander divided the Trichoptera into two well-separated groups which can be distinguished by the structure of their genitalia. The first of these included the family Limnophilidae and was characterized by a funnel shaped chitinized penis pouch, a membranous retractile penis, terminating in long processes or filaments, small gonopophyses or valvae, and very large anal appendages. The second group which included the remaining families possess an opposite set of characters, i.e. a membranous penis sheath, a penis of which at least the base is chitinous, large valvae, and small or moderabely large anal appendages. The genitalia of the Lepidoptera resemble this second group in the following respects: penis pouch membranous, penis chitinized, with the exception of the Hepialidae and Prototheoridae, gonopophyses (harpes or valves) large, and anal appendages, (socii), small. Both orders offer some few exceptions to this set of characters but they hold for the majority of the families. In addition to the above there is a tendency in both orders for the development of a dorsal and a ventral appendage of the ninth somite which as already mentioned are named the uncus and gnathos in the Lepidoptera.

Aside from describing the adult structures Zander worked out their pre-pupal and pupal development and in his later paper (1903), has compared the manner

of development of the various parts in the two orders. His general summary of this phase of his work is as follows: The prepupal development of the genitalia in the Trichoptera is parallel to that of the Lepidoptera with respect to the formation of a genital pouch, the primary differentiation of the penis and harpes, and the migration of the latter to the caudal margin of the ninth sternum. The pupal development of the two is quite different especially with respect to the penis. This structure is developed in a penis pouch, as in the Lepidoptera, but the pouch does not become deeply invaginated and the base of the penis remains linear, and receives the ejaculatory duct at the termen instead of some distance from it.

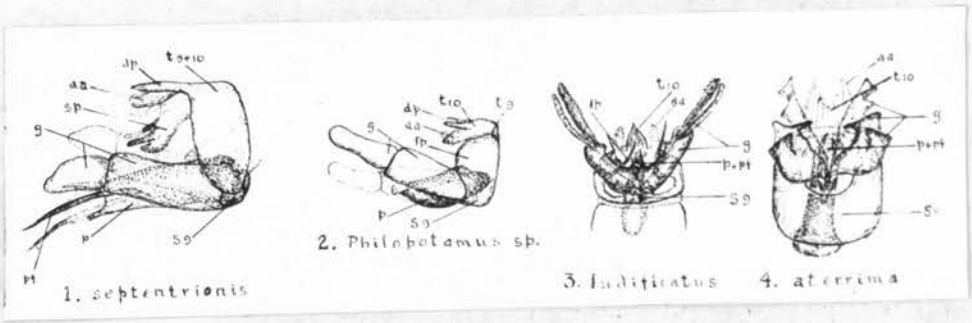
Cholodkovsky described the structure of the testes, vasa deferentia and accessory glands in the more important families of the Trichoptera and found, as he had already described for the Lepidoptera, (1884), four distinct types of testes which he named the embryonic, the larval, the pupal, and the definitive, according to their degree of specialization. The first two types he found present in the more generalized Trichoptera and the primative Lepidoptera, i.e. Hepialidae and Tineoidea, while the two latter more specialized types occured only in the higher families of both orders. The direct comparisons which he made between certain families will be included in the subsequent discussion.

The general morphology of the external genitalia of the order has been already mentioned in the discussion of the work of Zander. The following additional features noted in our own study should be added before proceeding to the special morphology of the different families. The tergum and sternum of the ninth somite are usually fused to form a solid ring, or the sternum is separated from the fused terga and pleura, and the two structures thus formed are comparable to the tegumen and vinculum of the Lepidoptera. The gonopophyses are one or two jointed but the basal joints

are never fused together as in the Mecoptera. Occasionally the terminal joint consists of two pieces which articulated side by side to the termen of the basal joint. The penis in all the families except the Limnophilidae consists of a chitinized tube containing the terminal portion of the ejaculatory duct and is quite similiar to the aedoeagus of the Lepidoptera. It is armed with spines, filaments or serrations in much the same manner. A chitinized plate resembling the juxta of Lepidoptera often supports the penis on the ventral surface, and in some instances the bases of the gonopophyses are attached to it.

In the subsequent discussion of the special morphology the conception and arrangement of the families according to Ulmer, (1907), has been adopted, along with certain suggestions offered by Dr. Cornelius Betten, (in literature).

Figure VII



Male genitalia of the Trichoptera: Rhyacophilidae and Philopotamidae.
1 - Rhyacophila septentrionis McLach., right side.
2 - Philopotamus sp., right side.
3 - Philopotamus ludificatus McLach., venter;
4 - Chimarrha aterrima Hag., venter.

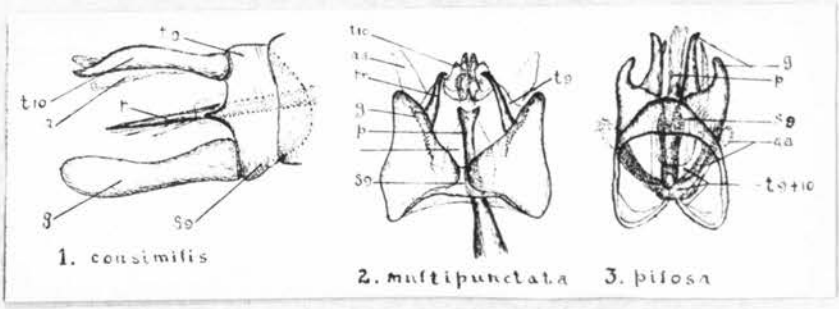
Abbreviations:
aa - anal appendages
dp - dorsal process of 10th tergite or fused 9th and 10th terga.
g - gonopophysis
lp - lateral lobe and process of 9th tergite
p - penis
pf - filamentous process of penis.
s_9 - 9th sternite
sp - subanal plate or process, i.e. homologue of gnathos in Lepidoptera.
t_9 - 9th tergite
t_{10} - 10th tergite.

Rhyacophilidae and Philopotamidae: (Text fig. VII, 1, 2, 3, and 4). The male genitalia of these two families are quite similar and represent one of the most generalized types in the order. The ninth sternum is either narrow and transverse as in Rhyacophila (VII, 1), or rectangular or U-shaped forming a distinct vinculum as in Philopotamus (VII, 2 and 3), and Chimharra (VII, 4), and in these has a close resemblance to the vinculum of the Micropterygid Lepidoptera. The ninth tergum forms a broad dorsal arch and is fused on the median line with the tenth tergum. In Philopotamus the lateral margins are produced and form lobes similar to the lateral lobes of the tegumen in the Micropterygidae, altho they lack spines and setae with which the latter are armed. The tenth somite is rudimentary and closely associated with the anus. In Rhyacophila and Philopotamus it bears a median simple or bifed process and two lateral appendages, the anal appendages of Zander, which, as already stated, may be homologized with the uncus and socii of the Lepidoptera. In Chimharra the entire anus is chitinized and only the anal appendages are present. In some species the tenth somite has a ventral appendage resembling the gnathos. The gonopophyses consist of one or two joints articulated to the medio-ventral portion of the ninth sternum. In most species they are joined together at the basal angles by membrane or a small chitinized bridge, in this respect resembling the harpes of the Micropterygidae. In no case however are the entire basal segments fused to form a V-shaped structure as in the Mecoptera but rather a vinculum, when present, is formed by the enlargement of the ninth sternum as in the Lepidoptera. The terminal portion of the gonopophysis is often emarginate, completely divided, or armed with spines and processes. All of these tendencies are characteristic of the harpes of the Lepidoptera. The penis is usually large and with the basal portion chitinized. The termen is either entirely membranous and eversible, with or without spines, or it is divided into a dorsal and ventral plate and

two lateral processes which surround a membranous central portion, i. e. the end of the ejaculatory duct. The ejaculatory duct enters the apex of the base of the penis except in a few species of Philopotamus where the base is bulb-like and the duct enters on the dorsum.

Species examined: Rhyacophila septentrionis McLach.
Rhyacophila sp. (two N.A. species from the collection of Dr. Betten).
Glossosoma sp.
Philopotamus ludificatus McLach.
Chimharra aterrima Hag.

Figure VIII.



Male genitalia of the Trichoptera: Hydroptilidae and Sericostomatidae.
1 - Hydroptila consimilis Mort., right side.
2 - Agrayles multipunctata Cart., venter.
3 - Goera pilosa Fab., venter.

Abbreviations:
a - arms
aa - anal appendages
g - gonopophysis
j - basal armature of penis, i.e. homologue of juxta in Lepidoptera.
p - penis
pr - process of fused lateral margin of 9th somite and gonopophysis.
s_9 - 9th sternite
t_9 - 9th tergite
t_{10} - 10th tergite

Hydroptilidae: (Text fig. VIII, 1 and 2). The genitalia of this family resemble those of the two preceding but are smaller, with the parts more closely fused, and frequently without gonopophyses. The ninth somite is highly chitinized, the sternum forms a quadrate vinculum, and the ninth and tenth terga are fused to form a hood-like tegumen. The anal appendages and the median dorsal process (uncus), are usually present but quite small. In Agrayles multipunctata Curt. the caudal margin of the tenth tergum forms

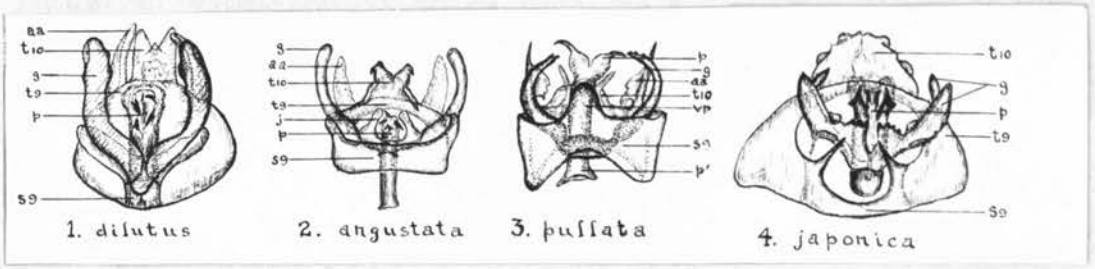
two large lobes one on each side of the median process and closely resembles the caudal margin of the tegumen in the Eriocraniidae. The gonopophyses when present are one jointed, but in many species they are absent or indistinguishably fused with the ninth sternum. A similar reduction and fusion of the gonopophyses occurs in the Eriocraniidae. The penis is heavily chitinized, usually with an enlarged basal portion and the apex is armed with one or more spines. A type of penis very similar to this occurs in many of the Micropterygidae, Eriocraniidae and Aculeate Tineoidea. From the preceding comparison it will be seen that the Hydroptilidae and Eriocraniidae present an interesting case of structural parallelism which is in reality of phylogenetic significance. Both families have arisen thru the most primitive groups of their respective orders, have become highly specialized thru reduction, and have produced as the end product very similar types of genitalia.

Species examined: Agraylea multipunctata Curt.
Hydroptila consimilis Mort.
Hydroptila hamata Mort.

The genitalia of the Hydroptilidae, Polycentropidae, and Psychomyidae are quite similar and appear to be modifications of the type described for the Rhyacophilidae and Philopotamidae. The Calamadoceratidae and Odontoceridae also come under this class but are even more greatly modified with respect to the penis and the tenth tergite. None of these modifications have any significance in relation to the Lepidoptera and need not be included in this discussion.

Species examined: Macronema hyalinatum Pictet.
Hydropsyche sp.
Polycentropus sp.)
Psychomyia sp.) N.A. species from collection of
Ganonema sp.) Dr. Betten.
Odontocerus sp.

Figure IX.



Male genitalia of the Trichoptera: Leptoceridae, Molannidae, and Phryganeidae (all views ventral).

1 - Leptocerus dilutus Hag., 3 - Berea pullata Curt.,
2 - Molanna angustata Curt. 4 - Phrygonea japonica McLach.

Abbreviations:

aa - anal appendages
g - gonopophysis
j - basal armature of the penis, i.e. homologue of the anellus and juxta of the Lepidoptera.
p - penis
p'- base of penis
s_9- 9th sternite
t_9- 9th tergite
t_{10} 10th tergite
vp - median process of the 9th sternum

Molannidae and Leptoceridae: (Text fig. IX, 1, 2, and 3). The genitalia of these families are quite different from those of the preceding families and present a type of structure which presents many features in common with the Hepialidae, Prototheoridae, and Mnesarchaeidae of the Lepidoptera. The ninth sternum usually forms a broad, U-shaped vinculum; the juxta, when present, is contiguous to its caudal margin andoften fused with it, and the one jointed gonopophyses articulate to its lateral margins or on the meso-ventral portion of the vinculum when the juxta is absent, thus duplicating the manner of articulation of the Harpes in the Hepialidae and Mnesarchaeidae. In Berasa, (Text fig. IX, 3), one of the Molannidae, the ventral margins of the vinculum bears a median process which resembles a similar structure in the Eriocraniidae. The ninth and tenth terga are fused and form the tegumen. In Leptocerus (Text fig. IX, 1), this is produced caudally and forms several lobes which resemble similar tegumen structures in the Eriocraniidae. The

two lateral ones are probably the anal appendages. In the Molannidae, the anal appendages are more laterally placed thus resembling the tegumen of the Mnesarchaeidae, while the median portion forms a bifed uncus, a structure which does not occur in the Lepidoptera just mentioned. The penis too is quite different from the plate like aedoeagus of the Jugate Lepidoptera. It is a chitinized tube more like the penis of the Micropterygidae and Tineoidea with an eversible membranous termen which often bears spines.

Species examined: Leptocerus dilutus Hag.
Leptocerus exquisita Walk.
Molanna angustata Curt.
Molanna cinerea Hag.
Molanna sp.
Beraea pullata Curt.

Phryganeidae: (Text fig. IX, 4). This family is usually placed further along in the series, near the Limnophilidae, but as the genitalia seem to be nearest in structure to those of the Molannidae and Leptoceridae it is inserted here. The eighth sternum is usually heavily chitinized, and forms a plate beneath the ninth sternum and the base of the genitalia much as it does in the Hepialidae and Bombycidae. The ninth sternum is small, quadrate, and often fused with the inner surface of the eighth. The gonopophyses are small, finger-like, sometimes with a short terminal joint, and are articulated to a small plate, possibly the homologue of the juxta. The ninth tergum forms the dorsal integument and the tenth tergum is a small rectangular sclerite usually closely fused with it, and produced laterally into spines or processes. The anal appendages are lobate, spine like, or absent. The penis is short, heavily chitinized, toothed or spined, and has an eversible membranous tip also armed with spines.

Zander studied many species of the Molannidae, Leptoceridae and Phryganeidae and made diagrams representing ideal cross sections of the typical genera. In the Leptoceridae and Phryganeidae these show the distal ends of the penis pouch and the anus contiguous or separated by thin membrane.

This same condition occurs in the Hepialidae where as already mentioned the membranous penis passes behind the plate like aedoeagus and opens directly beneath the anus and the two are separated by their membranous walls.

The testes of the Molannidae and the Phryganeidae were examined by Cholodkovsky (1913), and found to be similar in type to those of Hepialus and Phassus.

Species examined: Phryganea japonica McLach.
Neuronia postica Walk.

Sericostomatidae: (Text fig. VIII, 3). Only two genera of this family were studied, but Zander and Klapalek have described the modifications occurring in the different subfamilies very completely. From a study of their descriptions and the species mentioned below the genitalia of the family show many resemblances to those of the Tineidae and Acrolophidae. The ninth sternum forms a quadrate or emarginate vinculum which in one of the subfamilies, Brachycentrinae, possesses a saccus much like the Telaeporine Tineidae. The gonopophyses are quite broad and are articulated to the lateral angles of the ninth sternum; in Helicopsyche the outer margin is divided and forms a sacculus and cucullus as in the lower Tineidae, or Acrolophidae. In Goera they are emarginate at the apex. The tegumen is composed of the fused ninth and tenth terga and may bear a central process, uncus, or several lateral processes. The anal appendages are usually small. The penis is thin, heavily chitinized, with a bulbous basal portion and a small eversible tip. The ejaculatory duct usually enters the dorsal side of the base. This type of penis is quite like the aedoeagus of the Tineidae or Acrolophidae.

The testes of Goera were examined by Cholodkovsky and found to be similar to those of Tinea and Tineola.

Species examined: Goera pilosa Fabr.
Goera sp. (Dr. Betten's collection)
Helicopsyche sp.

Limnophilidae: The nature of the specialization in this family has already been mentioned in our review of Zander's work. The peculiar penis and

penis pouch, the large anal appendages, and the greatly reduced gonopophyses find no homologues in the Lepidoptera. The genitalia of the subfamily Apataniinae have gonopophyses and a dorsum very similar to the Rhyacophilidae showing that the type is a specialization from a very generalized form, probably from the ancestral stock of the order.

Species examined: Platyphylax sp.
Apatania sp. (Ulmer's figures)

Diptera, Hemiptera and Hymenoptera

Crampton, (1919, 1920, 1922, (a) and (b)), has described the genitalia in a number of the families of these orders and compared them with those of the Orthoptera, Neuroptera, Mecoptera, and Trichoptera. Since they do not show as close resemblance to the Lepidoptera as do the Mecoptera and Trichoptera and these similarities when they do exist show their relation to these orders rather than to the Lepidoptera; further discussion of them is unnecessary.

The Special Morphology of the Male Genitalia of the Primative Lepidoptera.

Suborder: Jugata.

Hepialidae: (Plates I and II). The male genitalia of this family were treated by the author, (1921), and an effort was made to homologize the nomenclature of Newell, (1918), with that of Pierce. Further study of the family has revealed the incorrectness of Newell's interpretation of the structures in the family and the following list of general characters is substituted.

The abdomen, as in most Lepidoptera, is composed of nine chitinized somites, and a membranous tenth, which is usually without appendages. Somites 3 - 8 usually bear a number of unchitinized areas or fossae which also occur on certain somites in the Jugo-frenate Lepidoptera.

The eighth somite possesses well developed spiracles; in the higher Lepidoptera these are rudimentary or absent. The eighth sternite is often heavily chitinized and forms a plate beneath the base of the genitalia, and the caudal margins of the eighth and ninth sterna are sometimes fused or articulated together. The eighth tergum in some species is produced caudally and forms a dorsal hood around the genitalia.

The ninth sternum forms the vinculum and is quadrate, U-shaped, or V-shaped. It is sometimes provided with a short, broad saccus. The juxta, a quadrate, chitinised plate, is situated directly caudad of the vinculum and on the ventral line of the venter. The harpes are short, finger-like appendages which articulate with the lateral margins of the juxta or occasionally, in part, with the lateral angles of the vinculum. Ordinarily the harpes are simple but in some species are emarginate, divided, or bear small appendages or processes.

The ninth tergum is large, hood-like, and weakly chitinized, or emarginate on the meson of the caudal margin. The caudal margin bears one or two pairs of processes which may fuse with the aedoeagus to form a suspensorium around the penis, or project caudad around the anus. The aedoeagus consists of a small, chitinised plate situated on the venter of the terminal portion of the ejaculatory duct or penis and caudad of the anellus. Its caudal margin may be produced into a spine or spatulate process, or the entire plate may be fused with the caudal processes of the ninth tergum. The tenth somite is entirely membranous and forms the base of the anus, from which it can not be distinguished. In a few species of Gorgopis the tergal portion is chitinised and may be recognised from the remainder of the anal tube.

The articulation of the harpes and juxta, the peculiar type of aedoeagus, the suppression of the tenth somite, and the caudal processes of the ninth tergite separates this family and the Prototheoridae from the remainder of the Lepidoptera. On the basis of the species studied the genitalia of the

family may be divided into ten groups or subtypes. The first five of these illustrate a progressive series; three of the latter five are derived from one of the former subtypes, while the last two subtypes seem bizarre and isolated.

Subtype I: This group comprises the most generalized forms of genitalia in the family, and is characterized as follows: ninth tergum without large processes; aedoeagus small, plate like and with a short, spatulate, median process. In some species the caudal margin of the eighth tergum is produced and forms two small lobes. The vinculum is without a saccus and the eighth sternum is only slightly chitinized. Hepialus lupalinus L. (Plate II, fig. 1), illustrates the simplest form of this subtype, and H. fusconebulosus Geer., one of the more specialized.

Subtype II: (Plate II, fig. 2) This group is distinguished from the preceding by having the processes of the ninth tergum enlarged and fused with the aedoeagus forming a "suspensorium" beneath the penis, and by a small saccus on the vinculum of many species. Most of the European species of Hepialus may be placed in this group, and Phassus schamyli Chr.

Subtype III: The species of the North American genus Sthenopis form this group, which differs from the preceding one only in the incomplete fusion of the aedoeagus and processes of the ninth tergum, and in the more constant occurrence of the saccus.

Subtype IV: (Plate II, fig. 3) The genitalia of this group represent modifications of subtypes I and III, and show considerable variation. The suspensorium is usually incomplete, the processes of the ninth tergum are hook-like or cygnate, and the saccus is small or absent. The harpes are subject to great modification being spined, emarginate or completely divided into a cucullus and sacculus (Plate I, figs. 3, 5, and 7). Most of the species of the group are from Australia and are classed in three related genera.

Subtype V: (Plate I, fig. 1) This group, consisting of the species of the Australian genus Oncopera, is characterized by having the contiguous

processes of the ninth tergum closely approximated and forming an uncus-like structure, by the small quadrate aedoeagus, and by the fusion of the vinculum and the eighth sternum.

Subtype VI: (Plates I, fig. 2) This type is a modification of the former in which the uncus is larger and more clearly defined. The penis lacks the chitinized ventral plate, or aedoeagus, and the vinculum is provided with a median, bifed, tooth on the caudal margin. The harpes are battledore shaped and their narrow bases articulate with the large juxta. The African genus Gorgopis forms this group.

Subtype VII; (Plate I, fig. 4, and Plate II, fig. 4) The genitalia of this group are characterized by the extreme fusion and chitinization of parts. The processes of the ninth tergum are fused dorsally behind the anus and ventrally beneath the penis, forming the boundaries of a large aperture containing the anus and penis. The juxta and harpes are greatly reduced in size and are forced forward owing to the expansion of the processes of the ninth tergum. The vinculum is often fused with the juxta and with the eighth sternum.

Subtype VIII: and IX: Both of these types seem to be modifications of VII, but are quite different in appearance. In VIII the processes of the ninth tergum form a large funnel-like orifice thru which the anus protrudes; the aedaoeagus is long, slender, and recurved, the harpes are absent, and the caudal margin of the eighth sternum is deeply emarginate. In IX (Plate I, fig. 6) the harpes are present but greatly reduced, the aedoeagus is vestigial, and the caudal margin of the eighth tergum forms a large asymmetrical hood consisting of several highly chitinized lobes.

Subtype X: (Plate I, fig. 8) In this type the genitalia are quite broad, the vinculum is short and quadrate, the anellus is broader than long, the harpes are truncate, and the aedoeagus narrow and recurved, fusing with the pair of narrow processes from the lateral margins of the ninth tergum.

The species which were examined are tabulated under their respective subtypes:

I - Hepialus lupulinus L., Hepialus fusconebulosus Geer. Hectomanes simulans Walk., Hectomanes crocea Luc.,

II - Hepialus amasinus HS., H. carna Esp., H. gallicus Ld., H. sylvinus L., H. humuli L., Phassus schamyli Chr.

III - Sthenopis argenteomaculatus Harr., S. quadriguttatus Gr., S. thule Spr.

IV - Porina fuscomaculata Walk. Hepialus eximius Scott., H. variabilis Br., H. hectoides Boisd. Perrisectis australasiae Donn.

V - Oncopera intricata Walk., O. mitocera Turn., O. sp.(Turner coll.)

VI - Gorgopis libania Stoll., Gorgopis sp. (Africa).

VII - Pielus hyalinatus HS., Trictena labyrinthicus Don., Porina umbraculata., P. cervinata ., P. nova-zealandae, Walk. Dalaca terea Schaus.

VIII - Hepialus hecta L.

IX - Phassus metellus DMU.

X - Hepialus medusa ., Palpifer sexnotatus Moore.

Prototheoridae: (Plate I, fig. 9) The genitalia of this family resemble those of the Hepialidae very closely. The tergum of the ninth somite is provided with a number of recurved processes very similar to those in group IV of the Hepialidae, the harpes are long and narrow and are articulated to the juxta, which is continuous with the caudal margin of the vinculum. The vinculum is narrow, U-shaped, and without a saccus. The aedoeagus consists of a recurved plate terminated by an elaborate armature made up of two lateral membranous, setose lobes, and a central, bifed, chitinized tongue. Only the genotype, Prototheora petrosema Meyr. was obtained for study.

Suborder: Jugo-Frenata.

Mnesarchaeidae: (Plate II, figs. 5 and 6). The genitalia of this group are intermediate in their structure between the Hepialidae on one hand and the Micropterygidae, Eriocraniidae, and the Aculeate Tineoidea

on the other. The absence of a tube-like aedoeagus and the form of the vinculum are suggestive of these structures in the Hepialidae; the shape and articulation of the harpes is similar to that of the generalized Micropterygidae and Aculeate Tineoidea, and the dorsal integument resembles the type which occurs in the Eriocraniidae. The general characteristics of the genitalia are as follows: Tegumen made up of the fused ninth and tenth terga, the tenth remaining entirely membranous; lateral margins of the tegumen expanded forming an inner pair of setose lobes and an outer pair of chitinized finger-like processes. Vinculum broadly U-shaped or quadrate. Harpes triangular, joined to the meson of the vinculum by their inner angles, and to the latus by their outer angles. Juxta, a membranous plate, heavily spined. Aedoeagus, membranous and in M. hamadelpha Meyr., terminated by two chitinized spines.

Species examined: Mnesarchaea loxoscia Meyr.
Mnesarchaea hamadelpha Meyr.

Micropterygidae: The genitalia of this family present a series of types which form a nucleus from which may be derived practically all the forms of genital structure occurring in the Eriocraniidae and the Aculeate Tineoidea. In the genus Sabatinca alone five distinct types of genitalia occur all of which foreshadow tendencies which later appear in the Tineoidea. The general characters of the family are as follows: Tegumen large and hood-like, composed of the ninth and tenth terga; uncus, when present, solidly fused with the tegumen; anus membranous; vinculum, U-shaped, much longer than broad and in some cases composed of the fused eighth and ninth sterna; harpes spoon-shaped, triangular, or finger-like, often cleft at the apex or with terminal spines, and articulating with the juxta in the meso-ventral portion of the vinculum. Aedoeagus, large, and usually as long as somites 7 - 9 inclusive, its base chitinized sometimes enlarged and receiving the ejaculatory duct on the dorsum, as in the higher

Lepidoptera, or slightly narrowed and receiving the duct at the apex as in the Trichoptera, tegmen membranous, eversible, sometimes spined. Anellus, membranous, juxta, composed of a small chitinized plate or bridge which connects the bases of the harpes. Abdominal fossae consisting of a pair of unchitinized apertures with a heavy chitinous margin which are situated on each side of the meson of the fifth sternum. The species of the family may be divided into six groups* based on the types of genitalia.

Subtype I: (Plate III, figs. 1 and 2) Tegumen large, uncus absent, vinculum composed of the fused eighth and ninth sterna; harpes large, spoon-shaped, and articulating with the quadrate, plate-like juxta on the meson of the vinculum; aedoeagus with the base slightly attenuate and receiving the duct at its apex. The group shows its relation to the Hepialidae thru the retention of a large juxta, and to the Aculeate Tineoidea, Prodoxidae, and Incurvariidae, in the shape of the vinculum, tegumen, and harpes.

Subtype II: (Plate III, fig. 4) This and the next two groups are modifications of the first. The tegumen bears a long uncus, the harpes are spoon-shaped and cleft at the apex, and the aedoeagus is enlarged basally and receives the ejaculatory duct on the dorsal side; its distal end is armed with short recurved spines.

Subtype III: (Plate II, figs. 3, 5, and 6, and Plate IV, figs. 1 and 2) Harpes, long and finger-like; lateral margins of the tegumen lobate and armed with spines and setae; juxta, small and triangular; uncus present in most species and sometimes partially or entirely fused with the lateral lobes

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*Since the writing of this Dr. Alfred Philpott, Cawthron Institute, New Zealand, informs me that he has divided the New Zealand species of the Genus Sabatinca into the same number of groups and has submitted the results of his investigation to the Transactions of the Entomological Society of London under the title, "On the Male genitalia in Sabatinca and Allied Genera, with observations on the same structures in Mecoptera". In this he includes a number of species which were not available to me for study and probably anticipates some of the conclusions already drawn from my study of the Nannochorostidae.

of the tegumen. i.e. (Plate III, figs. 3 and 6).

Subtype IV: (Plate III, fig. 7) This group is composed of the single Australian species of the genus Sabatinca and resembles subtype I with the following exceptions: The vinculum is shorter and consists only of the 9th sternite and the harpes are slender, finger-like, and deeply toothed at the apex.

Subtype V: (Plate III, fig. 8) This group is a modification of Subtype I and forms the transition between it and Subtype VI. Tegumen as in I; harpes, small, triangular with the inner angles of their broad bases articulating with a small linear juxta on the meson of the vinculum, and their outer angles to the latus of the vinculum.

Subtype VI: (Plate IV, fig. 3) This group is a modification of the former in which the harpes are more slender and bear a pair of inner processes; the juxta is entirely membranous; the tegumen is emarginate and possesses a small gnathos; the aedoeagus has a subterminal process. Subtypes V and VI represent intermediate forms which connect the generalized Micropterygidae, as illustrated in Subtype I, with the Eriocraniidae and the Aculeate Tineoidea, Incurvariidae, Adelidae and Nepticulidae. The species of Micropterygidae which were examined are tabulated below under their respective Subtypes.

I - Sabatinca chrysargyra Meyr., S. incongruella Walk.

II - Sabatinca aurella Huds., S. canthina Philp., S. doroxena Meyr.

III - Micropteryx thunbergella Fabr., M. aruncella Sc., M. sepella Fabr., M. calthella Linn., M. ammanella Hb., M. rablensis Zell., M. rothenbachii Frey.

IV - Sabatinca calliplaca Meyr.

V - Sabatinca eodora Meyr.

VI - Epimartyria auricrinella Wlsm.

Eriocraniidae: (Plate IV, figs. 4, 5, and 6) The characters of this family are as follows: Fifth sternum with a pair of fossae as in the

Micropterygidae. Ninth somite a heavily chitinized cylinder, sternum slightly longer than the tergum and forming the vinculum. Anterior margin of the vinculum deeply emarginate, caudal margin heavily chitinized and often with a median process. Tegumen emarginate at the apex forming two large lobes which assume the position of a dorsal hood. Zander has labeled these lobes the tenth tergite and their close association with the anus and the presence of a transverse suture between them and the remainder of the tegumen supports this view. Harpes small, triangular or quadrate, with median basal processes which are attached to muscles in the region of the juxta, while their outer basal angles are attached or firmly fused with the lateral margins of the vinculum. Often the harpes are greatly reduced and so fused with the vinculum as to be scarcely distinguishable, i.e. Plate IV, fig. 6. Juxta large, quadrate, partially or entirely chitinized. Aedoeagus with heavily chitinized dorsal and ventral surfaces and membranous lateral ones so that it assumes the appearance of two separate narrow, elongate pieces with acute apices; vesica enlarged and plicate; base of aedoeagus enlarged and receiving the ejaculatory duct on the dorsum. Anellus membranous, sometimes with short spines.

The structural resemblances of the genitalia to those of the Micropterygidae have already been mentioned. The harpes, tegumen, especially the terminal lobes, and the aedoeagus offer reliable characters for the separation of all the species that were examined.

Species examined: Mnemonica fastuosella Zell.
Mnemonica auricyania Walsm.
Mnemonica unimaculella Zett.
Eriocrania semipurpurella Stph.
Eriocrania purpurella Haw.

Suborder: Frenata

Superfamily Tineoidea; Group Aculeata

This group of the Tineoidea includes seven families all of which possess minute spicules, aculeae, on the wing membrane. The significance of these

structures has been discussed by Forbes, (1914), and the separation of the Tineoidea (sens. str.) into two groups on the basis of these structures is accepted by most microlepidopterists. From a survey of the male genitalia the group seems to be a perfectly natural one comprised of a series of nearly related families which, with the exception of the Tischeriidae, are most closely related to the Micropterygidae. They form a connecting series between the genitalia types of the Micropterygidae on the one hand and those of the generalized Tineidae on the other. The group may be distinguished by the following characters: Tegumen small and hood like, usually without an uncus, lateral margins sometimes produced to form two setigerous lobes or processes. Gnathos usually present. Vinculum composed of the ninth sternum, ordinarily large and in the form of a long U or V; apex usually covered by the eighth sternum. Harpes triangular, clavate, or spoon shaped, sometimes armed with tubercles, or spinose plates. Aedoeagus either a slender chitinized tube or in some species shorter and more heavy; its base is usually enlarged and the ejaculatory duct enters the apex or slightly on the dorsal side. Anellus membranous, often spined and with the free margin cleft or emarginate. Juxta usually absent. Certain modifications of these parts occur in the different families of the group and will be considered more fully under the following discussion of the special morphology.

Prodoxidae: (Plate VI, figs. 1 and 2) The genitalia of this family are a modification of the first type described in the Micropterygidae. The tegumen is reduced and shortened and forms a narrow hood, and is without either an uncus or gnathos; the vinculum is very long and in the form of an acute V; the harpes are spoon-shaped or clavate, and frequemtly possess chitinous tubercles on the outer margin. The juxta is absent.

Species examined: Prodoxus quinquepunctella Chamb.
Tegaticula alba Zell.

Incurvariidae: (Plate V, figs. 5, 7, and 9) The genitalia of this

family resemble those of the preceding quite closely. The tegumen is quite narrow and in some species is provided with a short uncus. The harpes are spoon-shaped or digitate; occasionally the inner margin is divided and forms a short clavus. The anellus in several forms has the free portion divided into lobes and is often spined.

Species examined: Incurvaria muscalella F.
Incurvaria humilis Wlsm.
Paraclemensia acerifoliella Fh.
Isocorypha mediostriatella Clem.

Adelidae: (Plate V, figs. 1, 2, 3, 4, 6, and 8) In structure this family is quite closely related to the preceding probably having been derived from a Micropterygid ancestor of the type described in group V. In certain respects the genitalia also resembles those of Epimartyria and Eriocrania. The family may be distinguished by the following characters: Tegumen small and hood like, with or without a gnathos; uncus absent; vinculum very large and usually longer than the eighth sternum under which it lies; it is U or V shaped often with a medio-ventral spine. Harpes short and triangular, or spoon shaped, and the inner margin is often adorned with scobinate or spinose plates. These structures anticipate similar ones found in the harpes of the Heliozelidae. The bases of the innermargins are sometimes fused to a small juxta. Aedoeagus, a long, thin, chitinized tube which is sometimes enlarged at the base and armed with a terminal spine. Anellus membranous, often with small spines and a lobed or emarginate free, portion. The family may be divided into at least three groups based on the shape of the harpes but insufficient material was at hand to allow a thorough working out of the species on this basis.

Species examined: Adela viridella Sc.
Adela ridingsella Clem.
Adela septentrionella Wlsm.
Nematois annae Zell.
Nematois sparsella Wlk.
Ceromitia wahlbergi Zell.
Lampronia pmaelatella Schiff.
Nemophora swammerdammella L.

Nepticulidae: (Plate VII, figs. 4, 5, and 6) The genitalia of this family resemble those of the preceding very closely and have probably been derived from them. The tegumen is short usually with a triangular uncus, and a well chitinized gnathos, composed of two lateral arms and a median plate, or a simple transverse plate. Vinculum large, quadrate, sometimes with the lateral margins expanded giving it an emarginate appearance. Harpes triangular with the spices acutely pointed, or clavate; inner basal angles meeting and articulating with the vinculum; hind margins frequently joined by a chitinized transtilla. Aedoeagus extremely large, usually two-thirds as long as the entire genitalia and quite broad. It is often armed with strong spines. Anellus membranous, occasionally armed with spines scattered over the entire surface or in a series around the margin. Margin sometimes produced into spine like processes. The presence of both gnathos and uncus, the emarginate vinculum, and the broad aedoeagus separates this family from the Adelidae.

Species examined: Nepticula slingerlandella Kearf.
Nepticula rosaefoliella Clem.
Ectoedemia populella Bsk.
Obrussa ochrefasciella Chamb.
Glaucolepis saccharalis Braun.
Trifurcula sp. (Europe)

Heliozelidae: (Plate VII, fig. 1, 2, and 3) The genitalia of this family resemble those of the genus Ceromitia of the family Adelidae, from which they have been probably derived. The characteristics are as follows: Tegumen, hoodlike; uncus, absent; gnathos, present; vinculum large, U-shaped, and extending up to the seventh somite; harpes finger-like or spoon-shaped with a pair of spinose plates on the innermargin, which may be firmly fused to it or elevated on a short process or "petiole". In Heliozela this petiole is long and recurved thus bringing the plate to one side of the harpe proper and foreshadowing a tendency which is more highly developed in the Opostegidae. Anellus membranous, usually with a row of recurved spines around the free margin. Aedoeagus long thin and heavily chitinized with an

eversible termen which in some species is quite complicated.

Species examined: Helizela stannella Tr.
Antispila isabella Clem.
Coptodisca splendoriferella Clem.

Opostegidae: (Plate VI, figs. 5 and 6) In this family we find a type of genitalia which is quite distinct from any other occuring in the Aculeate Tineoidea and, although it shows some resemblance to the Heliozelidae, it can hardly be classed as a direct derivation. The characters are as follows: Tegumen, a narrow transverse hood with two lateral setose papillae, or a chitinized plate bearing a row of setae on the margin. Gnathos, when present, quite large and made up of two lateral arms and a median tongue shaped plate. This structure articulates to the base of the tegumen and swings below the membranous aedoeagus much in the same manner as the suspensorium which was described in the Hepialidae. The absence of a chitinized aedoeagus and the structure of this peculiarly modified gnathos suggests that it serves as an intromittant organ. When the gnathos is absent the aedoeagus is chitinized and normal in structure. Vinculum narrow and quadrate, or emarginate. Harpes, an extreme modification of the type described in Heliozela. The harpe proper is greatly reduced in size, while the spinose pad is enormously enlarged and bent laterad on its petiole so that it forms a clavate terminal lobe. Anellus, membranous. The family may be divided into two subdivisions, the one including those species in which the gnathos is present and the aedoeagus is membranous and the other with the opposite characters.

As a whole the genitalia offer no better suggestion as to the relationships of the family than the mouth parts and wing venation. The structure of the harpes suggests that the family might be related to the Heliozelidae but all of the other parts are quite dissimiliar. The substitution of the gnathos for a chitinized aedoeagus in some species is analagous to the replacement of this structure by a suspensorium in the Hepialidae, but the

modification is evidently developed entirely within the family. The quadrate vinculum which sometimes occurs in the family resembles the same type in the Nepticulidae, but the emarginate form is much more extreme than any found in Nepticula. Heinrich (1918), from a study of the larval characters of Opostega and allied genera finds its closest affinities with the Nepticulidae and the Tischeriidae. From the study of the genitalia just summarized it will be seen that certain resemblances exist between the Opostegidae and the Nepticulidae indicative of relationship, but from the following summary of the Tischeriidae it will also be seen that there is nothing to indicate even a distant relationship between this family and Opostega. It is unfortunate that Heinrich omitted from his work the Heliozelidae which seem to be most closely related to Opostega in their genital characters, and the Adelidae which furnish the intermediate steps from the generalized Aculeates, Incurvariidae and Prodoxidae, to these other more highly specialized families.

Species examined: Opostega monstrigella Chamb.
Opostega auritella Hb.
Opostega saliciella Tr.

Tischeriidae: The position of this family is uncertain for although the wing membrane possesses aculeae, they are large and not typical. Other structures, (Meyrick, 1895 and 1912), indicate that the family may be related to the genus Bedellia of the Gracilariidae or Glyphipterygidae. The genital characters support this latter view particularly in the shape of the vinculum, the articulation and shape of the harpes and the presence of specialized hair tufts on the eighth sternum. Aside from the resemblance of the spined anellus to the same structure in the Heliozelidae the family has no genital characters in common with the other Aculeates. The bifed tegumen which occurs in some species slightly resembles the same structure in the Acrolophidae and Tineidae but the bifed condition is carried much further resulting in two large earlike appendages which have no parallel in any of the forms treated in this paper.

Species examined: Tischeria tinctoriella Chamb.
Tischeria marginea Hn.
Tischeria angusticolella Z.
Tischeria complanella Hb.
Tischeria malivorella Clem.
Coptotricha zelleriella Clem.

Group: Nonaculeata

This group includes all of the remaining families of the Tineiodea about thirty five of which are represented in North America. Most of these are highly specialized and cannot be regarded as primitive Lepidoptera. The Tineidae, Acrolepiidae, Acrolophidae, Psychidae, Cossidae, Bombycidae, and three families comprising the Eucleoidea possess structural characters in common and with the groups already described. The special morphology of their genitalia will be described in the following discussion.

Tineidae: This family forms the basis for practically all of the types of genitalia which occur in the Tineoidea. It may be separated into several fairly well defined divisions which correspond to subfamilies or groups of subfamilies already established on other morphological characters. It is a difficult family to characterize as a whole because these divisions are the result of several lines of specialization, which have culminated in widely separated types. The most satisfactory idea of the genitalia of the family may be obtained by a discussion of these types within their respective divisions.

Division I: (Plate VIII, figs. 1-7) This division contains those Tineids commonly classed under the subfamilies Eriocottinae, (= Xysmatadominae), and Crinopteryginae, and is characterized as follows: Tegumen very large and hood-like, probably made up of the ninth and tenth terga although there is no distinct suture between them, posterior margin emarginate or deeply bifed. Uncus not distinct although the posterior margin of the tehth tergite is sometimes produced and forms a triangular lobe, i.e. Timaea. The gnathos

consists of two chitinized arms and a median plate which may be membranous or chitinized. Vinculum U or V shaped, with or without a saccus. The form of the saccus varies from a shallow pocket to a long keel-like spur. The harpes are broad and spoon shaped, either undivided with a small spur near the base of the outer margin, (Eriocottis), or divided into a distinct cucullus and sacculus, (i.e. Narycia). The Transtilla is well developed in some species and forms a bridge behind the aedoeagus. The anellus is usually membranous, sometimes with short spines, and the juxta, when developed forms a small chitinized plate which may bear a pair of lateral lobes. The aedoeagus varies greatly in size and degree of chitinization, but is usually a linear tube without armature.

The origin of this type of genitalia is difficult to trace for it seems somewhat isolated from the Jugo-frenata and Aculeata. From the characters offered by the European genera, Crinopteryx and Eriocottis and the Australian genera Mallobathra, Mesopherna, and Timaea, it seems most logical to regard it as a derivation of the Micropterygidae, probably from group I. The large tegumen composed of the ninth and tenth terga, the simple U or V-shaped vinculum, the spoon shaped harpes and the linear aedoeagus are all structures which could be derived from a generalized form of genitalia such as already described in Sabatinca.

The more highly specialized members of this first group i.e. Rhodobates, Apreta, and Dryotopasta serve as a basic type from which may be derived the genitalia of the Acrolophidae, while the generalized type represented by Eriocottis etc., are closely related to the second division of the Tineidae thru the genus Solenobia.

Division II: (Plate IX, figs. 1, 2, 4, 5, 6, 7, 8,and 9) This division includes the sub-families Telaseriinae, Teichobiinae, and certain Tineid genera placed by some authors in the Psychidae. The group forms a transition on one side between the Eriocottinae and the Psychidae in which all of the

intermediate steps in genitalia development have been preserved, and on the other between the Eriocottinae and the Tineidae in which only a few intermediate forms have been preserved. The characters of the group are difficult to define because of the wide variation. The more generalized forms such as Solenobia resemble Eriocottis and Crinopteryx, but the more specialized ones are quite distinct. The tegumen is large and hoodlike in the generalized forms, but tends to become narrow in the forms more closely related to the Psychidae. It is usually without an uncus or gnathos altho the latter is sometimes present. The vinculum is V-shaped moderately large and usually possesses a short, blunt, or obtuse saccus. The harpes are either spoon shaped with a short projection near the base of the outer margin, or completely divided. The juxta is well developed in most species and is in the form of a large plate in front of or surrounding the aedoeagus. Its lateral margins frequently bear a pair of hairy lobes. The aedoeagus is usually large, especially in those forms resembling the Psychidae, well chitinized and with little armature.

Division III: This division contains most of the species placed by authors in the Tineidae with the exception of a few which have already been included under Divisions I and II. Two quite distinct types of genitalia occur in the group, which appear to be the result of two diverging lines of specialization from a form similar to Teichobia or Diachorisia. Both of these types occur in the genus Tinea and will be referred to as subdivisions A and B.

Subdivision "A": (Plate X, figs. 1-6). In this group is included all of the Tineidae in which the saccus is well developed, i.e. The genotype of Tinea, most of the North American and European species of the genus, and closely allied genera such as Monopis and Tineola. In the more typical of the group the uncus, gnathos, and saccus are all extremely well developed, but in reduced forms such as Oenoe and Homostinea the entire tegumen and its armature is greatly abbreviated. The Australian genus Moerarchis is

intermediate between the two subdivisions but cannot be considered as a transitional form because this separation on the basis of the presence or absence of a saccus is hardly a natural one. It is possible that such reduced forms as Ischnosia, Meesia, etc., which I have placed in the second subdivision may have lost the saccus thru reduction just as they have the uncus and gnathos. These genera are exceedingly difficult to place due to the absence of these structures. Isocorypha which has been placed by some authors among the genera included in this group bears more resemblance to the Incurvariidae, especially Paraclemensia, and is placed in that family. The aedoeagus in this subdivision is usually linear, quite long, and needlelike. The harpes are usually spoon shaped or finger-like.

Subdivision "B": (Plate X, figs. 7 and 8; Plate XI, figs. 1 and 2). As already mentioned this subdivision differs from the former in the absence of the saccus and in having the vinculum usually enlarged, forming a rectangular, U-shaped, or emarginate plate. The uncus and gnathos are absent or reduced and the former is sometimes replaced by socii. The harpes are very irregular, often with spines and processes. The aedoeagus is usually large at the base and acutely pointed at the apex and often abruptly curved. Homosetia which is placed in this subdivision closely resembles Diachorisia and Ateliotum of Division II. It has been very difficult to ascertain the positions of these three genera from the genitalia because they are somewhat intermediate in their structure between Divisions II and III.

Division IV: (Plate XI, figs. 4-7) This division includes the two genera Amydria and Scardia, which are usually placed in the Tineidae. Their genitalia resemble those of the Acrolophidae, and they were probably derived along with this family from a form similar to Alavona, Dryotopasta or Rhodobates of Division I. They are characterized by having a bifed or emarginate uncus, a U-shaped vinculum, an incomplete or rudimentary gnathos, and emarginate or divided harpes. These are large and irregular and are

composed of two or three lobes, the inner one sometimes forming a hook or process. The anellus is small and sometimes armed with short spines; and the juxta is well developed. In Scardia it forms a plate which surrounds the aedoeagus. The aedoeagus is large and linear, slightly dilated at the base and often armed with small spines or teeth at the termen, vesica,prominent. Most of the species of Scardia answer the foregoing description, but Amydria is divided into two distinct groups. The first of these represented by the genotype effrentella Clem. (Plate XI, fig. 4) possesses irregular harpes and a curved, acutely pointed aedoeagus, and the second, represented by margoriella Dtz. (Plate XI, fig. 5) has simple spoon shaped harpes and a linear aedoeagus.

Species examined:

Division I.

Crinopteryx familiella Peyr.
Eriocottis pyrocoma Meyr.
Eriocottis andalusiella Z.
Eriocottis fuscanella Z.
Mallobathra crataea Meyr.
Timaea bivittatella Wlk.
Mesopherna palustris Meyr.
Alavona barbarella
Roeslerstammia pronubella Schiff.
Roeslerstammia erxlabenella F.
Lypusa maurella F.
Narycia saxosa Meyr.
Narycia heliochares Meyr.
Narycia trifasciata Wlk.
Lepidoscia palleuca Meyr.
Rhodobates laevigatellus H.S.
Rhodobates pallipalpellus Rb.
Dryotoposta yumaella Kearf.
Apreta paradoxella Dietz.

Division II.

Telaeporiinae:

Solenobia manii Z.
Solenobia walshella Clem.
Telaeporia tabulosa Ritz.
Diplodoma marginapuncta Stph.
Melasina lugubris Hb.
Kearfottia albifasciella Fern.
Dissoctona granigerella St.
Dysmasia parietariella H.S.
Euplocamus delagrangei Rag.
Mymecozela danubiella Mn.

Teichobiinae:

Diachorisia vilatella Clem.
Teichobia verhuellella Stt.
Ateliotum hungaricellum Z.

Division III:

Subdivision "A":	Moerarchis	australasiella	Zell.
	Moerarchis	inconcisella	Wlk.
	Tinea	fuscipunctella	Hw.
	Tinea	pellionella	L.
	Tineala	bisselliella	Hum.
	Trichophaga	abruptella	Woll.
	Monopis	rusticella	Hbn.
	Monopis	dorsistrigella	Clem.
	Monopis	crocicapitella	Clem.
	Monopis	unibractella	Wlk.
	Xylesthia	pruniramiella	Clem.
	Setomorpha	insectella	Fab.
	Oenoe	hybromella	Clem.
	Homostinea	curviliniella	Dtz.
Subdivision "B":	Homosetia	miscecristatella	Chamb.
	Ischnosia	boreonella	Mill.
	Tinea	purella	Wlk.
	Tinea	xystidophora	Meyr.
	Tinea	misella	Zell
	Meesia	argentimaculella	H.S.
	Meesia	vinculella	H.S.
Division IV:	Amydria	effrenatella	Clem.
	Amydria	margoriella	Dtz.
	Scardia	boleti	F.
	Scardia	fiskeella	Busck.
	Scardia	coloradella	Dtz.

Acrolepiidae: From an examination of the genitalia of the North American species of the genus Acrolepia and the European genus Roeslerstammia which has also been placed in the family by some authors it seems very doubtful if these genera are to be regarded as separate from the Tineidae. Roeslerstammia is quite similar to Eriocottis and the genera forming Division I of the Tineidae and has been placed there. Acrolepia resembles the reduced Tineids, Ischnosia and Meesia, and unless further examination of the European species reveals a different type of genitalia it may be regarded as one of the saccus-bearing Tineidae. The family shows no close affinity with the Plutellidae, where some authors have placed them.

Species examined: Acrolepia incertella Chamb.
Roeslerstammia pronubella Schiff.
Roeslerstammia erxlabenella F.

Acrolophidae: (Plate XII, figs. 1-7) The characteristics for the genitalia of this family are much the same as in Division IV of the Tineidae.

The uncus is usually bifed, but the two portions are often approximated or fused. The harpes are spoon shaped and when divided form a spoon shaped or finger like cucullus and a clavate or pointed sacculus. The aedoeagus is large, slightly bulb like at the base, and has a large eversible vesica which bears one or more strong spines (cornuti); occasionally, the termen is acutely pointed. The anellus is unchitinized but sometimes armed with spines; the juxta is rudimentary or absent. The North American species which were described under a series of new genera by Walsingham (1887), were later combined under the original genus Acrolophus by Barnes and McDunnough (1917). From an examination of the genitalia this seems advisable. Anaphora and Acrolophus show no difference in genitalia; both being subject to the same variations, and none of the remainder of Walsingham's genera which were examined appear at all distinct. In fact, Walsingham admits as much in his revision when he says that, "the sexual appendages on the ultimate segments of the bodies of the males have been found reliable in separating the species, although certainly not uniform throughout the genera". As already mentioned the type of genitalia in this family is nearest Division IV of the Tineidae both of which have been derived from the first division of the latter family. In fact, it has been difficult to place such intermediate forms as Apreta and Dryotopasta, and if it were not for the characters furnished by the wing venation and mouth parts of the Acrolophidae the family could easily be regarded as a fifth group of the Tineidae.

Species examined:	Acrolophus	(Pseudanaphora)	arcanellus Clem.
	"	(Felderia)	filicornis Wlsm.
	"	(Orthrolophus)	variabilis Wlsm.
	"	(Anaphora)	popeanellus Clem.
	"	(Atopocera)	barnesi Dyar.
	"	( )	plumifrontellus Clem.
	"	(Hypoclopus)	mortipennellus Grt.
	"	(Eulepiste)	kearfotii Dyar.
	"	(Neolophus)	punctellus Bsk.
	"	(Panama)	
	Amisthus	gigas (Peru)	

In the figures illustrating the genitalia of this family Acrolophus mortipenellus (Plate XII, fig. 4) serves to illustrate the genotype for both Anaphora and Hypoclopus in which I see no difference; and A. plumifrontellus (Plate XII, fig. 1) shows the type in those species of Acrolophus, which have the harpes divided and the sacculus produced to form an acute clavus. Most of the species examined belong to the first type.

Psychidae: (Plate IX, fig. 3; Plate XIII, figs. 1-3) The genitalia of this family as already mentioned are a modification of the type described in the Telaeporiinae, (Tineidae Division II), the genera Melasina, Dissoctena, and Dysmasia forming the intermediate forms between the typical Telaeporiids and such types as Chalia and Eurycyttarus of the Psychidae. The Australian genus Ellasoptila also represents an intermediate type but seems to constitute an independent line of genital specialization which has preserved many tendencies in common with the Acrolophidae and Cossidae. Strand (1912), suggests that the family is not monophyletic, but from an examination of species from all parts of the world we find it is a very homogeneous one, Elassoptila being the only exception. Since the Psychidae have originated from a generalized Tineid ancestor, as have also the Cossidae, it is not surprising to find in some species tendencies in common with the latter. The characters of the family are as follows: Tegumen elongate and narrow forming a dorsal hood, which is sometimes emarginate at the apex. Vinculum long and narrow with an extremely long saccus. Harpes very small, emarginate or bifed at the apex often forming a short sacculus. Aedoeagus very large and long, sometimes with a bulb-like base and funnel shaped termen. Juxta chitinized and fused with the harpes. Sometimes the vinculum and transtilla fuse laterally and form a ring around the aedoeagus. Eighth sternum heavily chitinized and forming a large plate with its anterior lateral margins produced to form two large lobes. The extreme elongation of the genitalia and the modification of

the eighth sternum separates the family from most of the Telaeporiinae. In some of the transitional forms however i.e. Dysmasia and Ksarfottia the last character does not apply.

Species examined:

Elassoptila	microxutha,	Turn.(Austr.)
Eurycyttarus	confederata	Grt.
Chalia	rileyi	Heyl.
Platoeceticus	gloveri	Pack.
Oiketicus	omnivorus	Wlk. (N.Z.)
Thyridopteryx	ephemeraeformis	Haw.
Eumeta	moddermanni	Heyl. (Africa)
Clania	ignobilis	Wlk. (Australia)

Cossidae: (Plate XIV, figs. 1-5) The genitalia of this family combine tendencies from the Tineidae and Hepialidae, but show closest affinities with the Acrolophidae. The tegumen is large and hoodlike with a simple or bifed uncus; the gnathos is usually present although the median portion is poorly developed. The vinculum is small U or V-shaped and usually possesses a short saccus. The harpes are large spoon shaped and simple. The aedoeagus is large well chitinized and has a broad membranous termen; occasionally it is acutely pointed. The anellus is membranous often with longitudinal plicae; the juxta is large, chitinized and has a pair of lateral processes. The bases of the harpes, the juxta, and the aedoeagus are closely associated or fused, suggesting a similar relation of these parts in the Hepialidae. The simple uncus in some species is suggestive of the dorsal processes which occur in some Hepialids, Gorgopis. The prevailing simplicity of the harpes aedoeagus and vinculum indicates a tendency on the part of this family to retain more generalized characters than those described in the higher Tineidae and Acrolophidae. In the figures illustrating this family Cossula magnifica (Plate XIV, fig. 3) presents a highly specialized type, in which the vinculum and anellus are reduced and the uncus inclined ventrad closely approximating the gnathos.

Species examined:

Givira	mucidus	H. Edw.
"	cleopatra	B and McD
"	ethela	N and D
Zeuzera	pyrina	L
"	asylas	
"	multistrigata	Mr.

Species examined { Eudoxyla strix
Hamilcara ramuscula Dy.
Cossula magnifica Stkr.
Fania namus Stkr.
Comadia bertholdi Grt.
" henrici "
" engelhardti B and Benj.
" dolli B and Benj.
" subterminata B and Benj.
Acossus orc Stkr.
Prionoxystus robiniae Pect.

Superfamily Eucleoidea

Limacoididae (Cochlididae and Eucleidae): (Plate XIII, figs. 4-10)

The genitalia of this family are intermediate between those of the Cossidae and Megalopygidae. The tegumen is much like that described for the Cossidae, although the uncus is usually longer, more acutely pointed, and the arms of the gnathos are fused to a central plate. The vinculum is usually quite long and without a saccus. In Cania bandura (Plate XIII, fig. 9) however, the vinculum is narrow and has a broad short saccus. The harpes are spoon shaped either divided into a valvula and sacculus or with a short spine on the outer margin as in the Eriocottinae. The anellus is usually heavily spined or occasionally completely chitinized forming a funnel around the aedoeagus. The juxta is similar to that in the Eriocottinae. The aedoeagus is quite long with a large heavily chitinized bulb-like base; the termen is sometimes armed with cornuti. The origin of the genitalia appears to be from a very generalized Tineid ancestor and the family has retained a majority of Tineid tendencies although these are some resemblances to the Hepialid type. The figures of Cochlidion avellana (Plate XIII, fig. 6) and Euclea delphinii (Plate XIII, fig. 5) illustrate the type which prevails in the North American and European species, while Heterogenea (fig. 4), Microleon (fig. 7), Miresa (fig. 10), Setora (fig. 8), and Cania (fig. 9) illustrate various lines of modification. The latter three are of interest because of their resemblance to certain Megalopygidae, (Norape and Trosia). (Plate XIV, figs. 6 and 8).

Species examined:

Cochlidion	avellana	L (= limacodes Hufn.)
"	christophi	Graes.
Limacodes	biguttata	Pack
"	rectilinea	G.and R.
Euclea	delphinii	Bdv.
"	"	quercicola H.S.
"	"	form paenulata Clem.
Heterogenea	asella	Schiff.
Adoneta	spinuloides	H.S.
Lithacodes	fasciola	H.S.
Packardia	geminata	H.S.
Microleon	longipalpis	Butl.
Doratifera	vulnerans	Lew.
Neaera (Parasa)	dispar	(Java)
Setora	nitens	(Java)
Susica	corones	Fab.
Miresa	flavescens	Wlk.
Cania	bandura	Wlk. (Sumatra)

Megalopygidae: (Plate XIV, figs. 6-9) The representatives of this family present two widely separated lines of genital specialization and as the author has been unable to examine material from localities other than in North America the family relationships have been difficult to ascertain. Judging from the material at hand they are derived from a primative Jugofrenate type, possibly similar to Mnesarchaea, but have preserved certain Hepialid characters. The group may be separated into two divisions, the first containing the genera Norape and Trosia (figs. 6 and 8) and closely resembling the Hepialidae, and the second containing Megalopyge and Lagoa (fig. 9) which show little resemblance to any other Lepidoptera except possibly the Dalceridae (fig. 10). The first is characterized by having a short tegumen, a rudimentary uncus and gnathos, and a small V-shaped vinculum, which is well chitinized near the median line, but membranous at the lateral angles. The harpes are divided into a spoon shaped cucullus and a clavate or triangular sacculus. The cucullus is articulated to the tegumen while the saccus is solidly fused with the anellus; in N. tener (fig. 6) practically the entire harp is fastened to the anellus only the costal angle being articulated to the tegumen. The anellus is large usually heavily chitinized and the juxta forms a plate occupying the entire mediventral portion of the genitalia. The aedoeagus is large heavily chitinized

usually armed with an apical spine and has at least one spine on the vesica. The second group is characterized by a complete separation of the cucullus and sacculus of the harpes so that the former valvulae are attached to the tegumen near the uncus and the latter retain their articulation with the juxta. The socci are often greatly reduced and fused with the vinculum. The uncus is placed on a large basal plate which is entirely separated from the tegumen by membrane. The tegumen is enlarged and forms a broad hood. The aedoeagus is much like that in the first group except that the vesica is armed with a number of small cornuti. The fusion of the harpes with the anellus and the shape of the vinculum and tegumen in the first group places this series very near the Hepialidae and the second group may be considered as a development of the first. Since these same Hepialid tendencies are shared by the Lacosomidae and Bombycidae, it is very likely that these two families and the Megalopygidae represent the remnants of a broken series which once connected the Hepialidae and the Bombycidae.

Species examined:

Norape	tener Druce
"	virgo Butl.
"	ovina Sepp.
Megalopyge	opercularis A. and S.
"	bissesa Dyar.
"	heteropuncta B. and McD.
Lagoa	crispata Pack.
"	pyxidifera A. and S.

Dalceridae: (Plate XIV, fig. 10) This small and unique family is represented in North America by a single species exhibits as peculiar genital characters as are found in the venation and larval habits. The harpes are greatly reduced and the saccus is fused with the anellus and vinculum on the medio-ventral line while the cucullus is indistinguishably fused with the tegumen forming a pair of dorsal ear-like lobes. The gnathos is represented by a pair of triangular setose lobes armed with a serrate ridge. The vinculum is small and bears a long saccus of the type similar to that described in the Tineidae. The aedoeagus is long and lightly chitinized. The status of the family is difficult to determine from the genitalia, but

it seems to be most closely related to the Megalopygidae, but has preserved a Tineid-like vinculum, saccus, and aedoeagus.

Hy Edw.

Species examined: Dalcerides ingenita.

Subfamily Bombycoidea

The only families of this group, which show close genital affinities with the primitive Lepidoptera are the Lacosomidae and Bombycidae. As already mentioned both of these families have the harpes articulated or fused with the juxta, a character already noted in the Hepialidae, Cossidae, Megalopygidae, et al. The Bombycidae have the vinculum and saccus well developed as in the Tineoidea, while the eighth sternum is chitinized resembling that of the Hepialidae. The remaining characters of the group are not of particular importance and an idea of the genitalia may be formed from the figures of Lacosoma chirodota Grt. (Plate XIV, fig. 11) and Bombys mori L. (Plate XIV, fig. 12).

Species examined; Lacosoma chirodota Grt.
Cincinnus melsheimeri Harr.
Bombys mori L.

CONCLUDING REMARKS ON THE RELATIONSHIPS OF THE PRIMITIVE LEPIDOPTERA AS DETERMINED FROM A STUDY OF THE MALE GENITALIA.

In any attempt to determine the phylogenetic relationships of a group of animals the entire structure of the body as well as the biology should be considered. It would be entirely beyond the scope of this paper to do this for the primitive Lepidoptera but an examination of the results obtained from a study of their genitalia with the additional consideration of opinions held by workers in other phases of their anatomy and biology will contribute to the sum total of our knowledge concerning the phylogeny of these interesting insects.

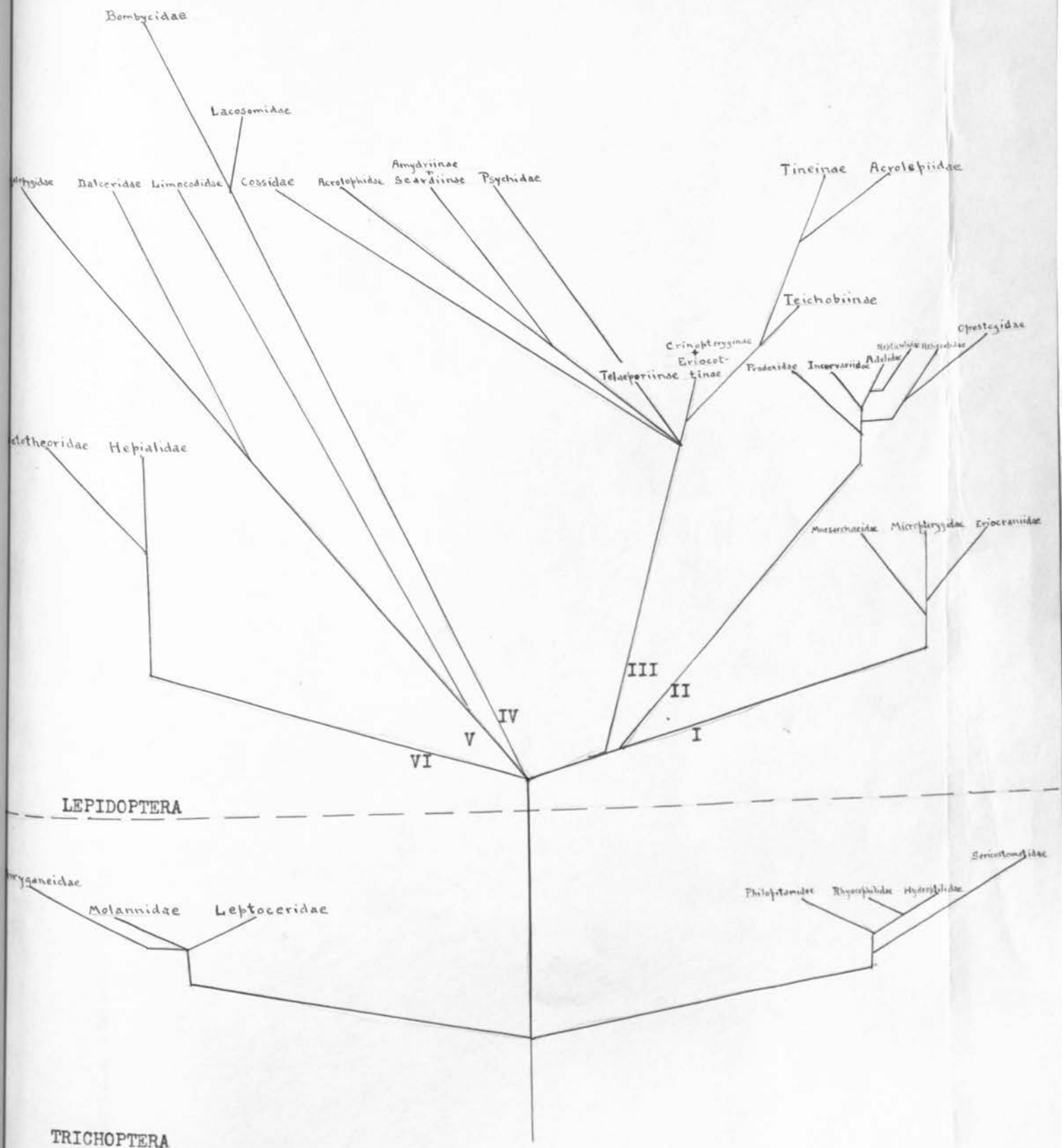
From our comparison of the structure of the male genitalia in the generalized representatives of various insect orders with those of the Lepidoptera

it was seen that the parts comprising the male genitalia can be homologized with little difficulty. Zander's conception of a common plan of structure for the Trichoptera, Hymenoptera and Lepidoptera may be extended to the Neuroptera and Orthoptera and to insects in general. The type of genitalia in all of these orders is quite similar and may be traced to tendencies developed in one of the most primitive orders of winged insects, i. e. the Ephemerida.

From a study of the wing venation, mouth parts, and other characters in the primitive Lepidoptera Packard, (1895), Meyrick, Busck (1914), et al. have concluded that the Lepidoptera have arisen from Trichopterous ancestors i.e. from the Rhyacophilidae thru the Micropterygidae. Quite apart from these investigations Zander and Cholodkovsky have shown that close resemblances exist between the external and internal genitalia of the Molannidae and Hepialidae on one hand and the Rhyacophilidae and Micropterygidae, and the Sericostomatidae and the Tineidae on the other. From our own investigations we have seen that the development of the different types of genitalia in the primitive Lepidoptera is paralleled by a development of similar ones in the Trichoptera, certain families in each order bearing a striking resemblance to each other. Two lines of development are discernible, the one represented by the Jugata (Hepialidae), which finds its parallel in the Leptoceridae, Molannidae and Phryganeidae, and the second represented by the Jugo-frenata and Tineoidea and finding its parallel in the Rhyacophilidae, Philopotamidae, Hydroptilidae and Sericostamidae.

Consequently in seeking for a generalized type of genitalia from which the various lines of specialization in the primitive Lepidoptera and Trichoptera have been derived we must expect to find characters intermediate between these two lines of development, a type however which we can hardly realize in any living insect of today. The nearest approach to such a form is most

PHYLOGENETIC TREE ILLUSTRATING THE RELATIONSHIPS OF THE FAMILIES OF PRIMITIVE LEPIDOPTERA AS ASCERTAINED FROM A STUDY OF THEIR MALE GENITALIA.



probably in Mnesarchaea of the Lepidoptera and in Leptocerus of the Trichoptera. In these we find the following generalized characters; a relatively simple tegumen, composed of the fused ninth and tenth terga, which is without a distinct uncus or gnathos; a vinculum composed of the ninth sternum which has retained its normal shape and size; simple harpes which are articulated to the mädio-ventral surface of the vinculum by a membranous or lightly chitinized juxta; a simply tube-like, membranous, or lightly chitinized aedoeagus. All of these characters exist in a slightly modified degree in the two generalized forms mentioned.

From such a type we may conceive of the Trichoptera as developing in two diverging lines, the one culminating in the present day Molannidae, and the other in the Rhyacophilidae. From these two branches have been derived the remaining families of our modern Trichoptera. Slightly higher in the scale, but from a similar generalized type the Lepidoptera have arisen as a dichotomous stem one branch of which has paralleled the Molannid branch of the Trichoptera resulting in the Hepialidae and the other paralleling the Rhyacophilidae resulting in the Micropterygidae. The accompanying phylogenetic tree illustrates the relations just described. Four main groups of Lepidoptera yet remain to be accounted for, i.e. the Aculeate and Non-aculeate Tineoidea, the Euclecidea, and the Bombycoidea. The first of these, the Aculeate Tineoidea have their closest affinities with the Jugo-frenata and are figured arising with these forms from a common stem. The nonaculeate Tineoidea are clearly related to the aculeate series and to the Jugo-frenata thru the subfamilies Eriocottinae and Crinopteryginae and this relationship is indicated by the origin of the stem from which they diverge. The Psychidae are also related to this series thru the Telaeporiinae. The Cossidae which resemble the Acrolophidae more closely than any other family are also included here,

The two remaining groups, Euclecidea and Bombycoidea have many characters in common with both Jugate Lepidoptera and Tineoidea but show little

direct connection with either thru transitional forms. Consequently the series is derived from the point of common origin of the Hepialidae and Tineoidea and the Megalopygidae which seem most closely allied to the Hepialidae, thru the genus Norape, are inclined toward the Jugate stem. The Bombycoidea which are quite isolated are tentatively placed in the central portion of the tree thus showing their relations to both sides.

In constructing the phylogenetic tree the rules laid down by Busck (1909) have been followed. The main branches I to VI, represent the larger groups or super-families into which the primitive Lepidoptera have been divided in our previous discussion. All of the families or sub-families, which originate from one of these main branches are to be regarded as separate systematic entities having a common ancestor. Their origins are indicated by the position of the bases of their respective branches and their degrees of specialization by their vertical elevations in the tree. Thus the Prodoxidae, Incurvariidae, and Adelidae are derived from a common ancestor and have attained the same degree of specialization along slightly divergent lines. The Heliozelidae and Opostegidae, although likewise derived from the same aculeate stock have surpassed these other families and attained a much higher degree of specialization. The Crinopteryginae and Eriocottinae, on the other hand, have attained the same relative degree of specialization as the generalized Aculeata (Prodoxidae and Incurvariidae) which they closely resemble in certain genital characters, but they have had their origin from a non-aculeate ancestor and have attained these similar characters along entirely separate lines.

EXPLANATION OF FIGURES

The figures illustrating the forms described in this discussion have been drawn from slides of the genitalia which were softened in potassium hydroxide, cleared in carbol xylol, and mounted in Canada balsam. The outline was first traced from the slide by using a projection lantern with a microscope

attachment thus insuring a correct depiction of the shape and position of the structures. The details were then added from a study of the parts under the high power of a compound microscope. No attempt was made to draw the figures to a definite scale for the great variation in size, often within the same family, made this impractical. If such a practice had been followed the genitalia of the largest species would require a full page cut and the smallest would be scarcely large enough for satisfactory reproducing. Consequently all of the figures were made of sufficient size to best show the structure of their component parts. Unless specified otherwise in an accompanying legend the figures depict the ventral aspects of the genitalia, and the harpes are opened laterad to reveal the inner structures which would be obscured by them. The aedoeagus also is frequently removed in order to obtain a better view of it and the parts which it overlies,

The custom which most taxonomists use of accompanying the figure with the name of the species has been followed, and in order to make this work useful to the taxonomist as well as to the comparative morphologists the genotype has been figured wherever possible. Whenever the type of the genus on which an important family is based was not available for study a large series of species from the genus were examined and the most typical one figured. When two or more distinct lines of specialization were observed to occur in a family or genus, figures illustrating these types were always included.

ACKNOWLEDGMENTS

The investigation of the use of the structures comprising the male genitalia of the Tineoidea as characters for determining the relationship of the various families and genera was begun at the suggestion of Dr. Wm. T. M. Forbes, and the author wishes to thank him for the direction

of the early part of this work. The subsequent enlarging and completion of this study was made under the direction of Dr. Wm. A. Riley, to whom the writer is deeply indebted for his patient personal supervision and valuable criticism. I am also grateful to Drs. Edward Meyrick, Alfred Philpott, Cornelius Betten, Oscar Oestlund and Mr. Carl Heinrich, for important suggestions and criticisms which they have made in connection with certain groups included in this paper.

The material on which the present study was based was obtained thru the courtesy of many specialists from a large number of educational institutions. For the gift and loan of these specimens, without which the work could not have been completed, I am especially indebted to Drs. J. C. Bradley, Wm. T. M. Forbes, J. G. Needham, Cornelius Betten, George P. Engelhardt, August Busck, A. N. Caudell, A. Philpott, A. J. Turner, V. Hudson, Wm. Barnes, R. J. Tillyard, A. F. Braun, J. C. Faure, Messrs. Carl Heinrich, F. H. Benjamin and V. Le Cerf.

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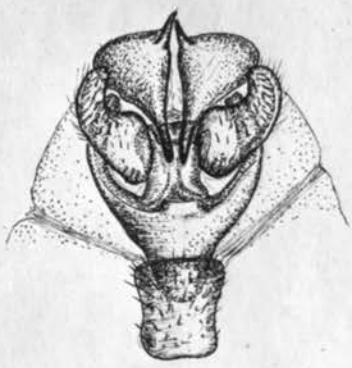
PLATES I - XIV

MALE GENITALIA OF THE PRIMITIVE LEPIDOPTERA.

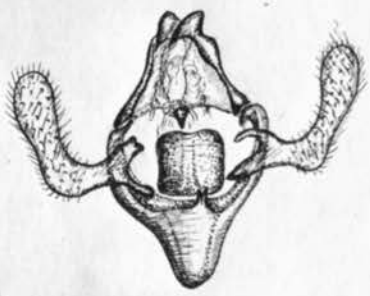
PLATE I

HEPIALIDAE AND PROTOTHEORIDAE

1. Oncopera intricata Walk.
2. Gorgopis libania Stoll.
3. Perrissectis australasiae Don., Right harpe
4. Porina novazealandiae Walk.
5. Hepialus (Charagia) eximius Scott., Right harpe
6. Phassus metellus DMU., Eighth tergite included
7. Hepialus hectoides Boisd., Right harpe
8. Palpifer sexnotatus Moore.
9. Prototheora petrosema Meyr.



1. intricata



2. libania

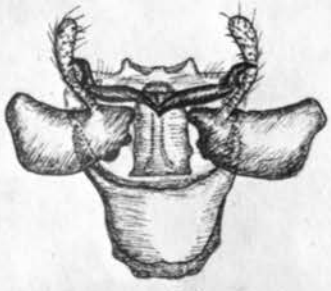
3. australasiae

4. novazealandiae

5. eximius

6. metellus

7. hectoides



8. sexnotatus

9. petrosema

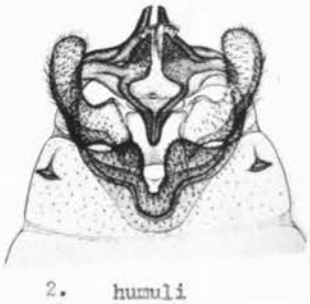
Hepialidae and Prototheoridae

PLATE II.

HEPIALIDAE AND MNESARCHAEIDAE

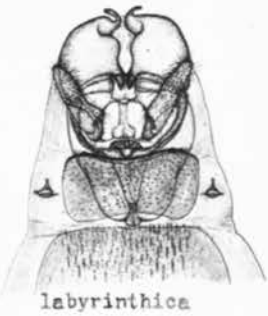
1. Hepialus lupulinus L.
2. Hepialus humuli L.
3. Porina fuscomaculata Walk.
4. Trictena labyrinthica Don.
5. Mnesarchaea hamadelpha Meyr.
6. Mnesarchaea loxoscia Meyr.

1. lupulinus

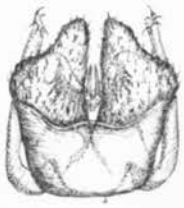


2. humuli

3. fuscomaculata



4. labyrinthica



5. hamadelpha

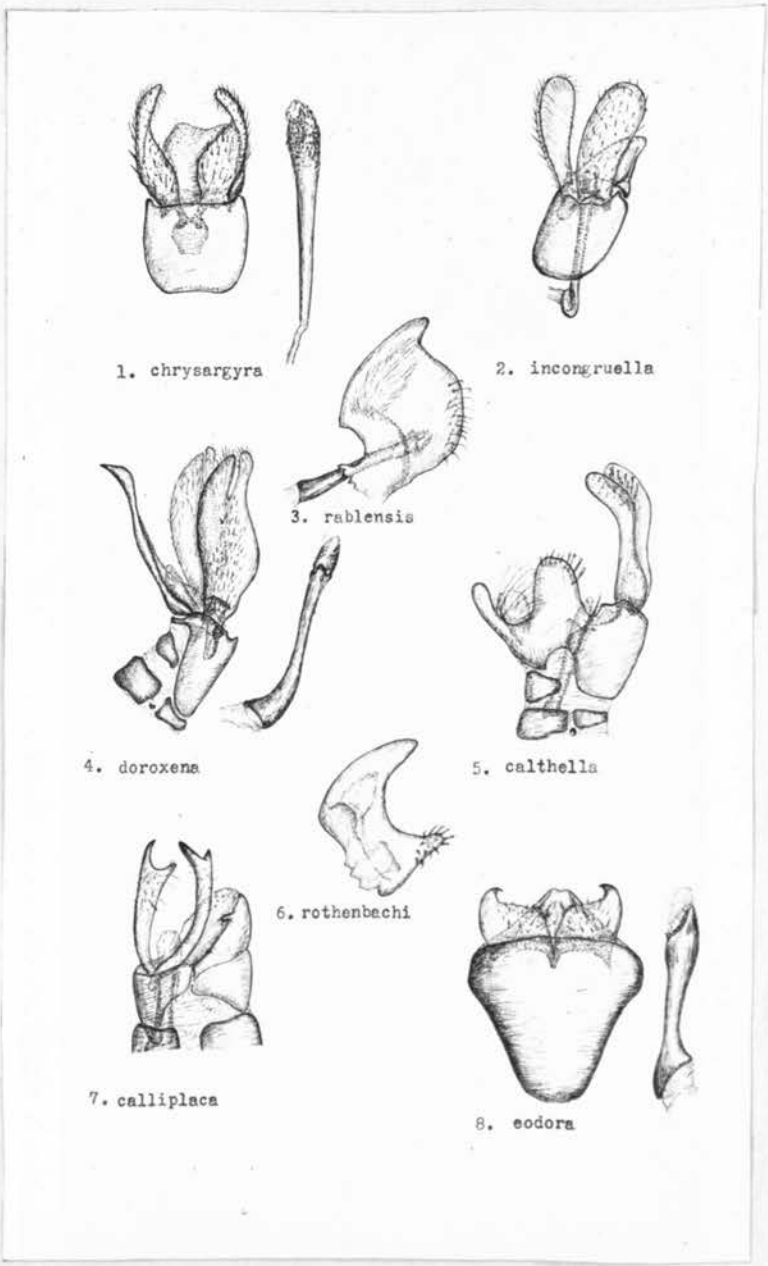
6. loxoscia

Hepialidae and Mnesarchaeidae

PLATE III.

MICROPTERYGIDAE

1. Sabatinca chrysargyra Meyr. Aedoeagus removed.
2. Sabatinca incongruella Walk. Ventro-lateral view of right side.
3. Micropteryx rablensis Zell. Latus of tegumen.
4. Sabatinca doroxena Meyr. Lateral view of left side, aedoeagus removed.
5. Micropteryx calthella L. Lateral view of left side.
6. Micropteryx rothenbachii Frey. Latus of tegumen.
7. Sabatinca calliplaca Meyr. Ventro-lateral view of right side.
8. Sabatinca eodora Meyr. Aedoeagus removed.

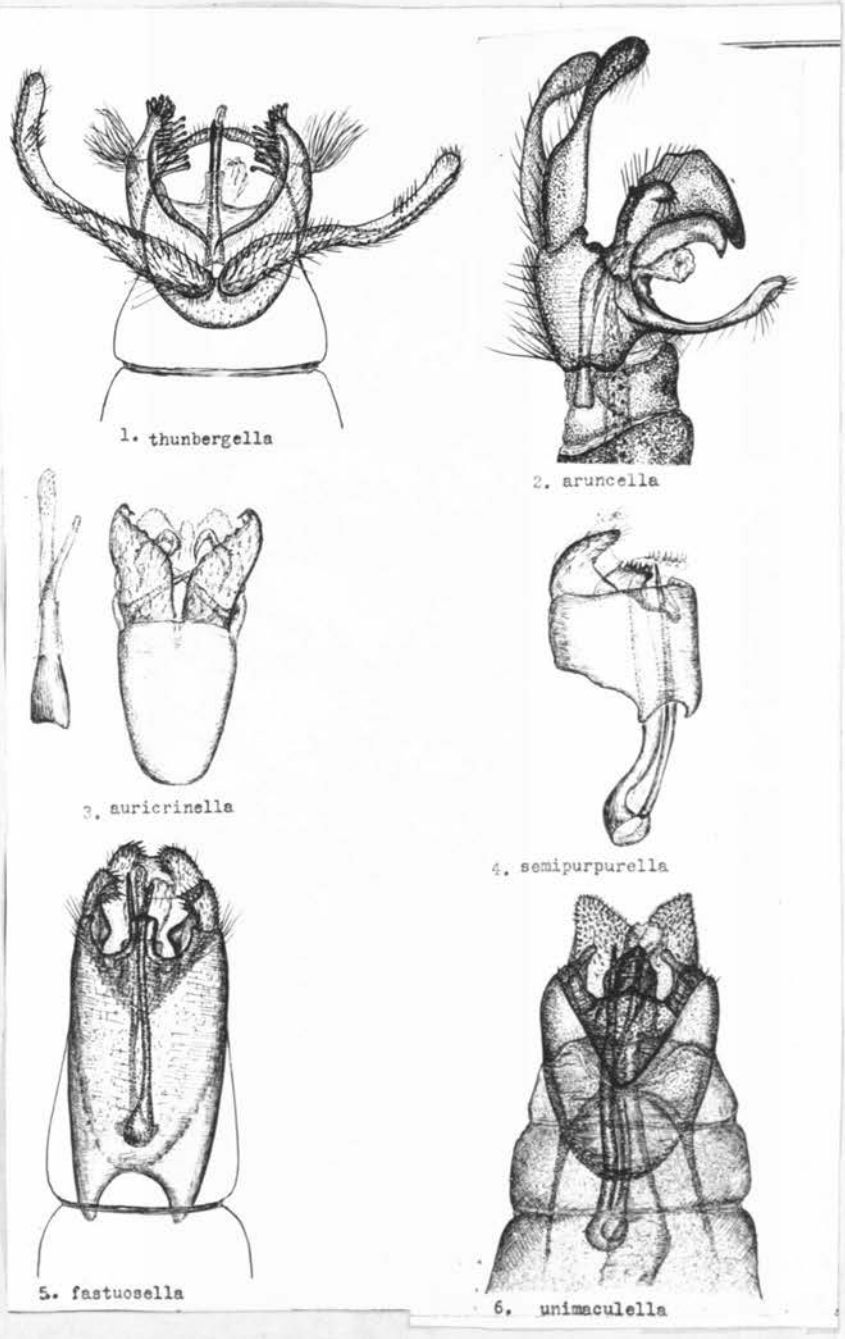


Micropterygidae

PLATE IV.

MICROPTERYGIDAE AND ERIOCRANIIDAE

1. Micropteryx thunbergella F.
2. Micropteryx aruncella Sc. Lateral view of right side.
3. Epimartyria auricrinella Wlsm. Aedoeagus removed.
4. Eriocrania semipurpurella Stph. Lateral view of left side.
5. Mnemonica subpurpurella Hw. fastuosella Zell.
6. Eriocrania unimaculella Ztt.



Micropterygidae and Eriocraniidae

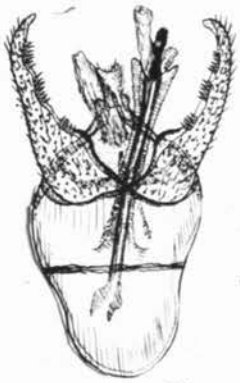
PLATE V

ADELIDAE AND INCURVARIIDAE

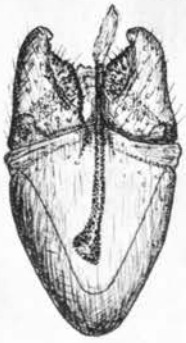
1. Adela septentrionella Wlsm.
2. Ceromitia wahlbergi Zell.
3. Nemophora swammerdammella L.
4. Adela viridella Sc.
5. Isccorypha mediostriatella Clem., Eighth somite included
6. Nematois annae Zell.
7. Paraclemensia acerifoliella Fh.
8. Lampronia praelatella Schiff., Left harpe reversed
9. Incurvaria muscalella F.

1. septentrionella

2. wahlbergi

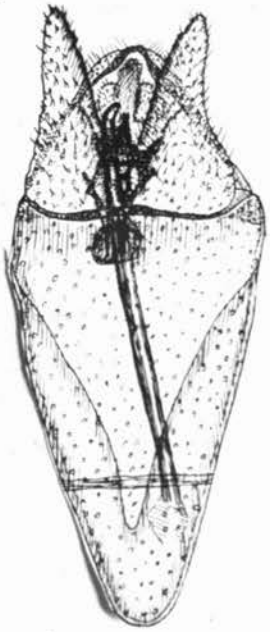


3. swammerdamella

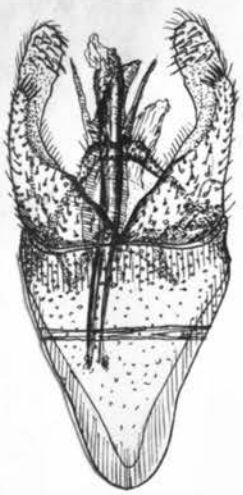


4. viridella

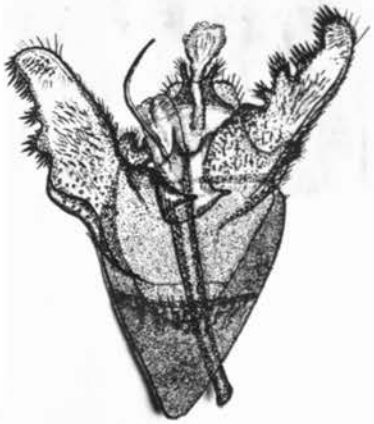
5. mediostriatella



6. annae



7. acerifoliella



8. praelatella

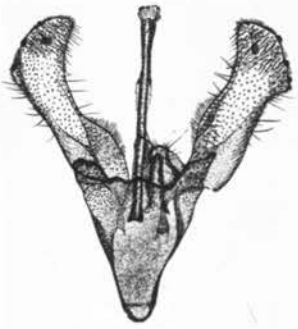
9. muscalella

Incurvariidae and Adelidae

PLATE VI

PRODOXIDAE, TISCHERIIDAE, AND OPOSTEGIDAE

1. Prodoxus quinquepunctellus Chamb.
2. Tegaticula alba Zell.
3. Tischeria malifoliella Clem.
4. Coptotriche zelleriella Clem.
5. Opostega salaciella Tr.
6. Opostega nonstrigella Chamb.



1. quinquepunctellus

2. alba

3. malifoliella

4. zelleriella

5. salaciella

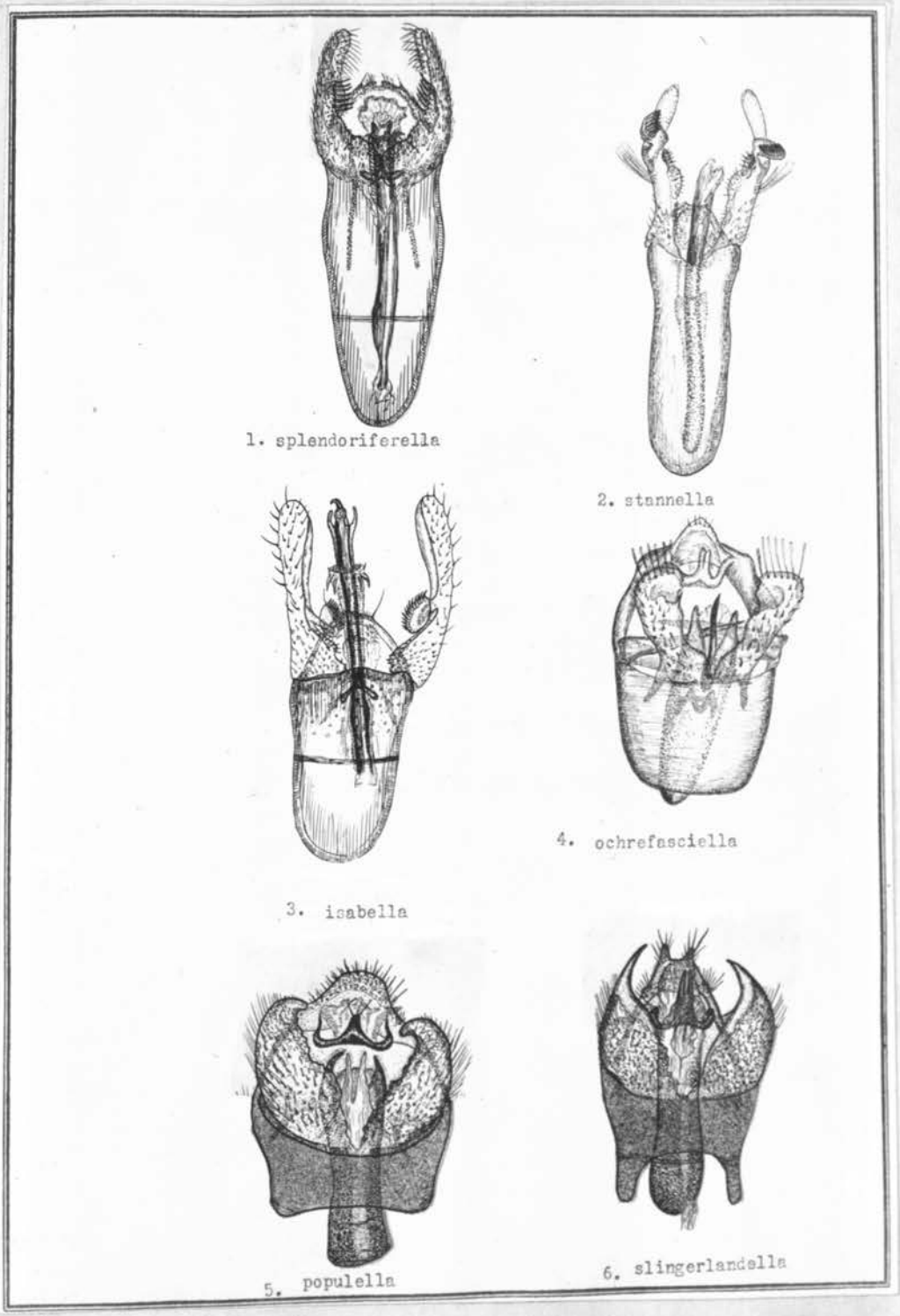
6. nonstrigella

Prodoxidae, Tischeridae, and Opostegidae

PLATE VII

HELIOZELIDAE AND NEPTICULIDAE

1. Coptodisca splendoriforella Clem.
2. Heliozela stanella Tr.
3. Antispila isabella Clem.
4. Obrussa ochrefasciella Chamb.
5. Ectoedemia populella Bsk.
6. Nepticula slingerlandella Kearf.



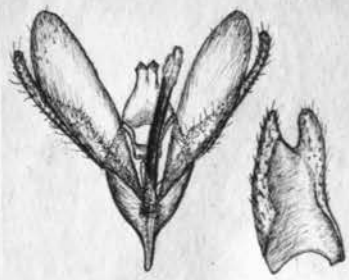
Heliozelidae and Nepticulidae

PLATE VIII

TINEIDAE

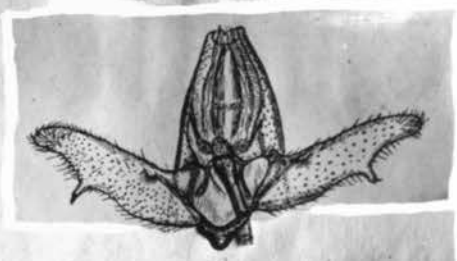
1. Narycia (Xysmatodoma) heliochares Meyr.
2. Narycia saxosa Meyr., Right harpe
3. Eriocottis fuscanella Z.
4. Apreta paradoxella Dtz., Aedoeagus removed
5. Rhodobates pallipalpellus Rb.
6. Dyotopasta yumaella Kearf.
7. Lypusa maurella F.

Plate VIII.

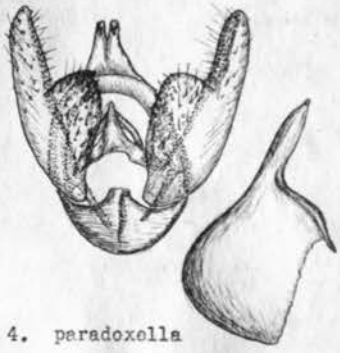


2. saxosa

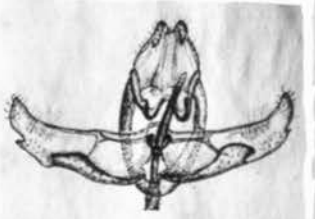
1. heliochares



3. fuscanella



4. paradoxella



5. pallipalpellus

6. yumaella

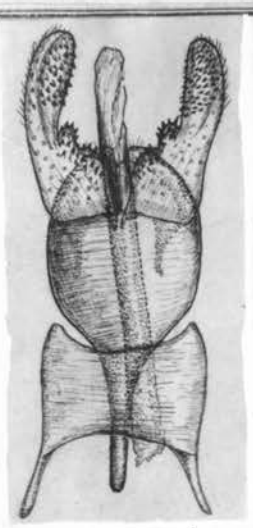
7. maurella

Tineidae

Plate IX.

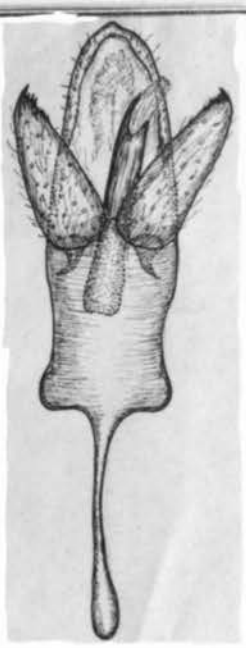
TINEIDAE, (TELAEPORIINAE AND TEICHOBIINAE) AND PSYCHIDAE.

1. Kearfottia albifasciella Fern.
2. Solenobia walshella Clem.
3. Chalia rileyi Heyl.
4. Telaeporia tabulosa Ritz.
5. Melasina lugubris Hb.
6. Diachorisia vilatella Clem.
7. Euplocamus delagrangei Rag.
8. Ateliotum hungaricellum Z.
9. Teichobia verhuellella Stt.

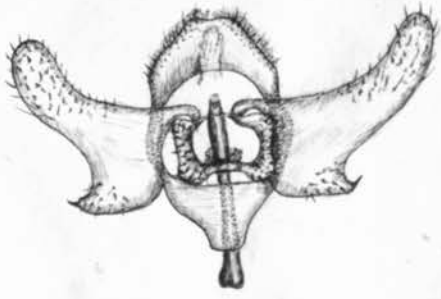


1. albifasciella

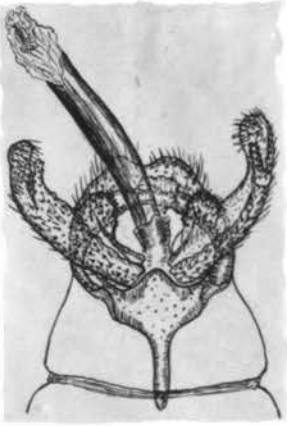
2. walshella



3. rileyi

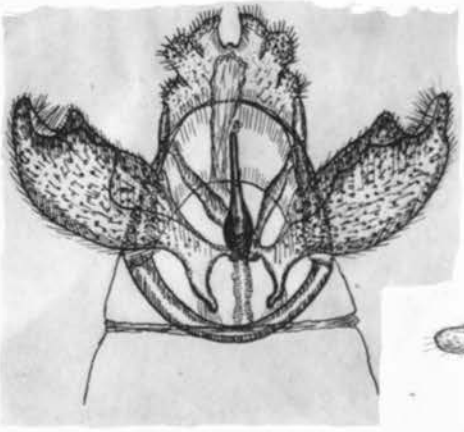


4. tabulosa

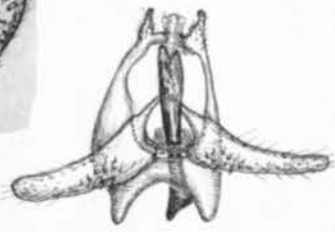


5. lugubris

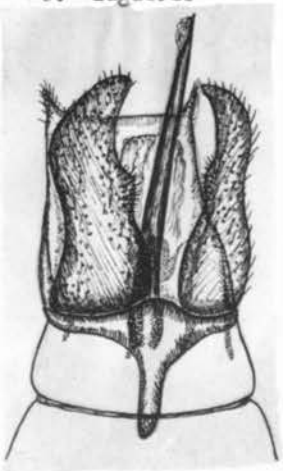
6. vilatella



7. delagrangei



8. hungaricellum



9. verhuellella

Tineidae, (Telaeporiinae and Teichobiinae) and Psychidae

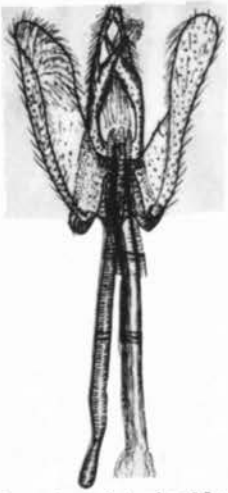
PLATE X.

TINEIDAE

1. Tinea pellionella L.
2. Moerarchis australasiella Zell.
3. Monopis dorsistrigella Clem.
4. Xylesthia pruniramiella Clem.
5. Setomorpha insectella Fab.
6. Oenoe hybromella Clem.
7. Homosetia miscocristatella Zell.
8. Meesia vinculella H.S.

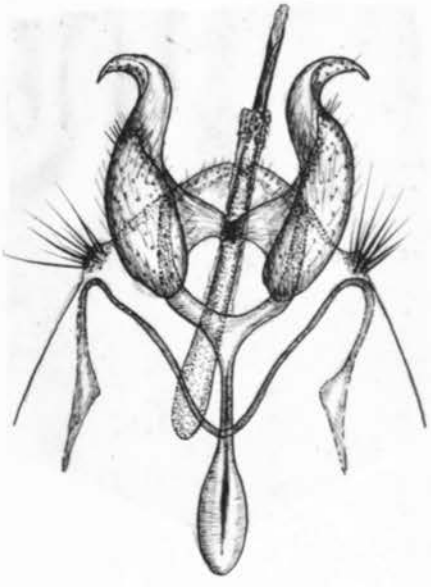
1. pellionella

2. australasiella

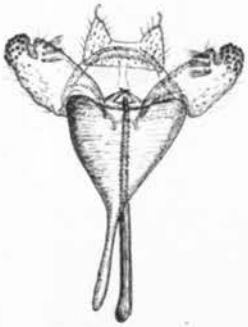


3. dorsistrigella

4. pruniramiella



5. insectella



6. hybromella

7. miscecristatella

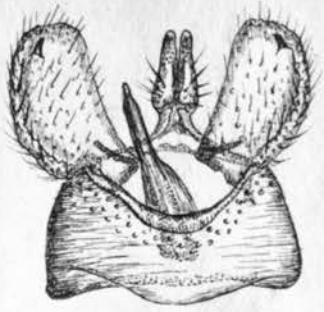
8. vinculella

Tineidae

PLATE XI

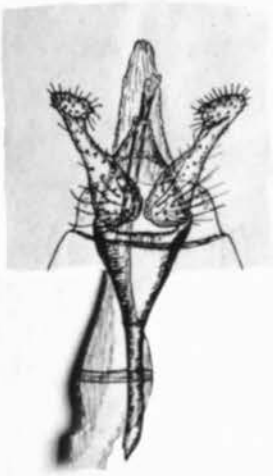
TINEIDAE, (SCARDIINAE AND AMYDRIINAE), AND ACROLEPIIDAE

1. Tinea xystidophora Meyr.
2. Tinea misella Zell.
3. Acrolepia incertella Chamb.
4. Amydria effrenatella Clem.
5. Amydria margoriecella Dtz.
6. Scardia boleti F.
7. Scardia coloradella Dtz.

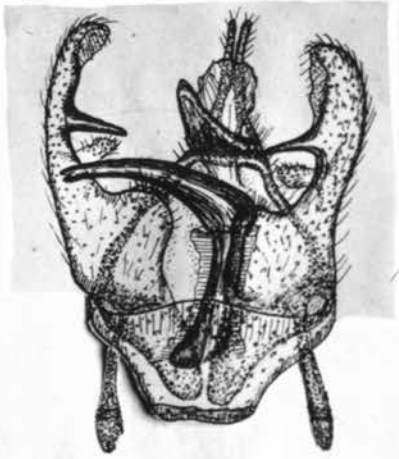


1. xystidophora

2. misella

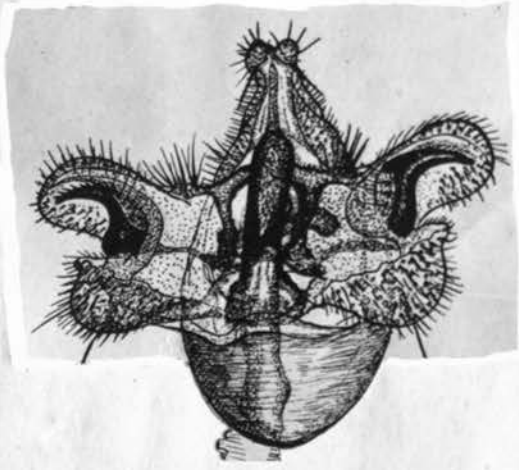


3. incertella

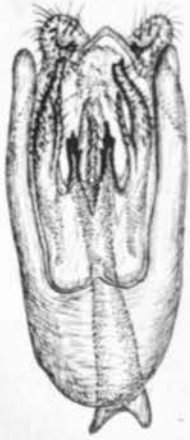


4. effrenatella

5. margoriella



6. boleti



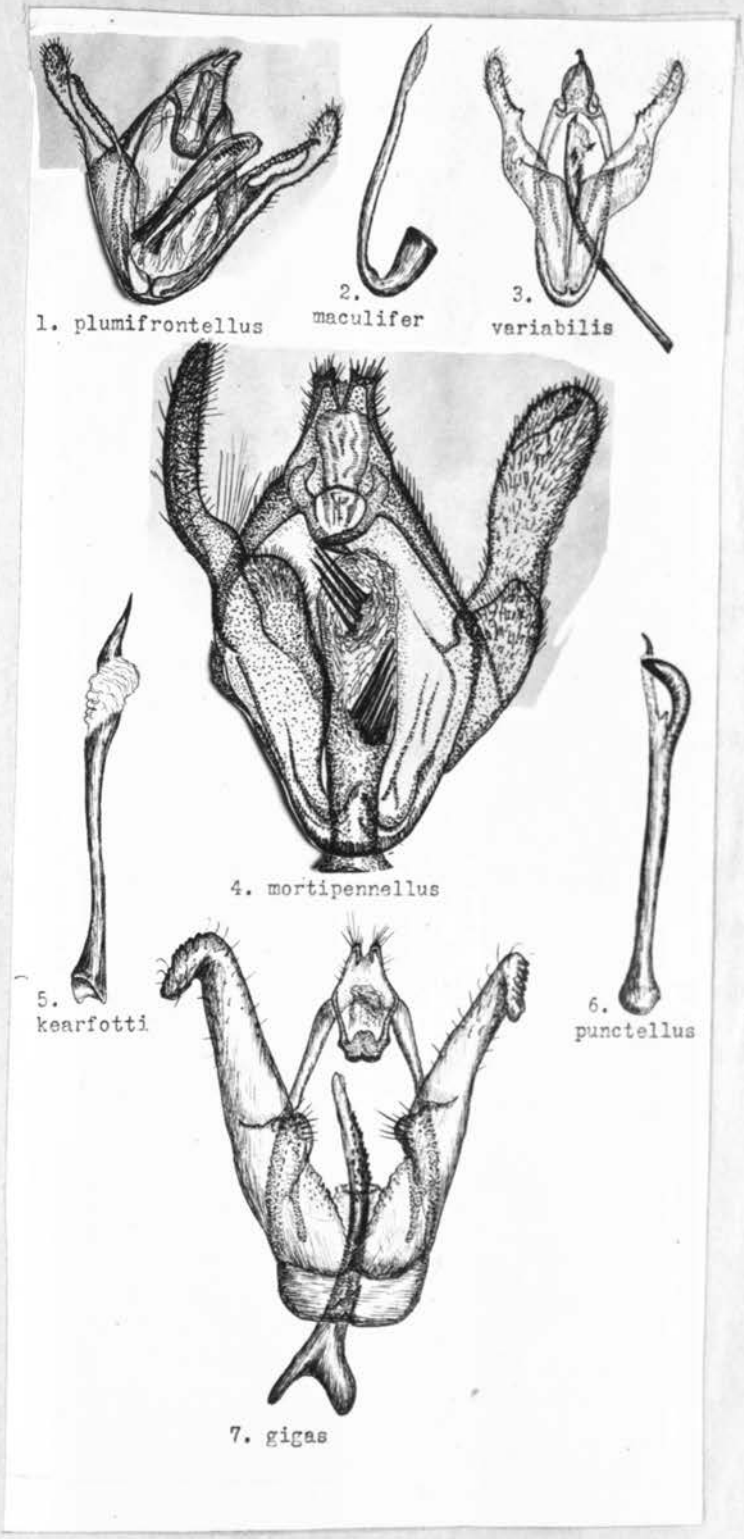
7. coloradella

Tineidae, (Scardiinae and Amydriinae) and Acrolepiidae

PLATE XII.

ACROLOPHIDAE

1. Acrolophus plumifrontellus Clem.
2. Acrolophus (Eulepiste) maculifer Wlsm. Aedoeagus.
3. Acrolophus (Ortholophus) variabilis Wlsm.
4. Acrolophus (Hypoclopus) mortipennellus Grt.
5. Acrolophus(Eulepiste) kearfotii Dyar. Aedoeagus.
6. Acrolophus (Neolophus) punctellus Bsk. Aedoeagus.
7. Amisthus gigas (Peru)

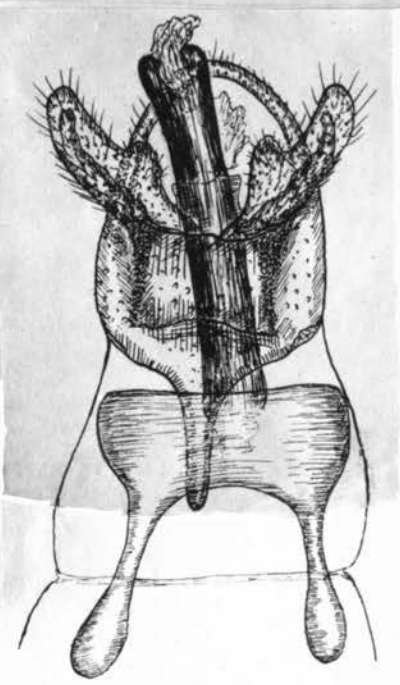


Acrolophidae

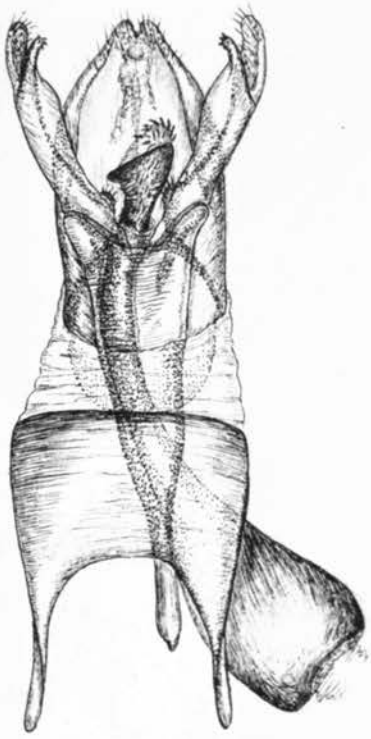
PLATE XIII

PSYCHIDAE AND LIMACODIDAE

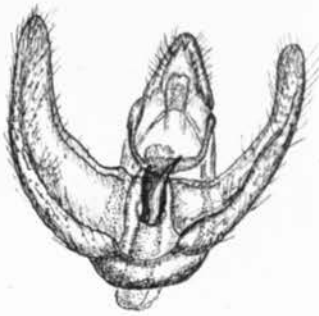
1. Eurycyttarus confederata Grt., Eighth somite included
2. Thyridopteryx ephemeraeformis Haw., Eighth somite included
3. Blassoptila microxutha Turn.
4. Heterogenea asella Schiff.
5. Euclea delphinii Bdv., Aedoeagus removed and right harpe cut off.
6. Cochlidion avellana L.
7. Microleon longipalpis Butl.
8. Setora nitens ., Central portion of aedoeagus cut out.
9. Cania bandura Wlk.
10. Miresa flavescens Wlk.



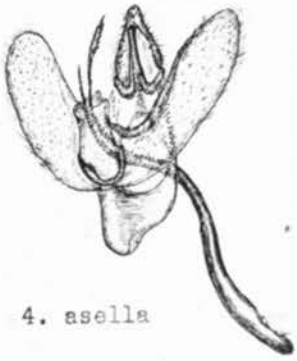
1. confederata



2. ephemeraeformis

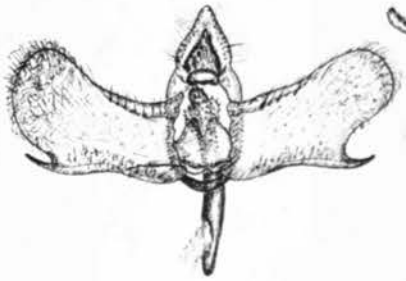


3. microxutha



4. asella

5. delphinii



6. avellana

7. longipalpis

8. nitens

9. bandura

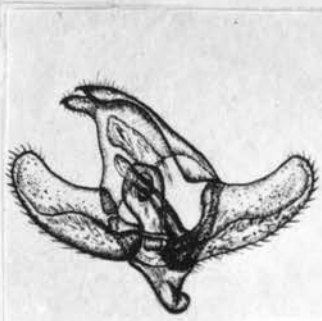
10. flavescens

Psychidae and Limacodidae

PLATE XIV

COSSIDAE, MEGALOPYGIDAE, DALCERIDAE, LACOSOMIDAE, AND BOMBYCIDAE

1. Givira mucidus H. Edw.
2. Eudoxyla strix Aedoeagus removed
3. Cossula magnifica Stkr.
4. Givira cleopatra B. & McD., Tegumen and uncus
5. Zeuzera multistrigata Mr., Tegumen, uncus, gnathos and juxta
6. Norape tener Druce.
7. Norape ovina Sepp., Aedoeagus
8. Trosia obsolescens Dy.
9. Megalopyge opercularis A. & S., Aedoeagus removed
10. Dalcerides ingenita H. Edw.
11. Lacosoma chirodota Grt.
12. Bombyx mori L.



1. mucidus

2. strix

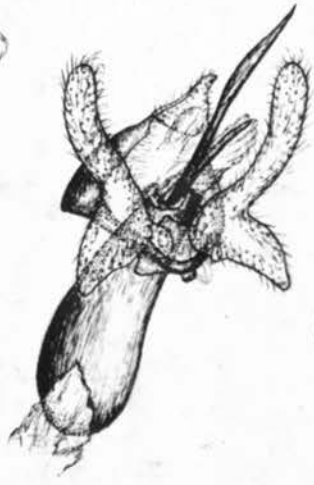
3. magnifica

4. cleopatra

5. multistrigata

6. tener

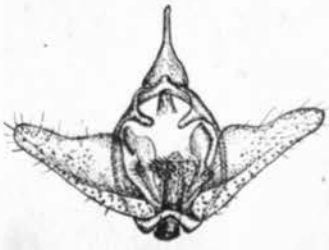
7. ovina



8. obsolescens

9. opercularis

10. ingenita



11. chiridota

12. mori

Cossidae, Megalopygidae, Dalceridae, Lacosomidae, and Bombycidae