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Title: TAXONOMY AND DISTRIBUTION OF THE LEAFHOPPER GENUS APHRODES CURTIS (HOMOPTERA:CICADELLIDAE) IN NORTH AMERICA

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Dr. Paul Oman

The subfamily Aphrodinae is represented in the Nearctic Region by eight species contained in a single tribe, Aphrodini, and genus *Aphrodes*. The external and internal morphology, biology and ecology of the Nearctic members of the genus *Aphrodes* were investigated.

Distributional evidence indicates that six of the eight species, belonging to the subgenera *Aphrodes* and *Anoscopus*, have been introduced from the Palearctic Region, presumably via maritime shipping. These six species occur either within the West Coast and adjacent land area or the East Coast and Great Lakes region and adjacent land areas, or both. The other two species, belonging to the subgenus *Stroggylocephalus*, are believed to be indigenous to North America and are not known to occur elsewhere. These two species have been recorded from numerous North American localities between

35°N and 58°N latitude. The irregular distribution of Nearctic members of the subgenus *Stroggylocephalus* indicates that these species now exist as relict populations. Two species of the subgenus *Stroggylocephalus* are recorded from Europe with one, *agrestis*, reported as occurring in North America. However, records of *agrestis* in North America were not verified, and prior records are believed to be erroneous. A single female of the subgenus *Stroggylocephalus* from Kentucky apparently represents a new species, the third known from North America.

The Nearctic species of *Aphrodes* are here assigned to three subgenera: *Aphrodes* *s. s.*, *Anoscopus* and *Stroggylocephalus*. Species differentiation is based primarily on features of the male genitalia. The structure, length, and number of retrorse spines of the aedeagus is unique for each species. The structure of the pygofer hook and style, the shape and setation of the genital plate and the absence or presence of a secondary papilliform structure adjacent to the pygofer hook were found to be useful in discriminating between some species and species groups. Morphological differentiation of females of some species is nearly impossible. The number of dentations on valve II of the ovipositor was found to be unreliable for discriminating species or species groups, in contrast to Readio's findings (1922).

Color and color pattern of the forewing, face and crown in males and some females were frequently found to be useful for recognition of some species and species groups even though considerable amounts of variation occur within a species. Wing venation is variable; the venation of the two forewings of the same insect are often different. However, the length of the forewing was found to be a reliable character for distinguishing members of *Aphrodes* *s. s.* and *Stroggylocephalus* from *Anoscopus*. Crown L:W ratios of the females are usually smaller than the males and ratios of both sexes are unreliable for species differentiation because of the amount of infraspecific variation.

Evidence regarding anatomy of the reproductive organs of species of *Aphrodes*, studied for the purpose of comparison with representatives of other genera and subfamilies of leafhoppers, although limited in scope, provides information useful for species differentiation in sexually mature males. The structure of the reproductive tracts supports the conclusion that the species studied belong to a single genus *Aphrodes*, or at most to two genera, *Aphrodes* and *Stroggylocephalus*.

The Nearctic species of the genus *Aphrodes* are characterized through illustrations, verbal descriptions and a diagnostic key. Infraspecific variation consists primarily of differences in color, color pattern and size. The male genitalia are relatively uniform with some minor differences occurring in the length and rugosity of the styles, rugosity and crenulations on the lateral margin and apex of the pygofer hooks, and length and position of the retrorse spines of the aedeagus. The nymphal instars of three species--*A. bicinctus*, *albifrons* and *serratulae*--are described. The color and color pattern were found to be distinct for each of these species from the second instar to the final molt.

Field and laboratory studies demonstrate that at least some of the species of *Aphrodes* are polyphagous. Two species, *serratulae* and *albifrons*, appear to prefer grasses, but will also feed on clovers. Those Nearctic species of *Aphrodes* that have been studied with reference to habitat preference are found in such places as near the base of plants, in soil surface litter, and under or around rocks and boards.

Members of *Aphrodes* *s. s.* and *Anoscopus* are univoltine, with a few females surviving the winter. Adults of *Stroggylocephalus* have been recorded during nearly every month which suggests a polyvoltine life cycle.

# Taxonomy and Distribution of the Leafhopper Genus *Aphrodes* Curtis (Homoptera: Cicadellidae) in North America

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# TAXONOMY AND DISTRIBUTION OF THE LEAFHOPPER GENUS <u>APHRODES</u> CURTIS (HOMOPTERA: CICADELLIDAE) IN NORTH AMERICA

## I. INTRODUCTION

Leafhoppers affect plants adversely in two ways; through direct injury caused by their feeding, and through the transmission of plant pathogens such as viruses and mycoplasma-like organisms. Numerous species have been incriminated as vectors of pathogens that cause diseases in certain crop plants (Nielson, 1968). However, their agricultural importance remains debatable because we know so little of their role in maintaining reservoirs of pathogens in non-crop plants, from which such organisms may be carried by leafhoppers to other susceptible plant hosts. An understanding of the complexities involved in the epidemiology of phytarboviruses and mycoplasma-like organisms requires, among many other things, knowledge of what species are capable of transmitting pathogens, where and when they occur, and how they behave. This dissertation is concerned with one small group of leafhoppers, the genus <u>Aphrodes</u> Curtis, two members of which have been incriminated as vectors of plant pathogens.

Most major insect pests of agricultural crops in North America are of foreign origin, chiefly from Eurasia (Clausen, 1956). Among the leafhoppers that transmit plant pathogens some (<u>e</u>.<u>g</u>.

Fieberiella florii, Euscelidius variegatus) are known immigrants; others (e.g. Circulifer tenellus) are of uncertain origin (Oman, 1969). In taxa that have a typical Holarctic distribution, such as Aphrodes, the geographic origin of individual species is frequently open to question. Published records for species of Aphrodes in North America strongly suggest that some are immigrants from the Old World, but because of doubt as to the accuracy of specific identifications relative to many of the records, a critical assessment of the evidence bearing upon their origins has not been possible. This study was undertaken in an effort to establish which of the numerous species of the genus actually occur in North America and, from an analysis of distributional patterns, determine which are immigrants and which are native to the Nearctic Region. To accomplish these objectives it was necessary, first of all, to develop a sound method for species discrimination. Additional objectives include an improved understanding of the host associations, ecology and general biology of those that occur in the northwestern United States.

Species now included in the genus Aphrodes were among those assigned to the genus Cicada by Linnaeus in 1758. The taxonomy and nomenclature of species belonging to this taxon have been in a state of confusion since that time. For example, published references pertaining to Aphrodes albifrons (L.) involve eight different generic names with 21 specific names as synonyms or recognized varieties, and 17 letter-designated varieties (Metcalf, 1963; 73-105). The literature pertaining to other common and widespread species such as A. bicinctus (Schrank) and A. serratulae (Fabricius) is fully as complex and confused. Two species occurring in North America have been for many years incorrectly synonymized with other species of Aphrodes. In addition, numerous species belonging to other genera and subfamilies have at one time or another been associated with Aphrodes.

The genus Aphrodes, as treated here, is the only genus in the subfamily Aphrodinae. Members of the subfamily Aphrodinae are characterized by a transverse ledge within the ocellocular area and above the antennae forming a distinct antennal pit, two ocelli located on or slightly above the anterior margin of the crown, lateral frontal sutures extending nearly to the ocelli, a flat or slightly convex clypellus, and a concealed episternum.

They are robust, medium sized leafhoppers, somewhat dorsoventrally flattened, and mottled light brown, or rufous to fuscous in color. Color dimorphism is readily apparent between the sexes of six species with the males being more contrastingly marked with characteristic transverse bands or stripes.

The genus Aphrodes Curtis is represented in North America by eight species. They inhabit grass/forb associations such as lawns, pastures, as well as some economic crops (strawberry, etc.) and are customarily found near or at the base of grasses and other foliaceous plants, especially in late summer and early fall.

This study summarizes the distribution and taxonomy of the genus Aphrodes in North America. Six of the species are believed to be adventive, probably as introductions from the Palearctic Region by maritime shipping. Two species are considered to be endemic to North America since they are not known from the Palearctic Region and their known distribution suggests that they exist as relict populations. Color and morphological characters were evaluated for taxonomic usefulness in species discrimination, especially among the females.

## II. LITERATURE REVIEW

Few groups of leafhoppers have had as turbulent a nomenclatorial history as have the species of Aphrodes Curtis. The specific and generic synonymy involved is covered in detail in Metcalf's Catalogue (1963) which includes references to all literature available prior to 1956, and the following summary of taxonomic literature deals only with the published actions that are necessary to understand the present status of the numerous generic and specific names applicable to the Nearctic elements. The more important contributions regarding biology and involvement in plant pathogen transmission are also summarized.

Leafhoppers now assigned to the genus Aphrodes Curtis include some of the first species described by early systematists. The tenth edition of Linnaeus' Systema Naturae contains descriptions of two species, Cicada albifrons and C. bifasciata. Linnaeus added still another species, C. striata, in 1776, but since the species name striata is a homonym, it is now known as A. bicinctus (Schrank), 1776. Several other 18th century or early 19th century workers added species under different generic names: Cicada serratulae Fabricius, 1775; Cicada flavostriata Donovan, 1799; Jassus albiger Germar, 1821; Tettigonia mixta Say, 1825 and Selenocephalus placidus

Provancher, 1889. The name Aphrodes first appeared in the literature in 1829 when Curtis published it without description but with a listing of 17 specific names.

Other generic designations used by early workers in connection with descriptions of species subsequent to Curtis' establishment of Aphrodes, some of which apply to various components of the genus as now recognized, are as follows: Acucephalus Germar, 1833 (and the unwarranted emendation or erroneous spelling, Acocephalus by Burmeister, 1835 and others); Pholetaera Zetterstedt, 1840; Anoscopus Kirschbaum, 1858 (now considered a subgenus of Aphrodes); and Stroggylocephalus Flor, 1861, originally proposed as a subgenus of Acocephalus, and improperly emended or misspelled as Strongylocephalus by Kirschbaum, 1868. Still another generic name that appears in literature pertaining to species of Aphrodes is Amblycephalus Curtis, 1833, a primary homonym of Amblycephalus Kuhl, 1826 (Reptilia).

The nomenclatural confusion resulting from the use of various generic names by early workers is clearly equaled by the divergent opinions of workers regarding the classification of the group at the generic, tribal and subfamily levels. Stroggylocephalus has been considered by many workers (e.g. Ribaut, 1952; Metcalf, 1963; Vilbaste, 1968; Nast, 1972; Hamilton, 1975) as distinct from Aphrodes; others (e.g. Oman, 1949; Ishihara, 1953) have treated it as a synonym or subgenus of Aphrodes. Similarly, though to a lesser extent, Anoscopus has appeared and disappeared in the literature. K.G.A. Hamilton (1975) proposes the division of Aphrodes into four genera, an arrangement that would recognize as genera, Anoscopus, Stroggylocephalus and Aphrodes s.s., here treated as subgenera. The situation is further confounded by some remaining uncertainties regarding type species fixations because several generic and subgeneris names involve problems that cannot be resolved until certain obscure literature becomes available for examination.

At the supergeneric level divergent opinions regarding both hierarchial rank and phylogenetic affinities are again evident. The group was first accorded family rank (as Acocephalidae) by Dohrn in 1859. Some subsequent authors (e.g. Oshanin, 1912; Van Duzee, 1917; Lawson, 1920; Medler, 1943; Delong, 1948; Oman, 1949; Ribaut, 1952) have accorded tribal or subfamily rank to taxa containing Aphrodes and close relatives, though with little uniformity as to composition of the tribe or subfamily, or higher category in which the group was placed. Evans (1947) recognized a subfamily Aphrodinae composed of four tribes--Aphrodini, Errhomenellini, Evacanthini and Signoretini--an arrangement followed by Metcalf in his Catalogue (1963). Oman (1949) included a single genus, Aphrodes, in the subfamily Aphrodinae with Stroggylocephalus, Acucephalus, Anoscopus, and Pholetaera treated as synonyms of Aphrodes.

Nast (1972) recognized two genera, Stroggylocephalus and Aphrodes, in the subfamily Aphrodinae. The latest published consideration of the Aphrodinae is that of Hamilton (1975) who contends, based largely on the spine and setal structures and their arrangement on the hind tibia, that the subfamily Aphrodinae also encompasses the subfamily Deltocephalinae (Euscellidae of Metcalf, 1967), with the name Aphrodinae having priority.

Hamilton's characterization of Aphrodinae includes a broad assemblage of leafhoppers with distinct differences in the external (and probably internal) morphology, behavior and habitat. These differences seem to justify the separation of the Aphrodinae and the Deltocephalinae since combining the two taxa results in a very heterogenous grouping. A preliminary study of the morphology of the internal reproductive system produced evidence that appears to support Oman's concept of the subfamily Aphrodinae as a separate subfamily, although such evidence is still not available for most deltocephaline species.

Evans (1955) has added one new species of Aphrodes (A. flavigera) from South Africa. However, his characterization of flavigera makes its affiliation with the Aphrodinae doubtful because the ocelli are located on the face below the anterior margin of the crown, and the crown and pronotum are pitted.

I consider Aphrodes to include three subgenera: Anoscopus, Aphrodes s. s., and Stroggylocephalus. I have not given generic status to these taxa because the Nearctic species are structurally very similar as are those members of the Palearctic species available to me for study. Examination of the world fauna may further clarify the status of these subgeneric names.

Published information regarding the morphology and biology of Aphrodes occurs primarily in the Old World literature. To a considerable extent the same is true of information dealing with the transmission of plant pathogens, there being relatively little published on these topics in North America. Metcalf's Catalogue (1963) lists all literature available to him prior to 1955, and includes annotations in each listing. The use of the catalogue alleviates much of the task of an extensive literature search. The annotated topics include such things as biology, ecology, listed, key, symbionts, food plants, predators, disease vectors, and others. The following resume is concerned only with the more important contributions concerning the Nearctic fauna, or with contributions that are relevant to both the Old and New World faunas.

Osborn (1916) made observations on the biology and behavior of two species of Aphrodes (bicinctus and albifrons). His observations included possible host plant relationships, ecology and limited information on the immature stages. Osborn's identification of albifrons is probably erroneous since the illustration of the immature stage resembles that of serratulae and because I have failed to verify albifrons' presence in Eastern United States. Chiychowski has also contributed to our knowledge of the biology, primarily the life cycle and pathogen transmission, of A. bicinctus in Canada. Nielson (1968) lists two species of Aphrodes, bicinctus and albifrons, that have been implicated in the transmission of plant pathogens. Both species have been shown to transmit plant disease in the Palearctic Region, but only bicinctus has been shown to transmit plant disease in the Nearctic Region (Chiykowski, 1961, 1970). Ossiannilsson (1949) described the morphology and function of sound producing organs of auchenorrynchous Homoptera which includes three species of Aphrodes, one of which is not known from North America.

# III. MATERIALS AND METHODS

The acquisition of potentially useful biological information, the precise association of immature stages with adults, and in some cases the proper association of the two sexes in the adult stage necessitated obtaining and culturing living specimens. Thus, the study required both live and preserved specimens. Preserved speciments, borrowed from numerous institutional collections or field collected, were used in studies of comparative morphology and anatomy. In all, more than 1300 preserved specimens from Nearctic localities and 200 from Palearctic localities were examined.

## Morphological Studies

External and internal morphological characters were examined for the usefulness in the taxonomic study of the genus Aphrodes. All general techniques used are outlined below. Definitions for certain morphological terms used in this section are given in the Appendix.

### Collecting, Preservation and Mounting Methods

Field collections were made with a canvas sweep net and aspirator, and with a motor operated suction device, "D-Vac." The sweep net was used primarily in areas of medium and tall vegetation and the captured leafhoppers were aspirated from the net and transferred to a killing bottle or rearing chamber. An aspirator was useful for collecting specimens from around and under rocks, boards and clumps of vegetation. However, the "D-Vac" was the preferred method for sampling for the presence or absence of leafhoppers. The nozzle of the "D-Vac" was held close to the ground and swept over the top of the vegetation. The collected material was then removed from the "D-Vac" net, placed in a container with appropriate collection data for transporting, and then transferred to a Berlese funnel if living specimens were needed, or put directly in 70 percent alcohol. When living material was desired, a wet filter paper was placed in the bottom of the Berlese collecting chamber. The collecting chamber was changed every 12-24 hours and the specimens then placed in a refrigerator (at apx. 35$^{o}$F) for one hour to reduce activity. The material was then examined and live Aphrodes removed with flexible forceps.

Adults desired for voucher specimens were killed in an ethyl acetate killing jar or in 70 percent alcohol. If specimens killed and preserved in alcohol were to be dry mounted they were processed through cellusolve and xylene as suggested by Sabrosky (1966). Nymphs that were killed in 70 percent alcohol were dehydrated through two 100 percent alcohol solutions. After the last solution of 100 percent alcohol, the alcohol was poured off and xylene added. Specimens were kept in xylene for 15-30 minutes, removed and then mounted on points. Setae and other integumental structures were more discernible after specimens were treated by these methods.

Dissection Techniques

Dissections were done with the aid of a dissecting scope at 15X or 45X magnification. When the dissection required the removal of the abdomen, the same initial steps and tools were used. The tools included a small loop, approximately 0.5 mm in diameter made from a 00 insect pin; a fine, slightly curved needle; a fine needle with a bent tip (approximately 45$^{o}$); a metal probe with a sharp oblique tip (23 gage hypodermic needle). watch makers forceps; and a cork dissecting block with a clay filled center. The fine needles and a small loop were shaped from minuten nadeln affixed to tapered wooden dowels of appropriate size.

To dissect a pinned insect, the specimen is placed venter up on a dissecting block by inserting the head of the insect pin into a clay filled hole in the block until the dorsum of the specimen comes to rest on the block. The abdomen is gently separated from the thorax by inserting the oblique probe between the thorax and abdomen. The abdomen is then heated in a 10-15 percent KOH solution to near boiling until the integument becomes soft and the contents macerated so that they are extruded as a stream of yellow-brown material when the abdomen is gently pressed with the small metal loop. The abdomen is then rinsed in water and placed in a watch glass with either glycerin or alcohol for further dissection.

The first step in dissection of the male inner genitalic structure from the genital capsule is orientation of the abdomen in a watch glass filled with glycerin. Then the dissecting needles are used to separate the inner structures from the genital capsule by tearing the membranes which connect them. One needle is inserted from the basal end of the abdomen while the other is inserted through the caudal opening between the pygofer and the external plates. The membrane connecting the aedeagal phallobase to the tenth tergum is gently torn, separating these two structures. The curved needle is again inserted anteriorly, this time hooking the connective and style ventrally. The styles are separated from the abdomen one at a time by drawing the hooked needle caudad and tearing the connective tissue that attaches the style to the genital capsule. After the styles are detached, the entire assemblage of styles, connective and aedeagus can be removed from the genital capsule. After examination, the dissected parts are placed in the abdomen for storage.

The ovipositor is removed with the same preliminary technique as described above for male genitalia. Watchmakers forceps are used to hold the abdomen while a fine curved pin is used to separate the ovipositor from the abdomen. Valve I can be separated from valves II and III by holding the latter with forceps and pulling on valve I with a second pair of forceps. Valve II can then be dissected from valve III by gently pressing along its lateral surface at the midpoint with a fine pointed curved pin. A scalpel with a size 11 blade is used to cleave each valve for further examination. Lacto-phenol is used for both temporary and permanent mounting media for slide preparations. Dissected parts are stored in a microvial containing a droplet of glycerin and kept with the appropriate pinned specimen by thrusting the pin through the stopper of the microvial at a slight angle so the glycerin will remain at the bottom of the microvial. Wings detached for study were glued to the paper point on which the leafhopper was mounted or dry mounted on slides with the appropriate information.

Dissections of the male and female reproductive system are best done with specimens that have been recently killed in 70 percent alcohol. The internal organs of specimens stored in alcohol for several years become brittle, making the dissection more difficult. The leafhopper to be dissected is placed venter up in a wax bottom dissecting pan that is flooded with 70 percent alcohol. A needle (minuten nadeln or small insect pin) placed through the thorax holds the specimen in place. Other needles may be placed along the margin of the abdomen to hold the specimen securely. The intersegmental membrane is torn with a fine curved needle along one side, between the second and third segments and just basad of the genital capsule.

The abdominal venter is then gently lifted to one side with watch makers forceps, cleared of attached tissue with a fine needle and pinned back. In males, the testes may be located anteriorly by references to the tubular vas deferens and are carefully removed with a curved needle. The pygofer, genital plates and styles are torn away with two pairs of fine forceps, leaving the aedeagus attached to the ejaculatory duct (sacculus ejaculatorius). The reproductive organs may then be lifted from the abdominal cavity and placed in another wax filled dissecting pan for further dissections and drawing. In females, the ovarioles are first detached anteriorly and the fat bodies and digestive organs then removed. The reproductive organs are lifted out by separating the ovipositor from the pygofer. The reproductive system of recently killed female specimens can be dissected by a modification of the Kamm and Ritcher method, described on p. 19.

## Measurements

Measurements were made using an American Optical Company Filar Micrometer, Model No. 426. Total body length of adults was measured as the distance from the apex of the crown to the wing tips for both macropterous and submacropterous forms. Total body length of nymphs was measured as the distance from the apex of the crown to the apex of the abdomen. The median length of the crown and its width immediately anterior to the eyes were measured and a ratio of length to width (L:W) was computed for each of 10 or more individual adults selected at random. The L:W ratio was computed as the quotient of the crown width divided by the crown length and is expressed in the technical descriptions of species as L:W, where L is always unity (1). Head width of nymphs was measured as the greatest distance between the outer margin of the eyes rather than immediately anterior to the eyes because of the difficulty to see the junction of the eye and crown. The length of the aedeagus was measured from its tip to its base.

Illustrations

Drawings were made of the reproductive system, genitalia, body, head and face with the aid of an ocular grid and dissecting microscope at 15X, 45X or 90X. Illustrations of the wings were made by tracing prints of slide mounted structures taken with a 3M "Filmac 400" Reader-Printer. Illustrations of the gonapophyses were made with a Wild Mark 5 stereomicroscope equipped with a drawing tube. Drawings of the aedeagi, styles and genital plates were made with the use of a Bausch and Lomb microprojector. Fine detail was added while structures were observed with a light microscope at 150X, 400X or 675 X magnification.

Photographs of aedeagi, connectives, and styles were taken with a Leica 35 mm camera, a Nikon PFM shutter system and a Zeiss Phase Contrast Research Microscope for quick reference. The genitalia were first oriented in a well-slide filled with glycerin with the aid of a dissecting microscope; the slide then placed on the stage of the compound microscope where the photograph was taken.

## Biological Studies

### Field Observations

Individuals were studied in their natural habitats by carefully removing rocks, boards and similar surface debris around which specimens tend to congregate, and observing their behavior and natural enemies. Metal probes were used to test tactile responses.

### Culture Methods

Laboratory cultures of *Aphrodes* were maintained on white clover, red clover, pasture grasses and two strawberry cultivars, Shasta and Hood, grown in four inch clay pots. Clover and strawberry plants were suggested as possible hosts and were used for rearing *A. bicinctus* by Chiykowski (1970). Pasture grasses were selected because they were the predominant plants in some areas where species of *Aphrodes* were collected. The leafhoppers were caged on small plants in either a glass lamp chimney (Corning Glass Works, No. 2, volume 950 cc) or a screened box cage with a sliding glass front. Plants were watered from below in order to keep the humidity in the cages at a minimum while maintaining suitable plant conditions. Plants were pruned as necessary to limit their size to the cages used. Temperatures were regulated between $60^oF$ and $70^oF$ by a warm and cold air ventilation system. Light intensity and duration were regulated by "Gro-Lux" fluorescent lamps.

Determination of Reproductive Development

A modification of the rapid dissection technique described by Kamm and Ritcher (1972) was used to determine the stage of egg development and if insemination had occurred. A leafhopper is first placed in 70 percent alcohol for two minutes, then transferred to a solution of insect ringers where it is rinsed and then placed in a wax filled dissecting pan flooded with insect ringers. A pin placed through the thorax holds the specimen in position. The pygofer is grasped with forceps while a fine curved dissecting needle is used to tear the intersegmental membrane connecting the pygofer to sternite VII. When the intersegmental membrane is completely severed, the tip of the abdomen is slowly pulled away to expose the reproductive tract.

Egg maturation was determined by visual inspection of eggs through the transparent walls of the ovarioles. Insemination was determined by removing the vagina, squashing it on a slide in an insect saline solution and then examining the preparation with a light microscope at 400X. Insect saline was used as a medium in which to observe live sperm.

To determine egg development in dried specimens, the abdomen is removed from the specimen and heated in near boiling water for approximately ten minutes. The abdomen is then removed, oriented in a small watch glass containing glycerin and cut along the lateral edge of the sterna with a scalpel. Forceps are used to pull the sternum across the abdomen while a dissecting pin holds the abdomen in place, exposing the eggs.

In males, sperm may be easily seen by removing the reproductive tract as previously described and examining squashed mounts of the testes and vesicles of adult males with a light microscope at 400X.

## Species Differentiation

Determination of adult females of *A. albifrons* and *serratulae* was accomplished by segregating fourth or fifth instar nymphs, which can be identified to species, and rearing adults from them. The emerging adults were killed and mounted on points along with the cast skin(s). Determination of adult females was accomplished by examining the color pattern of the nymphal skin associated with the adult.

## IV. INFRASPECIFIC VARIATION AND CHARACTERISTICS USEFUL IN CLASSIFICATION

Except for the structural detail of the aedeagus, no single character was found to be consistently reliable for species differentiation. In some cases, color or color pattern was useful for differentiation of subgenera or species, but it is subject to such a great degree of variation that it needs to be used in conjunction with structural details. The shape of the apical portion of the styles, structure of pygofer hook apex, shape of genital plate, size(s) of setae on genital plate, body length and presence or absence of a secondary papilliform structure near the pygofer hook of the male were found to be especially useful when used in conjunction with color and color pattern. The following discussion is an attempt to summarize the limitations of the various characters used in classification.

### Color

Sexual dimorphism, involving both color and size, is apparent in species of the subgenera Aphrodes and Anoscopus (Figs. 14-23, 27-29). Males and females of the subgenus Stroggylocephalus are very similar in color, although mixtus females are often darker than the males (Figs. 24, 25, and 31).

Color and color pattern were both found to be helpful in discriminating between males of some species of Aphrodes. Males of the subgenus Anoscopus have either opaque and/or hyaline transverse bands alternating with colored (fuscous, rufous to light brown) transverse bands, or opaque and rufous diagonal stripes that parallel the veins on the forewings (flavostriatus). A. serratulae and bifasciatus males usually have black or fuscous transverse bands on the forewings while albiger and albifrons have rufous to light brown transverse bands. However, occasionally the transverse bands of serratulae are rufous or light brown, which causes them to closely resemble those of albiger and albifrons (Figs. 14-20). Although the forewings of male albifrons and albiger usually have alternating transverse bands, occasionally the forewings are nearly rufous with opaque spots or are almost totally opaque with contrasting color present only along the claval suture and the proximal part of the forewing, as in Figure 22. The diagonal striping of flavostriatus males is sometimes incomplete with contrasting color almost absent in the forewing. Individuals in which this condition occurs cannot be distinguished from albiger males by color alone (Figs. 21 and 22). The forewings of both males and females of Aphrodes s. s. and Stroggylocephalus were found to be similar with the exception that in Stroggylocephalus there are irregular fuscous markings along the lateral margins and males of Aphrodes s. s. are nearly concolorous.

The color and pattern of the forewings of the females of the subgenus Anoscopus are extremely variable and identifications cannot be made with certainty (Fig. 27). However, two of the species usually have either indistinct transverse bands (bifasciatus) or indistinct diagonal stripes (flavostriatus) (Figs. 27 and 28).

The color of the pronotum, face and crown in the members of Anoscopus is variable, but usually similar to the color of the fore-wings. The crown is usually mottled except in flavostriatus males which usually have a distinct, irregular rufous pattern.

A. bicinctus males can be distinguished from others by a characteristic cream colored transverse band across the entire width of the crown and pronotum (Fig. 23). The crown and pronotum are nearly concolorous in bicinctus females and both sexes of placidus, but are usually mottled light brown to dark brown in mixtus (Figs. 24, 25, 29, and 31).

The first instar nymphs of bicinctus, serratulae and albifrons are very similar in color with bicinctus being usually lighter, larger and appearing brown-green late in the first instar (Fig. 8). The second through fifth instars have a distinct color and/or color pattern for each species (Figs. 9-13, 26 and 30). However, the intensity of pigmentation for each species is variable.

Harries and Douglass (1948) have shown that different temperatures during the final nymphal instar have a direct effect on the coloration of the adult beet leafhopper, Eutettix tennelus (Baker). They have also shown that seasonal color forms are determined primarily by temperature conditions, and are of the opinion that intensity of coloration is largely determined during the latter part of nymphal development and probably mostly during formation of the wings and hypodermis preceding the final molt. Musgrave (1975) suggested that either temperature and/or photoperiod directly affects coloration of Scaphytopius acutus. Specimens kept at a cooler temperature (18°C) and shorter day light (10 hr) were darker than those kept at warmer temperatures (21°C) and longer day length (16 hr). At present there is no reliable criteria for variation in pigmentation of Aphrodes. However, from preliminary observations, and extrapolation from studies of other leafhopper species, it is suggested that temperature during nymphal development may influence adult coloration.

## Length and Crown L:W Ratios

Body length is a good character for discriminating members of Anoscopus (4.8 mm or less) from members of Aphrodes s.s. and Stroggylocephalus (4.9 mm or greater). In general, representatives of Stroggylocephalus are smaller than Aphrodes s.s., but because length measurements in both subgenera extensively overlap, I do not consider them reliable.

The range of variation in body length as well as crown length, wing length, crown width and aedeagal length is shown in Table 1.

Table 1. Range of measurements of body length, crown length, crown width, wing length, CL:CW ratios and aedeagal length of species of <u>Aphrodes</u>. All measurements except crown L:W ratios are given in mm.

| Species | Body length | Wing length | Crown length | Crown width | CL:CW | Aedeagal length |
|---|---|---|---|---|---|---|
| | | | **Males** | | | |
| albifrons | 3.35-4.00 | 2.52-3.03 | 0.35-0.53 | 0.90-1.10 | 1.94-2.71 | 0.60-0.70 |
| albiger | 3.12-3.62 | 2.33-2.70 | 0.39-0.53 | 0.91-1.07 | 1.96-2.37 | 0.52-0.60 |
| serratulae | 3.24-3.84 | 2.44-2.92 | 0.38-0.56 | 0.87-1.06 | 1.92-0.49 | 0.60-0.70 |
| flavostriatus | 2.86-3.43 | 2.36-2.52 | 0.36-0.51 | 0.82-0.93 | 1.85-2.42 | 0.50-0.60 |
| bifasciatus | 3.50-3.80* | | | | | 0.81 |
| bicinctus | 5.00-6.50 | 4.05-4.95 | 0.51-0.79 | 1.36-1.74 | 2.10-2.67 | 0.78-0.99 |
| mixtus | 5.24-6.21 | 4.03-4.83 | 0.54-0.64 | 1.42-1.68 | 2.37-2.65 | 0.56-0.61 |
| placidus | 4.97-5.18 | 3.83-4.04 | 0.51-0.60 | 1.36-1.39 | 2.27-2.69 | 0.56-0.61 |
| | | | **Females** | | | |
| albifrons, albiger, serratulae | 3.75-4.40 | 2.70-3.25 | 0.51-0.63 | 0.82-0.94 | 1.37-1.80 | |
| flavostriatus | 4.14-4.36 | 2.95-3.25 | 0.44-0.53 | 0.89-0.99 | 1.74-2.13 | |
| bifasciatus | 4.00-4.80* | | | | | |
| bicinctus | 5.73-7.52 | 4.14-5.46 | 0.51-0.79 | 1.36-1.74 | 1.60-1.85 | |
| mixtus | 5.81-6.44 | 4.39-5.04 | 0.57-0.69 | 1.38-1.44 | 2.08-2.41 | |
| placidus | 5.52-5.72 | 4.18-4.29 | 0.54-0.60 | 1.16-1.39 | 2.07-2.50 | |

*from Ribaut (1952).

Members of <u>Anoscopus</u> can be distinguished from those of <u>Stroggylocephalus</u> and <u>Aphrodes</u> <u>s</u>. <u>s</u>. on length alone, but the length of species within a subgenus is unreliable for species discrimination. The body lengths given for species of <u>Anoscopus</u> were taken from the anterior margin of the crown to the apex of the wing. Because the males of <u>Anoscopus</u> are submacropterous, the length measurements do not represent total body length measurements.

Crown L:W ratios were also examined. Species of <u>Stroggylocephalus</u> had the least amount of variation in the L:W ratios, but this may be partially due to the small number of individuals available for measurement. The L:W ratios of <u>bicinctus</u>, <u>albiger</u>, <u>albifrons</u> and <u>serratulae</u> females are distinctly different from males of the same species while the ranges of the L:W ratios of both sexes of <u>flavostriatus</u>, <u>mixtus</u> and <u>placidus</u> extensively overlap. A comparison of the L:W ratio of <u>bifasciatus</u> is not given since only one male of that species was examined.

## <u>Pygofer</u>

A pair of hooks on the ventromedial margin of the pygofer and projecting caudodorsally, setal structure and the presence or absence of a setose papilliform projection near the pygofer hook were found to be useful characters in discriminating between some species and subgenera of <u>Aphrodes</u>.

The papilliform projection near the pygofer hook is lacking in members of *Stroggylocephalus*, but present in all others. The shape of the pygofer hook is distinct for each species except for *flavostriatus* and *albiger*. The pygofer hook is relatively uniform in structure for each species, but variation does occur in the degree of bluntness of the apex, curvature, crenulations and dentations along the margin of the hook.

The size of the setae on the pygofer corresponds to the size of the setae found on the genital plate.

## Male Genital Plates

The shape of the genital plates is basically similar for all species of *Aphrodes* with the exception of *serratulae* which have genital plates that are longer in relation to their width and with lateral margins that are nearly straight for the basal two-thirds of their length, bending dorsolaterally and becoming broadly rounded at their apex (Fig. 42). The lateral margins of the genital plates of other species of *Aphrodes* are nearly straight with the apex broadly rounded from the lateral to mesal margin.

Representatives of each subgenus can be separated by the type, size, and location of setae present on the genital plates. In *Stroggylocephalus*, there are two distinct types of setae. Those of the first types are located laterally, very long, hairlike, uniform in width and flexible. Setae of the second type, located on the medial one-half of the genital plate, are tapered from a relatively broad base to a pointed apex (Figs. 38 and 39). In Aphrodes s. s., the lateral setae are not as long and the medial setae are not as stout as in Stroggylocephalus (Fig. 44). In Anoscopus, the setae are relatively uniform in size over the entire genital plate although the setae along the median are stouter (Figs. 40-43).

Size of the genital plate is proportionate to the size of the specimen and can also be used to discern Anoscopus from the other subgenera.

## Male Styles

The styles are similar in general structure for all species of Aphrodes. The distal one-fourth of the styles is the most variable at the species level, mainly varying in the amount of rugosity, and is useful in discriminating between some species. Styles of members of Stroggylocephalus and Aphrodes are distinguished from those of Anoscopus by the presence of two rows of irregular teeth distally along the ventromedial margin. Styles of species of Aphrodes s. l. are very similar in shape with the exception of serratulae in which they are club-shaped distally and placidus in which they are rotundate apically (Figs. 46 and 48). The length of the styles is related in general to the length of the leafhopper and can be used to distinguish bicinctus from species of the subgenus Anoscopus. The number of setae along the dorsolateral margin of the distal one-half of the styles is variable, and frequently the setal pattern is different for the two styles of the same leafhopper.

## Aedeagus

The internal male genitalia, especially the aedeagus of Aphrodes accounts for the most evident interspecific variation. Length, shape of the shaft, number, position and shape of aedeagal spines and shape of phallobase were considered. In Stroggylocephalus, the aedeagal shaft has one pair of large retrorse spines with differences between species being in the length of the spines, curvature and shape of the aedeagal shaft (Figs. 52 and 53). The aedeagus of mixtus is similar to that of other Palearctic species of Aphrodes belonging to the subgenus Stroggylocephalus (agrestis and livens) in that the retrorse spines are nearly straight. However, the shape of the aedeagal shaft and location of the retrorse spines are different from those of both agrestis and livens.

The aedeagus of bifasciatus is unique among Aphrodes in North America in having three pairs of retrorse spines, although a similar condition occurs in some Palearctic species. The aedeagus is also laterally flattened with the shaft broadest medially unlike other species of Aphrodes (Fig. 58). The other species of Aphrodes s. s.

and Anoscopus in North America have two pairs of retrorse spines on the aedeagal shaft. A. serratulae, albifrons and bicinctus have two subequal pairs of retrorse spines while albiger and flavostriatus have one pair of retrorse spines greatly enlarged. The location of the retrorse spines along the length of the aedeagal shaft provides good characters for the differentiation of species. The length of the aedeagus, shape of the aedeagal shaft, and position of the gonopore in relation to the retrorse spines are also reliable characters for species differentiation.

Müller (1958) has shown that different day lengths cause a considerable amount of variation in the aedeagus of some species of Euscelis. In E. plebejus, variation of the aedeagus is so great that several variants of that species had been previously described as different species. Temperature, humidity and quantity and quality of nutrition only modify the effect of the photoperiod (Müller, 1958). I have no evidence to indicate that variations in the aedeagal structures of Aphrodes result from photoperiod effects because the aedeagus of both lab reared and field collected specimens are relatively uniform.

The greatest amount of variation found in the aedeagi is length and, in bicinctus, proximity of the retrorse spines. The variation in the length of the aedeagus appears to be correlated with the variation in the body length of the leafhopper. For example, in bicinctus, the mean length of the aedeagal shaft was 0.84 mm for males less than

6 mm in total body length and 0.94 mm for males 6 mm or greater in total body length. In all species of Aphrodes, the retrorse spines show a small degree of variability in size, diameter, and location on the shaft. A. bicinctus, in North America, shows the greatest amount of variation of all species of Aphrodes, especially in the distance between the two pair of medial retrorse spines. The spines may be very close, distinctly separate or intermediate of the two. Ribaut (1953) has defined the subspecies A. bicinctus bicinctus as having spines close together and A.b. diminutus as having spines distinctly separate. Both variants and intermediates of the variants of bicinctus have been taken from eastern United States. In western United States A.b. diminutus has been taken only from Pacific City (Tillamook Co., Ore.) with no intermediates being found.

## Ovipositor

The females of three species of Aphrodes found in North America cannot be distinguished based on morphological characteristics. Readio (1922) suggested that the gonapophyses (valves) might be useful in discriminating between females, especially by the number of denticles on the dorsal margin of valve II (Figs. 4c-4e). However, examination of the gonapophyses of females of all North American species of Aphrodes, except bifasciatus (not examined), failed to reveal any characters that were reliable for species determination.

The base of the ovipositor within each species is also variable, being round in some and angular in others.

## Reproductive System

The female reproductive system is similar in all of the species of Aphrodes that were examined (bicinctus, serratulae and albifrons). The most evident difference is the size of the ovarioles and length of the oviducts in specimens in the same state of development. Mature eggs found in the ovarioles of A. bicinctus, albifrons and serratulae were longer and more cylindrically shaped than in species of the subgenus Stroggylocephalus.

The male reproductive system is similar in shape in species of bicinctus, albifrons and serratulae, but variable in size. The variation in size is dependent upon the state of maturation of the reproductive system and size of the individual. The testes and vesicles of bicinctus are larger in comparison to albifrons and serratulae at the same stage of development. The accessory gland of serratulae in the early stage of development has a small protrusion anteriorly, but as maturation continues, the protrusion elongates into a cylindrical lobe (Figs. 68 and 69). The accessory gland of bicinctus is similar to serratulae, but is more chordate with a long, cylindrical lobe (Figs. 6 and 67). The mature accessory gland of albifrons is similar to that of bicinctus, but the anterior protrusion is narrow proximally and clubbed distally (Fig. 70). When comparing the male reproductive system between species, care must be taken to compare males of nearly the same maturation. Reproductively mature males have an enlarged vesicle that is distinctly different in texture than other parts of the reproductive system. Those that are not sexually mature are opaque, but gradually become pinkish white and shiny with maturity. The combined general structure of the reproductive tract may be useful in differentiation at the generic or higher category, but because of variation, due to maturation of the reproductive tract, it is impractical to use at the specific level.

# V. CHARACTERIZATION AND TAXONOMY OF THE SUBFAMILY APHRODINAE

## Subfamily Characteristics

Members of the subfamily are medium-sized leafhoppers ranging from 2.85-7.55 mm in length. Within a species, the females are usually larger than the males, although the length of the largest male may exceed that of the smallest female.

The Aphrodinae may be characterized as follows: Episternum concealed. Clypellus slightly convex, with lateral margins nearly parallel, narrowing slightly distally and extending just beyond the gena (Fig. 2). Lateral frontal sutures extending nearly to ocelli; ocelli on anterior margin of head or on crown near anterior margin of head; distance between ocelli greater than or equal to distance between antennal pits; base of antennae in a distinct pit bounded dorsally by a transverse ridge formed from the ocellocular area. Forewing with setae along margins of veins. Hindwing with submarginal vein evanescent apically (Figs. 32b-37b). Male genital plate at least three times as long as its basal width; valve concealed. Styles roughly falcate, their total length equal to or greater than the total length of genital plates (Figs. 45-51); styles bent mesad and slightly ventrad just distad of the connective. Connective broadly Y-shaped; stem flattened with apex slightly expanded laterally

(Figs. 45-51). Aedeagal shaft and phallobase fused and roughly U- or V-shaped in lateral view.

The anatomy of the reproductive system of both sexes of Aphrodes (based on a study of three species; bicinctus, serratulae and albifrons) may be characterized as follows:

Females (Figs. 7 and 60).--Paired ovaries, each composed of seven spindle shaped ovarioles uniting at a common junction forming a lateral oviduct. Sperm stored in swelling of the median oviduct (vagina). Accessory gland uniting distad of vagina.

Males (Figs. 6 and 67-70).--Testes composed of lobes enclosed by a membranous sheath. Paired vesicles enclosed by a membranous sheath, appearing united, especially in immature males. Lateral duct leading from vesicle united with an accessory gland just caudad of the vesicle. Sacculus ejaculotorius bulb shaped.

Hamilton (1975) has included in the subfamily Aphrodinae the subfamily Deltocephalinae (Euscelidae of Metcalf). As previously indicated, Hamilton's conclusion for including the Deltocephalinae with the Aphrodinae was based largely upon the structure and arrangement of setae on the hind tarsi. In an effort to obtain evidence other than that customarily used in deducing relationships among the higher categories of Cicadellidae, I studied the anatomy of the reproductive tracts of 13 species representing six nominal subfamilies; also one species of Cercopidae and one species of Membracidae. The following discussion deals with the significance of the evidence obtained.

In some orders of insects reasonably good correlation between reproductive tract anatomy and accepted classification has been established. For example, in the Coleoptera, Ritcher (1974) has shown generic and higher category relationships for some groups. Pentegrast (1957) has illustrated a limited number of Heteroptera for both sexes, but has also indicated that the structure of the reproductive organs is only one aspect of the already many criteria used for family definitions. Lumm (1961) has shown relationships at the generic and species level for some male mosquitoes and has also found that the variation in the reproductive organs at the infraspecific level is small. From the limited information available it appears that there is a considerable range of structure within the Hemiptera s.l. For example, although the auchenorrhynchous Homoptera studied are of relatively uniform structure as regards ovariole number and shape, shape and number of accessory glands, and structure of the oviducts, they differ considerably from most Heteroptera and stennorrynchous Homoptera (as illustrated by Grassé, 1964; Pesson, 1951; and Pentegrast, 1957) and seem to have more in common with many of the Coleoptera (as illustrated by Grassé, 1964, and Ritcher, 1974).

My studies indicate that the basic structure of reproductive tracts in leafhoppers conforms to that described above for Aphrodes.

Differences found in the reproductive tract of some Cicadellidae and related families are summarized in Tables 2 and 3.

In general terms, on the basis of reproductive tract structure the Aphrodinae form a distinct group. The females have seven ovarioles, unlike other species examined, and males have two testicular lobes, "fused" seminal vesicles and distally dilated accessory gland with a finger-like projection, a combination of characters not found in other Homoptera studied. In the tribe Errhomenellini, the three genera examined had many similarities, i.e. six testicular lobes attached to a dilated vas deferens and a long tubular accessory gland in the males and six ovarioles of similar shape and two long tubular accessory glands in the females. There are few differences between males of the genera Errhomus (separated seminal vesicles) and Carsonus and Lystridia "fused" seminal vesicles). However, within the Cicadellinae, males of the tribe Cicadellini, of which only one species (Hordnia circellata) was examined, differed from the tribe Errhomenellini by having testicular lobes with a more terminal attachment and seminal vesicles similar to Carsonus, but different from Errhomus. The reproductive organs of members of the subfamily Megophthalminae and Idiocerinae are very different in many respects and are not close to either the Aphrodinae or Errhomenellini. The males of Tiaja (Megophthalmini) have only four resticular lobes. The females of Idiocerous (Idiocerini) have 15 or more ovarioles/ovary and in this respect are similar to some Cercopidae.

Table 2. Summary of male reproductive system (Homoptera: Auchenorrhyncha).

| | Follicle number | Follicle attachment | *Vas deferens* apex | Paired vesicles | Accessory gland |
|---|---|---|---|---|---|
| Cercopidae | | | | | |
| *Philaenus spumarius* | 10+ | palmate | tubular | separate | tubular |
| Membracidae | | | | | |
| *Gargara genitsae* | 7 | palmate | tubular | separate | tubular |
| Cicadellidae | | | | | |
| Aphroninae | | | | | |
| Aphrodini | | | | | |
| *Aphrodes bicinctus* | 8 | opposite | dilated | contiguous | dilated |
| *albifrons* | | | | | |
| *serratulae* | | | | | |
| Cicadelinnae | | | | | |
| Cicadellini | | | | | |
| *Hordnia circellata* | 4 | palmate | tubular | contiguous | tubular |
| Errhomenellini | | | | | |
| *Errhomus montanus* | | | | | |
| *lineatus* | 6 | palmate | dilated | separate | tubular |
| *similis* | | | | | |
| *Carsonus irroratus* | 6 | opposite | tubular | contiguous | tubular |
| *Lystridea uhleri* | 6 | opposite | tubular | contiguous | tubular |
| Deltocephalinae | | | | | |
| Cochlorhinini | | | | | |
| *Cochlorhinus* | 8 | palmate | tubular | contiguous | tubular |
| Euscelini | | | | | |
| *Euscellis ohausi* | ? | ? | ? | separate | ? |

(Continued on next page)

Table 2. (Continued)

| | Follicle number | Follicle attachment | Vas deferens apex | Paired vesicles | Accessory gland |
|---|---|---|---|---|---|
| Cicadellidae (continued) | | | | | |
| Tetigellinae | | | | | |
| Proconiini | | | | | |
| _Cuerna yuccae_ | 6 | palmate | tubular | separate | dilated |
| Tettigellini | | | | | |
| _Draeculcephalus crassicornus_ | 8 | alternate | tubular | separate | ? |
| Idiocerinae | | | | | |
| Idiocerini | | | | | |
| _Idiocerus_ sp. | ? | palmate | tubular | separate? | tubular |
| Megophthalminae | | | | | |
| Megophthalmini | | | | | |
| _Tiaja_ sp. | 4 | palmate | tubular | separate | oblong |

Table 3. Summary of female reproductive system (Homoptera: Cicadellidae).

| | Ovariole shape | Ovariole no. | Accessory gland no. | Accessory gland shape |
|---|---|---|---|---|
| Cicadellidae | | | | |
| Aphrodinae | | | | |
| Aphrodini | | | | |
| *Aphrodes bicinctus* | | | | |
| *albifrons* | elliptical | 7 | 1 | dilated distally |
| *serratulae* | | | | |
| Cicadellinae | | | | |
| Errhomenellini | | | | |
| *Errhomus montanus* | | | | |
| *similis* | constricted medially | 6 | 2 | dilated distally and one tubular |
| *lineatus* | | | | |
| *oregonensis* | | | | |
| *Carsonus irroratus* | as above | 6 | 1 ? | dilated distally |
| *Lystridea uhleri* | as above | 6 | 2 | dilated distally and one tubular |
| Idiocerinae | | | | |
| Idiocerini | | | | |
| *Idiocerus* sp. | as above | 15+ | 1 | dilated distally |
| Deltocephalinae | | | | |
| Cochlorhinini | | | | |
| *Cochlorhinus* sp. | as above | 6 | 1 | dilated distally |

The shape and number of ovarioles and accessory glands of females and the number of testicular lobes and structure of the seminal vesicle and accessory gland of males appear to be significant in evaluating category relationships of some Cicadellidae. These preliminary observations of the comparative anatomy of the reproductive tracts of leafhoppers indicate that, in combination with other structural characters, such evidence may have value in development of classification, but that it is not reliable as a sole criterion.

## Generic Characteristics

In the absence of coordinate taxa within the subfamily, characterization of the tribe Aphrodini and genus *Aphrodes* is largely speculative and, therefore, separate characters for the tribe are not given.

The genus *Aphrodes* may be characterized as follows: Body robust and somewhat dorsoventrally flattened. Head usually distinctly wider than the pronotum; anterior margin of head carinate or subcarinate. Face broad, short; texture finely to coarsely granulose. Crown flat or concave, anterior margin broadly rounded. Pronotum not more than one-third as long as its median width; surface transversely striate posteriorly; lateral margins carinate or subcarinate. Scutellum granulose. Hind tibia broadly flattened and subrectangular in cross section. Females macropterous; males macropterous or submacropterous. Forewings lacking an appendix, usually sparsely setose, especially along the veins; outer anteapical cell one-half as large as the central anteapical cell; spurious crossvein sometimes present within the central anteapical cell, giving the impression that the outer and central anteapical cell are approximately equal in size.

Aedeagus approximately two-thirds the total length of the styles; symmetrical with one, two, or three pairs of retrorse spines. Pygofer hooks present, originating internally, medially and ventrally on the pygofer and giving the appearance of supporting the aedeagus (Fig. 5).

Ovipositor similar in general structure to other members of the Cicadellidae (Readio, 1922); extending just beyond the pygofer and composed of three pairs of valves or gonapophyses; outer gonapophyses narrow proximally, becoming broadly expanded medially and broadly rounded distally (Fig. 4); innermost gonapophyses laterally compressed, arcuate and knife-like, sharply pointed at apex. The two innermost gonapophyses rod shaped and curved basally (Figs. 4d, e); valve II similar to valve III except dorsal margin irregularly dentate and with conspicuous ducteoles extending distally to the ventral apical margin and branching along most of its length to where the valve fuses anteriorly (Fig. 4d). Seventh sternum of female two times as long as preceding sternum and with a shallow median notch (Fig. 3).

Immature stages of three species were available for morphological study. Except for color differences the several developmental stages of different species were similar in appearance. The gross habitus of the different stages was as follows:

First instar (Fig. 8): Head and thorax broad in relation to abdomen; anterior margin of crown broadly rounded. Abdomen roughly V-shaped in dorsal view; color usually a dark brown. Wing pads not evident.

Second instar (Fig. 9): Color variable; form similar to first instar. Mesothoracic wing pads small but distinct, metathoracic pair not evident.

Third instar (Fig. 10): Color and form similar to second instar. Mesothoracic wing pads extending to one-half the length of the metathorax. Anterior one-half of abdomen nearly parallel sided, posterior one-half roughly V-shaped in dorsal view; head not nearly so broad in proportion to body.

Fourth instar (Figs. 11-13): Color and form similar to third instar. Mesothoracic wing pads more than three-fourths the length of the metathorax. Metathoracic wing pads appear as lateral extensions of the metathorax.

Fifth instar (Figs. 26, 30): Color and form similar to fourth instar. Mesothoracic wing pads extending beyond metathorax.

## Subgeneric Characteristics

As treated here, the genus *Aphrodes* contains three subgenera; *Aphrodes* *s. s.*, *Anoscopus* Kirshbaum and *Stroggylocephalus* Flor.

*Aphrodes* (*Anoscopus*): Face finely granulose; distal edge of clypellus nearly straight, appearing slightly bilobed in some females (Fig. 2). Crown granulose and almost flat; head L:W ratio 1:1.37-2.71. Pronotum granulose anteriorly, gradually becoming punctate and transversely striate posteriorly. Distal one-fourth to one-third of styles scabose ventrally (Figs. 47-50). Aedeagal shaft with two or three pairs of retrorse spines. Gonopore dorsal, a long lenticulate opening, occupying one-half to one-third of the distal end of the aedeagus (Figs. 54-58). Secondary papilliform projection near pygofer hook present (Figs. 40c, 41c, 43c). Genital plates setose (Figs. 40c-43c). Females macropterous, males submacropterous.

*Aphrodes* (*Stroggylocephalus*): Face granulose. Clypellus slightly wider basally than distally. Crown short; head L:W ratio 1:2.07-2.69. Aedeagus with only one pair of large retrorse spines (Figs. 52, 53). Distal one-third of styles with two rows of irregular teeth along ventromedial margin and scabose ventrally. Gonopore dorsal; a narrow sub-rectangular or lenticulate opening on the basal one-half of the aedeagal shaft (Fig. 53b). Genital plates heavily setose (Figs. 38, 39). Male pygofer lacking secondary papilliform projections near pygofer hooks. Both sexes macropterous.

Aphrodes (Aphrodes): Face coarsely granulose; head L:W ratio 1:1.6-2.67. Anterior margin of clypellus bilobed. Aedeagal shaft with two pairs of retrorse spines (Fig. 59). Distal one-fourth of styles scabose ventrally; with two rows of irregular teeth along ventromedial margin. Gonopore similar to A. (Anoscopus) (Fig. 59b). Secondary papilliform projection near pygofer hook present (Fig. 44b). Genital plates setose (Fig. 44a). Both sexes macropterous.

## Key to Subgenera and Species of Aphrodes in North America

Males

1. Gonopore situated distad of all aedeagal processes. Aedeagal shaft with two pair of subequal, medial, retrorse spines. Color from tan to dark brown; crown and anterior margin of pronotum with a yellow-white transverse band. Length 5.0 mm or greater . . . . . Aphrodes (Aphrodes) bicinctus (Schrank)

\- Gonopore situated basad of at least one pair of the aedeagal processes. Retrorse spines variable. Color variable, but crown and pronotum without yellow-white transverse bands. Length variable . . . . . . 2

2. Aedeagal shaft with one large pair of retrorse spines (Figs. 52, 53); genital plates heavily setose (Figs. 38, 39); pygofer hooks recurved and usually sharply pointed. Macropterous. Length greater than 4.9 mm . . . . . . . . . . . . . . . . . . . . subgenus Stroggylocephalus Flor. 3

- Aedeagal shaft with two or three pairs of retrorse spines (Figs. 54-58); genital plates less setose (Figs. 40a-43a); pygofer hooks variable, but not recurved. Submacropterous. Length 4.0 mm or less . . . . . . . . . . . subgenus Anoscopus Kirshbaum 4

3. Retrorse spines located subapically on the aedeagal shaft (Fig. 53); no retrorse teeth located on anterolateral margin of aedeagal shaft . . . . . . *A. placidus* (Provancher)

- Larger retrorse spines originating one-fifth distance from apex of aedeagus; two rows of retrorse teeth on anterolateral margin extending from retrorse spines to apex (Fig. 52) . . . . . . . . . . . . . . *A. mixtus* (Say)

4. Two pairs of retrorse spines . . . . . . . . . . . . . . . . . 5

- Three pairs of retrorse spines (Fig. 58) . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. bifaciatus* (Linnaeus)

5. Retrorse spines subequal; adjacent or distinctly separated . . . . . . . . . . . . . . . . . . . . . . . . 6

- Medial pair of retrorse spines at least three times the length of the apical pair . . . . . . . . . . . . . . . . 7

6. Retrorse spines on aedeagal shaft curved, lateral and subapical (Fig. 55); aedeagal shaft uniform width. Forewing usually fuscous, and opaque and hyaline, usually forming distinct fuscous bands with opaque and/or hyaline transverse bands . . . . . . . . . . . . . . . . . . . . . . . . . . *A. serratulae* (Fabricius)

- Retrorse spines on aedeagal shaft straight; one pair medial (slightly larger) and one pair subapical (Fig. 54). Aedeagal shaft in lateral view not uniform width; distinctly dorsoventrally flattened at its apex. Forewing usually rufous and opaque and/or hyaline, forming distinct transverse bands as in *serratulae* . . . . . . . . . . . . *A. albifrons* (Linnaeus)

7. Medial retrorse spines decurving along its median length and parallel to the aedeagal shaft (Fig. 56). Forewing rufous with transverse hyaline bands or spots; usually forming distinct transverse bands . . . . . . . . . . . . . . . . . . *A. albiger* (Germar)

- Medial retrorse spines not decurving along its length (Fig. 57). Veins of forewing rufous; cells opaque; giving the appearance of angular longitudinal stripes (Fig. 21) . . . . . . . . . . . . . <u>A. flavostriatus</u> (Donovan)

<u>Females</u>

1. Length 5.5 mm or greater. Crown usually convex . . . . . . . 2

- Length 4.8 mm or less. Crown usually flat or slightly concave . . . . . . . . . . subgenus <u>Anoscopus</u> Kirschbaum 4

2. Distal margin of clypellus bilobed. Crown distinctly convex and subcarinate. Face coarsely granulose . . . . . . <u>Aphrodes</u> (<u>Aphrodes</u>) <u>bicinctus</u> (Schrank)

- Distal margin of clypellus straight. Crown slightly convex, shorter than in <u>bicinctus</u>. Face granulose . . . . . . . . . subgenus <u>Stroggylocephalus</u> Flor.

3. Crown striate; color variable, usually with distinct brown mottling . . . . . . . . . . . . . . . <u>A. mixtus</u> (Say)

- Crown finely striate; light brown and usually without brown mottling . . . . . . . . . . <u>A. placidus</u> (Provancher)

4. Submacropterous. Surface of forewings dull occasionally with a series of light patches of transverse bands . . . . . . . . . _A. bifasciatus_ (Linnaeus)

\- Macropterous. Surface of forewing more or less shiny, unevened, but not roughened . . . . . . . . . . . . . . . . . 5

5. Forewings rufous to fuscous with usually distinct opaque longitudinal veins (Fig. 28). ._A. flavostriatus_ (Donovan)

\- Forewings entirely rufous or opaque and/or hyaline with irregular fuscous spots . . . . _A. serratulae_ (Fabricius)
_A. albifrons_ (Linnaeus)
_A. albiger_ (Germar)

## Species Descriptions

### _Aphrodes_ (_Anoscopus_) _albifrons_ (L.)

(Figs. 1, 2, 5, 8-11, 18, 19, 26, 27, 35, 40, 47, 54, 70)

_Cicada albifrons_ Linnaeus, 1758, Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 10, rev, 1:437.

Males.--Length 3.35-4.00 mm (mean 3.36 mm). Crown L:W ratio 1:2.21; range 1:1.94-2.71. Forewings usually with wide rufous bands alternating with narrower opaque and/or hyaline transverse bands; proximal transverse band rufous, distal transverse band narrow and usually hyaline.

Females.--Length 3.75-4.40 mm (mean 4.12 mm). Crown L:W ratio 1:1.56; range 1:1.37-1.84. General form of the females similar to the males. Crown and pronotum fuscous or rufous, usually mottled. Forewings usually hyaline with opaque and dark brown spots; occasionally rufous and nearly unicolorous. Pygofer finely setose.

Male genitalia.--Dorsolateral margin of genital plates nearly straight; distal one-fourth of mesal margin of plate broadly rounded (Fig. 40a). Pygofer, hook broadly recurved basally, becoming sharply recurved apically; internal margins weakly serrate and crenate (Figs. 40b, 40c). Styles 0.8-0.95 mm long; distal one-fourth to one-third scabose ventrally and angularly rounded (Fig. 47). Aedeagus 0.6-0.7 mm long; with a subapical and a medial pair of straight subequal retrorse spines; shaft dorsoventrally flattened apically, gradually becoming rotundate medially (Fig. 54). Gonopore occupying one-half to one-third of length of aedeagal shaft and opening dorsally just anterior to its midpoint.

Nymphs.--Measurements for nymphs are shown in Table 4 (p.76).

First instar: Dark rufous to dark brown. Abdominal terga 3-8 each with six distinct setae located near the posterior margin, one middorsal pair and two lateral pair (Fig. 8).

Second instar (Fig. 9): Light brown to dark mottled brown. Body shape similar to first instar. Setal pattern similar to first instar.

Third instar (Fig. 10): Light brown to mottled dark brown. Abdominal segments 1-5 nearly as wide as thorax, not distinctly V-shaped. Head not appearing as broad in relation to body size. Setal pattern similar to second instar.

Fourth instar (Fig. 11): Mottled light brown to dark brown. Body shape similar to third instar. Six rows of setae on abdomen similar to third instar.

Fifth instar (Fig. 26): Form and color similar to fourth instar. Mottling may form an indistinct longitudinal middorsal stripe, but never a lateral longitudinal stripe. Wing pads distinctly separate. Setal pattern similar to fourth instar.

Specimens examined.--200+ .

Distribution.--Nearctic (Oregon and Nova Scotia, presumably adventive); Palearctic (Western Europe, Asia and N. Africa). See Map 1 for Nearctic distribution.

Remarks.--The forewings are variable; occasionally almost entirely rufous, but usually with alternate rufous and opaque and/or hyaline transverse bands. The males can usually be distinguished from serratulae by the color of the forewing and shape of genital plate.


Map 1. Confirmed Nearctic distribution of Aphrodes albifrons (L.).

Examination of the genitalia will readily distinguish albifrons from albiger.

In North America this species has been collected frequently in Oregon. Metcalf (1963) gives a complete summary of published distribution records for this species; however, my studies indicate that much of the Nearctic distribution data is erroneous due to misidentification of samples of albiger and serratulae. In the Willamette Valley it occurs in relatively large numbers in open fields, pastures and lawns, but is readily overlooked because of its habit of hiding when disturbed. I have found it in association with serratulae and bicinctus, but usually in fewer numbers than serratulae. Although I have no records of albifrons further north than Oregon, it probably occurs in Washington and possibly into western Canada. This supposition is based on one observation of an Aphrodes nymph resembling albifrons seen but not captured in western Washington.

Aphrodes (Anoscopus) albiger (Germar)
(Figs. 20, 36, 41, 49, 56)

Jassus albiger Germar, 1821, Bermerkungen über einige Gattungen der Cicadarien. Mag. Ent. 4:88.

Males.--Length 2.86-3.62 mm (mean 3.41 mm). Crown L:W ratio 1:2.13; range 1:1.92-2.38. Body color light brown to rufous. Ocelli usually reddish. Color of forewings similar to albifrons but transverse bands usually less distinct, sometimes appearing as several large opaque spots.

Females.--Length 3.75-4.40 mm (mean 4.12 mm). Crown L:W ratio 1:1.56; range 1:1.37-1.84. Similar to <u>albifrons</u> and cannot be distinguished with certainty from <u>albifrons</u> where both occur.

Male genitalia.--Setae and form of genital plates similar to <u>albifrons</u> (Fig. 41a). Styles 0.78-0.90 mm long and similar in structure to <u>albifrons</u>. Pygofer hook recurved with subapical internally projecting lobes; crenulate apically (Fig. 41b). Aedeagus 0.52-0.60 mm long with two lateral pairs of retrorse spines; apical pair short and directed anteroventral; medial pair located one-third the length of the aedeagus from the anterior pair, directed caudoventrally, and greater than three times the length of the shorter spines. Medial lateral retrorse spines project slightly outward, recurving and becoming parallel to the aedeagal shaft (Fig. 56). Gonopore similar to <u>albifrons</u>.

Specimens examined.--75+ .

Distribution.--Nearctic (Oregon, British Columbia, north eastern North America and Great Lakes region). Palearctic (Europe). See Map 2 for Nearctic distribution.

Remarks.--The genitalia, pygofer hook and genital plates are very similar to <u>flavostriatus</u>. However, <u>flavostriatus</u> males are generally smaller and usually have a striped pattern on the forewings


Map 2. Confirmed Nearctic distribution of **Aphrodes albiger** (Germar).

that can be easily distinguished from the transverse bands or spots of albiger.

This Palearctic species is presumably adventive to North America and occurs primarily in northeastern United States and southeastern Canada. Its habitat is probably similar to albifrons, and it has been collected with serratulae in some localities. The color pattern of the nymphs is unknown.

A complete synonomy and distribution of albiger is found in Metcalf's catalogue (1963). Most Nearctic records of albifrons from eastern North America probably refer to albiger.

Aphrodes (Aphrodes) bicinctus (Schrank)
(Figs. 6, 7, 23, 29, 30, 37, 44, 51, 59, 60, 67)

Cicada bicincta von Schrank, 1776, Beyträge zur Naturegeschichte. p. 75.

Males.--Length 5.00-6.50 mm (mean 6.01 mm). Crown L:W ratio 1:2.29; range 1:2.10-2.67. Crown and pronotum with an irregular transverse yellow-white band. Forewings translucent, light brown to rufous, and usually without fuscous markings. Veins of slightly lighter color.

Females.--Length 5.73-7.52 mm (mean 6.13 mm). Crown L:W ratio 1:1.70; range 1:1.6-1.85. Similar to albifrons in shape, but larger. Head and pronotum variable; rufous, mottled brown, to fuscous. Forewings translucent or opaque with irregular fuscous spots, almost entirely dark brown, or rufous. Tergum often striped with red along the intersegmental membrane.

Male genitalia.--Genital plate form similar to albiger; but larger, more coarsely setose, and more broadly rounded apically (Fig. 44a). Pygofer hooks gently recurved basally, sharply bending distally and pointed apically (Fig. 44b). Styles similar in structure to albifrons, but larger (Fig. 51). Aedeagus 0.78-0.99 mm in length; with two pair of retrorse spines medially and sublaterally; anterior pair project laterally, posterior pair projecting laterally and caudally. Retrorse spines close or distinctly separate. Lateral edges of distal one-fourth of aedeagal shaft dorsoventrally flattened, serrate and curving caudally at its tip; non-flattened distal portion angling sharply to a point in dorsal view (Fig. 59). Gonopore occupies distal one-third of aedeagal shaft, similar to albifrons.

Nymphs.--Measurements for nymphs are shown in Table 4.

First instar: Similar to albifrons in shape, but larger and often becoming a brownish-green near end of stadium. Setal rows on abdomen absent in all instars.

Second to fifth instar: Light green to dark green with fuscous spots on the body; spots usually more concentrated on head and pronotum.

Specimens examined.--700+ .

Distribution.--Nearctic (northeastern United States, southeastern Canada, Great Lakes region, northwestern United States and eastern Canada). Palearctic (western Europe, Asia and N. Africa). See Maps 3 and 4 for Nearctic distribution.

Remarks.--Males are readily distinguished from species of Anoscopus by the absence of color pattern on the forewing and from those of Stroggylocephalus by the presence of two transverse light stripes on the crown and pronotum.

Ribaut (1952) recognizes a subspecies, A. bicinctus diminutus (Figs. 59a, 59b). It is distinguished from A. bicinctus bicinctus (Fig. 59c) by having the pairs of lateral spines distinctly separate. It occurs primarily in the eastern United States, but three males from Pacific City (Tillamook Co., Ore.) are recorded from western United States. Intermediates of the two subspecies are common in eastern United States, but have not been found in western United States.

This species is Palearctic, apparently adventive into North America, and is very abundant in eastern and western North America. It apparently feeds on grasses, legumes, and strawberry, but is also collected (less often) on other herbaceous plants and some cultivated crops. Its habitat is similar to albifrons, but it usually occurs on higher parts of the plant. It has been collected wherever albifrons has


Map 3. Confirmed Nearctic distribution of Aphrodes bicinctus (Schrank).


Map 4. Confirmed Nearctic distribution of *Aphrodes bicinctus diminuatus*.

been collected in the Willamette Valley (Oregon). In lawns where albifrons has been found, only a few bicinctus have been collected.

Aphrodes californiensis Bliven (1957) was described from 23 specimens collected at Eureka, California (July 4, 1955). Although none of Bliven's material was available for study, A. bicinctus is known to occur in that area, and on the basis of his description, I consider A. californiensis to be a junior synonym of A. bicinctus.

A complete synonomy and distribution of bicinctus is found in Metcalf's Catalogue (1963).

Aphrodes (Anoscopus) flavostriatus (Donovan)
(Figs. 21, 22, 28, 43, 50, 57)

Cicada flavostriata Donovan, 1799, Homoptera Natural History of British Insects 8, p. 88.

Males.--Length 2.86-3.43 mm (mean 3.16 mm). Crown L:W ratio 1:2.02; range 1:1.85-2.42. Ocelli usually brown. Forewings striped, rufous and opaque; veins rufous to dark brown, opaque proximally, becoming light brown to rufous distally forming an irregular transverse dark band; a narrow opaque transverse band apically.

Female.--Length 4.14-4.36 mm (mean 4.22 mm). Crown L:W ratio 1:1.88; range 1:1.74-2.13. Similar to albifrons in form. Forewings fuscous and usually with opaque longitudinal veins. Pattern of of forewing may not be distinct.

Male genitalia.--Form and setal structure of genital plates similar to albifrons (Fig. 43a). Form of pygofer hook similar to albiger (Figs. 43b, 43c). Styles 0.8-0.85 mm long, similar to albifrons but usually less scabose (Fig. 50). Aedeagus 0.5-0.6 mm long, similar to albiger except that the phallobase forms an almost right angle with the aedeagal shaft where they meet; large medial spines gently curving laterally; distal one-third of aedeagus narrowing into a blunt dorsolateral flattened point (Fig. 57). Gonopore similar to albiger.

Specimens examined.--59.

Distribution.--Nearctic (Great Lakes region, northeastern United States, southeastern Canada). Palearctic (Europe and western and central Asia). See Map 5 for Nearctic distribution.

Remarks.--Although the pygofer hooks, styles and aedeagus of flavostriatus and albiger are similar, the color pattern of the fore-wings is usually distinctly different.

In North America A. flavostriatus has been collected only in the vicinity of the Great Lakes region. The color pattern of the nymphs is unknown.

A complete synonomy and distribution of flavostriatus is found in Metcalf's catalogue (1963).


Map 5. Confirmed Nearctic distribution of *Aphrodes flavostriatus* (Donovan).

Aphrodes (Stroggylocephalus) mixtus (Say)
(Figs. 24, 31, 32, 38, 45, 52)

Tettigonia mixta Say, 1825, Descriptions of new Hemipterous insects collected in the expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under command of Major Long. Acad. Nat. Sci. Phila. Jour. 4:341.

Males.--Length 5.24-6.21 mm (mean 5.58 mm). Crown L:W ratio 1:2.51; range 1:2.37-2.65. Crown striate, light brown to rufous with darker mottling. Face similar in color to crown but usually darker. Forewings opaque with brown or rufous mottling.

Females.--Length 5.81-6.44 mm (mean 6.12 mm). Crown L:W ratio 1:2.24; range 1:2.08-2.41. Similar to males, but generally darker in color. Crown striate; color lighter than face. Crown usually distinctly mottled.

Male genitalia.--Genital plate similar in shape to albifrons but larger and more setose with stout setae present on ventromedial one-half and hairlike setae present on ventrolateral one-half (Fig. 38a). Distal one-third of pygofer hook recurved, sharply pointed and dentate at its apex (Fig. 38b). Styles similar to bicinctus; angularly rounded apically and crenulate; two rows of recurved teeth subapical, becoming crenulate (Fig. 45). Aedeagus 0.56-0.61 mm long; dorsoventrally flattened and broadly rounded at the apex; distal one-fifth of the aedeagal shaft with two rows of short stout spines along the lateral margin, terminating in a pair of retrorse spines that extend latero-ventrally (Fig. 52). Width of aedeagal shaft nearly uniform. Phallobase dorsoventrally compressed and at least two times broader at base than aedeagal shaft; narrowing apically into a blunt point. Gonopore opening in the anterior one-fourth of aedeagal shaft.

Specimens examined.--61.

Distribution.--Nearctic (northern United States and southern Canada). See Map 6 for distribution.

Remarks.--Males and females show little sexual dimorphism although the females tend to be larger and darker in color. They can be easily distinguished by the aedeagus being dorsoventrally flattened apically with two rows of denticles on the apical lateral margin and terminating in a pair of larger retrorse spines.

This species is endemic to North America. Its general habitat is unknown, but it may occur near marshes and similar habitats.

Most recent American workers have considered mixtus to be a junior synonym of the Palearctic agrestis (Fallen), and it is so treated by Metcalf (1963). However, none of the Nearctic specimens that I have examined is specifically identical with examples from the Palearctic Region; thus mixtus is considered as a valid species.


Map 6. Confirmed Nearctic distribution of *Aphrodes mixtus* (Say).

Aphrodes (Stroggylocephalus) placidus (Provancher)
(Figs. 25, 33, 39, 46, 53)

Selenocephalus placidus Provancher, 1889, Deuxième sous-ordre les Homopteres. Petite Faune Entomologique du Canada, précédée d'um traité élémentaire d'entomologie. 3:280.

Males.--Length 4.97-5.18 mm (mean 5.11 mm). Crown L:W ratio 1:2.52; range 1:2.27-2.69. Crown finely striate, light brown to rufous, occasionally with darker mottling. Face usually mottled brown.

Females.--Length 5.52-5.72 mm (mean 5.60 mm). Crown L:W ratio 1:2.29; range 1:2.07-2.50. Similar to mixtus, but generally lighter in color. Crown finely striate, light brown and usually without mottling. Face usually mottled.

Male genitalia.--Genital plates similar to mixtus (Fig. 39a). Pygofer hook recurving dorsally and then decurving near its tip, sharply pointed at its apex (Fig. 39b). Shape of styles similar to albifrons but broadly rounded and crenulate apically; two rows of recurved teeth subapical, becoming crenulate (Fig. 46). Aedeagus length 0.56-0.61 mm long; with one pair of long apical retrorse spines, curving laterally and anteriorly. Aedeagal shaft rotundate, apically and laterally expanded basally; with lateral margins dorso-ventrally flattened basally, narrowing sharply near its base (Fig. 53).

Gonopore opening in the distal two-thirds of aedeagus and similar to mixtus.

Specimens examined.--14.

Distribution.--Nearctic (northern United States and southern Canada). See Map 7 for distribution.

Remarks.--Sexual dimorphism is not readily apparent in this species, although females tend to be larger and darker in color than the males. A. placidus can be distinguished by stout setae on the genital plate; a finely striate crown; and aedeagus with one pair of curved apical retrorse spines.

This species is endemic to North America with a similar distribution as mixtus. Both of the latter species have been collected from the same locality and probably have similar habitat.

A. placidus has been considered a junior synonym of the Holarctic flavostriatus and is so treated by Metcalf (1963). In collections, placidus has been usually found identified as agrestis, a Palearctic species, and less often as mixtus, a Nearctic species. Individuals of placidus from the U.S. have been compared and species identification verified with the type specimen in the Canadian National Collection by K.G.A. Hamilton (personal communication).


Map 7. Confirmed Nearctic distribution of Aphrodes placidus (Provancher).

Aphrodes (Anoscopus) bifasciata (L.)

(Fig. 58)

Cicada bifasciata Linnaeus, 1758, Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 10, rev, 1:436.

Males.--Length 3.5-3.8 mm (Ribaut, 1952). Crown L:W ratio 1:1.78. Forewings with fuscous or black transverse bands (three) alternating with opaque transverse bands (two or three); proximal transverse band fuscous; distal transverse band opaque or black.

Females.--Length 4.00-4.8 mm (Ribaut, 1952). Similar to albifrons but usually larger. Submacropterous. Forewings sometimes with two transverse light patches as in males.

Male genitalia.--Form and setae of genital plate similar to albifrons. Shape of styles similar to albifrons. Aedeagus 0.81 mm long; shaft laterally compressed; distal one-fourth of its posterior margin expanded in a transverse irregular ledge; anterior margin sharp. Aedeagal shaft with three pairs of subequal retrorse spines; two pair somewhat medial and on the posterior margin; one pair somewhat medial and on the lateral side (Fig. 58). Gonopore opening in the anterior one-half of aedeagal shaft.

Specimens examined.--One male.

Distribution.--Nearctic (Newfoundland); Palearctic (Europe, Asia, N. Africa and Japan). See Map 8 for Nearctic distribution.

Remarks.--The general appearance of this species is very similar to serratulae, but it can be distinguished from the latter by a larger aedeagus and the presence of three retrorse spines on the aedeagal shaft. This species is widespread in Europe and Asia and has been recorded from Japan. I have only one record of bifasciatus in North America, a male specimen taken from Newfoundland and possibly representing a recent introduction. The data are insufficient to make any kind of judgment of its true distribution in North America.

A complete synonomy and distribution of bifasciatus is found in Metcalf's catalogue (1963).

Aphrodes (Anoscopus) serratulae (Fabricius)
(Figs. 3, 4, 12-17, 27, 42, 48, 55, 68, 69)

Cicada serratulae Fabricius, 1775, Ryngota. Systema Entomologiae. Sisten insectorum classes, ordines, genera, species, adietis synonymis, locis, descriptionibus, observationibus, Korte p. 686.

Males.--Length 3.24-3.84 mm (mean 3.56 mm). Crown L:W ratio 1:2.15; range 1:1.92-2.49. Ocelli usually reddish. Forewings usually with fuscous transverse bands alternating with opaque and/or hyaline transverse bands; proximal transverse band fuscous; distal transverse band narrow and usually hyaline.

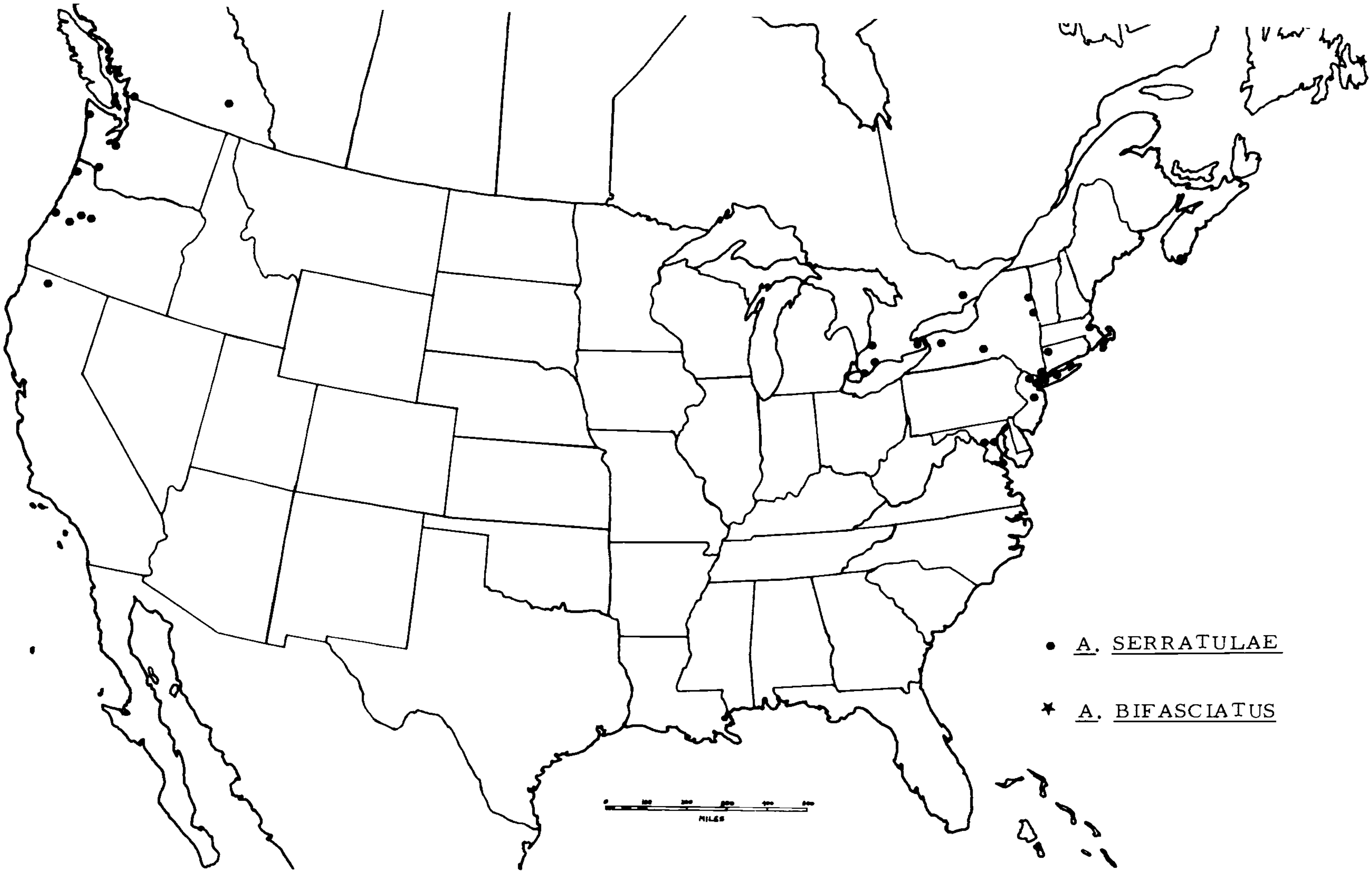
Females.--Length 3.75-4.40 mm (mean 4.12 mm). Crown L:W ratio 1:1.56; range 1:1.37-1.80. Similar to albifrons and cannot be distinguished with certainty from females of albifrons. Forewings usually hyaline and rufous with some fuscous spots. Seventh sternite with a medial rufous patch, usually lighter in color than albifrons.

Male genitalia.--Genital plate with basal two-thirds of dorsolateral margin nearly straight; curving posterodorsally and terminating in a blunt point (Fig. 42a). Pygofer hook recurved; apically irregular and blunt; internal margin irregular (Figs. 42b, 42c). Styles 0.85-0.95 mm long; similar to albifrons but somewhat clubbed distally (Fig. 48). Aedeagus 0.6-0.7 mm long; rotundate for most of its length, becoming somewhat dorsoventrally flattened apically; two pair of lateral, subequal, subapical retrorse spines; apical pair projecting anteriorly; posterior pair projecting posteriorly. Aedeagal shaft broader basally (Fig. 55). Gonopore similar to albifrons, but wider distally.

Nymphs.--Measurements for nymphs are shown in Table 4.

First instar: Similar to albifrons and indistinguishable from that species.

Second to fifth instar: Similar to albifrons, but differing in having a distinct color pattern consisting of a fuscous longitudinal stripe from anterior margin of crown to terminalia and lateral




Map 8. Confirmed Nearctic distribution of *Aphrodes serratulae* (Fabricius) and *Aphrodes bifasciatus* (L.).

longitudinal stripes from posterior margin of eye to terminalia. Setae on abdomen as in albifrons.

Specimens examined.--250+ .

Distribution.--Nearctic (northwest North America, northeastern United States and Great Lakes region). Palearctic (western Europe, Asia and N. Africa). See Map 8 for Nearctic distribution.

Remarks.--The forewings are variable; usually with distinct fuscous transverse bands; occasionally completely hyaline, or with rufous transverse bands. The males of this species can be distinguished from other species of Aphrodes by size, color of forewing and position of retrorse spines on aedeagal shaft.

This Palearctic species is presumably adventive in North America. It occupies the same basic habitat as albifrons and in the Willamette Valley (Oregon) has always been collected in association with albifrons, but is usually more abundant than that species.

A complete synonomy and distribution of serratulae is found in Metcalf's Catalogue (1963). However, on the basis of my study of specimens, some of the Nearctic records of albifrons probably refer to serratulae.

Aphrodes (Stroggylocephalus) sp.

(Fig. 34)

Males.--Unknown.

Females.--Length 5.09 mm. Crown L:W ratio 1:2.49. Similar to _mixtus_ in form. Crown, convex, short, mottled, finely striate. Anterior margin of crown carinate. Face and crown uniformly mottled and pigmented. Clypellus slightly convex. Submacropterous, exposing ovipositor and tip of pygofer. Forewing rufous with irregular opaque spots. Hind wing brachypterous and somewhat triangular (Fig. 34b). Tibia 1-3 light brown. Posterior margin of sternum 3-5 and tergum 3-8 with a transverse pink to red color, mostly on intersegmental membrane.

Specimens examined.--One female.

Distribution.--Nearctic (Mt. LeCont, Kentucky).

Remarks.--This is believed to be a new species of _Aphrodes_ belonging to the subgenus _Stroggylocephalus_ and similar to _placidus_ and _mixtus_.

Table 4. Range of body length and crown width of larval instars of bicinctus, serratulae and albifrons.

| Instar | Length (mm) | Crown width (mm) |
| --- | --- | --- |
| | A. bicinctus | |
| 1 | 1.16-1.62 | 0.46-0.58 |
| 2 | 1.74-2.32 | 0.70-0.81 |
| 3 | 2.55-3.71 | 1.04-1.16 |
| 4 | 3.71-4.52 | 1.28-1.51 |
| 5 | 4.64-6.61 | 1.74-1.97 |
| | A. albifrons | |
| 1 | 0.83-0.96 | 0.51-0.56 |
| 2 | 1.21-1.43 | 0.65-0.71 |
| 3 | 1.75-2.22 | 0.87-0.92 |
| 4 | 2.30-2.93 | 1.00-1.12 |
| 5 (cast skins) | 3.88-4.02 | 1.21-1.28 |
| | A. serratulae | |
| 1 | 0.83-0.96 | 0.51-0.56 |
| 2 | 1.21-1.39 | 0.64-0.72 |
| 3 | 1.91-2.18 | 0.87-0.94 |
| 4 | 2.30-2.93 | 1.00-1.16 |
| 5 (cast skins) | 3.76-4.04 | 1.21-1.28 |

# VI. BIOLOGY AND ECOLOGY

## Habitat and Behavior

Information on the biology of members of the genus Aphrodes in North America is incomplete for most species and lacking altogether for others. The biology of species of Aphrodes occurring in Eurasia has been studied in greater detail because A. bicinctus and albifrons have been implicated as vectors of plant pathogens. However, those studies deal mostly with disease transmission and are very incomplete regarding other aspects of the biology of Aphrodes.

In Oregon, specimens of A. serratulae, albifrons and bicinctus can often be collected from the same locality and often from under the same rocks. Adults of bicinctus are usually found on the basal one-half of plant stems or at the base of plants and can be collected easily with a sweep net. A. albifrons and serratulae adults are usually found at the base of plants and among ground litter, under boards and rocks, in cracks in the soil, etc., and are less readily collected with a sweep net than is bicinctus. Collection records for North America indicate that other species of the subgenus Anoscopus occupy similar habitats and probably behave as do albifrons and serratulae. A species of the subgenus Stroggylocephalus, probably mixtus or placidus, was reported (under the name agrestis) as taken from vegetation in sandy soils and from a grass marsh in Illinois (Delong, 1948).

In grazed pastures, both nymphs and adults of albifrons and serratulae often aggregate at the edge of rocks, boards, debris, and around foliaceous weeds not normally eaten by grazing animals. The increased population density near or under rocks and large plants is most likely a response to temperature and humidity conditions that exist in the surrounding vegetations. In late summer they tend to congregate under objects more than in spring or early summer. The presence of nymphs around objects in heavily grazed pastures may be partially due to females having deposited their eggs where they tend to congregate in late August or early September.

In ungrazed vegetation, early instars are found in open areas and were not observed to congregate under or around rocks or other debris. The first nymphs, under relatively wet conditions, are found on the lower part of the stems of plants and can easily be collected in a "D-Vac."

In grazed pastures, bicinctus tends to congregate somewhat around rocks and boards as does albifrons, but is more often found around herbaceous plants (tansy, etc.) not normally eaten by grazing animals. In ungrazed areas, bicinctus is found usually on the lower one-half of the stem, but, in dense populations, can be collected in relatively large numbers by sweeping the upper parts of the plants.

As summer progresses, bicinctus also moves to lower parts of the plants and is not so readily collected.

Aphrodes (except bicinctus) are not commonly collected and for the most part go undetected because of their behavior and habitat. A "D-Vac" with a wide nozzle proved to be successful in the early detection of nymphs. In the early spring the nymphs occur higher on the plant, and the plants are shorter, leaving the leafhopper more accessible to the suction of the "D-Vac." However, as the season progresses, and grass increases in height, the leafhoppers move nearer the base of the plant or below the mat of grass which decreases the efficiency of the wide nozzle. A nozzle of smaller diameter is more efficient later in the season because it provides more suction and accessibility around the base of plants, rocks, etc. where the leafhoppers are then congregated. The "D-Vac" may prove to be an important device for the ready detection of vectors of plant pathogens that frequent environments such as those inhabited by bicinctus and albifrons.

Nymphs and adults of bicinctus, serratulae and albifrons have the same basic behavioral patterns. Normally members of these three species are relatively sluggish, moving very slowly and jumping only when prodded. The females tend to be more sluggish than the males, often requiring several prods in order to get them to jump.

However, once the leafhopper jumps, less stimulus is required to get it to hop again.

The males react to a disturbance more readily than do the females, which often remain motionless until touched. Both nymphs and adults of serratulae and albifrons, and to a lesser degree bicinctus, will feign death when disturbed by falling on their backs, drawing in their legs and remaining motionless. Usually, within a minute or so they begin to move, right themselves, and then either remain motionless, or crawl away to the shelter of grass, cracks in the soil, etc. When air (breath) is blown over the leafhopper, the death feigning response is interrupted. The leafhopper rights itself by moving its legs rapidly and then retreats to shelter. All three species will also, when on a plant, move to the protected side of the stem and sometimes move up or down the stem when air (breath) is blown directly on them or when an object is moved toward them. Bright light from an illuminator will also cause them to retreat to the lower part of the plant or at least out of the range of the light. A. serratulae and albifrons, when on the ground away from plants, will seek protection in cracks or holes in the soil, under clods of soil or other debris. They do so by backing into the cracks. Once the source of disturbance (e.g. a probe) is removed, the leafhopper will usually crawl partially out of hiding, exposing the anterior portion of its body. If a probe is moved closer, or other disturbance occurs, the leafhopper will again back into the hole and move forward only if the probe is removed. After an extended period of time, the leafhopper will crawl completely out and retreat to a clump of grass. This behavioral trait has not been observed in bicinctus.

## Sound Production

Sound production is widespread among auchenorrhynchous Homoptera (Ossiannilsson, 1949). In most cases, both sexes have sound producing organs, although the sound producing organs of females may be weaker or less developed. Most of the sounds produced have been characterized as courtship songs (males) or invitation songs (females), but distress songs have also been observed. Because of the secretive habits of at least some species of Aphrodes, courtship songs presumably improve the probability of mating. Ossiannilsson has reported that bicinctus, bifasciatus (as trifasciatus), and flavostriatus have the ability to make sounds, and gives an account of the morphology of the sound producing organs of bicinctus as well as other leafhoppers and auchenorrhynchous Homoptera. A. bifasciatus has been observed making a distress sound (Ossiannilsson, 1949). I have observed a serratulae male, and a female presumed to be of same species, producing sounds while the male was riding on the back of the female. The sounds may be described as a fast tat-tat-tat-tat-tat-etc.-tat-buzz, buzz, buzz. Buzzing usually occurred after the tat-tat-tat-tat-tat-etc. sequence. Copulation did not follow and it was not determined which individual, or if both, produced the sounds. In the greenhouse, it was frequently observed that males of serratulae and bicinctus were found riding on the backs of females. A. serratulae and albifrons males appear to be non-selective, riding as frequently on bicinctus females as other females. However, males of bicinctus were never observed riding on the backs of A. (Anoscopus) females. Copulation was not observed to follow the "riding" behavior.

House and Claridge (1970) have found a structure on the antennae of Oncopsis favicollis (Macropsinae) that may have an auditory function. This idea was supported by observations that the antennal flagella could be made to resonate to tones with frequencies approximating the pulse repetition frequencies of the songs. Examination of the antennae of bicinctus, albifrons, and serratulae at 400X magnification reveals that the external structure of the antennae is nearly the same in form as that of O. flavicollis.

## Natural Enemies

A large number and variety of spiders were collected in association with Aphrodes and appear to be their main predator. Nabis americoferus Caray (Nabidae) has also been observed feeding on serratulae and has commonly been found, along with other species of Nabidae, where populations of Aphrodes have been collected in

Oregon. No parasites were observed in field collected specimens or specimens that were reared from field collected nymphs. However, nematode parasites have been reported by Dlabola (1945), and another parasite by Grandi (1934) in Europe.

## Host Plants

*A. bicinctus* is polyphagous, and in Canada, has been reared on ladino clover and strawberry (Chiykowski, 1970). In Oregon, *bicinctus* has been reared on *Trifolium repens* L. and *Vicia* (Leguminosae), strawberry, cultivars Shasta and Hood (Rosaceae), and pasture grasses (*Lolium perenne* L., *Poa* sp. L., *Hordeum murinum* L., and *Festuca bromoides* L.; (all Gramineae) ). Chiykowski (1970) reports *bicinctus* taken from *Trifolium pratense* L. and *T. hybridum* L. (Leguminosae), *Plantago major* L. (Plantaginaceae), *Taraxacum officinale* Weber and *Erigeron canadensis* L. (Compositae), *Capsella bursa-pastoris* (L.) Medic. and a species of *Brassica* (Tourn.) L. (Brassicaceae). *A. bicinctus* was reared through third and fourth instars on a species of *Brassica*. Observations indicate that *bicinctus* prefers to feed on clover, but will also feed on some grasses and will accept clover and strawberry about equally. However, when food plants were changed, strawberry to clover or vice-versa, there was a higher mortality rate among larval instars than if they were transferred to another plant of the same species. The mortality rate decreased among fifth instars and still more among adults subjected to the same type of host changes.

Some _bicinctus_ fifth instars and adults were reared on bean plants. There was no mortality for the first three weeks, but most were dead after four weeks. This indicates that they can survive temporarily on bean, but probably do not reproduce.

_A. albifrons_ and _serratulae_ are also polyphagous, but appear to be more restricted to grasses. Attempts to rear nymphs of both species on strawberry cultivars failed, but they were reared on _Trifolium repens_ L. When clover and grasses were placed in the same rearing chamber, a majority of the specimens were always found on the grasses.

_A. bicinctus_, _albifrons_ and _serratulae_ have been collected in the field from pasture grasses, at the base of tansy ragwort (_Senecio jacobaea_ L., Compositae), _Plantago major_ L. (Plantaginaceae), _Phalaris arundinacea_ L., _Deschampsia caespitosa_ (L.) Beauv. and _Festuca rubra_ L. (Gramineae), and clover. Presumably, _Plantago major_ L. and tansy are not utilized as a food source, but provide shelter and a level of relatively constant humidity at the base of the plant and also access to exposed roots of grasses and clovers. Osborn (1916) reported a species (probably _serratulae_) under the name _albifrons_ as occurring and feeding on timothy grass, and not occurring in the surrounding area where timothy was absent.

## Disease Transmission

Two species, _A. bicinctus_ and _albifrons_, have been implicated as vectors of plant pathogens. In Europe and North America, _bicinctus_ has been shown to be a potential vector of clover phyllody virus (CPV), clover dwarf, European aster yellows in Europe, and stolbur virus disease of tomato and tobacco in Czechoslavakia (Nielson, 1968). _A. albifrons_ has been implicated in the transmission of clover phyllody virus in Europe, but confirmation is lacking (Chiykowski, 1962). Because of the potential economic importance of _bicinctus_, this species has been more critically studied than have others of the genus.

## Life Cycle (Charts 1-4)

In three species (_bicinctus_, _albifrons_ and _serratulae_) that have been examined in Oregon (Benton and Marion Co.), the females become gravid by mid August or early September. Usually one complete set of eggs (14, 7 per ovary) develops at a time with the remaining oocytes developing very slowly until after oviposition of the ripe eggs. After oviposition, the following oocytes develop more rapidly.

Through October and November, the numbers of females present decrease rapidly. In Oregon, a few females survive the winter as adults, but this population does not represent a significant number of individuals. One adult female of either albifrons or serratulae was taken in early March. Examination of the spermatheca revealed the presence of sperm.

The eggs overwinter and begin to hatch in late February or early March. The time of emergence appears to depend on prevailing weather conditions, latitude and elevation. For example, in Ottawa, Canada, the hatching of bicinctus may occur as late as May (Chiykowski, 1970).

My observations indicate that early instars feed on the lower one-half of the stem of the food plant, gradually migrating to the base of the plant as they develop. Movement from the upper portion of the plant to the lower part of the plant may be due to humidity requirements, a photonegative response, and/or their ability to penetrate coarser material with the mouth parts. Nymphs of serratulae and albifrons exhibit greater vertical movement than those of bicinctus which remains on the upper portion of the basal one-half of the stem.

On the basis of field observations, development is very slow at first, increasing as the days lengthen and the mean temperature increases. By June, a few adult males appear in the field. In the greenhouse, where the mean temperature is higher than normal ambient temperatures, first and second instars developed into adult males by the end of April with females appearing shortly thereafter. In newly emerged males, the testes rapidly increase in size and the seminal vesicle becomes enlarged as it becomes packed with sperm. The accessory gland increases in size and the testes later begin to deteriorate. Adult females begin to appear shortly after the males. Examination of female spermatheca indicates that insemination does not occur immediately after emergence, but within a short time (up to 5-10 days) thereafter.

The ovarioles develop very slowly through mid July. Shortly after emergence the developing oocytes are barely discernible, but become easily visible with a light microscope at 100X by late July in some females. By mid August or early September most females have mature eggs.

Toward the end of August males of bicinctus, serratulae and albifrons are present only in very small numbers and have not been found later than 10 September in Benton or Marion Counties, Oregon. Females of these same species are relatively abundant through September, declining in October, and are found only rarely in November.

The life cycles of albiger and flavostriatus appear to be similar to that of albifrons, with adults appearing in June. Males disappear from the populations by early September but females are present until November. Mature eggs were not found in preserved specimens of flavostriatus collected during June through September, but egg maturation is believed to occur at the same time as in albifrons.

Information on the life cycle of bifasciatus in North America is incomplete because only one male has been collected in North America.

Females of bicinctus caged on clover plants in the greenhouse usually oviposited in the basal portion of the petiole, completely burying the eggs in the plant tissue, although some occasionally deposited eggs in pieces of peat moss (part of the soil mixture) or strewn over the surface of the soil (Chiykowski, 1970). My attempts to find eggs of serratulae and albifrons under greenhouse conditions failed. Eggs of these latter species are most likely deposited in the basal portion of grass stems, but, like bicinctus, may be deposited randomly over the surface of the soil.

Aphrodes bicinctus, albifrons and serratulae have five nymphal instars. Under laboratory conditions (70-75°F, 16 hr/day), bicinctus developed into adults in about 40 days; male development required slightly less time (38.5 days) than females (41.3 days) (Chiykowski, 1970). However, under natural conditions, the duration of the instars is longer. This is believed to be primarily due to cooler temperatures which prevail in the earlier part of the season. When nymphs of serratulae, albifrons and bicinctus were brought into the greenhouse in March, and kept in a rearing room at 65-70°F with natural light conditions, males appeared as early as 27 April and females appeared in early May. Judging from field observations, the length of the nymphal stages of albifrons and serratulae are similar to bicinctus.

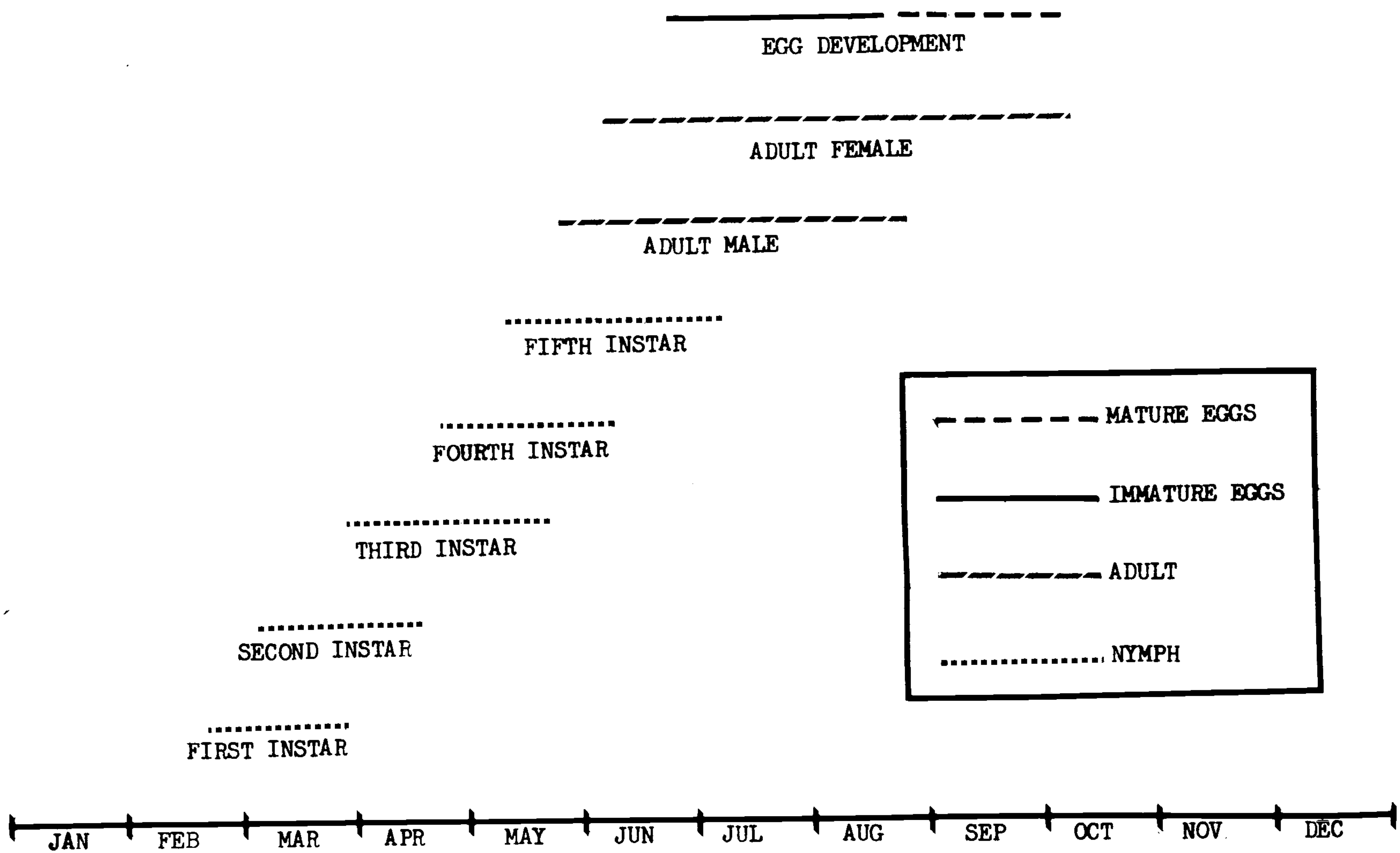



Chart 1. Seasonal sequence of developmental stages of *A. albifrons*. Oregon, Benton Co., 1974-1975.

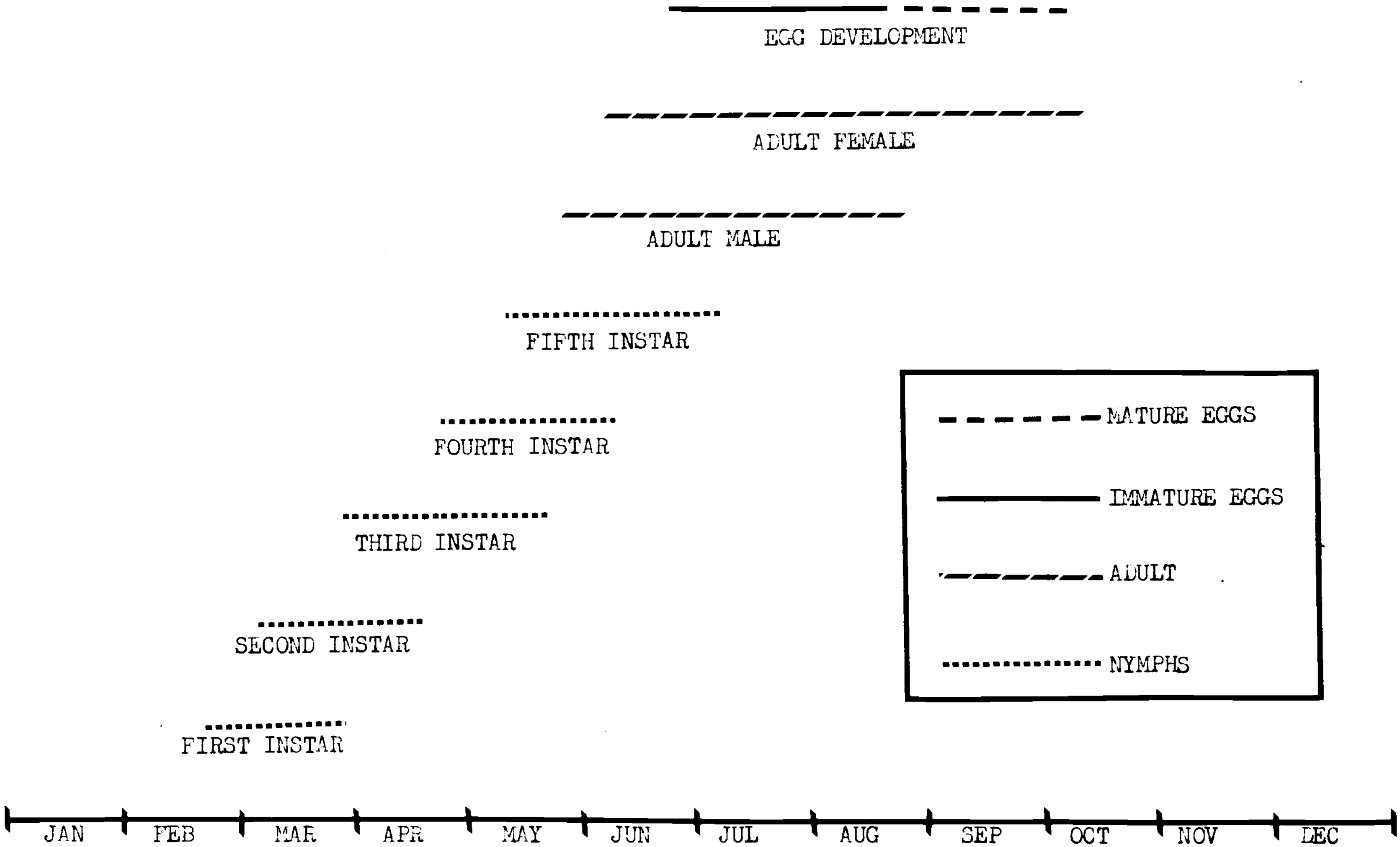



Chart 2. Seasonal sequence of developmental stages of A. serratulae. Oregon, Benton Co., 1974-1975.

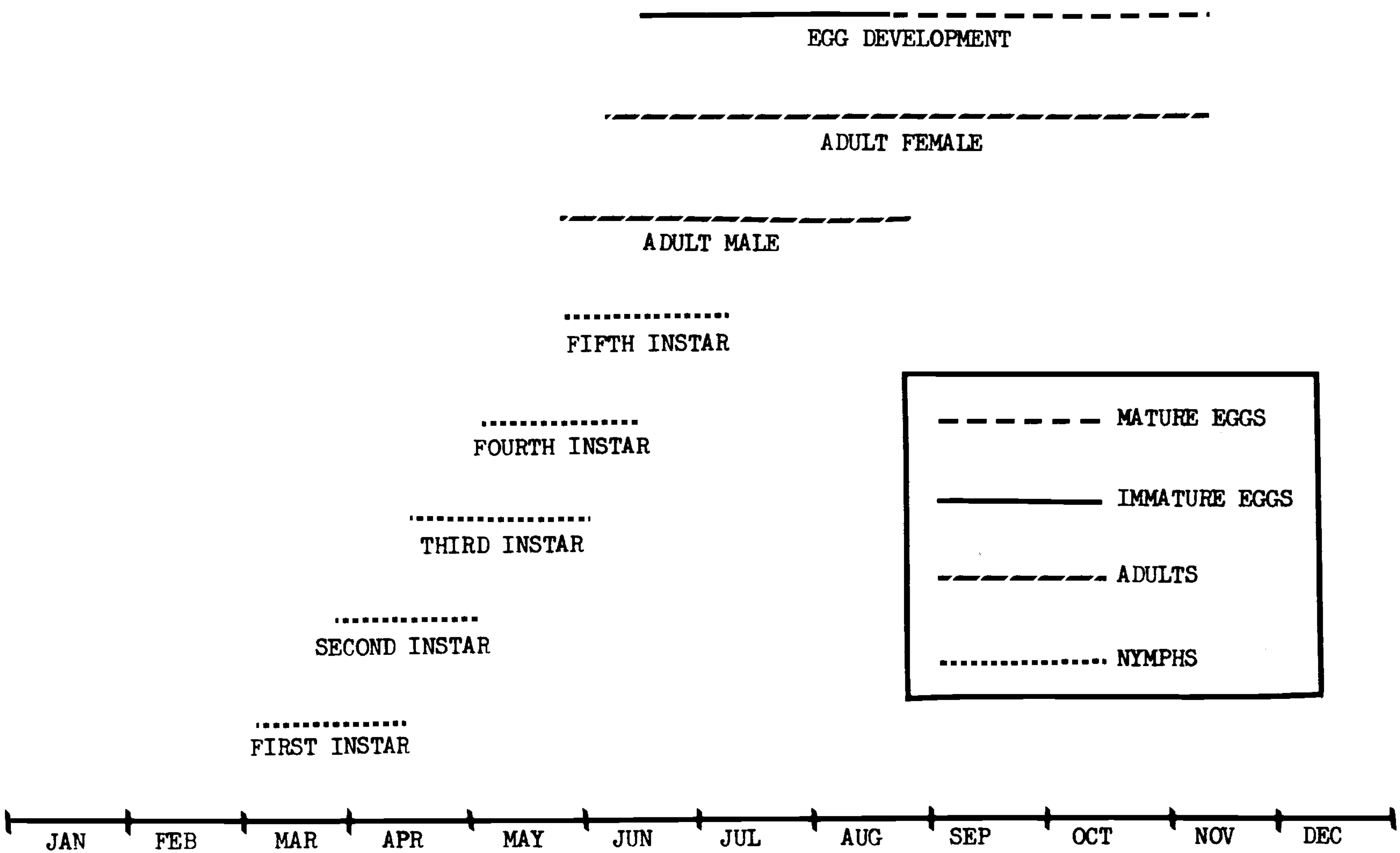



Chart 3. Seasonal sequence of developmental stages of A. bicinctus. Oregon, Benton Co., 1974-1975.

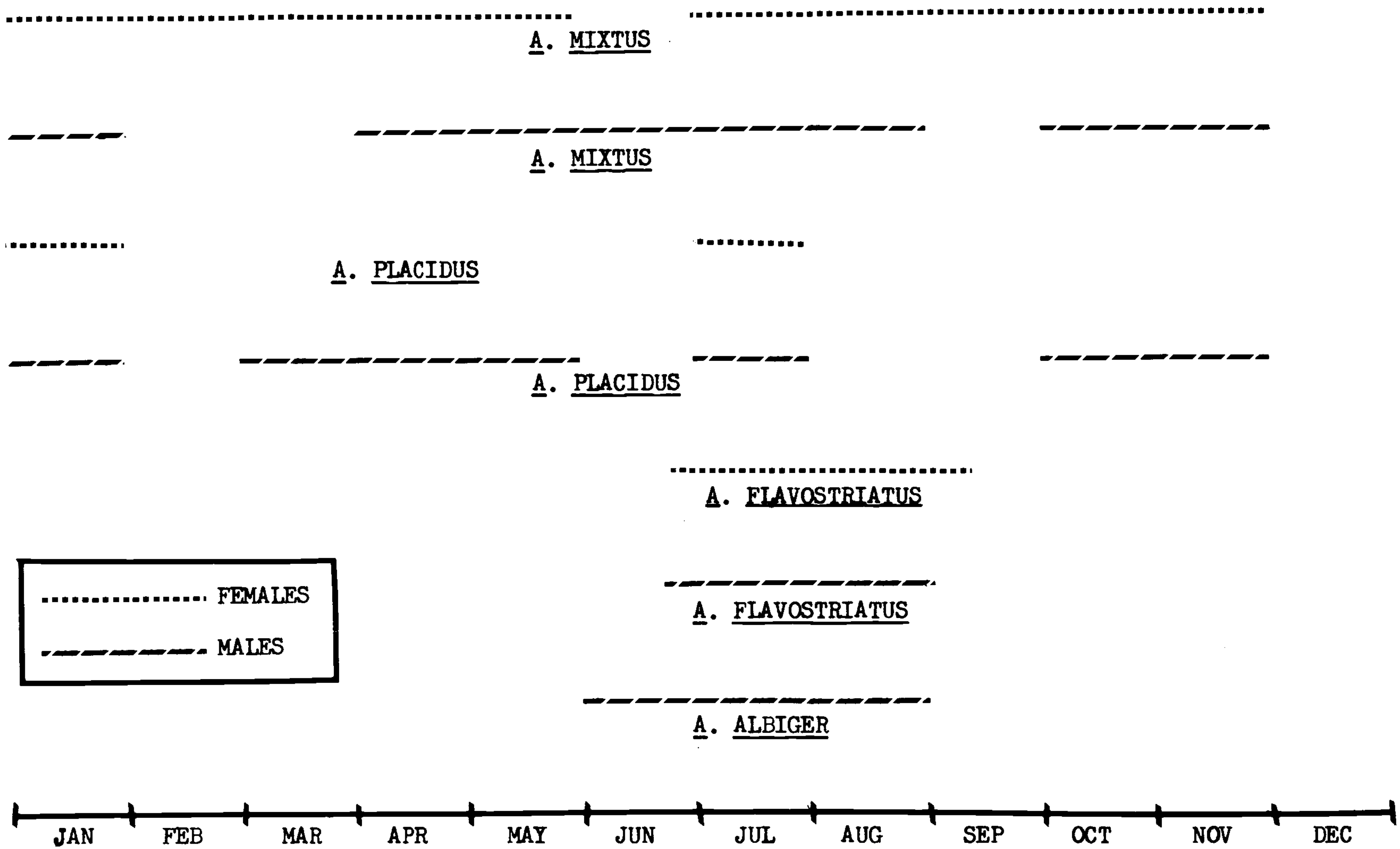



Chart 4. Seasonal distributions of adult stages of species of Aphrodes in North America.

The life cycle of members of the subgenus *Stroggylocephalus* in North America appears to be somewhat different from that of other species of *Aphrodes*. The adults of *mixtus* probably occur throughout the year but have not been collected in December. *A. placidus* probably also occurs throughout the year but has not been collected during February, June, August, September, and December. No information is available on the nymphs. Mature eggs were found in *mixtus* collected in April and June and in one female of *placidus* taken in late August.

Apparently most species of *Anoscopus* and *Aphrodes s.s.* are univoltine. Information on the life cycle of *bifasciatus* is incomplete, but it is assumed to be similar to the other species of *Anoscopus*. Species of *Stroggylocephalus* may or may not be univoltine.

## Reproductive System

### Females (Figs. 7, 60)

The reproductive system has two ovaries that are connected anteriorly to the lateral prothoracic region by long filaments leading from the ovarioles. Forbes and McCarthy (1969) reported that the ovarioles were attached to fat bodies. My findings do not support that observation since I find no evidence of attachment of the terminal filament to the fat bodies. The fat bodies are contiguous with the anterior part of the ovarioles near the base of the terminal filament in reproductively immature females, becoming indistinct masses prior to egg deposition. Each ovary has seven ovarioles which join at a common point to form the lateral oviducts. The ovarioles are spindle shaped, gradually becoming more elongate as the eggs mature. The median oviduct is formed by the union of the lateral oviducts. The vagina occupies the basal portion of the median oviduct and is pink or white in color and distinctly hyaline. Sperm bundles presumably occupy the periphery of the vagina where the vagina is swollen or enlarged. One accessory gland joins the vagina basally. It is greenish or yellowish in color in bicinctus and opaque in serratulae and albifrons. The vagina joins the ovipositor at its base (Fig. 7). Normally seven eggs mature at the same time in each ovary (Fig. 60) with the other developing eggs being very small. Following the passage of eggs, the lateral oviduct and pedicel (when present) do not return to their original shape, leaving these structures wrinkled. The eggs of albifrons, bicinctus and serratulae are similar, resembling opaque, slightly curved cylinders, gradually tapering toward the apex and becoming broadly rounded. Eggs of mixtus and placidus are similar to bicinctus, but are generally wider medially.

Males (Figs. 6, 67-70)

The paired testes are opaque and composed of several lobes or spermatheca that are enclosed in a thin, membranous sheath. They are located laterally in the anterior one-fourth of the abdomen. The testes first appear as round balls with inconspicuous lobes enclosed in the membranous sheath. The testes increase in size as they mature which causes the membranous sheath to stretch and the lobes to become more distinct. The degeneration of the testes becomes noticeable in specimens that have enlarged and shiny vesicles where the sperm bundles that are produced in the testes are stored. The vesicles are small, opaque, paired and enclosed in a membranous sheath, having the appearance, in young adult male specimens, of a single structure. As sperm accumulates the vesicles become white and somewhat shiny and distended, stretching the membrane that encloses them. The two vesicles are closely appressed medially and when distended appear to be tightly enclosed by a membranous sheath. The vas deferens is a long, tube-like structure that extends to the base of the vesicle and connects the vesicle and testes before it loops and enters the vesicle anteriorly. The paired vesicles are located medially with an accessory gland closely appressed to each vesicle laterally. The accessory gland is opaque and distinct for each species of leafhopper that has been examined. At first, the accessory glands are small, gradually becoming larger as the vesicles enlarge and fill with sperm. The ejaculatory duct and accessory gland duct unite caudad of the vesicle. The paired ejaculatory ducts then unite near the aedeagus to form the *sacculus ejaculatorius*. The *sacculus ejaculatorius* narrows posteriorly where it connects with the penis at the base of the phallobase.

# VII. DISTRIBUTION

With few exceptions, collection data indicate a distribution for Aphrodes between 30° and 65°N latitude. Of the eight species of Aphrodes that occur in North America, six also occur in the Palearctic Region. The North American distribution patterns of those species that occur also in the Palearctic Region show certain similarities that suggest they were introduced through maritime commerce at some of the major seaports and subsequently extended their ranges inland along some of the major waterways and/or have been further trans-located by man. Collection data support the hypothesis that these species are adventive to North America as relatively recent introductions from Europe and/or Asia.

Both species of Aphrodes (Stroggylocephalus) that occur in North America are presumed to be endemic and have not been recorded from the Palearctic Region. Collection records are sparse and scattered which may indicate that they are represented only by populations. A. mixtus (Say) is the most widespread of the two species, having been recorded from numerous localities in the United States and Canada. It ranges west to central British Columbia and east to Massachusetts (110°W-70°W longitude), north to Churchill, Manitoba, and south to North Carolina (35°N-58°N latitude). It has been most often collected in northeastern United States and southeastern Canada, to north-central United States and south-central Canada (Map 6).

The distribution pattern of _A. placidus_ (Provancher) is similar to that of _mixtus_, but its range does not extend as far north or west (Map 7). Only a few specimens of _placidus_ have been available for study and may give a very incomplete picture of its true distribution.

I have examined one female specimen collected from Mt. Lecont, Tennessee that I have placed in the subgenus _Stroggylocephalus_. I believe it represents an undescribed species. However, because the criteria for species discrimination are based primarily on male genitalia, and because considerable variation is found among females of the genus _Aphrodes_, evidence of the precise identity of the specimen is inconclusive.

Metcalf (1963) records _A. agrestis_ from numerous localities in the United States and Canada (New York, Michigan, Iowa, Colorado, New Hampshire, Ohio, Indiana, Manitoba, Minnesota, Illinois, Ontario and New Jersey). Beirne (1954) also reports it from Canada. However, Beirne's illustration of the aedeagus of what he considered to be _agrestis_, is actually _mixtus_. Examination of preserved material from the United States and Canada, having failed to verify the occurrence of _agrestis_ in North America, leads me to conclude that this species does not occur in the Nearctic Region and that records of it in North America apply to either _mixtus_ or _placidus_.

A. albiger occurs in the northeastern coastal states and inland along the Great Lakes region (Map 2). On the west coast, it is found in isolated areas in Oregon and along the border of British Columbia and Washington, with only a few specimens taken from each locality. A. albiger may occur in some of the same localities as albifrons, but the evidence is still fragmentary. A. albiger has not been commonly recorded as occurring in North America probably because it has been confused with albifrons since the color patterns of the males are very similar.

A. bicinctus is by far the most abundant, or at least the most conspicuous species of Aphrodes in North America (Maps 3 and 4). It is widely distributed in northwestern and northeastern United States, extending into Canada along each coast. In northeastern United States its distribution parallels the east coast and Great Lakes. Occurrence records indicate that populations occur near areas of the shipping industry and adjacent land areas in eastern and western North America and Great Lakes region. Along the northwest coast and parallel to the Columbia River, population levels appear to be very dense, becoming more sparse inland. With the exception of one record from Texas (a female, and possibly an error in labeling), records for bicinctus are north of the 35°N latitude and below the 65°N latitude.

The distribution of flavostriatus is similar to albiger, with the exception that it does not occur in northwestern United States (Map 5). Collection data show flavostriatus to be widespread, but indicate that the populations are relatively dispersed. Beirne's (1954) record of flavostriatus from British Columbia presumably applies to albiger as the illustration of the aedeagus is of that species.

A. serratulae occurs along northeastern North America, the Great Lakes, and northwestern North America, primarily along the coast and inland a short distance (Map 8). It occupies the same basic habitat as albifrons and is very abundant, although it is not often collected because of its secretive habits. It could possibly be the most abundant of the species of Aphrodes occurring in western North America. Wherever serratulae has been found in Oregon, albifrons has also been found, but in fewer numbers. A. serratulae occasionally occurs with albiger in northeastern North America where albifrons is practically absent, but its range does not extend as far west along the Great Lakes as does albiger.

A. albifrons has been collected in Oregon and Nova Scotia (Map 1). The record from Nova Scotia is represented by only one male specimen. Because the females of albifrons cannot be distinguished from albiger and serratulae and since males of albifrons are only present from June to early September, distribution data depend upon collections made during this period. Populations of albifrons appear to be very localized and discontinuous. This can be exemplified by the situation observed in a well grazed pasture. Specimens of albifrons (and serratulae) were collected in a 30 meter radius where large rocks and boards were found centrally in the field; beyond that distance large rocks and boards were absent and no specimens were taken.

A. albifrons has probably been recorded erroneously from Maine, Indiana, Quebec, New York, New Hampshire, District of Columbia, Ohio, Pennsylvania, New Jersey, Wisconsin, Ontario, Massachusetts, Connecticut, British Columbia, Virginia, Minnesota, and Illinois (Metcalf, 1963). However, most of these records cannot be verified because of lack of specimens, illustrations or adequate descriptions of the male genitalia. Osborn's (1916) record of albifrons from Maine is accompanied by an illustration of a nymph that strongly resembles serratulae with its characteristic striping. J. L. Buys (1923) records albifrons from Ithaca, New York, but his illustration of the aedeagus is that of albiger (or possibly flavostriatus). Beirne (1954) and K. G. A. Hamilton (personal communication) are both of the opinion that most of the North American records of albifrons are erroneous.

Aphrodes albifrons, albiger, serratulae, bifasciatus, flavostriatus and bicinctus are Palearctic and presumably adventive to North America. In North America, all occur on the east coast and/or west coast along major waterways, and somewhat inland. Thus, the Palearctic and Nearctic distribution patterns of these species indicate that they are introductions from the Old World.

C.H. Lindroth (1968) suggested a means of introduction of plants and animals into North America from the Old World through sea travel. According to Lindroth, early in the Seventeenth Century the dumping of ballast into the sea was forbidden off the coast of Newfoundland and a similar law was later established for other ports in North America. The ballast, consisting of sod, rocks and soil, that contained plant materials etc., was required to be brought ashore. Movement of such material from one land mass to another provided excellent opportunities for small animals that inhabit the surface litter to move from one land mass to another.

Lindroth further states:

> The evidence gained from studies of the ballast transport of animals to Newfoundland is applicable not only to other parts of Atlantic North America but also to the Pacific Northwest. Southern British Columbia and Washington State, with Vancouver and Seattle as the main ports, have served as similar centers of introduction. . . . The explanation is similar: The large vessels loading wheat and lumber in the years before and during World War I often arrived from Europe in ballast.

The polyphagus and ground inhabiting behavior of adults and immature stages of <u>Aphrodes</u> makes them ideal candidates as introductions by means of a ship's ballast. Eggs laid on the ground or in a host plant could also have been transported in the same manner, not hatching until the following spring. Many of the possible host plants (clover and grasses), as well as the environmental conditions, are common to both continents. The habitat preferences of Aphrodes s. l. (excluding the subgenus Stroggylocephalus), their behavior, biology and patterns of distribution in North America support the hypothesis that maritime commerce played an important role in their introduction into this hemisphere. It is also noted that their Nearctic distribution patterns are similar to those of some other insects known to have been introduced from the Old World. However, collection records showing immigration from the coastal ports to the inland of North America, as has been done for some species of ground inhabiting Carabidae (Lindroth, 1968), are inconclusive.

Whatever the mechanism of introduction, some species of Aphrodes that became established in North America appear to be slowly extending their ranges inland. The slow rate of dispersal is probably due to their secretive habits and behavior. Although the females of most species are macropterous, they have never been observed to fly, and jump only when greatly disturbed. Long range movements are probably dependent on the movement of soil and plant products from one area to another.

# PLATE I

Figure

1 *Aphrodes albifrons* (L.). Crown and pronotum.

2 *Aphrodes albifrons* (L.). Face.

3 *Aphrodes serratulae* (Fabricius). Seventh sternum.

4 *Aphrodes serratulae* (Fabricius). (a) Ventral view of female genital capsule; (b) sclerotized rod of valve III; (c) valve I; (d) valve II; (e) valve III.

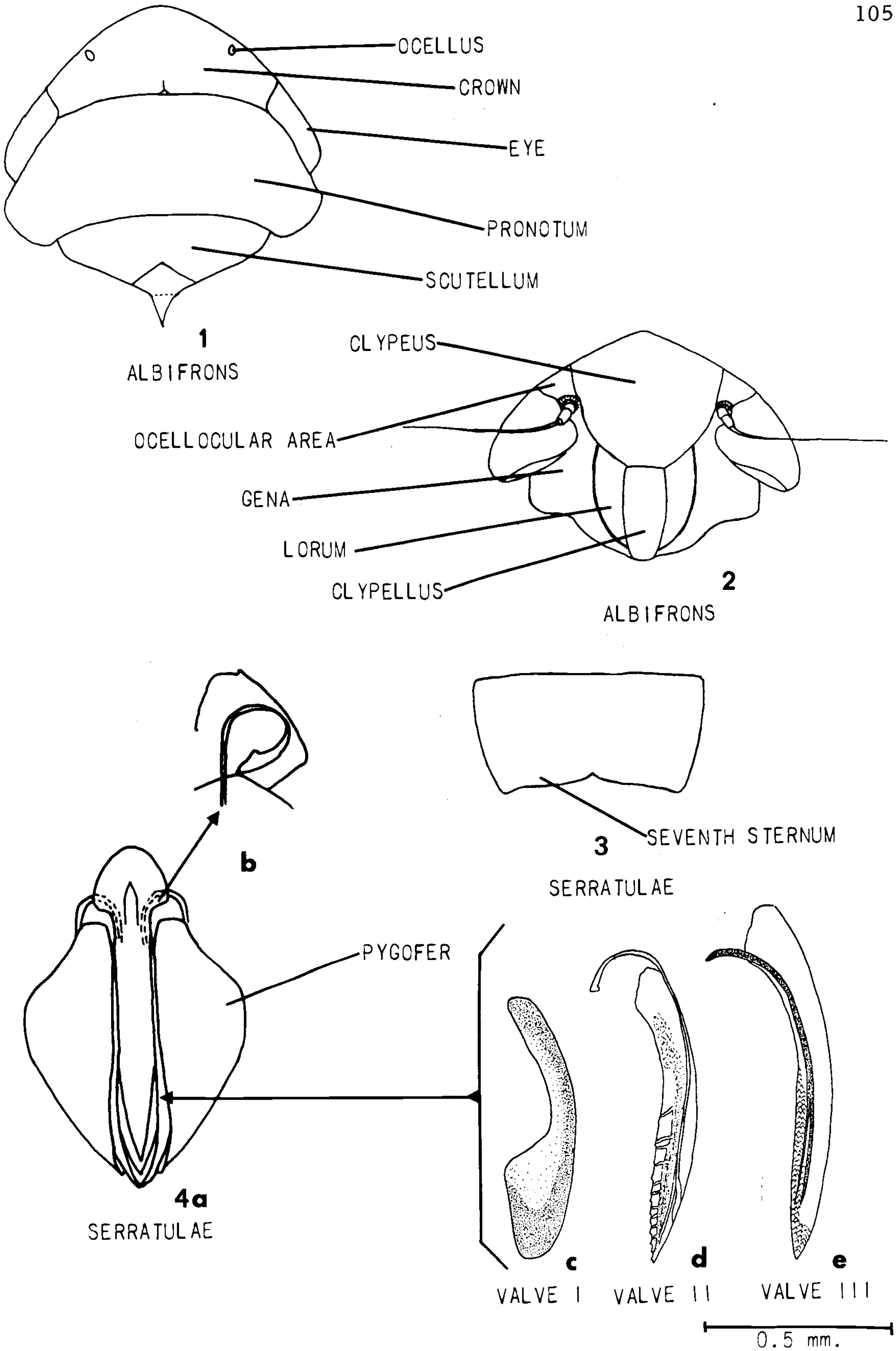



PLATE I. STRUCTURAL CHARACTERS OF APHRODES.

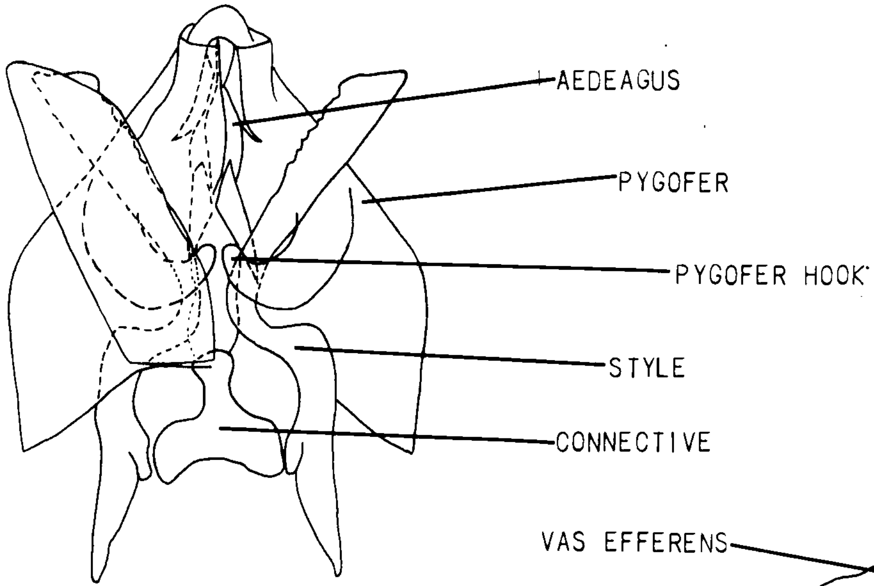
## PLATE II

Figure

5 Aphrodes albifrons (L.). Ventral view of male genital capsule.

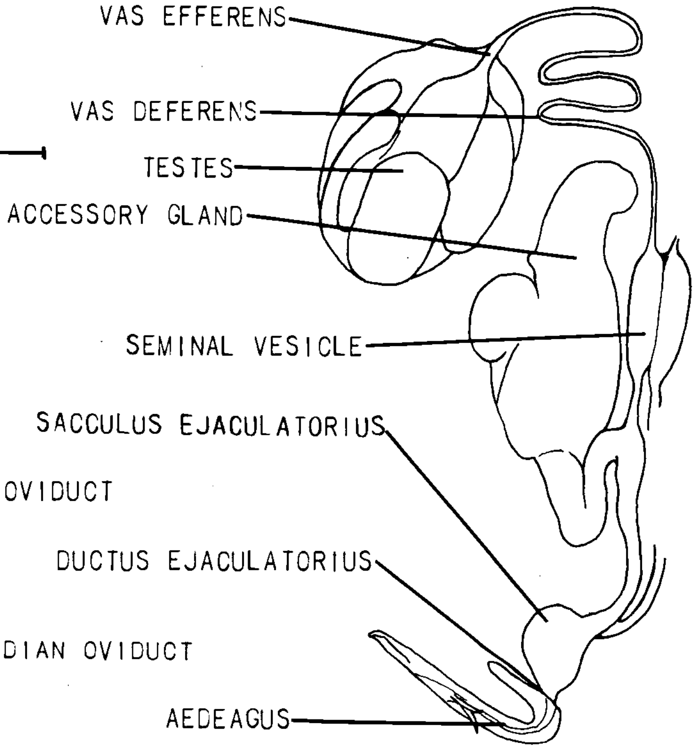
6 Aphrodes bicinctus (Schrank). Male reproductive organs.

7 Aphrodes bicinctus (Schrank). Female reproductive organs.

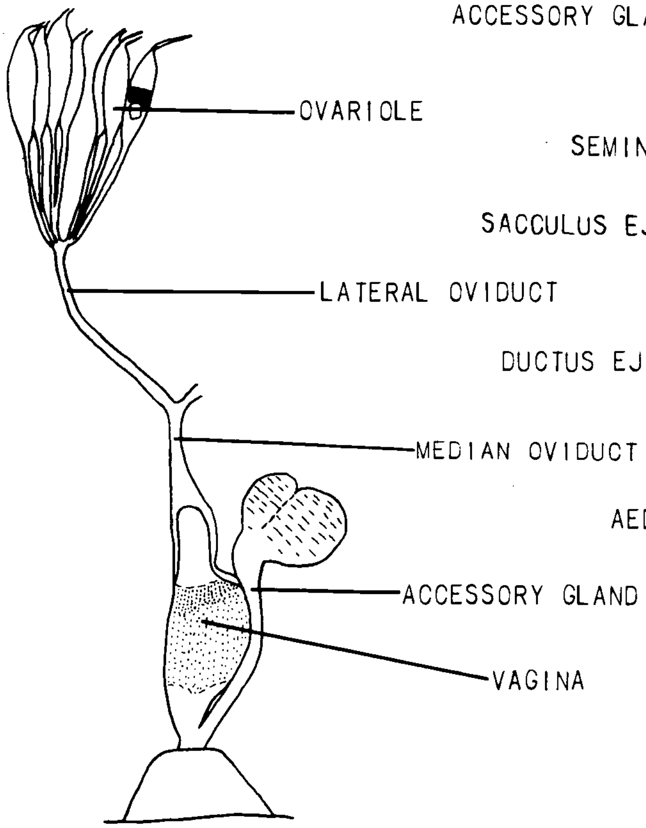



ALBIFRONS 5

0.5 mm.




6
BICINCTUS




7
BICINCTUS

1.0 mm.

PLATE II. STRUCTURAL CHARACTERS OF MALE GENITALIA AND MALE AND FEMALE REPRODUCTIVE TRACT OF APHRODES.

# PLATE III

| Figure | |
|---|---|
| 8 | *Aphrodes serratulae* (Fabricius) or *A. albifrons* (L.). First instar larva. |
| 9 | *Aphrodes albifrons* (L.). Second instar larva. |
| 10 | *Aphrodes albifrons* (L.). Third instar larva. |
| 11 | *Aphrodes albifrons* (L.). Fourth instar larva. |
| 12 | *Aphrodes serratulae* (Fabricius). Fourth instar larva. |
| 13 | *Aphrodes serratulae* (Fabricius). Fourth instar larva. |

8

serratulae or albifrons

9

albifrons

10

albifrons

11

albifrons

12

serratulae

13

serratulae

___ = 1 mm

# PLATE IV

Figure

14 *Aphrodes serratulae* (Fabricius). Adult male.

15 *Aphrodes serratulae* (Fabricius). Adult male (abdomen removed).

16 *Aphrodes serratulae* (Fabricius). Adult male (abdomen removed).

17 *Aphrodes serratulae* (Fabricius). Adult male (abdomen removed).

18 *Aphrodes albifrons* (L.). Adult male.

19 *Aphrodes albifrons* (L.). Adult male (abdomen removed).

14

serratulae

15

serratulae

16

serratulae

17

serratulae

18

albifrons

19

albifrons

___ = 1 mm

# PLATE V

Figure

20 *Aphrodes albiger* (Germar). Adult male (abdomen removed).

21 *Aphrodes flavostriatus* (Donovan). Adult male (abdomen removed).

22 *Aphrodes flavostriatus* (Donovan). Adult male (abdomen removed).

23 *Aphrodes bicinctus* (Schrank). Adult male (abdomen removed).

24 *Aphrodes mixtus* (Say). Adult male (abdomen removed).

25 *Aphrodes placidus* (Provancher). Adult male (abdomen removed).

20
albiger

21
flavostriatus

22
flavostriatus

23
bicinctus

24
mixtus

25
placidus

— = 1 mm

# PLATE VI

Figure

26 Aphrodes albifrons (L.). Fifth instar larval cast skin.

27 Aphrodes albifrons (L.) or A. serratulae (Fabricius). Adult female.

28 Aphrodes flavostriatus (Donovan). Adult female.

29 Aphrodes bicinctus (Schrank). Adult female.

30 Aphrodes bicinctus (Schrank). Fifth instar larva.

31 Aphrodes mixtus (Say). Adult female.

26

albifrons

27

serratulae or albifrons

28

flavostriatus

___ = 1 mm

29

bicinctus

___ = 1 mm

30

bicinctus

___ = 1 mm

31

mixtus

___ = 1 mm

# PLATE VII

Figure

32 *Aphrodes mixtus* (Say). (a) Forewing; (b) hindwing.

33 *Aphrodes placidus* (Provancher). (a) Forewing; (b) hindwing.

34 *Aphrodes* (*Stroggylocephalus*) sp. (a) Forewing; (b) hindwing.

35 *Aphrodes albifrons* (L.). (a) Forewing; (b) hindwing.

36 *Aphrodes albiger* (Germar). (a) Forewing; (b) hindwing.

37 *Aphrodes bicinctus* (Schrank). (a) Forewing; (b) hindwing.

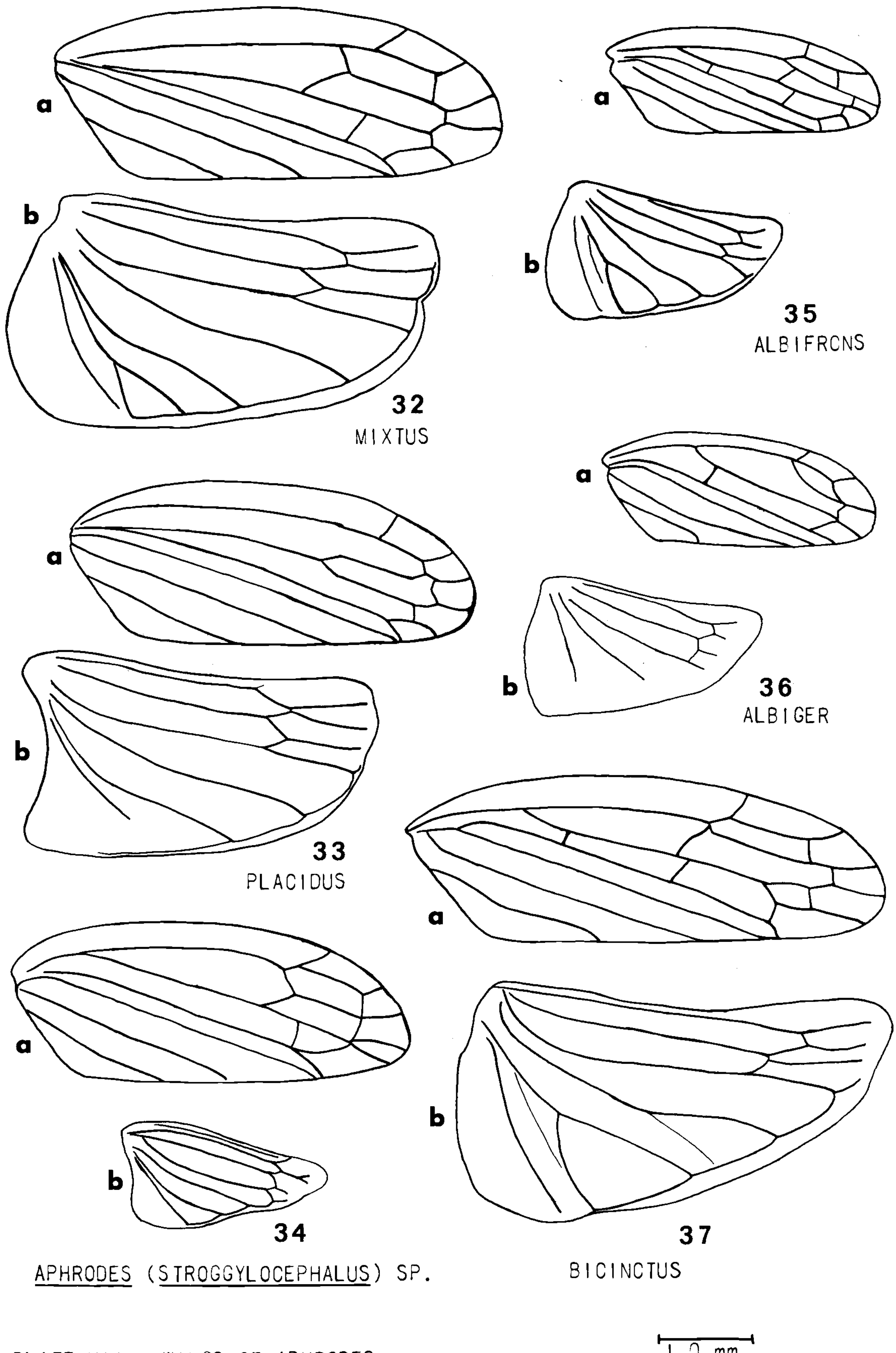



PLATE VII. WINGS OF APHRODES.

PLATE VIII

Figure

38 *Aphrodes mixtus* (Say). (a) Ventral view of genital plate; (b) pygofer hook.

39 *Aphrodes placidus* (Provancher). (a) Ventral view of genital plate; (b) pygofer hook.

40 *Aphrodes albifrons* (L.). (a) Ventral view of genital plate; (b) pygofer hook; (c) pygofer hook (enlarged).

41 *Aphrodes albiger* (Germar). (a) Ventral view of genital plate; (b) pygofer hook.

42 *Aphrodes serratulae* (Fabricius). (a) Ventral view of genital plate; (b) pygofer hook; (c) pygofer hook (enlarged).

43 *Aphrodes flavostriatus* (Donovan). (a) Ventral view of genital plate; (b) pygofer hook; (c) pygofer hook (enlarged).

44 *Aphrodes bicinctus* (Schrank). (a) Ventral view of genital plate; (b) pygofer hook.

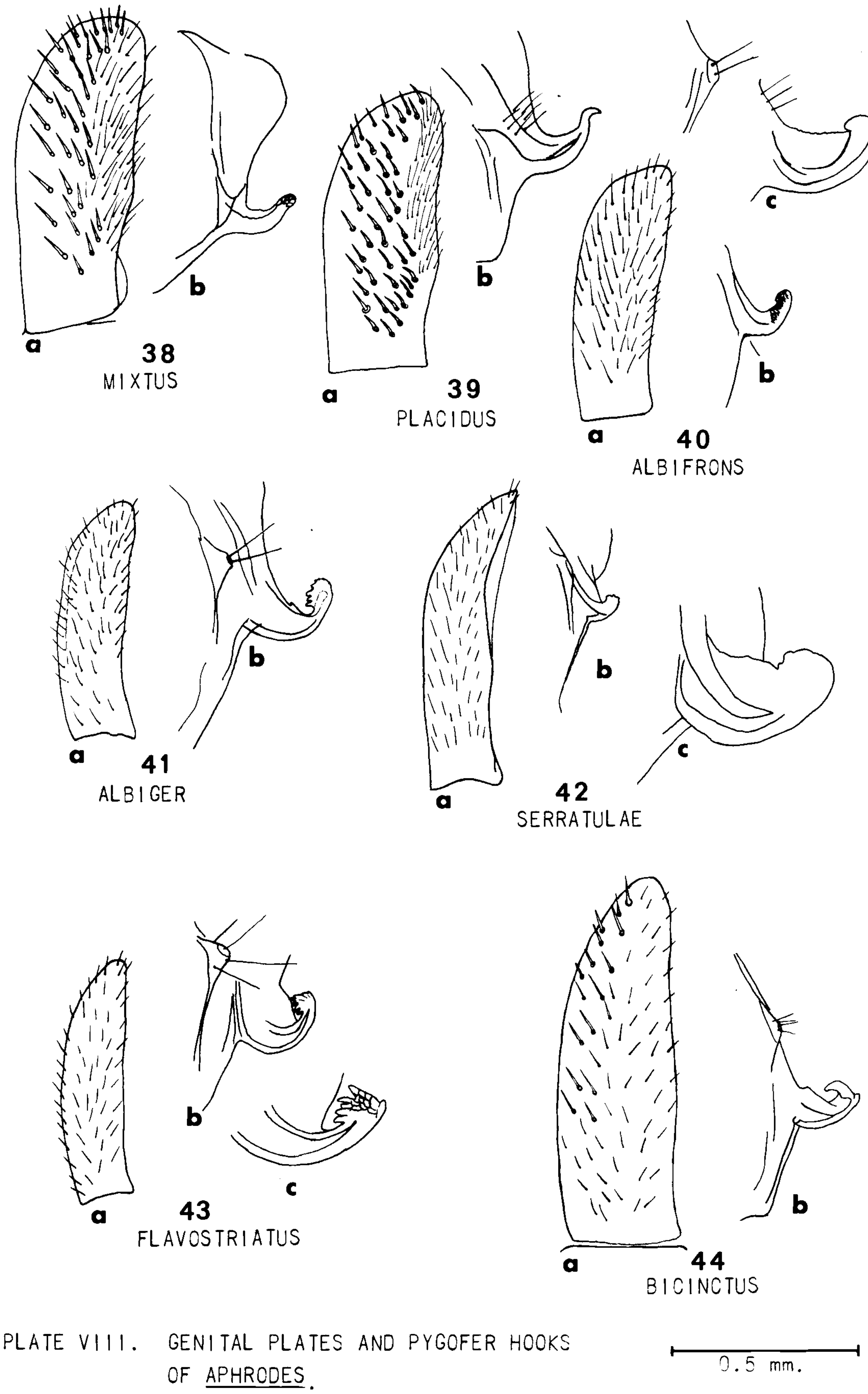



PLATE VIII. GENITAL PLATES AND PYGOFER HOOKS OF APHRODES.

# PLATE IX

Figure

45 Aphrodes mixtus (Say). Dorsal view of style and connective.

46 Aphrodes placidus (Provancher). Dorsal view of style and connective.

47 Aphrodes albifrons (L.). Dorsal view of style and connective.

48 Aphrodes serratulae (Fabricius). Dorsal view of style and connective.

49 Aphrodes albiger (Germar). Dorsal view of style and connective.

50 Aphrodes flavostriatus (Donovan). Dorsal view of style and connective.

51 Aphrodes bicinctus (Schrank). Dorsal view of style and connective.

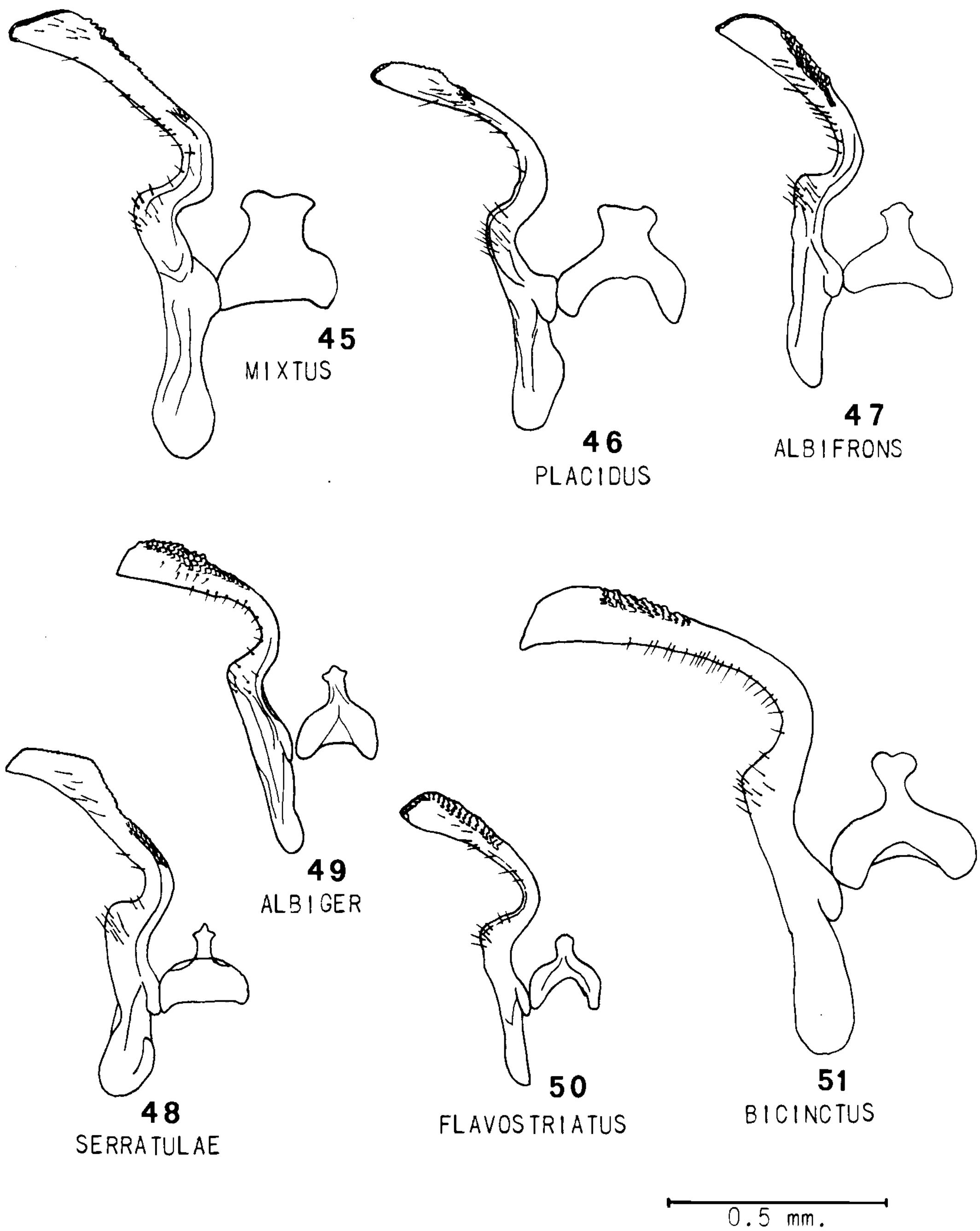



PLATE IX. STYLES OF APHRODES.

# PLATE X

Figure

52 Aphrodes mixtus (Say). (a) Lateral view of aedeagus; (b) ventral view of aedeagus.

53 Aphrodes placidus (Provancher). (a) Lateral view of aedeagus; (b) ventral view of aedeagus.

54 Aphrodes albifrons (L.). (a) Lateral view of aedeagus; (b) ventral view of aedeagus.

55 Aphrodes serratulae (Fabricius). (a) Lateral view of aedeagus; (b) ventral view of aedeagus.

56 Aphrodes albiger (Germar). (a) Lateral view of aedeagus; (b) Ventral view of aedeagus.

57 Aphrodes flavostriatus (Donovan). (a) Lateral view of aedeagus; (b) ventral view of aedeagus.

58 Aphrodes bifasciatus (L.). (a) Lateral view of aedeagus; (b) dorsal view of aedeagus; (c) ventral view of aedeagus.

59 a and b. Aphrodes bicinctus diminutus (Schrank). (a) Lateral view of aedeagus; (b) ventral view of aedeagus.

c. Aphrodes bicinctus bicinctus (Schrank). (c) Ventral view of aedeagus.

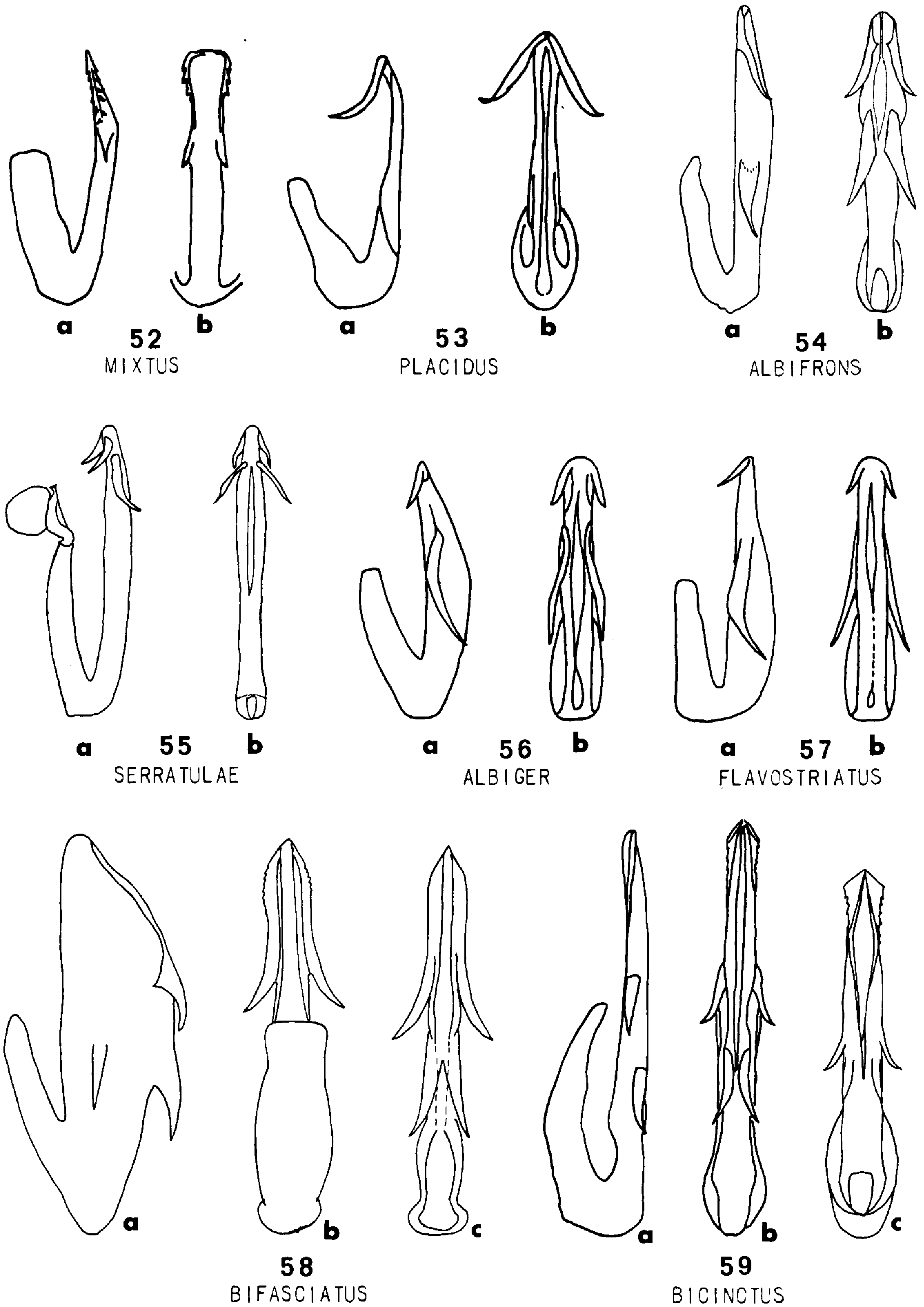



PLATE X. AEDEAGI OF <u>APHRODES</u>.

0.5 mm.

# PLATE XI

Figure

| | |
|---|---|
| 60 | *Aphrodes bicinctus* (Schrank). Female reproductive tract. |
| 61 | *Carsonus irroratus* (Ball). Female reproductive tract. |
| 62 | *Lystridea uhleri* Baker. Female reproductive tract. |
| 63 | *Errhomus lineatus* (Baker). Female reproductive tract. |
| 64 | *Errhomus montanus* (Baker). Female reproductive tract. |
| 65 | *Errhomus similis* Oman. Female reproductive tract. |
| 66 | *Idiocerus* sp. Female reproductive tract. |

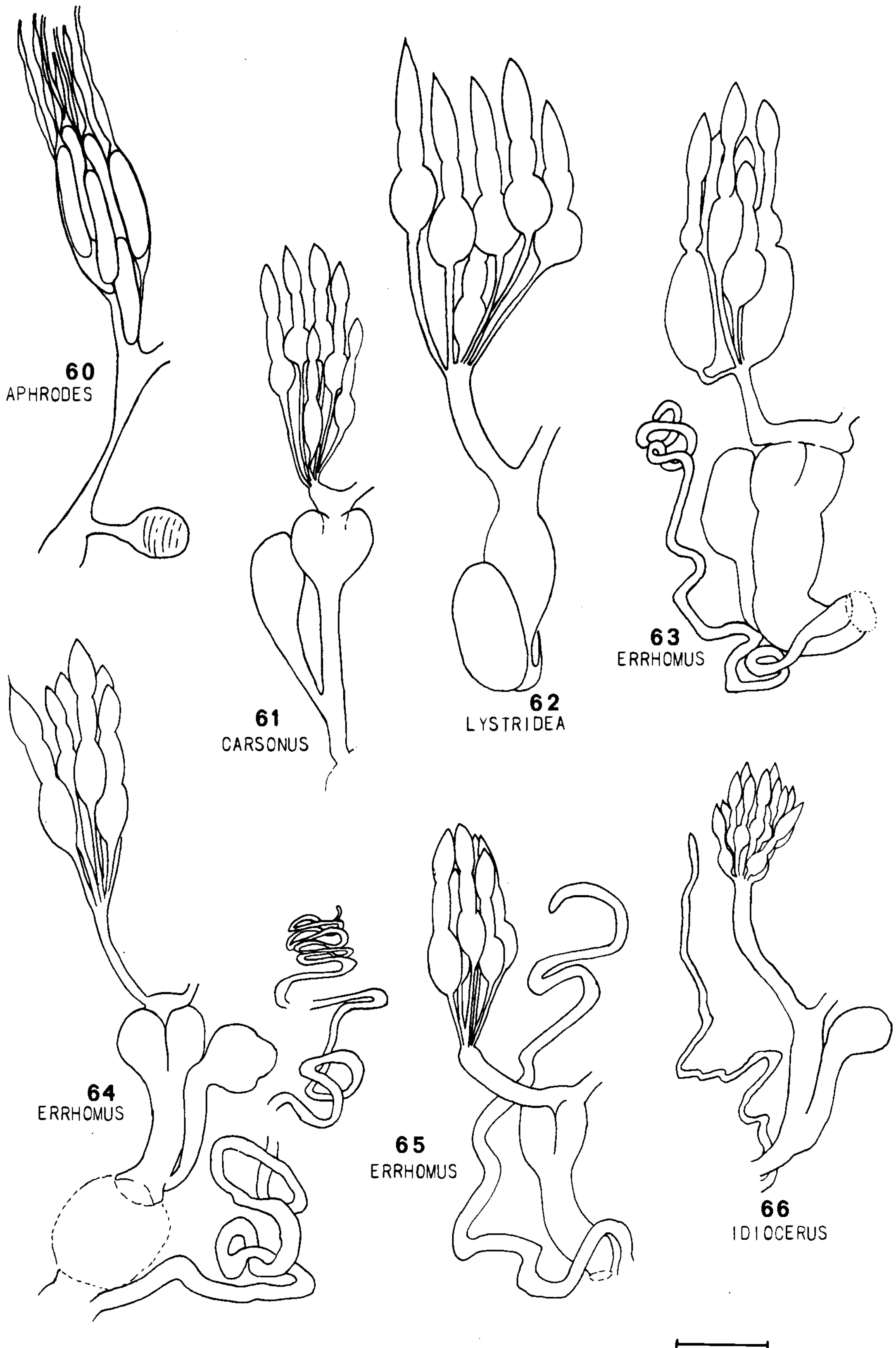



PLATE XI. FEMALE REPRODUCTIVE SYSTEM.

## PLATE XII

Figure

67 *Aphrodes bicinctus* (Schrank). Male reproductive tract and aedeagus.

68 *Aphrodes serratulae* (Fabricius). Male reproductive tract and aedeagus.

69 *Aphrodes serratulae* (Fabricius). Male reproductive tract and aedeagus.

70 *Aphrodes albifrons* (L.). Male reproductive tract and aedeagus.

71 *Tiaja* sp. Male reproductive tract.

72 *Idiocerus* sp. Male reproductive tract.

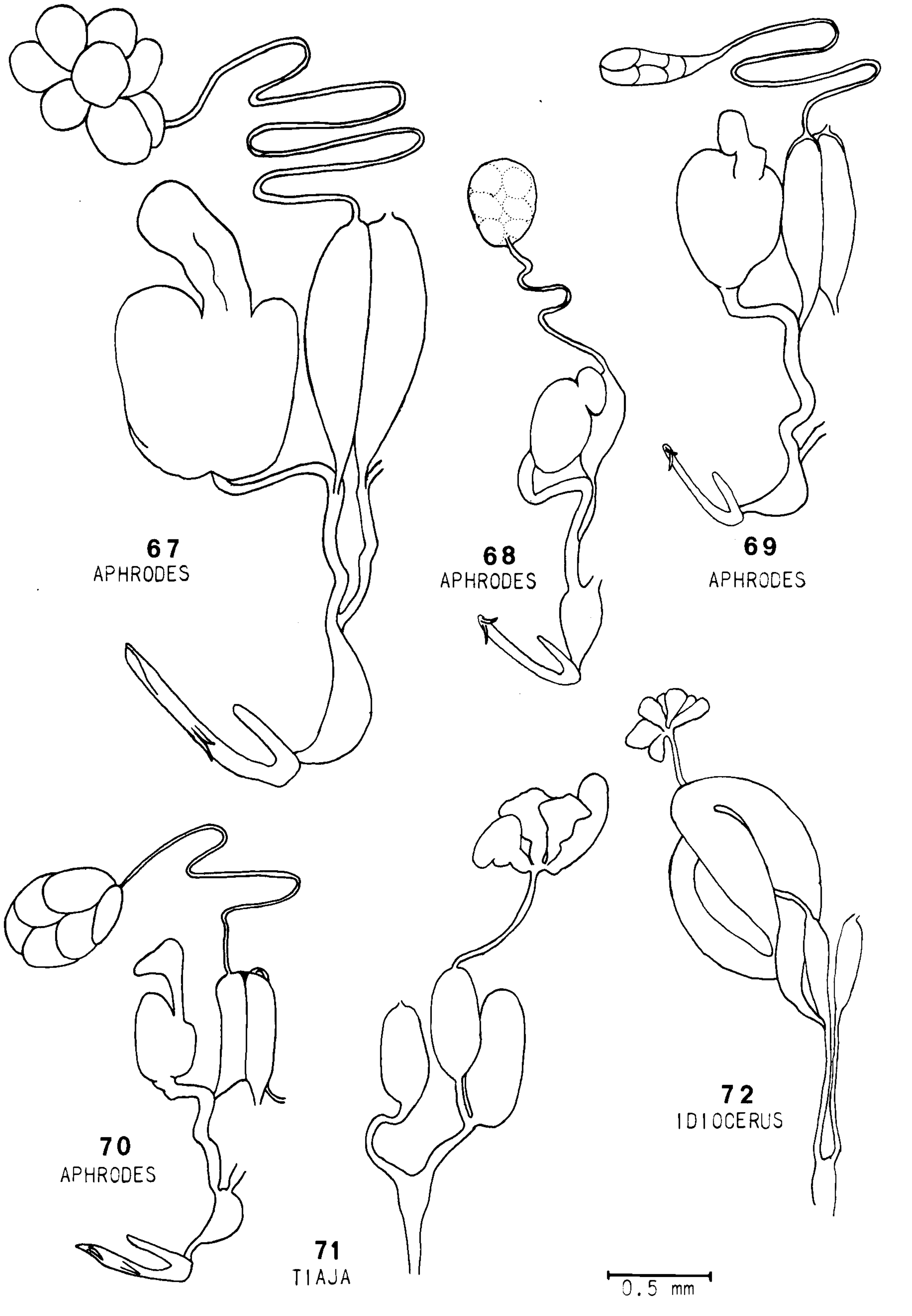



PLATE XII. MALE REPRODUCTIVE SYSTEM.

# PLATE XIII

Figure

73 *Errhomus montanus* (Baker). Male reproductive tract.

74 *Errhomus lineatus* (Baker). (a) Male reproductive tract; (b) testes.

75 *Errhomus similis* Oman. (a) Male reproductive tract; (b) testes.

76 *Lystridea uhleri* Baker. Male reproductive tract.

77 *Carsonus irroratus* (Ball). Male reproductive tract.

78 *Hordnia circellata* (Baker). Male reproductive tract.

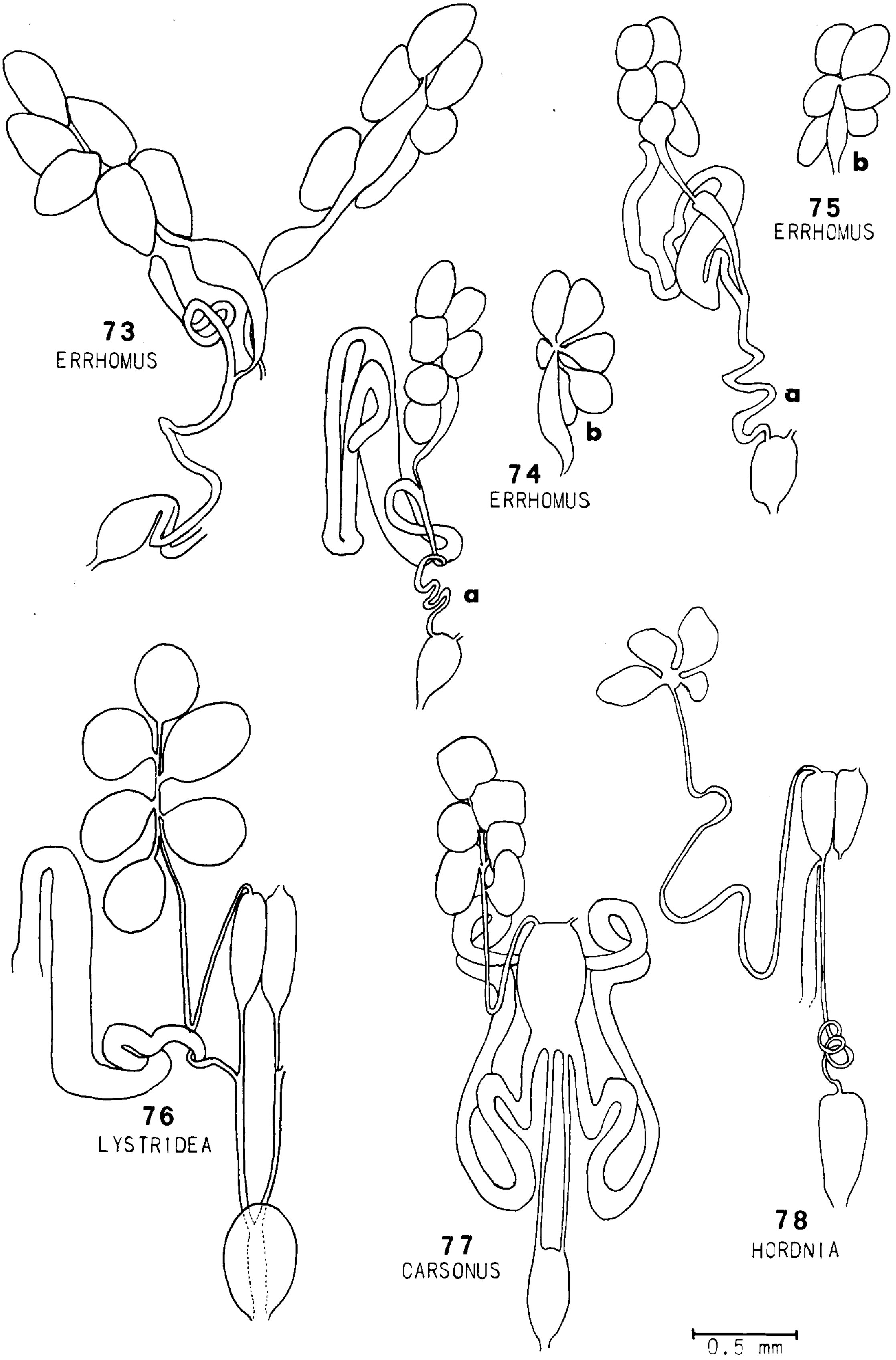



PLATE XIII. MALE REPRODUCTIVE SYSTEM.

# BIBLIOGRAPHY


Ball, E.D. 1932. The food plants of leafhoppers. Annals of the Entomological Society of America 25:497-501.

Bei-Bienko, G. Y. et al. 1967. Keys to the insects of the European U.S.S.R. Apterygota, Palaeoptera, Hemimetabola. U.S. Department of Commerce 1:1-1214.

Beirne, B.P. 1964. Notes on the North American species of _Aphrodes_ (Homoptera: Cicadellidae). The Canadian Entomologist 86:199-200.

Black, L.M. and A.N. Nagaraj. 1962. Hereditary variation in the ability of a leafhopper to transmit two unrelated plant viruses. Virology 16:152-162.

Blackwelder, R.E. 1941. Zoology--the gender of names in zoology. Journal of the Washington Academy of Sciences 31(4):135-140.

Brown, R.W. 1954. Composition of scientific words. George W. King Printing Co., Baltimore, MD. 882 p.

Buys, J. L. 1924. The Cicadellidae of the vicinity of Ithaca, New York, with special reference to the structure of the gonapophyses. Cornell University Agricultural Experiment Station. Memoir 80:1-115.

Chapman, R.F. 1969. The insects, structure and function. American Elsevier, New York, NY. 819 p.

Chiykowski, L.N. 1962. Clover phyllody and strawberry green petal diseases, caused by the same virus in eastern Canada. Canadian Journal of Botany 40:1615-1617.

__________. 1970. Notes on the biology of the leafhopper _Aphrodes bicincta_ (Homoptera: Cicadellidae) in the Ottowa area. The Canadian Entomologist 102:750-758.

Claridge, M.F. and P.E. Howse. 1970. The fine structure of Johnston's organ of the leafhopper, _Oncopsis flavicollis_. Journal of Insect Physiology 16:1665-1675.

Delong, D.M. 1948. The leafhoppers, or Cicadellidae, of Illinois (Eurmelinae-Balclutinae). Bulletin of the Illinois Natural History Survey 24(2):97-367.

Dlabola, J. 1954. Fauna ČSR Xvazek 1. Křísi-Homoptera. Práce Československé Akademie Véd (Sekce Biol.). 339 p.

Evans, J.W. 1947. A natural classification of leafhoppers (Jassoidea, Homoptera). Entomological Society of London Transactions 98:105-271.

________________. 1955. Cicadellidae (Hemiptera Homoptera). Exploration du parc national de l'Upemba, mission G.F. De Witte (1946-1949), Brussels fascicle 37:3-44.

Forbes, A.R. and H.R. MacCarthy. 1969. in Viruses, vectors, and vegetation, Karl Maramorosch, ed. Interscience Publishers, New York, NY. p. 211-234.

Hamilton, K.G.A. 1975. Review of the tribal classification of the leafhopper subfamily Aphrodinae (Deltocephalinae of Authors) of Holarctic Region (Rhynchota: Homoptera: Cicadellidae). The Canadian Entomologist 107:477-498.

________________. 1975. A review of the northern hemisphere Aphrodina (Rhynchota: Homoptera: Cicadellidae), with special reference to the Nearctic fauna. The Canadian Entomologist 107(10):1009-1027.

Harries, F.H. and J.R. Douglass. 1948. Bionomic studies of the beet leafhopper. Ecological Monographs 18:45-79.

International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology, London, July 1958. 1964. London, International Trust for Zoological Nomenclature. 176 p.

Kamm, J.A. and P.O. Ritcher. 1972. Rapid dissection of insects to determine ovarial development. Annals of the Entomological Society of America 65(1):271-274.

Kamm, J.A. and W.H. Reissig. 1975. Reproductive development of male Draeculacephala crassicornis. Annals of the Entomological Society of America 68(1):58-60.

Lawson, P. B. 1920. The Cicadellidae of Kansas. Kansas University Science Bulletin 12:5-306.

LeQuesne, W.J. 1964. Some taxonomic changes and additions in the British Cicadellidae (Hemiptera) including a new species and subspecies. Proceedings, Royal Entomological Society of London 33(5-6):73-82.

Lindroth, C.H. 1968. Distribution and distributional centers of North Atlantic insects. Bulletin of the Entomological Society of America 14(1):91-95.

Lowry, P.R. 1933. Cicadellidae leafhoppers of New Hampshire. Ohio Journal of Science 33(1):59-80.

Lumm, T.M.P. 1961. The reproductive system of some Florida mosquitoes. I. The male reproductive tract. Annals of the Entomological Society of America 54:397-401.

Maramorosch, K. 1963. Arthropod transmission of plant viruses. Annual Review of Entomology 8:369-414.

Medler, J.T. 1943. The leafhoppers of Minnesota. Homoptera: Cicadellidae. Minnesota Agriculture Experiment Station Technical Bulletin. 196 p.

Metcalf, Z.P. 1964. General catalogue of the Homoptera. Fascicle VI. Part 8. Aphrodidae. Agricultural Research Service. USDA. 349 p.

Müller, H.J. 1958. The taxonomic value of the male genitalia in leafhoppers in the light of new studies on the seasonal forms of Euscelis. Proceedings 10th International Congress of Entomology 1:357-362.

Musgrave, C.A. 1975. Taxonomy of the Scaphytopius (Cloanthanus) acutus Complex (Homoptera: Cicadellidae). Annals of the Entomological Society of America 68(3):434-438.

Nast, J. 1972. Palearctic Auchenorrhyncha (Homoptera), an annotated checklist. Polish Scientific Publishers, Wasszowa. 550 p.

Nielson, M.W. 1968. The leafhopper vectors of phytopathogenic viruses (Homoptera, Cicadellidae). Taxonomy, biology and virus transmission. Agricultural Research Service, USDA. Technical Bulletin. 1382 p.

Oman, P.W. 1949. The Nearctic leafhopper (Homoptera: Cicadellidae). A generic classification and check list. Washington Entomological Society 3:1253.

________________. 1969. in Viruses, vectors, and vegetation, Karl Maramorosch, ed. Interscience Publishers, New York, NY. p. 1-22.

Oman, P. and C.A. Musgrave. 1975. The Nearctic genera of Errhomini (Homoptera: Cicadellidae). Melandaria 21:1-14.

Oshanin, V.T. 1912. Katalog der paläarktischen Hemipteron (Heteroptera, Homoptera-Auchenorhyncha und Psylloideae) i-xvi:1-187.

Ossiannilsson, F. 1949. Insect drummers. A study on the morphology and function of the sound-producing organs of Swedish Homoptera auchenorrhyncha. Opuscula Entomologic 4 Supplementum X. 142 p.

Ossiannilsson, F., L.M. Russell, and H. Weber. 1970. in Tuxen, taxonomists' glossary of genitalia of insects. p. 179-190.

Osborn, H. 1916. Studies of life histories of leafhoppers of Maine. Maine Agricultural Experiment Station Bulletin 248:53-80.

________________. 1915. Leafhoppers of Maine. Maine Agricultural Experiment Station Bulletin 238:106-108.

Pendergrast, J.G. 1957. Studies on the reproductive organs of the Heteroptera with a consideration of their bearing on classification. The Transactions of the Royal Entomological Society of London 109(1):1-107.

Pesson, P. 1951. Ordre des homopteres. Traité de Zoologie, Anatomie Systématique, Biologie. Publie sous la direction M. Pierre-P. Grassé 10:1390-1656.

Provancher, abbe L. 1886. Petite Faune Entomologique du Canada, et particulierement de la province de Quegec. Quebec, C. Darveau 3:271-281.

Readio, P.A. 1922. Ovipositors of Cicadellidae. The Kansas University Science Bulletin 14(8):217-298.

Ribaut, H. 1952. Faune de France. Homoptères Auchénorhynques. II. (Jassidae). Librairie de la Faculte des Sciences, Paris. 474 p.

Ross, H.H. 1958. Evidence suggesting a hybrid origin for certain leafhopper species. Evolution 12(3):337-446.

Say, T. 1830. Descriptions of new North American Hemipterous insects belonging to the first family of the sections Homoptera of Latreille (continued). Academy of Natural Sciences (Philadelphia) Journal 6:299-314.

Sabrosky, C.W. 1966. Mounting insects from alcohol. Bulletin of the Entomological Society of America 12(3):349.

Snodgrass, R.E. 1935. Principles of insect morphology. McGraw-Hill Book Company, New York, NY. 667 p.

__________________. 1960. Some words and their ways in entomology. Proceedings, Entomological Society of Washington 62(4):265-270.

Stone, A. et al. 1965. A catalog of the Diptera of America north of Mexico. Agricultural Research Service, USDA. p. 9.

Torre-Bueno, J.R. de la. 1937. A glossary of entomology. Brooklyn, Brooklyn Entomological Society, NY. 336 p.

Van Duzee, E.P. 1912. Synonomy of the Provancher collection of Hemiptera. The Canadian Entomologist 44(11):317-330.

Vilbauste, J. 1965. Über die Zikadenfauna altais. Eesti NSV Tead. Akad. Toim., Tallinn (Biol.). 143 p.

# APPENDIX

# DEFINITION OF TERMS

To facilitate understanding the sections on taxonomy and morphology the following definitions are provided (after Snodgrass, 1935; Oman, 1949; Torre-Bueno, 1962; Imms, 1964). Illustrations of some features are on Plates I and II.

Accessory gland: a secondary structure usually located near the base of the vagina or ovipositor.

Aedeagus: sclerotized intromittent organ, including the phallobase.

Aedeagal shaft: tubular portion of the aedeagus.

Crown: the entire dorsal surface of the head except for the compound eyes.

Clypellus: the anteclypeus of Snodgrass. A rectangular shaped facial sclerite bounded by the clypeus dorsally, the lorae laterally and the stylets ventrally.

Clypeus: the post-clypeus of Snodgrass. A trapezoidal facial sclerite lying just below the vertex. It is bounded laterally by the lateral frontal sutures and ventrally by the clypellus.

Connective: a component of the internal male genitalia which articulates with the paired styles and the aedeagus.

Face: the entire cephalic aspect of the head.

Forewing: the outer, mesothoracic wing, often called the tegmina.

Gena: part of the maxillary plate of Snodgrass. These lateral facial sclerites lie just posterior to the eyes and are limited medially by the lateral frontal sutures and lorae.

| | |
|---|---|
| Genital capsule: | includes the pygofer, valve, plates and internal genitalia of the male. |
| Gonopore: | Phallotreme of Snodgrass. Distal opening in the aedeagus through which sperm is passed from the male to the female. |
| Hindwing: | the inner or metathoracic wing, which is often membranous. |
| Insect ringers: | 11 g NaCl, 1.6 g KCl, 0.85 g $CaCl_2$, and 0.17 g $MgCl_2$/1000 ml water. |
| Instar: | The form assumed by an insect during a particular stadium (Imms). |
| Length of crown: | length along the median suture. |
| Lorum: | the mandibular plate of Snodgrass. Paired, almost semicircular facial sclerites on either side of the clypeus and clypellus. |
| Genital plates: | The paired sclerites on the ventral surface of the genital capsule, behind and articulating with the valve. |
| Ocellocular area: | the area of the head between the eye and the lateral suture of the clypeus. |
| Pygofer: | the saddle-like dorsal and lateral sclerotized portion of the genital capsule. |
| Seventh sternum: | the seventh ventral sclerite of the female leafhopper abdomen. |
| Styles: | the parameres of Snodgrass. The pair of lateral sclerites articulating with the connective. |
| Submacropterous: | condition of the forewing when it extends beyond the seventh abdominal segment, but does not extend beyond the apex of the last abdominal segment. |
| Valve: | ventral plate of the male genital capsule. |

| | |
|---|---|
| Width between the eyes: | the longest width between the eyes. |
| Width of pronotum: | distance from one lateral margin to the other on the pronotum. |