PHYLOGENY OF THE EUSIMULIUM - GROUP OF BLACK FLIES

AN INTERPRETATION OF THE PHYLOGENY OF THE EUSIMULIUM-GROUP (DIPTERA: SIMULIIDAE) WITH DESCRIPTIONS OF SIX NEW SPECIES

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SCOPE AND CONTENTS:

The female, male, last stage larva and pupa of seventeen Ontario species of the Eusimulium-group are described, illustrated and keyed. Morphological and ecological knowledge of these and other species is used as a basis for interpreting the phylogeny within the group. This approach is extended, with the help of other representative species, to the derivation of a tentative phylogeny and zoogeography of the family Simuliidae. The findings from these studies contributed to the formation of a hypothesis of speciation.

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INTRODUCTION

Blood-sucking insects have harassed mankind through the ages by their often severe attacks and by the disease organisms which they transmit. Among the most important of these insects are the black flies of the family Simuliidae. In the tropics simuliids are responsible for the spread of one of the most serious human parasites, Onchocerca. In North America, although not significant in the transmission of human disease organisms, they can make life unbearable outdoors by their numbers and the severity of their biting. In addition, they pose a hazard to both wild and domestic birds by transmitting to them blood protozoa and filariae (Anderson, 1956; Fallis and Bennett, 1958; Bennett, 1961), resulting in heavy mortality in certain cases.

An understanding of species involved in transmission, and of their ecology and subsequent control is limited because the taxonomy of this family is difficult. This is because of the homogeneity of the whole family and, on the other hand, the apparent interspecific variability. In addition, Dunbar (1958, 1959, 1962) and Rothfels (1958) have demonstrated in some species the presence of two or more distinct cytological entities.

Of prime concern in this research has been the diagnosis and definition of both the described and undescribed species. Prior to 1958 thirteen species, that are herein assigned to the Eusimulium-group, were known from eastern North America. The generic concepts of earlier workers differed and the species were treated under both Simulium and Eusimulium. The two earliest papers (Coquillett, 1898; Malloch, 1914) mentioned only one species - bracteatum Coq. from eastern North America which was synonymized later with the European aureum Fries by Dyar and Shannon (1927). The last authors described several new species including two in the Eusimulium-group, congareenarum D. & S. from South Carolina in the east and pugetense D. & S. from Washington State in the west, the latter being found in the east (New York State) many years later by Stone and Jamnback (1955). A more extensive treatment of the eastern Canadian species was made by Twinn (1936). He added two European species (latipes Meigen and subexcisum Edwards) to the North American fauna and described three new ones (rivuli, baffinense and quebecense). Five additional species were described later, i. e. euryadminiculum by Davies (1949), croxtoni by Nicholson and Mickel (1950), innocens and furculatum by Shewell (1952), and gouldingi by Stone (1952).

More extensive collecting of large series of specimens and more careful evaluation of these and of other collections made earlier has allowed a better understanding of existing species and disclosed new ones. Five new species from Ontario are described in this thesis, descriptions of four of these being published recently (Davies, Peterson and Wood, 1962). One of these, Twinn (1936) had originally called *subexcisum*, a species that is evidently not found in North America.

The *Eusimulium*-group is well represented in Ontario, and also in the Palaearctic and Ethiopian regions. Fortunately the Palaearctic black flies have been monographed by Edwards (1915, 1920), Petersen (1924), Séguy (1925), Grenier (1953) and Rubtzov (1956, 1959-62), and the Ethiopian species by Freeman and de Meillon (1953). The group is almost absent from the Neotropical region, being represented only by a member of the *aureum*-complex in the mountainous regions of Mexico (Vargas and Diaz Najera, 1957) and Guatemala (Dalmat, 1955). Edwards (1931) also listed *costatum* Friederichs from Patagonia. A few species are also known from the Oriental region (e.g. *aureohirtum* Brunetti and the *aureum*-complex (Puri, 1933)) and one species, *ornatipes* Skuse from the Australian region (Mackerras and Mackerras, 1949). A study of the literature, however, has disclosed that the Ontario black-fly fauna contains representatives of most of the Holarctic species groups; thus it has been possible to develop an interpretation of the phylogeny within the *Eusimulium*-group. This study has been supplemented by a study of specimens of several species from western North America, Europe, Africa and Asia.

A natural corollary to the study of the phylogeny of the *Eusimulium*-group is an attempt to understand the phylogeny of the family as a whole with emphasis on the path that might have led to the origin of the *Eusimulium*-group. Special attention has been devoted to the structure and development of the larval labrum and its head fans in simuliids and related Diptera. Many Holarctic species of *Prosimulium*, *Cnephia*, and *Simulium* were examined, with particular attention being devoted to the species of *Cnephia* most closely related to the *Eusimulium*-group. Two new species of *Cnephia* have recently been found, one *denaria*, already published by Davies, Peterson and Wood (1962) and the other described as new in this thesis. Additional specimens of *Cnephia*, *Austrosimulium*, *Gigantodax* and *Simulium* from South America, New Zealand and Australia were studied as well. Rubtzov (1956) has presented his interpretation of the phylogeny of the family, which is similar in several respects to the scheme developed in this thesis.

Discontinuities of distribution and phylogeny in the Simuliidae have led to the development of a pattern of zoogeography similar to that found for vertebrates by Darlington (1957), in which dominant animal groups have arisen in Asia, and spread to the surrounding continents, pushing the older and relict forms into the extremities (Australia, South America and Africa) where they often form a relatively high proportion of the fauna. These areas in addition tend to have highly indigenous faunas because of their isolation during the Tertiary.

Some understanding of what species are, and of the nature of their formation is a necessary foundation for the diagnosis of the species in any group of organisms. Darwin (1859) conceived of the forces of natural selection operating to direct the evolution of a species in time, and the evolution of different species in geographically isolated parts of the population of the parent species. Since this time, controversy has arisen about the process of speciation, much of it because of the diversity of organisms. Dobzhansky (1937) was one of the first (Dodson, 1960) to incorporate the accumulated knowledge of heredity into a better understanding of the mechanism of evolution. His theory has since been refined to include the assistance of reproductive isolating mechanisms which would keep the two new species separate wherever they met (Sinnott, Dunn and Dobzhansky, 1958).

Several isolating mechanisms were discussed by these authors. Other theories of speciation have also been advanced; for example, Goldschmidt (1940) postulated that new species are produced by chromosomal rearrangements. These theories are evaluated in the final discussion of this thesis and from them a hypothesis of speciation, perhaps most applicable to insects, is developed, which is amplified and modified to suit the reproductive peculiarities of other organisms.

MATERIALS AND METHODS

The procurement and correct preservation of an adequate series of specimens is important in taxonomic studies of black flies. The most satisfactory method of obtaining material was the collection of the immature stages from flowing water. One or more species were usually encountered in streams and rivers of all sizes, from a few inches to many feet in width. In collecting, all types of removable material - grass, leaves, sticks and stones of all sizes - were examined for larvae and pupae, which were transferred with fine forceps to wet filter paper in plastic petri dishes. Pupae were dislodged and handled by grasping the anterior or lateral edges of the cocoon. Since Twinn (1936) showed that black-fly pupae could withstand exposure to the air, the rearing of adults from pupae placed only on a damp substrate has permitted the acquisition of large series of specimens associated with their exuviae and cocoons. In addition, the last larval skin may sometimes be found inside the cocoon. Mature larvae were related to pupae by the number and arrangement of the respiratory filaments in the pupal histoblast. Some of the larvae, preferably last instars with histoblast of the pupal respiratory apparatus half-darkened, were prepared for cytological examination by immediately cutting them open in a shallow film of water in the shade to expose the salivary glands, and fixing them in Carnoy's fixative. Later, they were stained in acetic orcein and squashed in 50% acetic acid by the technique of Rothfels and Dunbar (1953). The remaining larvae were fixed in 95% ethanol (without added glycerine) to distend the larva and expand the head fans. This treatment also minimized colour change, and descriptions of colour in the following account are based only on larvae fixed in this way. On a few occasions where pupae were not available and the time between collection and return to the laboratory was short, larvae were brought back (kept cold with ice), and reared to maturity in artificial streams.

In the laboratory, the pupae were transferred to fresh filter paper for mass rearing or to a rearing tray (Fig. 81) for individual rearing. The latter consisted essentially of a sheet of acrylic plastic louvre with openings 1/2 inch square, laid on top of wet filter paper in a shallow tray. A single pupa was placed on the wet paper in each compartment and a 2-inch length of glass tubing was inverted over the pupa. This tube was stoppered at the open upper end with cotton to allow some diffusion of air and to prevent changes in pressure from drawing water up into the tube. The pupae were usually retained at about 50°F until emergence. Adults were removed daily from the tray and each with its exuvia placed in a small shell vial stoppered with cotton. After a few hours had elapsed for hardening of the cuticle, they were killed in a deep freezer. The adult was then quickly glued to the side of an insect pin above its exuvia by the method of Shewell (in Beirne, 1955) and returned to the freezer (at minus 10°F) for two to five weeks until completely frozen dried. This method of drying minimized the shrinkage and collapse of the head and abdomen that is usually characteristic of pinned black flies, and facilitated later clearing in potassium hydroxide. In this way, many adults each associated with its exuvia can be reared.

Adult females of a few species were obtained, sometimes in large numbers, by exposing a chicken or other bird according to the methods described by Bennett (1960). The bird (with legs tied and eyes covered with a leather hood to minimize activity) was placed in a small cage (about 7 x 7 x 11 inches) covered with chicken wire (3/4 x 1 in. mesh) or fitted with vertical 1/4 inch dowels, 1 - 1 1/4 inches apart. The cage was raised by rope and pulley into the forest canopy (10 to 30 ft. above the ground) for fifteen to twenty minutes, then brought down and placed on a 1-yd. square white board where a much larger cage of fine white nylon mesh (23 x 28 mesh per in.) was placed over it for fifteen to twenty minutes. The engorged flies leaving the bird collected within this larger cage, and were removed with an aspirator and immediately transferred to a wooden holding cage (8 to 10-inch cube) (Anderson, 1956). The floor of this small cage was covered with damp paper and a lump of sucrose wrapped in gauze was suspended in the cage (Davies, 1953).

After ten days in darkness at about 60°F, the females were induced to oviposit. Only one species, *E. aureum*, could be induced to lay egg masses regularly. Each female was confined in a petri dish with a short length of green wet grass (several types of grass of varying texture were used successfully) at room temperature in moderate light. Eggs were laid on the wet part of the leaf, but just at the water's edge. Those individuals which did not oviposit in one or two hours were returned to the holding cage; the process was repeated the following day.

After egg masses were laid the female was removed and either preserved in 95% alcohol or re-fed on a bird the following day. By confining the fly in a 1/2 inch length of glass tubing (1/2 inch diameter) covered at each end with nylon mesh (after the method of Sommerman) re-feeding was readily achieved by applying one end of this tube to the exposed skin of the comb or wattle of a bantam rooster. The use of carbon dioxide in the form of dry ice to stimulate feeding (Dalmat 1950, 1955) was occasionally helpful.

If a gravid female fly would not oviposit, fertilized eggs were obtained by transferring them from the fly's abdomen with fine forceps into a drop of carbon-filtered water. They were fertilized as quickly as possible after removal by crushing the same fly's spermatheca in the water surrounding them. More water was added after a few minutes had elapsed.

By using the spermatheca from a previously mated (wild caught) female of a different sibling species cross fertilization was attempted.

Egg masses were flooded with filtered water and stored at 60^{o}F. In early summer, complete embryonic development usually occurred in all eggs, but as the season progressed, the development of most eggs in each mass was arrested at an early stage of embryogeny when eye-spots had appeared, and refrigeration at 40^{o} for two months or more was necessary to break the diapause. Incipient hatching could be detected by the appearance of sclerotized details of the head capsule, notably the egg burster and mouth parts. Prior to hatching the egg mass was transferred to an artificial stream for larval development.

The apparatus for rearing larvae consisted of three interconnected components: a tank containing activated carbon for filtering tap-water and another tank for storing it; a series of small troughs where the larvae were maintained; and an apparatus to disperse a dilute suspension of baker's yeast to the larvae as food. All containers were made of glass or acrylic plastic; the tubing connecting them was of polyvinyl chloride, polyethylene, Tygon (Canadian Laboratory Supplies Ltd.) or rubber. The use of water continually from the city mains avoided the difficulties of maintaining recirculation pumps or air pumps together with the hazards of power failures.

The tank for filtering the water was a vertical rectangular chamber (5 ft. x 2 ft. x 2 ft.) with 1/2 inch thick walls containing about 12 cu. ft. of highly activated granular carbon, suitable for dechlorination (made from coke by Atlas Powder Co. and supplied by J. W. Anderson Co. Ltd., Dundas, Ontario), held in place by gravel and sand above and below. Tap-water was introduced at the bottom of the tank and passed up through the carbon core. Air coming out of solution was forced up by the rising water, and allowed to escape at the top. The filtered water overflowed through a black polyvinyl chloride pipe into a storage tank. The water in this tank was maintained at a depth of 10 inches to provide a uniform head pressure. Both the filter and storage tank were enclosed in black cloth to exclude light and thus inhibit algal growth.

The troughs for rearing the larvae each had a flat bottom and vertical sides (1/2 inch wide, 1 inch deep and 4 ft. long). Ten or eleven troughs were assembled together as a unit and two units (21 troughs in all) were supported, 2 to 3 feet below the water level in the storage tank, in a single galvanized pan and serviced by a single manifold (Fig. 83). Each manifold was an acrylic plastic tube, one inch inside diameter, with a row of 1/16 inch holes each fitted with a short one-inch length of plastic tube to direct the flow of water into each trough. The tube was kept from touching the side or bottom of the trough as otherwise larvae would migrate into the manifold. Clean pebbles of suitable size were placed along each trough at intervals of 3 to 4 inches to provide a variety of current velocities and of attachment sites for the larvae. The troughs were inclined at a slope of 1 inch in 36 inches. To prevent the escape of larvae, the foot of each trough was deepened into a reservoir terminating in a stainless steel screen (100 mesh per inch), (Fig. 84).

The larvae were fed baker's yeast (Fleischmann's) exclusively. Each day, 1/2 lb. of moist yeast cake was suspended with a food blender in filtered water, and then released by a separate apparatus which could be regularly dismantled for cleaning without interrupting the water flow in the troughs. The feeding apparatus consisted of three parts: a container for the concentrated yeast suspension, a series of small tanks for dilution, and a manifold for releasing the diluted suspension at the desired rate into each trough (Fig. 82). The container for the concentrated yeast suspension was a glass florence flask (A) with side arm (B), modified to provide an additional opening (D). Water was admitted into D, one drop per 2-10 sec., the rate depending on the number of larvae being reared. The resulting overflow from tube B collected in a small acrylic plastic tank (E), measuring 6 inches x 2 inches x 4 inches. An electrically driven stirring rod (C) inserted into the florence flask maintained the yeast continually in suspension. The yeast suspension in container E was greatly diluted by filtered water (F); the excess overflowed at G into the drain. The diluted suspension was drawn from tank E by one or more siphons (H). Each siphon, controlled by a Hoffman clamp, conveyed the suspended food to another small container (J), similar to E, where it was further diluted by more filtered water from tube (K). This suspension overflowed from J through a plastic tube (L), of 1/4 inch inside diameter, to an acrylic plastic manifold (M), which was located above each group of troughs. Above each trough was a 1/32 inch hole in the manifold (M) and the suspension was conveyed to the trough by a short plastic tube (N) of 1/8 inch inside diameter. The rate of flow of the suspension into the stream varied directly with the level of suspension in the manifold. This level was controlled by regulating, with a Hoffman clamp, the amount of water entering through K.

The feeding apparatus, described above, supplied only one rack of 21 troughs. When it was desirable to service another rack of troughs, an additional siphon H was installed to draw off more suspension from container E, and the apparatus from J to N was duplicated (Fig. 85). It was necessary now to increase the flow of water both at D and at F. When this many streams were in operation at one time the supply of baker's yeast in the flask A had to be renewed twice daily.

Preparation of Material for Study

For the preparation of larval drawings the mandibles, maxillae and pharyngeal region were removed in one piece by severing their cuticular attachments around the anterior edge of the head capsule. The capsule, cut from the body, was then cleared for four hours in cold 10% potassium hydroxide and washed in water where the softened contents were removed. It was then transferred to a glass depression slide into a drop of water and glycerine. Study was completed after the water had evaporated. Drawings were made with the aid of a Bausch and Lomb "Speed Matic" micro-projector (Cat. No. 42-63-56-48) with a carbon arc light source. Stability of orientation in glycerine was obtained by attaching the specimen to a small amount of petroleum jelly.

The preparation of adult structures differed from the treatment above only in that the clearing required twenty-four hours in cold 10% potassium hydroxide and dissection was done in glycerine. Interpretation of the arrangement of the genital structures of the male was often made from specimens dissected from pupae, as the distal portion of the aedeagus is invaginated after emergence, placing the spines associated with it in a position difficult to observe. The study of specimens suspended in glycerine minimized the distortion that is often associated with permanently slide-mounted material, and permitted a consistent angle of view for each specimen. Drawings were prepared as described above for the larvae.

MORPHOLOGY AND TERMINOLOGY

The morphology of the known species of Simuliidae is notoriously homogeneous and the early classification within the family has been based almost entirely on small variations found in the wing venation and the hind leg of the adult (Edwards, 1931; Enderlein, 1921, 1930), whereas the adult genitalia and larval structures played an inferior role. It is the purpose of this section to describe the structures that serve for distinguishing and grouping species, and when possible, to interpret their homologies among other Nematocera.

Adult Structures

Wing

As would be expected in such a homogenous group, the wing (Fig. 5) shows only slight variations. Except for Parasimulium which is unusual in several respects (Stone, 1941), and which was unavailable for study, all other known species show variations in merely four features and these may be divided into variation in the venation itself and in the presence and arrangement of hairs on the veins: (1) the radial sector is often bifurcate and the unforked basal portion may be long or short (Fig. 5); (2) the presence or absence of the m-cu cross vein forming a second basal cell; (3) the presence or absence of short, thick setae (spinules) among the finer hairs along the costal vein; and (4) the presence or absence of hairs on the upper basal portion of the radius. The arrangement of these hairs, whether they are in one or two rows or scattered over the whole of the vein, now appears to be of significance and as important as their presence or absence.

Hind Leg

The ratios of the lengths of the various segments to one another and to their widths have been given prominent treatment by some authors, notably Enderlein (1921, 1930) but there is often marked sexual dimorphism and they have not been used in classification except by Enderlein. The degree of development of two other features, the calcipala and pedisulcus, introduced first by Enderlein (1930) have been widely used. The calcipala is a flattened projection of the first tarsal segment or basitarsus; its sharp, serrated distal edge is a continuation of the keeled ventral edge of the segment. It may be absent, be very small in which case the first tarsal segment appears truncate, or be well developed and produced on the postero-ventral margin as a flattened lobe, extending past the point of attachment of the second segment and mesad of it. A part of the dorsal surface of the second hind tarsal segment is often weakly sclerotized and frequently indented in the form of a shallow notch or deep V-shaped groove which is termed the pedisulcus.

There is much variation in these two features and their development is often independent of one another causing confusion. The calcipala and pedisulcus have been given much weight in classification. Their development or reduction evidently does not always indicate close relationship, as will be discussed later, and until their function has been explained, their use in elucidating phylogeny may be open to misinterpretation.

Each tarsus terminates in a pair of small claws; each usually bears a basal ventral tooth whose shape is often characteristic. In many species the basal tooth is as long as half the claw itself and is a broad rounded lobe. Its presence in most bird feeding species has led to the assumption that it is a modification for crawling in the feathers (Shewell, 1955). In other species, which feed on mammals or do not suck blood, this tooth may be reduced or absent. Petersen (1958) has described how the simple, untoothed claws of S. equinum L. are folded to grasp the hair in the ears of domestic mammals.

Structures of the Head

The number of segments in the antenna is usually eleven, but in some species may be reduced to 9 or 10. The basal two segments, the scape and pedicel are differentiated from the remaining segments which constitute the flagellum. These two segments are usually larger, with longer hairs, and their length and width relative to one another has been used taxonomically to characterize species groups.

The mandibles and maxillae have been described in detail by Wenk (1962). In blood-sucking species the lower edges of these organs are set with a row of recurved teeth. These teeth are weak, and replaced with a few hairs in some species, and this reduction has been interpreted as indicative of non-blood-feeding (Dorogostajskij _et al_, 1935; Krafchick, 1942), and may be used for species identification. Reduction in the serrations on the mouth parts is generally correlated with autogeny, and nearly or fully developed eggs in the female on emergence (Davies, 1958; Davies and Peterson, 1956).

The palp of the maxilla has five segments (Nicholson, 1945); the third segment is usually enlarged and contains an internal sclerotized sensory vesicle, or Lauterborn's organ, which opens to the exterior anteriorly through a small canal, or directly by a pore (Syme and Davies, 1958; Wenk, 1962). The extent, shape and position of the canal, and the shape, complexity and size of the vesicle relative to the third segment, are useful in the female for characterizing species groups. The vesicle is usually smaller in the male.

In the female, and in the males of a few species, the eyes are not contiguous above the antennae, and the frons thus formed is variable in width. Its width, at the narrowest point, is usually expressed as a ratio of the greatest total width of the head; (this character is suitable only for specimens frozen-dried, or preserved in alcohol).

Thorax

The prosternum or basisternum is a small sclerite lying between the fore coxae. In newly emerged flies, it is only partly sclerotized along its posterior W-shaped border, becoming fully sclerotized a few hours after emergence. In the males of all species, and in the females of some (most species of Eusimulium) each anterior corner of the basisternum is connected to the episternum by a narrow band, the precoxal bridge, that is fully sclerotized even in teneral specimens (Fig. 6c). Its presence is useful in grouping species.

In at least one species, (S. emarginatum), in which it is normally absent (Fig. 6a), a slender connection may occur in occasional specimens (Fig. 6b). When the precoxal bridge is absent, the shape of the anterior corners of the basisternum are also of diagnostic value.

The sternites between the mid and hind coxae are almost entirely invaginated apodemes, each of a characteristic shape. The sternite between the hind coxae, called the metasternum (Fig. 8a-c), may bear ventrally directed lobes on its internal dorsal arms (Fig. 8c); their presence is of diagnostic value.

Integument and its Vestiture

The integument of most species is more or less pollinose; the colour of the pollen varies from white or yellow to pale gray, darker grayish-brown, or grayish-black and may also show bluish or violet reflections. When the pollen is sparse or absent on sclerotized regions, the integument is usually shining to some extent.

The vestiture of both sexes is usually characteristic in each species as to colour and arrangement. The frons and clypeus of the female are usually partly or wholly covered with recumbent scale-like hairs that are directed anteroventrally. In the male, the hair on the clypeus is longer, more erect and directed postero-dorsally (reclinate); there may be a row of widely spaced reclinate hairs between the eyes. The posterior surface of the head in both sexes bears outwardly directed hairs that project slightly beyond the dorsal and lateral edges.

The scutum is covered with recumbent, scale-like hairs. These hairs are usually shining, and may be brown or yellowish to metallic silver or gold. The colour of the hairs laterally and along the anterior margin is often paler. The hairs may be sparse, leaving much of the underlying integument exposed, or dense, virtually obscuring the integument. The scutellum is usually covered with longer erect hairs. The postscutellum is usually bare; in a few species, however, two lateral patches of recumbent scale-like hairs may be present. The pronotum, proepisternum, and mesepimeron each bear a tuft of erect hair. The fore coxae are covered anteriorly with recumbent hair; the mid and hind coxae usually bear a narrow vertical patch of hair. Mostly recumbent hair entirely covers the remainder of the legs; that on the femora and tibiae of females and males of some species is usually pale, coloured similarly to the thoracic hair, and contrasting to the dark brown hair of the tarsi.

The costa of the wing, the stem vein, the upper surface of the radius and the lower surfaces of the subcosta and radial sector usually bear one or more rows of fine hair. In some species the hair at the base of the costa and on the stem vein may be pale, or with pale and dark hair mixed, but the remaining hairs are usually dark brown. The costa and distal part of the radius in most species bear smaller, stouter spinules, set among the longer hairs. In the males of many species, the hairs are absent (or greatly reduced in number) on the lower surface of the subcosta.

The first tergite of the abdomen extends part way around the abdomen and bears a marginal fringe of unusually long hair; this is termed the basal fringe, and its colour may be of importance in identification. Most of the remaining part of the abdomen bears hair; their arrangement, density and colour are diagnostic.

External Genitalia

In most insect groups and probably among other arthropods as well, the external genitalia, particularly those of the male, have been fully exploited for the determination of species. Often they show great complexity and variety and have been used (Robach, 1954) as virtually the sole basis for the development of phylogenetic concepts.

The external genitalia of black flies, especially of the male, show greater interspecific variety in the shape of their component parts than does any other structure. Consequently, advantage has been taken of this variation in determining relationships between species groups and the resulting phylogenetic concepts may be compared with those based on wing and leg structure. The external male genitalia consists of two paired structures and three median ones all originating posterior to the ninth sternite. Snodgrass (1957) has shown that the male genitalia of nematocerous Diptera (among which the black flies are included) and indeed of most insects whose ontogeny has been studied, arise as a pair of lobes on the ventral surface behind the ninth abdominal sternum of the last larval instar. These lobes enlarge and each divides longitudinally into an outer pair of lobes, the parameres, and an inner pair, the mesomeres. The parameres then elongate to form the claspers which in Nematocera become segmented into the basimeres or basistyles and telomeres or dististyles. The mesomeres fuse medially to form the tubular aedeagus. In some forms, secondary lobes may appear on the basistyles and dististyles and the walls of the aedeagus may contain sclerotized plates.

Snodgrass (1957) does not specifically refer to the Simuliidae and the accepted terminology for the genitalic structures in this family does not necessarily bear a relationship to the homologous structures in other Diptera, even in other families of Nematocera. His treatment of some of these families, however, is sufficiently clear to enable an interpretation of the male blackfly genitalia and homologies may be attempted.

a) Male genitalia

The claspers, which Snodgrass (1957) has shown must be called parameres, are clearly homologous among all the Nematocera and Brachycera and are almost universally articulated into a distal segment or dististyle and a basal segment or basistyle. In the Simuliidae the large and massive basistyles are rather uniform in shape and position. They closely approximate one another medially and the ring-like ninth sternite anteriorly, and each narrows apically to the region of articulation of the dististyle. The latter is usually more slender and curved, arching dorso-medially and bearing at its apex one or more short, stout, peg-like setae. The shape of these structures and the number and placement of the apical pegs are of considerable value in associating species into groups, but usually not useful for species identification, i.e., they usually vary little among closely related species, and on the other hand may show intraspecific variability (Davies, 1949a).

The ventral plate or adminiculum is a flap-like triangular or rectangular extension of cuticle arising between and dorsal to the basistyles. Each antero-lateral corner bears an anteriorly projecting apodeme. The apex is usually produced into a ventrally curved lip which bears small hairs arranged in a distinctive pattern. This structure assumes many shapes and is perhaps one of the most useful structures in characterizing both species and species groups. The ventral plate appears to be homologous with the claspettes of the mosquitoes and the inferior lobes of the Chironomidae. Both the claspettes and the inferior lobes are by derivation medially directed outgrowths of the basistyles (Snodgrass, 1957) and are usually narrowly fused to one another medially. In Anopheles, they are broadly fused, and the resulting structure strongly resembles the simuliid ventral plate.

The remaining genitalic structures which are dorsal to the ventral plate are here interpreted as sclerotized plates in the walls of the tubular aedeagus. In the Culicidae, the aedeagus is slender and tubular, encircling the vas deferens and is evidently adapted for intromission. In some species of Culex the encircling edges are narrowly fused dorsally. The simuliid aedeagus however is much broader, being adapted to pass a spermatophore, which is affixed to the exterior of the female (the process in Cnephia dacotensis is described below in more detail). The thin, flat median sclerite forms the floor of the aedeagus. It is articulated by its anterior end to the dorsal wall of the ventral plate. Distally it is widened, often forked, and the tips of the arms thus formed are sometimes dorsally recurved. The median sclerite is possibly homologous with the entire so-called aedeagus of the Culicidae.

The sclerotized plates in the lateral walls of the aedeagus are called the 'parameres' by most authors (Fig. 41). Snodgrass (1957) has shown that this term is correctly applied to the claspers, but an alternate term is evidently not available and the old usage is best continued here until their homology is more thoroughly established . In the mosquito a pair of minute plates connect the aedeagus to the basistyles. They are also called 'parameres' (Carpenter and La Casse, 1955) and in spite of the disparity in size are probably homologous to the simuliid parameres. Typically each is a triangular plate; its antero-dorsal corner is articulated with a prong on the basistyle (as in the mosquito); its antero-ventral corner may be articulated with the ventral plate or may bypass the ventral plate dorsally to articulate with the median sclerite; its apex is usually produced into an arm. This parameral arm may vary from merely a simple inflexible extension of the paramere (Fig. 34) to a long, flexible band along each side of the distal portion of the aedeagus (Fig. 35), or forming a fingerlike projection from it (Fig. 40). Terminally it often bears a comblike row of long spines (Fig. 44). The paramere itself may also bear a long spine directed dorsally, antero-laterally or, in one species, ventrally (Fig. 41). Small short spines are usually scattered over the remaining transparent membrane of the aedeagus and in a few species, patches of longer spines are also present (Fig. 41). The parameres and associated arms and spines are here considered in detail and because of their variability have been most useful in elucidating phylogeny.

The flat, dorsal sclerite, of limited taxonomic value, lies in the dorsal wall of the aedeagus.

b) Female genitalia

The genitalia of the female, although showing less variability than in the male, are nevertheless useful in distinguishing species and in segregating species groups. The ninth sternite is produced posteriorly to form a pair of flaps, the ovipositor lobes. Their shape and the shape of the cleft between them are often of value. The tenth sternite, usually called the genital fork, and the anal lobes are the most variable structures. The genital fork is a Y-shaped sclerite; the arms are continuous with the tenth tergite and the stem runs anteriorly as a reinforcement in the upper wall of the common oviduct. The arms are expanded into terminal plates of variable size and shape which are usually slightly concave, each bearing an internal, anteriorly directed apodeme which is variously shaped. The articulation of each of these plates to the tergite is also variable and characteristic, and is often folded and convoluted, ribbon-like, either dorsally or ventrally (Fig. 10).

The anal lobes on either side of the anus usually project ventrally to varying degrees and their medio-ventral margins bear characteristic areas of specialized fine setae.

c) Genitalia *in copulo*

A study of the coupled genitalia (of *Cnephia dacotensis* (Fig. 55)) has made possible the elucidation of the function of the genitalic structures of the male. In this species and probably in all black-fly species, the genitalia are modified for the transfer of a spermatophore. The male of *C. dacotensis* appears to approach and mount the female from behind, curling its abdomen forward and down until the terminalia come in contact with the ventral apex of the female abdomen. The claspers grasp the female from beneath between the ninth and tenth segments; in this position, the ventral surface of the claspers face posteriorly (in reference to the female). The ventral plate is evidently used to pull the anal lobes posteriorly, thus enlarging the genital chamber. In some species (*aureum*, and some non-*Eusimulium* species of *Simulium*), however, the ventral plate appears to be too narrow to perform this function and is evidently merely inserted between the anal lobes. Nevertheless in this position, the setae on the lip of the ventral plate will evidently come in contact with the specialized setae on the inner margins of the anal lobes and is thus suggestive of a sensory function on the part of both these patches of setae. The aedeagus is then everted, pushing the ovipositor lobes forward to lie inside and directed anteriorly on the floor of the genital chamber. The parameral spines are arranged along the dorsal and lateral (in respect to the male) edges of the aedeagus and appear to grip the lateral and ventral walls of the genital chamber of the female (anterior to the infolded ovipositor lobes). In this position, they also appear capable of pulling the ovipositor lobes back to their original position, but a study of those species in which parameral spines are lacking (*Prosimulium*) is necessary before this can be asserted.

While the genitalia are coupled in this manner, the spermatophore, which appears from dissection to be already formed in the genital tract of the male, is evidently passed out and pressed against the roof (formed by the genital fork) of the female genital chamber. On withdrawal of the aedeagus the spermatophore is left in position held anteriorly by the ovipositor lobes and posteriorly by the anal lobes. In the specimens of Cnephia dacotensis examined, the spermatophore was an almost spherical transparent capsule containing two opaque pyriform bodies side by side closely approximated medially (presumably sacs filled with spermatozoa). On the dorsal surface of the spermatophore was a small papilla which extended into the spermathecal opening of the female.

Larval Structures

Labrum

A characteristic feature of most black-fly larvae is the pair of prominent mouth or head fans, on either side of the anterior end of the head, for straining food particles from the water flowing past. The stalk of the fan is a tubular outgrowth, and is derived from the lateral wall of the labrum (Puri, 1925). The dorsal half of the stalk is a rigid slightly convex plate; its ventral wall is mostly membranous and flexible, containing mid-ventrally a longitudinal rod, which is probably homologous with the torma of the mosquito larva (Snodgrass, 1959). The torma expands distally into a rounded tip, the connective sclerite (Fig. 58). The long, flattened slender rays of the head fan are each attached along one edge at their bases to the end of the stalk between the dorsal wall and the ventral connective sclerite, and are directed ventrally.

The head fans are evidently extended by internal fluid pressure (mechanical pressure on the larva will produce this effect); there is no evidence of a muscle for this purpose. Folding is accomplished by a longitudinal postero-mesad movement of the torma in relation to the dorsal wall, whose distal edge serves as the fulcrum. The torma is moved in this way by a single large muscle inserted on a slender, transparent, tendon-like apodeme attached to the anteromedial corner of the torma (Fig. 58 a, d). At the point of muscle insertion the apodeme is heavily sclerotized in some species and is not readily hydrolyzed by potassium hydroxide, indicating that it is of cuticular origin. The muscle has two portions, each with a different origin. The median portion of the muscle originates along the mid-line of the large shield-like dorsal area of the head which Snodgrass (1959) has called the cephalic apotome. The lateral portion crosses the midline, interdigitating with its homologue of the opposite side at this point (Grenier, 1949) to originate in the opposite corner of the cephalic apotome.

Snodgrass (1959) has shown that the tormae of the mouth brushes of the mosquito larva are musculated in a similar fashion to that described above. The arrangement of the labral muscles and sclerites in the larva of Aedes aegypti L. is shown in Fig. 58e. Mechanical elevation of the connective sclerite causes downward folding of the hairs of the mouth brushes simulating the normal movement of the feeding mosquito larva. The mouth brushes may be returned to their extended position by mechanical pressure on the body, although Snodgrass (1959) stated that their extension was a result of the elasticity of their basal connections.

In the first instar of Simulium pictipes Hagen, the torma and connective sclerite form a single flat, lightly sclerotized structure (Fig. 58c), the torma not showing the rotation and heavy sclerotization characteristic of later instars. The primary fan rays are reduced in number, and the secondary fan and most other structures are absent. However, the second instar has all the component parts of the head-fan apparatus that are found in mature larvae. L. Davies (1960) has shown that in the first instar of a species of Prosimulium, the entire head fan was absent, but that it appeared in the second instar.

In a few aberrant simuliid species the head fans are reduced (Cnephia crozetense Womersley and Simulium oviceps Edw. (Dumbleton, 1962)) or absent (Twinnia spp. and Gymnopais spp.) even in the last instar. In the mature larva of Twinnia tibblesi S. & J. there is scarcely a vestige of any of the complex sclerites that make up the head fan of other species; nevertheless, the pair of muscles that are associated with them are present. Each is a thin undivided strand and both originate side by side on the mid-line of the cephalic apotome, just posterior to the origins of the pair of much larger epipharyngeal muscles. Each muscle is inserted on a minute transparent tendon-like apodeme (as described above), that is attached to a small fold in the membranous lateral wall of the labrum, in the region where the base of the fan would normally be. In *Gymnopais* sp. (only a penultimate instar from Pelly Lake, Keewatin Dist., N.W.T. was available) some of the sclerites, including the torma, are present although much reduced in size (Fig. 58a) and a slender apodeme for muscle attachment is present in a similar location to that described above for *Twinnia tibblesi.* In the larvae of both these species the head is ovoid and reduced in size; the mandibles and maxillae are closer to one another basally and are modified for browsing. In *Gymnopais*, the distal mandibular surfaces bear several rows of radula-like teeth, and the well-developed palatine brush is composed of many stiff curved bristles.

The secondary fan rays of the simuliid head fan are actually a continuation of the primary rays and are separated from them by a few short, blunt, aborted rays. They arise in a nearly straight row along the posterior edge of the connective sclerite, and are not appreciably different in structure from the primary fan rays. Each is flattened, and bears a single row of hairs along the edge facing the connective sclerite. These hairs are much longer than those of the primary rays. The secondary fan is absent in the first instar of Simulium pictipes, and this may be true of the first instar of other simuliid species. The arrangement of the secondary rays has been shown to be of two types (Sommerman, 1953). The fundamental difference between the two types is that one contains many more rays in a slightly longer row, and when the entire head fan is extended, these secondary rays open up in two different ways, forming two distinct patterns. One pattern, the less complex of the two, is found in Prosimulium spp., in Gigantodax igniculum Coscaron and Wygodzinsky (and presumably in other Gigantodax as well), and in Cnephia strenua Mackerras & Mackerras and C. tonnoiri M. & M. (and probably the other Australian species of Cnephia). When the head fan is extended, the flattened secondary rays are erected to form a small, flat triangular fan projecting ventrally, perpendicular to the primary fan (Fig. 58b, d). The hairs along the morphologically anterior edge of each ray now extend laterally because each ray is oriented with its flattened sides facing antero-posteriorly. Another peculiarity of the head fans of the species mentioned is the presence of many fine hairs attached to and around the edge of the connective sclerite, at the bases of the primary fan rays. Furthermore, in C. strenua and C. tonnoiri the connective sclerite arises near the base of the torma rather than at its apex (Fig. 58b). In C. strenua the two structures are broadly fused along their adjacent edges; this region is mostly membranous in C. tonnoiri. These structural peculiarities are reminiscent of the culicid mouth brush (Fig. 58e).

The second, more complex type of head fan is found in *Simulium* (including the *Eusimulium*-group), all Holarctic *Cnephia* examined, and *Austrosimulium longicorne* Tonnoir, *A. furiosum* Skuse and *A. bancrofti* Taylor (and presumably in the remaining species). As indicated above, there are many more secondary rays, although they are still attached in a straight row. In addition to forming a small, flat triangular fan perpendicular to the body axis, as was described above for *Prosimulium* spp., the additional, more medially placed secondary rays form a small cupped fan, inside and below the primary fan, and thus cover the connective sclerite. The flattened triangular portion and cupped portions are continuous (not separated or distinguished from one another). This arrangement may be more effective in keeping the areas around the bases of the primary fan rays free of particles. The small hairs on the connective sclerite and around the bases of the primary rays are absent.

Antenna

The antenna of the larva appears to be basically composed of three segments. In nearly every species, however, the basal segment is divided into two or more annuli, separated by a weak, sometimes incomplete, crease. The second annulus is, in some species, further subdivided into two to seven secondary annuli, that are usually separated from one another more distinctly than are the two primary annuli (Fig. 64). Nevertheless most authors have referred to the two primary annuli of the basal segment, as segments one and two (Crosskey, 1960), while further annulations in the second portion are called secondary division of the second segment (Sommerman 1953).

Because of the conflicting views, this region with its primary and secondary annuli will be called the basal portion of the antenna in the present thesis. This portion is often unsclerotized and transparent, or may be unsclerotized medially and more or less sclerotized laterally and dorsally. The distal portion of the antenna is made up almost entirely of the penultimate segment. It is completely sclerotized and is usually narrower than the basal portion, from which it is distinctly separated by a flexible joint which bears two minute conical papillae. A small conical tip forms the apical segment. The ratios of the lengths of the various segments and annuli to one another, and the number of annuli are of diagnostic value.

Hypostomium

The hypostomium is the antero-medial region of the ventral wall of the head capsule. It is double walled, being a flattened, wedge-shaped anterior extension of the ventral edge of the head capsule. The fold (labio-hypostomial fold - Fig. 59) where the dorsal wall of the hypostomium turns forward to become the membranous connection to the venter of the labium, is visible through the semi-transparent ventral wall of the hypostomium, as a semi-circular line. The position of this line often changes after fixation and is unreliable taxonomically.

The anterior edge of the hypostomium is produced into a row of heavily sclerotized sharp points, the hypostomial teeth, that are of value in segregating species groups. Basically these teeth are arranged in three groups. The central group, with one long median tooth and two smaller ones flanking it, is usually slightly inclined dorsally. Each lateral group of teeth contains about five teeth and the median one in this group is usually the longest. The hypostomium thus appears at low magnification to be tricuspidate with the central tooth and the two longest lateral ones most prominent. The lateral teeth are not tilted dorsally as are the central teeth. In some species groups, the lateral teeth are born on pointed or rounded lobes flanking and extending well beyond the central teeth (Figs. 59-62). The size and shape of these lobes has been found, in at least one species, to differ between the penultimate and final instars, suggesting an allometric type of growth from one instar to another. Thus the teeth of the last instar of _E. congareenarum_ are not as much like those of its relatives, as are the teeth of the penultimate instar.

The teeth are usually believed to serve as a scraper for removing food or detritus from the substrate, but may also provide a serrated edge for cutting the secreted 'silk' strand. In this respect, the labio-hypopharyngeal complex which bears the common opening of the salivary glands, is grooved to slide forward and backward over these teeth. The labio-hypopharyngeal complex may be extended by internal pressure, while silk is being expressed onto the substrate, and then retracted, drawing the orifice of the salivary glands over the teeth. There is evidently only one pair of retractor muscles which originate on either side of the throat cleft and are inserted on the postero-lateral corners of the labium. Whether or not there is a sphincter controlling the opening of the salivary glands has not been ascertained.

Postgenal Cleft

On the ventral surface of the head, the point of union of the postgenae is usually partly unsclerotized, leaving a rounded or V-shaped cleft which appears to be a ventral extension of the occipital foramen. This cleft has been variously called the "throat cleft", "gular cleft", "epicranial cleft" and "postgenal cleft" (the last term is here used) and its shape is of the utmost value in characterizing species.

Pattern of Dorsal and Ventral Head Spots

Another feature which is of taxonomic value is the head pattern. It is formed by the differential deposition of pigmentation, both at the sites of the origins of the muscles that operate the mouthparts and head fans, and in the surrounding areas. Usually the positions of muscle origin are relatively constant and thus pigment associated with them forms a pattern which differs among different species. The components of this pattern most used are the origins of the labral and pharyngeal muscles on the cephalic apotome (Fig. 59).

As indicated by Snodgrass (1959), and above, the labral muscles are of two pairs. One pair, inserted on the epipharyngeal apparatus, originates on the mid-line, the associated pigment forming the antero-median spot. Each muscle of the other pair, which is inserted on the torma of the head fan is divided into two portions with two origins. The associated pigment forms the postero-median spot and the second postero-lateral spot. The three remaining pairs of spots, the first and second antero-lateral spots and the first postero-lateral spot are formed by the pigmented origins of the dorsal pharyngeal muscles. The first and second antero-lateral spots may be close together appearing as a single spot (Figs. 77, 80), and their positions relative to one another are diagnostic. The first postero-lateral spot may be pale and indistinct, or may be so close to the second that the two appear as one.

Lateral to the cephalic apotome are the origins of the mandibular and maxillary muscles and the ventral pharyngeal muscles, while on either side of the postgenal cleft are the origins of the labial muscles. As diagnostic features, the spots formed by these muscles have not been as useful taxonomically as those on the dorsum of the head.

Abdomen

At the posterior end of the larva, ventral to the anal opening, is a ring of many radiating rows of minute hooks, the number of hooks in each row being variable among different species. Antero-ventral to this ring of hooks are, in many species, a pair of cone-shaped ventral tubercles, whose presence and degree of development are diagnostic. In some species, the two tubercles are united medially to form a single mid-ventral fold: or the tubercles may be present on a similar fold.

An X-shaped sclerite (Y-shaped in a few species) lies dorsal to the ring of hooks. Its dorsal arms are usually short, extending anteriorly in the ventral wall of the rectum, but in some species of the Southern Hemisphere, these arms are postero-ventrally recurved as internal apodemes (Fig. 57a)(Mackerras & Mackerras, 1948; Dumbleton, 1960, 1962). Its ventral arms extend laterally along the anterior edge of the ring of hooks for a short distance; in <u>Gigantodax igniculum</u> and <u>Austrosimulium longicorne</u> and probably other species of these genera, there is an additional ring sclerite encircling, and anterior to the ring of hooks. The tips of this sclerite approximate the ventral arms of the anal sclerite in Gigantodax (Fig. 57b).

Abdominal Chaetotaxy and Colour

The dorsal surface of the abdomen may be ornamented with cuticular hairs; in some exotic species these hairs may be larger and compound. Some species bear articulated flattened fan-shaped scales, and a few are ornamented with two rows of tubercles, dorsally or ventrally. Larval body pigment is usually associated with chromatophores lying near the surface and usually aggregated into patches. It is often of two colours, one colour, usually reddish, is confined to two longitudinal rows of spots or patches that overlie the background, usually greenish, pigment and partially obscure it.

Pupa

The pupae are conservative except for their respiratory organs, which arise from the antero-lateral corners of the prothorax. The base of each organ is a single, short petiole which subtends from two to over 100 filaments, usually directed anteriorly. The pattern of branching, the shape, thickness, texture and to some extent even the number of filaments reflect relationships between species and species groups. They are invaluable for associating mature larvae with pupae and adults.

The position and direction of spines on abdominal tergites and sternites shows minor variation within the Eusimulium-group. Greater variations occur, however, in some species of Cnephia. The shape and texture of the cocoon which is believed to reflect innate spinning behaviour is of taxonomic value (Shewell, 1958).

DESCRIPTIONS OF ONTARIO SPECIES

This section contains the original citations and descriptions of the female, male, last stage larva and pupa of the seventeen Ontario species of the Eusimulium-group of the genus Simulium. The limits of the known distribution for each species, both in Ontario and elsewhere, are included; a more detailed account of the Ontario distribution has been published recently (Davies, Peterson and Wood, 1962). In addition, four of the Ontario species of Cnephia are similarly treated. Interpretations of the morphological and ecological relationships of these and other related species throughout the world are discussed in following sections.

Genus Simulium Latreille

Simulium aestivum, new species

Female. A small, brown and grey pollinose species with pale yellow hair, sparsely haired abdomen and narrow frons.

Posterior surface of head, frons and clypeus grey pollinose; ventral half of clypeus and dorsal half of frons with recumbent, yellow hair. Frons narrow, about one-ninth the width of head. Antenna and palpus uniformly dark greyish-brown pollinose. Flagellum of antenna with pale pubescence, and longer, pale hairs basally. Hair of palpus nearly all brown; sensory vesicle of third segment about one-half the length of the segment.

Scutum grey pollinose, covered with recumbent, uniformly pale, yellow hair. Scutellum with long, erect, yellow hair, interspersed with a few darker ones. Postscutellum bare, lightly pollinose, brown, shining. Pleuron greyish-brown pollinose; pleural membrane and subalar area dull brown. Mesepimeral tuft and hair on pronotum and proepisternum long, erect, pale yellow. Precoxal bridge present. Hair on stem vein pale yellow, interspersed with a few dark hairs; hair on dorsal surface of radius black; ventral surface of subcosta and radial sector with dark hair. Legs brown, tarsi darker brown; basal segments with pale yellow hair, hair darker on the distal tips of the tibiae, mostly dark brown on the tarsi. Claw with a large, basal lobe. Calcipala and pedisulcus well-developed.

Abdomen brown, tinged with a greyish-brown pollinosity, more pronounced on second tergite. Basal fringe pale yellow, hair on second and third tergites short, pale yellow; hair on remaining segments short, sparse, recumbent, entirely brown apically.

Genitalia as in Fig. 24. Arms of genital fork moderately broad at point of bifurcation; postero-medial areas of terminal plates large and rounded, or bluntly angulate.

Male. General body colour dark brown, with gold hair on scutum.

Posterior surface of head, frons and clypeus dark greyish-brown pollinose, with erect, brown hair. Antenna dark, with pale pubescence on flagellum, scape and pedicel with dark hair.

Palpus with dark hair, third segment dark brown, distal segments paler; sensory vesicle of third segment minute, less than one-sixth the length of the segment.

Central portion of scutum dull blackish-brown, margins of scutum, pleuron, scutellum and postscutellum paler greyish-brown pollinose. Hair of pronotum and proepisternum gold, long, erect. Scutum covered with short, fine, recumbent, gold hair. Scutellum with black, long, erect hair laterally, interspersed with shorter gold hair. Postscutellum and katepisternum bare. Mesepimeral tuft brown, with pale tips. Legs brown, concolorous with thorax (paler in teneral specimens). Hair on fore coxa gold, interspersed with a few darker hairs; hair on femora and tibiae, and mid- and hind coxae dark brown, interspersed with a few gold hairs; tarsi with dark hair. Calcipala present; pedisulcus well-developed.

Abdominal tergites dull brown in both lateral and terminal views, grey pollinose only on second tergite; lateral regions and sternites paler, grey pollinose. Tergites 2-6 with long, erect, brown hair, this paler, shorter and recumbent posteriorly; sternites with brown, erect, sparse hair.

Genitalia as in Fig. 49. Clasper dark brown with black hair; diststyle enlarged and rounded terminally, with a flattened, triangular flange medially, the small spine at its apex directed antero-medially. Paramere broadest at base with a concave ventral margin, the apex produced ventrally and bearing a long, dorsally recurved spine. Median sclerite weakly forked, often with infilling between the arms. Dorsal sclerite clavate, three or more times as long as wide.

Larva. Abdominal pigment pale reddish-brown diffusely scattered over the dorsum of the larva, transverse bands broad and poorly defined, leaving small transparent, intersegmental patches between segments 1 and 4. Segments 3-8 each with two laterally placed patches of darker, reddish pigment overlying the paler, brown pigment. Postgenal cleft small with square or rounded anterior margin. Median hypostomial tooth relatively large. Basal portion of antenna elongate, longer than head-fan stalk. Head capsule yellowish-brown; head pattern enclosed in a darkly pigmented area (Fig. 76) excluding only the antero-median head spot. Pigmented area antero-ventral to eye small.

Pupa. Respiratory organ about 3.0 mm. long, composed of 4 filaments in two, petiolate pairs; the petiole of the ventral pair slightly longer and thinner than petiole of dorsal pair. All four filaments closely subparallel, rugose, grey, and subshining. Cocoon slipper-shaped, with a thickened, anterior margin.

Holotype. Female, reared from a pupa collected June 25, 1959, from a small stream flowing into the Ottawa River at the North Star Lodge, Point Alexander, Rolph Twp., Renfrew Co., Ontario, D.M. Davies and D.M. Wood.

Allotype. Male, same data as holotype.

Paratypes. Fourteen males, eight females, same data as holotype. Three males, four females, from a small stream crossing the Laurentian Point Road, three miles west of Point Alexander, Rolph Twp., Renfrew Co., Ontario, June 25, 1959, D.M. Davies and D.M. Wood. Types (No. 7992) and paratypes deposited in the Canadian National Collection. Paratypes deposited in the U.S. National Museum, and McMaster University.

Distribution. Thunder Bay Dist., Nipissing Dist. and Renfrew Co., Ont. Great Whale River (C.N.C.) and Mt. Tremblant, Que. (B.V. Peterson).

Simulium anatinum new species

Simulium (Eusimulium) "H", Bennett, 1960, Canad. J. Zool. 38: 379 (female bloodsucking habits).

Female. A small grey species with white hair and grey legs similar to innocens from which it may be separated by the wider frons.

Posterior surface of head, frons and clypeus, grey pollinose with whitish hair, that on frons and clypeus proclinate and recumbent. Frons about one-eighth the width of the head. Antenna dark grey with pale pubescence; scape and pedicel paler with pale hair. Palpus grey pollinose with whitish hair; length of sensory vesicle of third segment about one-fourth the length of the segment.

Scutum grey pollinose with recumbent white hair. Scutellum with long, somewhat recumbent, medially directed white hair mixed with a few darker hairs. Pleuron and postscutellum grey pollinose, concolorous with scutum. Pleural tuft and hair on pronotum and proepisternum white. Postscutellum and katepisternum bare. Precoxal bridge present. Costa, stem vein, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair, a few white hairs at the base of the costa and on the stem vein. Fore coxa grey pollinose, concolorous with pleuron. Legs greyish-brown, paler in teneral specimens. Tibiae and tarsi dark brown; with white hair basally and brown hair on the tarsi. Calcipala minute, pedisulcus shallow. Claw with large thumb-like basal lobe.

Abdomen grey, paler ventrally with long, dense, white hair on top and sides, sparser and shorter ventrally; last three to four segments with a few long, dark hairs dorsally.

Genitalia as in Fig. 17. Arms of genital fork moderately slender; terminal plates with infolded posterior margin, appearing as a sclerotized edge in ventral view, the anteriorly-directed apodeme minute or absent.

Male. Clypeus greyish-black, with sparse grey pollen and dark reclinate hair. Antenna dark grey with pale pubescence. Maxillary palpus greyish-black with dark hair.

Scutum dark brown with a slight, greyish pollinosity in anterior view and moderately sparse recumbent hair, brownish medially (yellowish in some specimens) changing to yellow laterally, paler at the humeral angles. Scutellum with erect dark hair. Pleuron greyish-black with grey pollen. Mesepimeral tuft and hair on pronotum and proepisternum brown. Legs dark with brown hair (sometimes with a few pale hairs). Abdomen dull, dark brown with sparse brown hair dorsally and longer, denser hair laterally.

Genitalia similar to innocens and congareenarum. Parameral spines are longer than those of either species, the longest teeth approximately equal to the distance from the tip of the basal arm of the ventral plate to its point of articulation with the paramere.

Larva. Abdominal pigment brown, diverse; transverse bands weakly differentiated, with a slender, transparent median stripe and a tendency to denser pigment on either side of the stripe, thus forming two weakly marked dorsal rows of spots. Postgenal cleft small and square. Lateral hypostomial teeth moderately elevated. Antenna pale, weakly sclerotized. Second annulus of basal portion with 5-7 (usually six) subdivisions, separated from one another by transparent, transverse lines; the distal subdivision the longest. The basal subdivisions are usually variable, often differing on either side of the same specimen. Articulation between the two primary annuli of the basal portion is not marked by a transparent area.

Head pattern relatively dark and discrete, antero-lateral head spots almost in a vertical line. Second postero-lateral head spots usually distinct, surrounded by a lighter area (i.e. without background pigment). Head narrowed basally (Fig. 64).

Pupa. Respiratory organ slightly longer than pupa, consisting of twelve long, slender filaments arranged in four groups, two dorsal petiolate groups of three filaments each, branching almost at right angles to the two ventral petiolate groups, also each with 3 filaments. Cocoon fragile, slipper-shaped, with long anterior median process, its edges somewhat thickened.

Distribution. Churchill, Man. (Dunbar, 1962; C.N.C.) east to Fort Chimo, Quebec (Shewell, pers. comm.) and Goose Bay, Nfld. (C.N.C.), and as far south as Frontenac Co. and Muskoka Dist., Ontario.

Simulium aureum Fries

Simulia aurea Fries, 1824, Observationes Entomologicae 1: 16 (females, male).

Cotypes. ? Two females, Zoological Institute, University of Lund, Lund, Sweden.

Type Locality. The types were collected by Zetterstedt in Scania, Sweden, from Esperöd and Björnstorp.

Female. A medium-sized greyish-brown species with metallic silvery and gold hairs and extensive yellow areas on the legs.

Frons and clypeus pale grey pollinose, almost entirely covered with metallic yellowish recumbent hair. Flagellum of antenna grey with pale pubescence; scape and pedicel orange with short, pale hair. Maxillary palpus dark greyish-brown with dark hair; a few paler hairs on the third segment; sensory vesicle of third segment over one-half the length of the segment.

Scutum grey pollinose with recumbent gold scale-like hair on the disk, changing to metallic silvery hair on the lateral and anterior edges. Scutellum with long, erect yellow hair. Postscutellum grey pollinose with two lateral patches of recumbent gold hair. Thorax greyish-brown pollinose. Pleural tuft and hair on pronotum and proepisternum white. Precoxal bridge present. Fore coxa yellow; mid and hind coxae grey, concolorous with thorax. All coxae with yellow hair. Trochanters, basal two-thirds of femora, of tibiae and of basitarsi yellow with yellow hair contrasting with the dark, dark-haired apices of the femora, tibiae and basitarsi. Remaining tarsal segments dark brown, with dark hair. Claw with thumb-like basal lobe. Base of costa and stem vein with pale hair; remainder of costa and upper surface of radius and lower surface of subcosta and radial sector with dark hair.

Abdomen grey, paler ventrally, thickly clothed dorsally and laterally with metallic flattened scale-like hair, mixed with a few longer, darker hairs apically.

Genitalia as in Fig. 31. Terminal plate of arm of genital fork triangular, with prominent anteriorly-directed apodeme. Ovipositor lobe produced posteriorly, acuminate, thickly covered with small, fine setae. Anal lobe narrow, strap-shaped, with rounded anterior margin.

Male. Clypeus pale grey pollinose with sparse, fine, mixed pale and dark reclinate hairs. Antenna dark grey with pale pubescence; scape and pedicel orange-brown. Scutum dull black with dense, recumbent gold hair, paler yellow on lateral and anterior margins and on humeri. Scutellum with erect yellow hair. Postscutellum with two small, lateral patches of recumbent gold hair. Pleuron greyish-brown pollinose. Mesepimeral tuft pale yellow. Hair on pronotum, proepisternum, fore coxa and fore tibia white. Hair on mid-coxa and mid-trochanter pale yellowish; with antero-lateral patches on mid- and hind femur and basal one-half of mid- and hind tibiae of yellow hair. Remaining hair on legs dark. Hair on stem vein mixed pale and dark; on costa,dorsal surface of radius and ventral surface of subcosta and radial sector dark.

Abdomen dull brownish-black, paler ventrally. Tergites one to six each with a dorsal, marginal patch of gold hair which becomes wider and higher on segments five and six to cover most of the tergite; segments seven and eight with smaller lateral patches of gold hair. Remaining dorsal abdominal hair short, brown. Lateral abdominal hair including hair on basal scale in basal fringe whitish, darkened basally.

Genitalia as in Fig. 54. Basistyle disproportionately large, appearing somewhat swollen, strongly tapered; dististyle relatively minute with small rounded end, terminal spine directed anteromedially. Ventral plate a laterally compressed, median keel that is more than twice as long as broad, its basal arms extending almost laterally. Keeled portion covered with hair, in form "A" rounded apically in profile (Fig. 54), more acutely pointed in forms "B", "C" and "D".

Larva. Abdominal pigment greenish-grey overlaid with laterally placed areas of reddish pigment which on some segments may meet in the mid-line. The reddish pigment is usually confined to the anterior half of the segment. Postgenal cleft of moderate size, usually almost square. Median and lateral hypostomial teeth slightly enlarged. Head capsule pale yellowish with dark brown pattern. Antero-lateral head spots placed close to one another. Pigment between antenna and eye not extending to cleavage line. Pigmented area anteroventral to eye, small and obscure (Fig. 77).

The larva of aureum B. is similar, differing as follows: reddish abdominal pigment more orange and more extensive, overlying and contrasting with the darker greenish pigment. Markings on head capsule darker and more extensive. Pigmented area between antenna and eye extending to cleavage line. Pigmented area in front of and below eye larger, more conspicuous. Antenna dark brown. Postgenal cleft usually wider above the middle, often with a slightly V-shaped anterior margin (Fig. 80).

Distribution. The aureum-complex is widespread in the Holarctic region and its distribution has been summarized by Dunbar (1958). It has been recorded from Europe (Edwards, 1920; Petersen, 1924; Grenier, 1953; Novak, 1956; Carlsson, 1962; Rubtzov, 1956) and northern Asia (Rubtzov, 1956), south to the Atlas Mountains of Morocco (Grenier, 1953) and Simla in northern India (Puri, 1933). In North America it occurs from Alaska (Stone, 1952) to Churchill, Man. (Twinn et al, 1948) and Labrador (Hocking and Richards, 1952), south to the mountains of Guatemala (Dalmat, 1955) and South Carolina (Dyar and Shannon, 1927).

Simulium baffinense Twinn

Simulium (Eusimulium) baffinense Twinn, 1936, Canad. J. Res., D, 14: 121-123, Fig. 8A, 1-5 (female, male).

Holotype. Female, Type No. 4126, Canadian National Collection.

Type locality. Lake Harbour, Baffin Island, August 10, 1935 (W.J. Brown).

Female. A small to medium-sized greyish-brown species with thin grey pollen and light yellow hair. Claw without large basal lobe. Sensory vesicle of third segment of maxillary palpus small. Mandibles and galea of maxilla without apical teeth.

Scutum dark brown with thin greyish-brown pollen, sparse recumbent hair, yellow on the disk, paler along the anterior margin. Scutellum with long erect yellow hair. Pleuron greyish-brown with thin grey pollen. Precoxal bridge present. Mesepimeral tuft and hair on pronotum, proepisternum, coxae, trochanters, femora and tibiae with pale hair; tarsi with dark hair. Hair at base of costa and on stem vein pale yellow, on remaining veins dark.

Abdomen greyish-brown, thinly pollinose, subshining, with sparse, scattered, short, yellowish hair slightly longer and denser laterally.

Genitalia as in Fig. 20. Terminal plate with infolded posterior edge and reduced apodeme along anterior edge.

Male. Clypeus brown with thin greyish-brown pollen and reclinate pale and dark hairs. Antenna dark grey with pale pubescence. Scutum dark brown, greyish-brown pollinose in anterior view, with long, dense, recumbent yellowish-white hair, slightly paler along the anterior margin. Scutellum with erect yellow hair. Mesepimeral hair and hair on pronotum, proepisternum and fore coxa yellow. Remaining hair on legs reddish-brown, with a few paler hairs on the anterior surfaces of the femora and tibiae. Hair on wing veins brown; sparse or absent on ventral side of subcosta.

Abdomen, brown with little pollen and sparse, pale hair, with longer hairs laterally on segments one to three that are dark at the base with paler tips.

Genitalia as in Fig. 39. Dististyle moderately curved and evenly tapering. Ventral plate broad, keeled medially, its ventral surface extensively haired. Paramere long and slender, parameral arm forming the base of a finger-like ventrolateral extension from the aedeagus. Dorsal and lateral walls of the aedeagus with numerous small spines.

Larva. Properly preserved mature larvae were unavailable. Partly grown larvae from Big Trout Lake (Patricia Subdist.), Ontario, were greenish-brown without paler intersegmental areas and median stripe. Postgenal cleft small and square. Lateral hypostomial teeth moderately elevated. Antenna dark brown, contrasting with head-fan stalk; Second annulus of basal portion with 6 or 7 subdivisions, separated from one another by transparent, transverse lines. Head capsule moderately sclerotized, the dorsal head pattern not strongly contrasting.

Pupa. Respiratory organ shorter than pupa, consisting of three, stout, inflated filaments; the dorsal filament extends dorsally at right angles to the two horizontal ventral filaments. Each filament with indistinct pseudo-segmentation. Cocoon slipper-shaped with moderately long anterior process which has thickened lateral margins.

Distribution. Holarctic, circumpolar. Sweden (Carlsson, 1962), northern Asia (Rubtzov, 1956) and Alaska (Stone, 1952) east to Frobisher, N.W.T. (Shewell, 1958), south at high elevations to Utah (Peterson, 1959) and in the east to Big Trout Lake, Patricia Subdist., Ontario, and Fort Chimo, Quebec (Shewell, 1958).

Simulium congareenarum (Dyar and Shannon)

Eusimulium congareenarum Dyar and Shannon, 1927, Proc. U.S. Nat. Mus. 69(10): 20, Plate 4, Fig. 45 (female).

Holotype. Female, Cat. No. 28333, U.S. National Museum.

Type locality. Congaree, Richland Co., South Carolina.

Female. A small, grey species with white and gold hair, wide frons and orange-brown legs.

Frons and clypeus grey pollinose, with whitish hair, recumbent on frons, more erect on clypeus. Width of frons about one-fifth the width of head. Antenna dark grey with pale pubescence. Scape and pedicel paler distally. Palpus grey with whitish hair; length of sensory vesicle of third segment about one-fourth the length of the segment.

Scutum grey pollinose, humeri slightly reddish, with recumbent yellow hair which is paler laterally and in the humeral area. Scutellum with long, erect yellow hair. Pleuron and postscutellum grey pollinose. Pleural tuft and hair on pronotum and proepisternum white, erect. Postscutellum and katepisternum bare. Precoxal bridge present. Costa, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair. Stem vein with yellowish hair. Legs paler than thorax especially in teneral specimens. Fore coxa orange-brown with thin greyish pollen, paler than adjacent pleuron. Mid- and hind coxae concolorous with pleuron. Trochanters, basal one-half of femora and basal half of fore- and mid tibiae orange-brown. Hind tibia grey, paler basally. Tarsi dark brown. Hair on legs white basally and brown on tarsi. Calcipala small; pedisulcus shallow. Claw with large thumb-like basal lobe.

Abdominal tergites grey pollinose. Remainder of abdomen grey, paler basally. Hair long, white, dense laterally and dorsally, sparser and shorter ventrally with a few longer, dark hairs on the last two segments.

Genitalia as in Fig. 13. Cleft between arms of genital fork square. Terminal plates triangular with rather straight medial and posterior edges; broadly connected to the tergite; sclerotized along anterior edge with small pointed apodeme.

Male. Clypeus greyish pollinose with reclinate pale hair. Antenna greyish-brown with pale pubescence; scape and pedicel paler.

Hair on scutum dense, entirely yellow becoming paler at the humeral angles. Hair on scutellum, pronotum, proepisternum and pleural tuft pale, whitish to yellowish. Hair on legs pale basally, tarsi and apex of tibiae with dark hair. Hair on basal scale and lateral and sides of abdomen pale, remaining abdominal hair dark.

Genitalia as in Fig. 35. Parameral spines intermediate in length between those of anatinum and innocens.

Larva. Abdominal pigment reddish-brown, conspicuously aggregated medio-laterally to form two dorsal rows of darker, reddish spots on either side of a slender, transparent median line. The spots are present on all body segments but are most prominent on the first thoracic segment and on segments 1-7 of the abdomen. Postgenal cleft small, square. Antenna pale; second annulus of basal portion subdivided into four weakly marked annuli. Lateral hypostomial teeth not strongly elevated. Dorsal head pattern pale, distinct, without surrounding background pigment (Fig. 65).

Pupa. Respiratory organ of 12 long, slender filaments with branching similar to that of anatinum. Cocoon similar to that of innocens and anatinum, with long anterior process.

Distribution. Bruce Co. and Algonquin Park, Ontario, east to Long Island, New York, and south to Florida and Louisiana (Jamnback and Stone, 1957).

Simulium croxtoni Nicholson and Mickel

Simulium croxtoni Nicholson and Mickel, 1950, Tech. Bull. Univ. Minn. agric. Exp. Sta. 192: 41-42, Fig. 20A-B (female, pupa).

Holotype. Female, University of Minnesota.

Type locality. West of International Falls, Koochiching Co., Minnesota, June 2, 1941 (reared).

Female. A moderate to large grey pollinose species with white hair and a small patch of hair on the katepisternum.

Posterior surface of head, frons and clypeus grey pollinose with white hair recumbent on frons and clypeus. Antenna dark grey with pale pubescence. Palpus greyish-brown, third segment enlarged with appressed white hair, remaining segments brownish with dark appressed hair. Sensory vesicle of third segment about one-half the length of the segment.

Scutum grey pollinose densely clothed with recumbent white hair which may have a yellowish tinge on the disk in some specimens. Scutellum with long, erect white hair mixed with a few dark hairs. Pleuron and postscutellum grey pollinose. Postscutellum bare. Katepisternum with a small patch of appressed white hairs along its dorsal edge. In a few specimens, only one or two hairs may be present. Pleural tuft and hair on pronotum and proepisternum white, somewhat recumbent. Basisternum connected to proepisternum by a precoxal bridge. Costa, stem vein, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair, sometimes basal area of costa with a few whitish hairs. Legs greyish-brown, paler than thorax; tibiae darker; coxae to tibiae with recumbent white hair; tarsi with short recumbent dark hair. Calcipala and pedisulcus present. Claw with large basal lobe.

Abdomen grey, paler ventrally, covered dorsally and laterally with moderately dense, long, white hair; segments 6-9 also with longer, darker hair.

Genitalia as in Fig. 28. Arms of genital fork with a small amount of infilling, sclerotized antero-dorsal edge of anal lobe with a row of 7-10 setae; setae lacking on ventral membranous area.

Male. General body colour blackish-brown with gold hair on the scutum.

Scutum dull black, grey pollinose on margins; hair on central portion short, recumbent, golden; hair along lateral margins paler and slightly longer, anterior margin and humeri with still paler yellow hair.

Pronotum, proepisternum and fore coxa with almost white hair. Pleuron pale grey pollinose. Pleural tuft with mixed pale and dark hair. Katepisternum bare. Legs brown; hair mostly brown, mixed with pale yellow hair on front femur and tibia and on anteroventral surfaces near the junctions of mid- and hind femora and tibiae.

Abdominal tergites greyish-brown pollinose in lateral view, becoming dull brown in posterior view except on the second tergite which remains pollinose.

Genitalia as in Fig. 51. Dististyle rather long. Body of ventral plate narrowing posteriorly, the small, central, hirsute lip projecting as a small tubercle beyond the distal margin.

Larva. Similar to latipes from which it can usually be distinguished by the browner abdominal pigment which shows a stronger tendency to form discrete transverse bands, by the narrower and longer postgenal cleft, and by the head pattern in which the background pigment extends anteriorly to form a usually distinct median stripe.

Pupa. Respiratory organ shorter than pupa, consisting of eight moderately stout, divergent filaments arranged in three groups. The dorsal group, consisting of two long filaments, is short petiolate, the dorsal filament diverges dorsally almost at right angles, then curves forward. A lateral group of three shorter almost sessile filaments and a ventral longer petiolate group of three make up the remainder. Cocoon slipper-shaped with short, broad anterior process and heavily thickened anterior margin; loosely and coarsely woven, particularly along the sides.

Distribution. Patricia Subdist., Ontario and Goose Bay, Nfld. (Hocking & Richards, 1952) south to Minnesota (type material), Wisconsin (Anderson & Dicke, 1960), southern Ontario, Quebec (C.N.C.) and New York (Stone & Jamnback, 1955).

Simulium emarginatum, new species

Female. A small, grey pollinose species, with almost entirely whitish hair.

Posterior surface of head, frons and clypeus grey pollinose. Hair on frons sparse, restricted to the dorsal one-half. Clypeus with sparse, recumbent hair. Antenna dark, relatively long, with pale pubescence. Third segment of maxillary palpus darker than remaining segments; sensory vesicle about one-half the length of the segment.

Scutum grey pollinose, slightly paler at the margins; sparsely covered with short, recumbent, white hair with a yellowish tinge. Scutellum with erect, white and brown hair. Postscutellum and pleuron grey pollinose, pleural membrane lighter. Postscutellum and katepisternum bare. Mesepimeral tuft, and hair on the pronotum and proepisternum whitish. Precoxal bridge incomplete, with a small gap near proepisternum (some older individuals may show a tenuously complete bridge on one or, rarely, both sides). Legs brown, slightly darker distally; basal portion of leg with white hair, that on the basitarsus interspersed with some dark hair, remainder of the tarsus with nearly all brown hair. Claw with a large, basal lobe. Hair on stem vein black, sometimes mixed with white; hair on base of costa white, remainder of costa, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair. Abdominal tergites greyish-brown, lightly pollinose; tergites rather sparsely covered with recumbent, white hair that is mixed with darker, longer hair on the last two tergites. Pleural membranes pale grey except for a darker spot at the base of each segment laterally (often obscured in the intersegmental folds), this spot is absent on segment one, smallest on segment two, but higher and extending to the tergite on the third and fourth segments, and is more obscure on distal segments. Lateral margins of segments 2-7 each with a patch of rather long, dense, white hair which is separated from the sparser hair of tergites 2-4 by a bare, or nearly bare, membranous area, but is continuous with the sparsely haired regions of the remaining tergites. Venter of abdomen pale grey, each segment with a row of widely scattered, small, white hairs.

Genitalia as in Fig. 19. Terminal plate of genital fork densely sclerotized, the posteromedial areas dark brown, the anteromedial angles, or tubercles, well-developed. Anal lobes with mixed white and dark hair; the membranous, ventral nipple located near the posterior margin.

Male. General body colour blackish-brown with greyish-brown pollinosity and brown hair.

Posterior surface of head and clypeus dark brown, with greyish-brown pollinosity and brown hair. Antenna dark, with pale pubescence on the flagellum; scape and pedicel with dark hair. Palpus greyish pollinose, third segment darker; segments with brown hair, a few paler hairs present on last two segments; sensory vesicle of third segment small, about one-fourth the length of the segment.

Scutum dull blackish-brown, margins faintly greyish-brown pollinose; with recumbent, shining brown hair. Humerus slightly lighter than scutum. Pleuron pale greyish-brown pollinose, paler and more shining than scutum; mesepimeral tuft brown. Katepisternum bare. Legs brown; hair brown, rather long and dense, especially along dorsal edge of femur.

Abdominal tergites greyish-brown pollinose in lateral view, duller and darker in posterior view; hair brown, long on basal scale, shorter and more erect on tergites 2-6, and recumbent on remaining tergites. Pleural membranes and sternites paler, grey pollinose, the latter with sparse, short, erect, brown hair.

Genitalia as in Fig. 42. Basistyle brown. Dististyle darker brown, with black hair, moderately curved, uniformly tapering and terminating in a small spine. Body of ventral plate thin and flat, unusually wide and with a broadly concave, distal margin and a subparallel, convex, proximal margin; most of central portion ventrally covered with pale, recumbent hair; basal arms short, slightly convergent. Paramere rectangular, about twice as long as broad, with an antero-ventrally directed spine at the junction of parameral arm; parameral arm lightly sclerotized at junction with paramere, forming the dorsal wall of a finger-like projection from the ventrolateral wall of the aedeagus. Dorsal wall of aedeagus with two lateral patches of anteriorly-directed, long spines.

Larva. Like a small, pale specimen of euryadminiculum, differing as follows: abdominal pigment paler and less extensive, median transparent line wider, not interrupted on segment 5. Head capsule paler, almost colourless; head spots pale but discrete with at most a suggestion of background pigment around and between them (Fig. 72).

Pupa. Respiratory organs about 2.5 mm. long, shorter than pupa; composed of four filaments in two petiolate pairs, the ventral petiole slightly longer and narrower than the dorsal petiole; filaments moderately divergent in a dorso-ventral plane; the integument greyish-white, paler basally, rather smooth and shining.

Holotype. Female, reared from a pupa collected May 5, 1959, from Sharpes Creek (also called Sparks Creek), where it crosses Highway No. 17, about one-half mile west of Rutherglen, Bonfield Twp., Nipissing District, Ontario, D.M. Davies and D.M. Wood.

Allotype. Male, same data as holotype.

Paratypes. Fifteen males and 45 females, same data as holotype. Types (No. 7994) and paratypes deposited in the Canadian National Collection. Paratypes deposited in the U.S. National Museum, McMaster University, and British Museum.

Distribution. Wisconsin (U.S. National Museum), east to Nipissing Dist., Wellington Co. and Wentworth Co., Ontario and Perkins, Quebec.

Simulium euryadminiculum Davies

Simulium euryadminiculum Davies, 1949, Canad. Ent. 81: 45-49, Figs. 1-3, 4A-B, 5A-C, 6 (female, male, pupa).

Holotype. Male, Type No. 5867, Canadian National Collection.

Type locality. Costello Creek, Algonquin Park, Ontario; May 20, 1940 (F.P. Ide).

Female. A medium-sized grey pollinose species with entirely white hair.

Scutum grey pollinose with short recumbent white hair that does not have a yellowish tinge. Hair on stem vein usually white, sometimes mixed with a few black hairs.

Genitalia as in Fig. 18. Terminal plate of genital fork membranous with contrasting more heavily sclerotized anterior edge and apodeme. Otherwise as in emarginatum.

Male. Hair on scutum somewhat variable in colour, sparse, dull yellowish-white to brown. Hair on pronotum and proepisternum whitish to brown, and on femora and tibiae brown, sometimes with whitish patches. Remaining hair on head, abdomen and wings brown. Mesepimeral tuft brown.

Genitalia as in Fig. 41. Dististyle bent slightly dorsomedially at mid-point. Ventral plate broad and flat with scarcely differentiated lip, nearly straight posterior border and convex anterior border. Paramere subquadrate, with strong apical spine directed ventro-laterally. Parameral arm forming the dorsal wall of a finger-like projection from the ventro-lateral wall of the aedeagus. Dorsal wall of aedeagus with two lateral patches of anteriorly-directed spines.

Larva. Abdominal pigment dark, purplish-brown forming distinct transverse bands contrasting strongly with transparent, intersegmental areas and narrow median line. Postgenal cleft of moderate size, square, usually with a broadly V-shaped anterior border. Hypostomial teeth relatively small, not strongly differentiated from one another; lateral teeth scarcely elevated. Antenna almost colourless; second annulus of basal portion of antenna with four indistinct secondary annuli. Head spots dark; entire area between and around dorsal head spots usually darkly pigmented (Fig. 69). Head widest behind the eyes, narrowing slightly basally.

Pupa. Larger than that of emarginatum, otherwise indistinguishable from it.

Distribution. Baker Lake, N.W.T. (C.N.C.); Port Harrison, Quebec (C.N.C.) and Goose Bay, Nfld. (C.N.C.); south to Prince Albert, Sask. (C.N.C.); Nipissing Dist. and Carleton Co., Ontario and Baie Comeau, Quebec (Wolfe & Peterson, 1959; C.N.C.).

Simulium excisum, new species

Simulium (Eusimulium) subexcisum, Twinn, 1936, Canad. J. Res., D, 14:118-120 (nec Edwards).

Eusimulium subexcisum, Twinn, et al., 1948, Canad. J. Res., D. 26:349.

Simulium subexcisum, Hocking and Pickering, 1954, Canad. J. Zool., 32:101.

Simulium sp. near subexcisum Edw., Wolfe & Peterson, 1959, Canad. J. Zool., 37:144.

Female. A small, grey to greyish-brown species, with whitish hair.

Posterior surface of head, frons and clypeus grey pollinose, with whitish hair, that on frons and clypeus recumbent. Antenna dark grey, with pale pubescence; scape and pedicel with pale hair. Palpus greyish-brown; length of sensory vesicle of third segment about one-fourth the length of the segment.

Scutum grey pollinose, paler on the humeri, with recumbent, white hair. Scutellum with long, erect, white hair mixed with a few darker hairs. Pleuron and postscutellum grey pollinose, concolorous with scutum. Mesepimeral tuft and hair on pronotum and proepisternum white, erect. Precoxal bridge present. Postscutellum and katepisternum bare. Costa, stem vein, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair. Legs brown, paler than thorax (especially in teneral specimens), with white hair basally, and brown hair on the apex of the tibiae and tarsi. Calcipala minute, pedisulcus shallow. Claw with large basal lobe (Fig. 7a).

Abdomen with relatively dense, long, white hair (especially long on basal fringe) covering top and sides, and sparser and shorter ventrally. Last two segments with a few dark hairs in addition to the white hair. Ground colour of tergites grey, paler on pleura and even paler on venter.

Genitalia as in Fig. 16. Arms of genital fork slender; terminal plates triangular. Their posterior edges turned dorsally, thus appearing sclerotized.

Male. General body colour blackish-brown to greyish-brown pollinose, with brown hair.

Posterior surface of head, and clypeus dark brown with scant, greyish pollinosity and brown hair. Antenna uniformly dark; flagellum with recumbent, whitish pubescence; scape and pedicel with dark hair. Palpus greyish-brown pollinose, paler on fourth and fifth segments, with brown hair; sensory vesicle of third segment small, its length about one-fifth the length of the segment.

Thorax uniformly greyish-brown pollinose. Hair on pronotum and proepisternum brown. Scutum greyish-brown pollinose with a slight bluish cast, which is usually visible on the central portion even in direct view; with a wide, paler marginal band. Hair brown, short, recumbent and rather sparse. Scutellum dark, with long, erect, brown hair. Postscutellum bare, greyish-brown pollinose, subshining. Pleuron slightly paler than scutum; mesepimeral tuft brown. Katepisternum bare. Legs uniformly brown concolorous with thorax (paler in teneral specimens); hair brown, with a few paler ones. Calcipala small; pedisulcus shallow.

Abdominal tergites greyish-brown pollinose with a bluish cast in lateral view, dull dark brown in posterior view; hair brown, dense and long, shorter and sparser on the last three segments. Pleural membranes and sternites paler, grey pollinose, the latter with sparse, moderately long, erect, dark hair.

Genitalia as in Fig. 36. Basistyle and dististyle greyish-brown pollinose, with dark hair. Dististyle moderately curved, uniformly tapering, with a small, apical spine. Body of ventral plate triangular, covered with pale, recumbent hair; ventrally recurved lip relatively weak; basal arms rather short, slightly curved inwardly. Paramere broadest at base, tapering distally to the slender parameral arm, which bears 5-6 relatively small and weakly sclerotized teeth. Median sclerite weak, broadest at the base, with a small, forked tip. Dorsal sclerite short, wide, strap-like.

Larva. Abdominal pigment in narrow, reddish-brown, transverse bands, with wide, transparent, intersegmental areas, almost as wide, between segments 1-5, as the bands of pigment. A median, transparent stripe on segments 5-7. Postgenal cleft square, slightly larger than that of *rivuli*. Lateral hypostomial teeth not strongly elevated. Antenna almost transparent, the second annulus of basal portion not subdivided. Dorsal head pattern paler than that of *rivuli*; second antero-lateral head spot slightly displaced laterally relative to first antero-lateral spot (Fig. 68).

Pupa. Respiratory organ about 3.0 mm. long, slightly longer than pupa; consisting of six slender filaments in three pairs; petiole of dorsal pair directed dorsally at right angles to the other two pairs, its point of attachment constricted and flexible; petioles of remaining filaments diverging in a horizontal plane. Cocoon slipper-shaped, with a long anterior process that has thickened margins and a more transparent, central strip.

Holotype. Female, reared from a pupa collected May 5, 1961, from a roadside ditch one and one-half miles west of Stanley Corners (C.P.H.#1 of Twinn, 1936), Goulbourn Twp., Carleton Co., Ontario, D.M. Wood and E. Bond.

Allotype. Male, same data as holotype.

Paratypes. Twenty-five males and 40 females, same data as holotype. Types (No. 7993) and paratypes deposited in the Canadian National Collection. Paratypes deposited in the U.S. National Museum, British Museum and McMaster University.

Distribution. Churchill, Manitoba (Twinn, *et al*, 1948; C.N.C.) and Baie Comeau, Quebec (Wolfe and Peterson, 1959; C.N.C.) south to Michigan (C.N.C.), Wentworth Co. and Carleton Co., Ontario.

Simulium furculatum (Shewell)

Eusimulium furculatum Shewell, 1952 Canad. Ent. 84: 40-42, Fig. 4A-G (female, male, pupa).

Holotype. Male, Type No. 5990, Canadian National Collection.

Type locality. Goose River, Churchill, Manitoba; July 9, 1947 (reared) (C.R. Twinn).

Female. A medium to large grey species with white to yellowish hair. Claw lacking the large basal lobe.

Posterior surface of head, frons and clypeus grey pollinose with sparse whitish hair recumbent on the frons and clypeus. Antenna dark grey with pale pubescence. Palpus grey with mixed pale and dark hairs; third segment darker; sensory vesicle of third segment over one-half the length of the segment.

Scutum grey pollinose somewhat paler and reddish on the humeri, with rather sparse whitish to yellowish recumbent hair. Scutellum with long somewhat recumbent yellowish hair, sometimes mixed with black hair. Pleuron and postscutellum greyish-brown pollinose. Mesepimeral tuft yellowish. Hair on pronotum and proepisternum white, erect. Precoxal bridge present. Postscutellum and katepisternum bare. Stem vein and base of costa and radius with pale yellowish hair; remainder of costa, radius and ventral surface of subcosta and radial sector with dark hair. Legs greyish-brown, fore coxa scarcely paler than thorax. Hair whitish basally, somewhat denser on tibiae, brown on the tarsi. Calcipala and pedisulcus well-developed. Claw with minute basal lobe..

Abdomen grey, darker dorsally. Hair white, rather sparse. Terminal segments with a few darker hairs.

Genitalia as in Fig. 21. Terminal plates narrowly connected to the tergites, with prominent rounded postero-medial lobes.

Male. Clypeus dark grey with sparse pollen and reclinate long, dark hair. Antenna dark grey with pale pubescence. Scutum black with sparse grey pollen, hair recumbent, gold, paler along anterior edge. Scutellum with erect, yellow and brown hair. Pleuron dark greyish-brown. Hair on pronotum, proepisternum, front and mid-coxae pale yellowish-white. Hair on anterior surfaces of femora yellowish, darker dorsally; silvery-white on basal two-thirds of fore tibia, basal one-half of mid tibia and basal one-third of hind tibia; central area of hind tibia with some yellowish hair; apex of all three tibiae and tarsi with dark hair. Mesepimeral tuft, abdomen and wing veins with dark hair.

Genitalia as in Fig. 45. Dististyle with a flattened flange-like, dorso-lateral lobe. Ventral plate broad, moderately keeled ventrally, with a triangular patch (broadest apically) of sparse hair. Paramere broad and square, the apex strongly curved ventrally and the apical spine recurved dorsally. Parameral arm with a series of two to three smaller spines lying parallel to the apical spines and decreasing in size medially; the first about 2/3 the length of the apical spine. Median sclerite forked to or beyond its midpoint.

Larva. Abdominal pigment dark greenish-brown; transverse bands extensive, leaving only narrow transparent intersegmental areas; each segment with two laterally placed reddish-brown areas on the anterior half of each segment,whichtend to fuse in the mid line. Ventral tubercles small, poorly developed. Postgenal cleft strongly widened in the middle, tapering to an acute point. Antenna almost colourless and relatively short, scarcely extending beyond the stalk of the head fan. Head capsule pale, almost colourless with strongly contrasting dark brown head pattern. Stripe above eye narrow and indistinct, anterior tentorial pit small, dark and discrete (Fig. 79).

Pupa. Respiratory organ about 2/3 of the length of the pupa, consisting of eight moderately stout, divergent, filaments, in three groups, a dorsal group of two with a very short petiole, a lateral group of three, the basal branch close to the base, and a ventral petiolate group of three. Cocoon slipper-shaped, with reinforced anterior margin and a slight dorsal projection.

Distribution. Alaska (Stone, 1952) east to Baker Lake, N.W.T. (Shewell, 1952) and Goose Bay, Nfld. (Shewell, 1952) south to Big Trout Lake, and Hastings Co., Ontario and Baie Comeau, Quebec (Wolfe and Peterson, 1959). (Crow R. ONT. before Hydro-dam built, pre. 1980) (cf. Ref. bottom p. 128)

Simulium gouldingi Stone

Simulium (*Eusimulium*) *gouldingi* Stone, 1952, Proc. ent. Soc. Wash. 54: 90-91 (female, male, pupa).

Holotype. Female, Cat. No. 61192 (U.S. National Museum).

Type locality. Route 115, 14.5 miles west of Wilkes Barre, Pennsylvania; June 5, 1948 (reared) (A. Stone).

Female. A small greyish-brown species with whitish hair tending to yellowish on the disk of the scutum and on the legs and abdomen.

Posterior surface of head, frons and clypeus, greyish-brown pollinose with whitish, recumbent hair. Antenna dark greyish-brown with pale pubescence. Palpus brown with brown hair; third segment only moderately enlarged; length of sensory vesicle of third segment about one-third or less the length of the segment.

Scutum greyish-brown pollinose, with dense recumbent hair; yellowish on the disk fading to white at the lateral and anterior margins and on the humeri. Scutellum with mixed yellowish and black erect hairs. Postscutellum and pleuron greyish-brown pollinose. Mesepimeral tuft and hair on pronotum and proepisternum white. Precoxal bridge present. Postscutellum bare. Katepisternum with a patch of white, recumbent hair usually covering its upper half. Hair at base of costa yellowish; on remainder of costa, stem vein, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair. Legs brown with pale yellow hair basally, and brown hair on the tarsi and the apex of the tibiae. Calcipala and pedisulcus well-developed. Claw with large basal lobe.

Abdomen brown, paler ventrally; tergites with thin greyish-brown pollen. Hair yellowish, moderately dense laterally, shorter and sparser dorsally and ventrally, mixed with brown hairs on segments 4-8.

Genitalia as in Fig. 29. Cleft between arms of genital fork shallow; postero-medial angles of terminal plates weakly developed. Terminal plates narrowly connected to the tergites; bearing a small seta mesad to the point of attachment. Sclerotized anterior margin of anal lobe bearing a row of setae. Setae absent from membranous area.

Male. Clypeus with mixed yellow and brown hair. Scutum with recumbent gold hair slightly paler along anterior margin. Hair on pronotum, proepisternum, fore and mid coxa paler, yellowish, on fore femur and basal half of tibia yellow, mid and hind femora with mixed yellow and dark hair, the remainder of tibiae and tarsi with dark hair. Mesepimeral tuft yellow with a few dark hairs. Upper half of katepisternum with yellow, recumbent hair. Abdomen with dark hair.

Genitalia as in Fig. 52. Ventral plate relatively narrow, tapering evenly to the moderately recurved lip. Serrations on either side of terminal patch of hair relatively large.

Larva. Thoracic and abdominal pigment yellowish-brown almost completely distributed over the dorsal surface of the larva. Postgenal cleft relatively high, rounded apically, only slightly enlarged in the middle. Head capsule pale yellowish-brown. Distal portion of antenna approximately equal in length to each of the two annuli in basal portion. Head pattern pale, indistinct. Areas between antennae and eyes lateral to the cleavage lines darker contrasting with the central area. Pigmented area antero-ventral to eye absent. Median and lateral hypostomial teeth moderately enlarged (Fig. 71).

Pupa. Respiratory organ of six filaments about as long as the pupa, arranged in three groups of two filaments each. The dorsal pair, short petiolate and not strongly divergent from the lateral and ventral pair, each of which has a slightly longer petiole. Cocoon as in *croxtoni*, loosely and coarsely woven, slipper-shaped, with short, broad anterior process, that is often irregularly thickened.

Distribution. Alaska (Stone, 1952; Sommerman, 1953: the illustrations and key given by the latter author suggest that a different species may be involved); Wisconsin (Anderson & Dicke, 1960) east to Nipissing Dist., Ontario and New York State (Stone, 1952) south to Highlands, North Carolina (C.N.C.).

Simulium impar, new species

Female. A minute, grey to greyish-brown species, with whitish hair.

Posterior surface of head, clypeus and frons grey pollinose. Hair on frons and ventral portion of clypeus whitish, recumbent. Flagellum of antenna dark greyish-brown; scape and pedicel pale yellowish-brown; segments all with whitish pubescence. Palpus dark grey pollinose, third segment almost black, hair brown; length of sensory vesicle of third segment about one-half the length of the segment.

Scutum grey pollinose with recumbent, white hair with a yellowish tinge. Humeri yellowish-brown, with a central spot of grey pollen and whitish hair. Scutellum with long, erect, brown and white hair mixed. Pleuron and scutellum brown to yellowish-brown, lightly brown pollinose. Mesepimeral tuft and hair on pronotum and proepisternum concolorous with that of scutum. Scutellum and katepisternum bare. Precoxal bridge present. Hair of costa brown except for a few longer, paler ones basal to the humeral cross-vein; hair of stem vein, dorsal surface of radius and ventral surfaces of subcosta and radial sector brown. Legs paler than thorax (all the available specimens appear teneral and the integument probably darkens with age) except for the coxae, distal ends of femora and tibiae, and all of the tarsi which are grey. Hair on legs whitish except mixed brown and white on the basitarsi and brown on the tarsal segments. Calcipala and pedisulcus well-developed. Claw with a large, basal lobe.

Abdominal tergites pale greyish-brown, slightly darker than the remainder of abdomen. Basal fringe white, relatively short. Hair on remainder of abdomen short, mostly brown and scattered, leaving most of the integument exposed.

Genitalia as in Fig. 23. Arms of genital fork narrow at point of bifurcation, with little infilling; arms long, the terminal plates rather widely separated. Antero-medial corners of anal lobes concave when viewed ventrally, the median margins in this region relatively well-defined.

Male. General body colour brown to pale greyish-brown pollinose, with pale gold hair on scutum. Posterior surface of head and clypeus grey-brown pollinose with mixed dark and pale hairs. Antenna greyish-brown with pale pubescence. Palpus uniformly pale greyish-brown pollinose, with light and dark hair; sensory vesicle of third segment minute, about one-sixth the length of the segment.

Thorax dull brown on scutum, pollinose on margins. Pleuron, scutellum and postscutellum pale greyish-brown pollinose. Hair of scutum pale gold, short and recumbent; hair on pronotum and proepisternum longer, golden in colour. Mesepimeral tuft pale. Postscutellum and katepisternum bare. Legs rather pale (all available specimens appear teneral); coxae of all legs with mixed pale and dark hair anteriorly, and darker hair laterally; hair on remainder of legs brown with interspersed paler ones. Calcipala and pedisulcus well-developed.

Abdominal tergites dull brown, somewhat greyish pollinose in lateral view, second tergite more pollinose than others; hair brown, erect, with a few recumbent, paler hairs distally. Pleural membranes and sternites paler, greyish-brown pollinose. Hair on sternites brown, erect and sparse.

Genitalia as in Fig. 46. Basistyle and dististyle brown, with dark hair. Dististyle enlarged apically, with a flattened, triangular, medially directed flange bearing a small spine at its apex. Body of ventral plate broadly V-shaped in terminal view, the lip moderately prominent; basal arms curved medially. Paramere broad basally, narrowing distally and bearing a long, dorsally recurved spine at its distal end. Median sclerite forked distally to one-half its length. Dorsal sclerite about as broad at base as long, tapering distally to a blunt point.

Larva. Thoracic and abdominal pigment bright orange-brown, almost continuously distributed over the larva dorsally, leaving small transparent intersegmental areas ventrally. Postgenal cleft rather small, rounded apically, only slightly widened in the middle. Median hypostomial tooth enlarged. Head capsule yellowish-brown; dorsal head pattern, especially anterior median and lateral spots discrete with distinct margins and without surrounding pigment. Pigmented area antero-ventral to eye absent.(Fig. 74).

Pupa. Respiratory organ about 2.0 mm. long, nearly as long as pupa, consisting of four filaments in two petiolate pairs; petiole of ventral pair narrower and five or more times as long as the short petiole of the dorsal pair. Filaments moderately divergent in vertical plane; integument pale grey, rugose, subshining. Cocoon slipper-shaped, with thickened anterior margin.

Holotype. Female, reared from a pupa collected June 25, 1959, from a small stream crossing the Laurentian Point Road and flowing into the Ottawa River about three miles west of Point Alexander, Rolph Twp., Renfrew Co., Ontario, D.M. Davies and D.M. Wood.

Allotype. Male, same data as holotype.

Paratypes. Fifteen males and 35 females, same data as holotype. Types (No. 8012) and paratypes deposited in the Canadian National Collection. Paratypes deposited in the U.S. National Museum, British Museum and McMaster University.

Distribution. Renfrew Co., Ontario and Franklin Co., Maine (U.S.N.M.) - the two female specimens examined were identical to the type material except for the pupal respiratory filaments in which the petiole of the ventral pair was only three times as long as the dorsal pair.

Simulium innocens (Shewell)

Eusimulium innocens Shewell, 1952, Canad. Ent. 84: 38-39, Fig. 3A-G (female, male, pupa).

Holotype. Female, Type No. 5989, Canadian National Collection.

Type locality. Bell's Corners, Ontario. Pupa collected June 2; adult emerged June 6, 1950 (G.E. Shewell).

Female. A small grey species with whitish hair, and narrow frons. Head, pale grey pollinose with sparse whitish hair on frons and clypeus. Width of frons, one-tenth or less the width of head. Antenna dark grey with pale pubescence. Palpus grey with pale hair; length of sensory vesicle of third segment, about one-fourth the length of the segment.

Scutum grey pollinose with recumbent whitish hair, sometimes with a yellowish tinge on the disk. Pleuron grey pollinose. Scutellum and katepisternum bare. Mesepimeral tuft, and hair on pronotum and proepisternum white. Precoxal bridge present. Legs greyish brown, paler than the thorax (in teneral specimens) with whitish hair basally and shorter dark hair on the tarsi. Costa, stem vein, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair; costa sometimes with a few white hairs basally.

Abdomen with long dense, white hair on the top and sides, sparser and shorter ventrally. Last two segments with a few longer, dark hairs. Tergites grey with thin grey pollen.

Genitalia as in Fig. 14. Terminal plates of genital fork broadly connected to tergites; the anteriorly directed apodeme small and truncate.

Male. Externally indistinguishable from anatinum. Scutum dark brownish-black with sparse pollinosity; hair recumbent, brown on the central area usually changing to pale yellowish on the humeri. The extent of the pale humeral hair is rather variable.

Genitalia as in Fig. 37. Length of parameral spines about two-thirds the distance between tip of basal arm of ventral plate and its attachment to the paramere. Otherwise as in anatinum.

Larva. Abdominal pigment of segments 1 to 4 greenish-brown, changing to reddish on the remainder of abdomen. Pigment of segments 1 to 7 somewhat denser along either side of a transparent median line, thus forming two longitudinal rows of weakly differentiated spots. Postgenal cleft small, usually strongly Y-shaped (i.e. with U or V-shaped anterior border). Antenna pale; second annulus of basal portion with four (rarely five) secondary annuli. Head pattern as in anatinum except that the second postero-lateral spots usually are not discrete, being enclosed in a darkly pigmented region (Fig. 63).

Pupa. Respiratory organ about as long as the pupa, consisting of three groups of slender filaments; the petiole of the dorsal group directed at right angles to the two horizontally directed petioles of the ventral groups. The dorsal group consists of four filaments branched dichotomously twice; each ventral group contains three filaments. Cocoon slipper-shaped, with long anterior process thickened along lateral margins; in some specimens there is a suggestion of a slight thickening along the mid-line of the dorsal projection, continuing back on the dorsal portion of the cocoon. Ventral corners of anterior opening strongly produced forward, extending almost as far as the anterior dorsal projection.

Distribution. Bruce Co. (C.N.C.) east to Nipissing Dist. and Renfrew Co. south to Frontenac Co. and Carleton Co. (type material), Ontario.

Simulium latipes (Meigen)

Atractocera latipes Meigen, 1804, Klassif, Beschr. Europäischen Zweiflüg. Insekten 1: 96 (male).

Holotype. Male (location not known to the author).

Type locality. Not known to the author.

Female. A medium-sized greyish-brown species with gold hair on the central area of the scutum, usually surrounded with whitish hair on the anterior and lateral margins.

Frons and clypeus greyish-brown pollinose with yellowish recumbent hair. Antenna dark grey with pale pubescence. Palpus grey, the third segment slightly darker; sensory vesicle of third segment over one-half the length of the segment.

Scutum grey pollinose, brownish on the humeri, with short, dense, recumbent hair, gold centrally, usually with whitish hair on the anterior and lateral margins. Scutellum with erect yellowish hair. Postscutellum usually bare, rarely with two small patches of gold hair. Pleuron greyish-brown, subshining, with thin grey pollen. Katepisternum bare. Mesepimeral tuft and hair on pronotum pale yellowish. Hair on proepisternum whitish. Precoxal bridge present. Base of costa with a few yellowish hairs, remainder of costa, stem vein, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair. Legs brown. Hair on coxae, trochanters and femora yellow, on tibiae usually whitish, brown on tarsi. Calcipala and pedisulcus well-developed. Claw with large basal lobe.

Abdomen greyish-brown. Tergites subshining with little pollen. Dorsal and lateral surfaces with short, sparse yellowish hairs mixed with longer brown hair. Basal fringe of long yellowish hair.

Genitalia as in Fig. 25. Cleft between arms of genital fork shallow and broad; terminal plates reduced, with long, low apodeme and narrow connection to the tergite.

<u>Male</u>. Clypeus grey pollinose with reclinate, long brown hair. Antenna greyish-brown with pale pubescence.

Scutum dull brown, slightly pollinose at the margins, with recumbent gold hair, sometimes brownish antero-medially. Remainder of thorax greyish-brown pollinose. Hair on pronotum, proepisternum and fore coxa yellow. Hair on remainder of legs, mesepimeral tuft and abdominal hair brown.

Genitalia as in Fig. 50. Diststyle relatively short and broad with rounded apex and median triangular keel. Ventral plate broad and flattened, truncate or slightly rounded apically; the lip broad and shallow; the apical patch of hair relatively broad. Paramere somewhat triangular, broadest basally, the narrowed apex directed postero-ventrally with a long apical spine directed antero-dorsally.

Larva. Thoracic and abdominal pigment greenish-brown covering the entire dorsal surface of the larva, not organized into transverse bands. Postgenal cleft widest at the middle, usually rounded anteriorly, extending only one-third of the distance from posterior tentorial pit to the hypostomial teeth. Median hypostomial tooth moderately enlarged. Second annulus of basal portion of antenna without subdivisions. Head capsule yellowish-brown, darker laterad of the cephalic apotome; head pattern pale to dark, usually not sharply defined and usually enclosed within a lightly pigmented area. Antero-lateral spots placed somewhat more anteriorly than in other members of the latipes-group. Pigment area antero-ventral to eye large (Fig. 75).

Pupa. Respiratory organ slightly longer than pupa, consisting of four slender filaments in two short-petiolate pairs. The filaments are slightly to moderately divergent in the vertical plane. Cocoon slipper-shaped with long anterior process which is entirely thickened; the thickening continues along the anterior margin of the remainder of the cocoon.

Distribution. Holarctic; Europe (Edwards, 1915; Grenier, 1953; Usova, 1961; Carlsson, 1962), Asia (Rubtzov, 1956) and Alaska (Stone, 1952) east to Chesterfield, N.W.T. (C.N.C.), Fort Chimo, Que. (C.N.C.) and Gander, Nfld. (C.N.C.) south to California (Stone & Jamnback, 1955) and Utah (Peterson, 1959) east to Connecticut (Stone & Jamnback, 1955).

Simulium quebecense Twinn

Simulium (Eusimulium) quebecense Twinn, 1936, Canad. J. Res., D, 14: 117-118, Fig. 6B, 1-5 (female, male, pupa).

Holotype. Female, Type No. 4124, Canadian National Collection.

Type locality. Blanche River, about five miles south of Perkins Mills, Quebec. Pupa collected May 22; adult emerged May 26, 1935 (C.R. Twinn).

Female. A small greyish-brown species with whitish hair; externally indistinguishable from impar, except for its slightly larger size and differences in the genital fork.

Genitalia as in Fig. 27. Arms of genital fork with moderate infilling; cleft rounded and shallow. Terminal plate of genital fork expanded dorsal-ventrally at point of attachment to the ninth tergite forming a strongly sclerotized, paddle-shaped structure.

Male. Similar in size and colour to male of impar from which it differs in the following respects. Hair on clypeus mostly or entirely dark. Hair on scutum more yellowish. Mesepimeral tuft usually dark. Genitalia as in Fig. 48. Lip of ventral plate greatly enlarged with thickened rim, deeper than wide. Basal arm of ventral plate not strongly bowed inwardly.

Larva. Abdominal pigment predominently greenish on thorax and first two abdominal segments, becoming mixed with reddish pigment on third and fourth abdominal segments; predominently reddish-brown on remainder of abdomen. Pigment on first abdominal segment conspicuously darker than that on adjoining segments, thus forming two dorsal and two ventral contrasting greenish-brown spots. Remaining abdominal pigment aggregated into discrete areas forming a blotchy pattern, contrasting strongly with the remaining transparent membrane. Postgenal cleft relatively long, rounded anteriorly. Hypostomial teeth not strongly differentiated from one another. Anterior half of head capsule almost colourless, usually contrasting strongly with the darker basal portion and head pattern (Fig. 70).

Pupa. Respiratory organ a little longer than pupa, consisting of four slender filaments in two short-petiolate pairs, moderately divergent in the vertical plane. Tubercles on dorsum of head and thorax small, not strongly grouped. Cocoon slipper-shaped, with reinforced anterior margin, but without anterior median process.

Distribution. Wisconsin (J.R. Anderson, possibly these were the same specimens reported as *pugetense*, Anderson & Dicke, 1960) east to Thunder Bay Dist. and Nipissing Dist., Ontario and Perkins, Que. (type material) south to Virginia (U.S.N.M.).

Simulium pugetense (Dyar and Shannon)

Eusimulium pugetense Dyar and Shannon, 1927, Proc. U.S. Nat. Mus. 69(10): 23, Plate 7, Figs. 121-123 (male).

Holotype. Male, Cat. No. 28338, U.S. National Museum.

Type locality. Seattle, Washington (C.V. Piper).

Female. A large greyish-brown species with pale yellow hair.

Frons and clypeus greyish-brown pollinose with pale yellowish recumbent hair. Antenna greyish-brown, with pale pubescence. Palpus brown with brown hair; third segment larger and darker with paler hair; length of sensory vesicle of third segment over one-half the length of the segment.

Scutum greyish-brown pollinose, paler and yellowish on the humeri with dense, recumbent pale yellow hair. Scutellum with long, erect yellow hair mixed with a few darker hairs. Pleuron and postscutellum greyish-brown pollinose. Postscutellum and katepisternum bare. Precoxal bridge present. Mesepimeral tuft and hair on pronotum and proepisternum pale yellow. Base of costa with pale hair, stem vein with mixed pale and dark hair, remainder of costa, dorsal surface of radius and ventral surface of subcosta and radial sector with dark hair. Legs yellowish-brown, paler than thorax, with pale recumbent yellow hair on coxa to tibia and on dorsal edge of basitarsus; remainder of tarsus with dark hair.

Abdomen yellowish-brown, paler ventrally with scattered, erect, dark hairs and sparse, short, inconspicuous paler hairs.

Genitalia as in Fig. 26. Arms of genital fork with moderate infilling (as in quebecense); cleft between arms shallow. Posteromedial angles of terminal plates moderately developed, usually with a sclerotized band along the medial edge. Terminal plate usually narrowly connected to the tergite.

Male. Clypeus greyish-brown pollinose with long reclinate brown hair. Scutum with recumbent yellow to gold hair. Pronotum, proepisternum and fore coxa and base of mid-coxa with yellow hairs. Mesepimeral tuft, and remaining hair on legs, abdomen brown. Subcosta with a ventral row of small, brown hairs.

Genitalia as in Fig. 47. Dististyle relatively long, ventral plate with long, slightly divergent basal arms; lip moderately developed and slightly thickened. Median sclerite deeply forked, the arms with dorsally curved tips.

Larva. Abdominal pigment reddish-brown in life (no properly preserved specimens available for colour determination on preserved material). Postgenal cleft rather variable, usually widest basally, tapering to a rounded or pointed apex. Toothed region of hypostomium relatively narrow; median hypostomial tooth not strongly differentiated. Antenna relatively dark. Head capsule yellowish-brown, darkly pigmented laterally behind the eyes; pigmented area antero-ventral to eye absent; dorsal head pattern paler, indistinct (Fig. 73).

Pupa. Respiratory organ slightly longer than pupa, consisting of four filaments arranged in two short-petiolate pairs. The petiole of the ventral pair is about one-half of the thickness of, and usually a little longer than the dorsal petiole, and arises from a ventro-lateral position, less than its own width from the point of attachment of the respiratory organ.

Distribution. Alaska (Stone, 1952; supplied by K.M. Sommerman) east to Goose Bay, Nfld. (Hocking & Richards, 1952; C.N.C.) south to California (U.S.N.M.) and Utah (Peterson, 1960) and east to Peel Co., Ontario and Bagotville, Que. (D.M. Davies). Stone &

Jamnbach (1955) list Maine, West Virginia and Oneida Co., N.Y. Specimens from these three localities were not available for study, but biological data given by these authors for the New York specimens indicate that they were probably *pugetense* and not *quebecense* or *aestivum*.

Simulium rivuli Twinn

Simulium (Eusimulium) rivuli Twinn, 1936, Canad. J. Res., D. 14: 120-121, Fig. 6D, 1-3 (male, pupa).

Holotype. Male, Type No. 4125, Canadian National Collection.

Type locality. Small stream near Carleton Place, Ontario. Pupa collected May 8; adult emerged May 13, 1935 (C.R. Twinn).

Female. A small to minute, grey species, with pale yellow hair and yellow legs.

Head grey pollinose, with pale yellow hair covering frons and most of clypeus. Antenna dark grey, with pale pubescence. Palpus dark grey, with pale hair; length of sensory vesicle about one-fourth the length of the segment.

Scutum grey pollinose, paler on humeri, with recumbent, pale yellow hair. Pleuron grey pollinose. Scutellum and katepisternum bare. Precoxal bridge present. Fore coxa yellow, slightly grey pollinose basally, but as a whole contrasting with the darker grey of the pleuron. Mid- and hind coxae grey pollinose; trochanters, basal five-sixths of femora and central portion of tibiae pale yellow to orange-yellow, remaining portions grey to dark grey on last three segments of tarsi. Hair on legs pale yellow basally, mixed with brown hair on basitarsus and entirely brown on remainder of tarsi. Calcipala small; pedisulcus shallow. Claw with a large basal lobe.

Abdominal tergites greyish-brown, slightly pollinose; remainder of abdomen yellowish-brown; hair pale yellow, relatively long, moderately dense and evenly distributed dorsally and laterally, sparser ventrally; a few longer, brown hairs on last two segments.

Genitalia as in Fig. 15. Arms of genital fork narrow at point of bifurcation, without infilling. Terminal plates lacking extensive, or deeply sclerotized areas.

Male. Clypeus dark brown, sparsely pollinose, with a few reclinate dark hairs. Antenna dark greyish-brown with pale pubescence.

Scutum dark brown, with thin greyish pollen visible only from extreme anterior view, and rather sparse recumbent brown hair. Pleuron greyish-brown pollinose. Mesepimeral tuft, hair on pronotum, proepisternum, legs, wings and abdomen brown. Abdomen dull brown.

Genitalia as in Fig. 38, similar to those of *innocens*.

Larva. Abdominal pigment greenish-brown, pale; transverse bands relatively broad leaving, narrow, intersegmental bands tending to become evanescent between segments 5-8. Postgenal cleft small, square. Lateral hypostomial teeth raised on moderately large lobes. Antenna long and relatively dark, the second annulus of basal portion not subdivided. Second antero-lateral head spot almost directly behind first antero-lateral spot (Fig. 67).

Pupa. Respiratory organ slightly longer than pupa, consisting of four slender filaments in two petiolate pairs; petiole of dorsal pair usually shorter, directed dorsally, almost at right angles to the stouter petiole of the ventral pair. Cocoon slipper-shaped, with a long, anterior median process in which only the margins are thickened, as in excisum.

Distribution. Nipissing Dist., Renfrew Co., Muskoka Dist., Frontenac Co. and Carleton Co., Ontario and Gatineau Co. Quebec.

Genus Cnephia Enderlein

Cnephia abdita Peterson

Cnephia abdita Peterson, 1962, Canad. Ent. 94: 96-102, Figs. 1-23 (female, male, pupa, larva).

Holotype. Female, Type No. 7525, Canadian National Collection.

Type locality. Small stream crossing Lake of Two Rivers Nature Trail approximately 1/4 mile north of Highway 60 at mile 20.0 from the west gate, Algonquin Park, Ontario; emerged from pupa collected June 3, 1959 (B.V. Peterson).

Female. A small to minute, grey pollinose species with dull whitish hair, elongate, flattened clypeus broadest below the middle with nearly straight edges, sparsely haired scutellum and long, nearly straight claw with long slender basal lobe. Wing veins lacking spinules. Radial sector unforked, with dark hair dorsally as well as ventrally. Precoxal bridge present. Calcipala minute, pedisulcus absent. Genitalia as in Fig. 9.

Male. Scutum black with grey pollen and sparse, recumbent, pale hair. Fore coxa with pale hair. Femora and tibiae with a few scattered pale hairs. Genitalia and other features similar to those of *abditoides* n. sp. (cf. Fig. 33).

Larva. Abdominal pigment diffuse, pale greenish-brown, transverse bands broad and indistinct. Postgenal cleft long and usually very narrow. Lateral hypostomial teeth strongly elevated on long narrow lobes. Antenna extremely long, dark brown; first annulus of basal portion twice as long as second annulus; distal portion of antenna long and slender, with numerous closely-set dark transverse bars imparting a multi-segmented appearance. Head capsule almost colourless; head pattern pale and indistinct (Fig. 59).

Pupa. Respiratory organ about two-thirds the length of the pupa, consisting of a variable (sometimes asymmetric) number, usually 18-21, slender, thread-like filaments arranged in four short-petiolate groups. Each group usually contains four or five (exceptionally 3 to 7) filaments, that usually arise together from the apex of their petiole.

Posteriorly directed spines absent on anterior border of abdominal tergites. Anteriorly directed hooks on posterior borders of tergites long and slender, present on segments 2 to 8 (4 pairs on tergites 3 and 4, with fewer spines on tergites 2 and 5-8). Terminal segment with a dorsal pair of long, stout hooks. Cocoon reduced to a few loose threads.

Distribution. Nipissing Dist. and Muskoka Dist., Ontario.

Cnephia abditoides new species

Female. A medium-sized, blackish species with thin greyish-black pollen and sparse dull yellowish hair.

Posterior surface of head, frons and clypeus greyish-black, subshining with thin, grey pollen. Hair sparse, recumbent, yellowish-brown on frons, somewhat erect and directed medially on clypeus. Clypeus only slightly longer than broad, shorter and more convex than that in abdita. Frons wide, V-shaped, at its narrowest point one-fifth the width of the head. Antenna black with paler greyish pubescence. Scape and pedicel slightly paler with short, dark hair. Palpus blackish with dark hair. Sensory vesicle of third segment about one-quarter of the length of the segment. Mouthparts fully developed.

Scutum black with thin greyish pollen and sparse, recumbent yellowish hair. Scutellum relatively bare with a few, erect hairs. Pleuron blackish, thinly grey pollinose. Precoxal bridge present.

Mesepimeral tuft with mixed pale and dark hair. Pronotum and proepisternum with erect paler hair. Costa, stem vein, dorsal surface of radius and ventral surface of subcosta and radial sector with fine dark hair; spinules entirely absent. Radial sector unforked. Legs dark greyish-brown with dull yellow hair darkening to brown on the apices of the femora and tibiae, and on the tarsi. Calcipala minute, pedisulcus nearly absent. Claw with small basal lobe.

Abdomen greyish-brown; tergites slightly darker with thin greyish pollen. Hair sparse, short and recumbent, mixed pale and dark. Basal fringe short, pale and relatively sparse.

Genitalia similar to abdita (cf. Fig. 9). Eggs mature in newly emerged females.

Male. Black with thin greyish pollen; hair entirely dark except on antenna. Clypeus black with long, reclinate black hair. Antenna black with pale pubescence and a few dark hairs on scape and pedicel. Palpi black with dark hair. Scutum blackish, thinly grey pollinose, subshining with sparse brown hair. Scutellum with sparse, erect black hair. Legs dark greyish-brown with entirely dark hair, which is somewhat long and shaggy along the dorsal edges of the femora.

Genitalia as in Fig. 33. Dististyle evenly tapering, with two small, stout, medially directed, apical spines. Ventral plate quadrate with deep, rounded median ventral keel. Paramere small, triangular, without arm or other associated spines.

Larva. Larger and darker than abdita from which it differs in the following respects: abdominal pigment greenish-brown, more extensive and diffused leaving only indistinct transparent intersegmental lines. Lateral hypostomial teeth not usually as strongly elevated as those in abdita. Basal portion of antenna longer, almost as long as penultimate portion; first annulus of basal portion about three times as long as second annulus. Head spots darker; head capsule as a whole more darkly pigmented (Fig. 61).

Pupa. Respiratory organ resembling that of abdita, the anterior petiole, however, giving rise to 9 or 10 filaments (instead of 4 or 5), making a total of about 25 instead of 20. Pupal chaetotaxy reduced, as in abdita. Cocoon of a few unorganized threads.

Distribution. Renfrew Co., Muskoka Dist., and Frontenac Co., Ontario.

Cnephia denaria Davies, Peterson and Wood

Cnephia denaria Davies, Peterson and Wood, 1962, Proc. ent. Soc. Ont. 92(1961): 97-100 (female, male, pupa).

Holotype. Female, Type No. 7995, Canadian National Collection.

Type locality. Roadside stream beside Hwy. 7, 9.2 miles east of Kaladar, Frontenac Co., Ontario; May 3, 1961 (B.V. Peterson and E. Bond).

Female. A small to medium-sized grey species with greyish-yellow hair.

Frons and clypeus dark greyish-brown pollinose with recumbent pale greyish-yellow hair. Antenna 10-segmented, dark grey with pale pubescence. Maxillary palp greyish-black with dark hair.

Scutum greyish-brown pollinose with recumbent greyish-yellow hair. Precoxal bridge present. Mesepimeral tuft, and hair on pronotum, proepisternum, coxae to tibiae and dorsal edges of basitarsi concolorous with scutum. Remainder of tarsi dark brown with brown hair. Mid-coxa densely haired. Calcipala minute; pedisulcus nearly absent. Claw with large basal lobe. Base of costa and stem vein with pale and dark hair, remainder of costa, upper surfaces of radius and distal one-third of radial sector, and lower surfaces of subcosta and radial sector with brown hair; spinules absent. Radial sector with minute fork, appearing as a small cross-vein at about one-third the distance from end of radius to the end of costa.

Abdomen grey with long greyish-white hair, dense laterally. Genitalia as in Fig. 12.

Male. Clypeus dull brown with brown, reclinate hair. Antenna 10-segmented.

Scutum dark brown with greyish-brown pollen and sparse recumbent yellowish-brown hair. Mesepimeral tuft brown. Hair on pronotum, proepisternum and fore coxae, all femora and tibiae with mixed pale and dark hair, mid- and hind coxae and tarsi with brown hair. Hair on wings and abdomen brown. Abdomen greyish-brown pollinose.

Genitalia as in Fig. 34. Dististyle slightly curved, evenly tapered, with a single small, stout, apical spine. Ventral plate almost square, with moderate, ventrally recurved lip; almost entirely haired on exposed portion. Paramere long and narrow, rigidly attached to basistyle, with a small, weakly sclerotized connection extending to articulate with ventral plate; arm and associated teeth absent.

Larva. Abdominal pigment pale purplish-brown, diffuse, indistinctly differentiated into transverse bands. Postgenal cleft small, narrow and rounded or inversely V-shaped. Lateral hypostomial teeth elevated on lobes that are broader and not as long as those in abdita. Antenna long; penultimate segment, dark brown but not excessively elongate; basal portion dark dorso-laterally, slightly swollen basally, tapering rather abruptly about three-quarters from the base. Head pattern moderately darkened and discrete. Second antero-lateral spot almost directly behind first antero-lateral spot. Second postero-lateral spot strongly curved anteriorly, closely approaching the postero-median spot (Fig. 62).

Pupa. Respiratory organ about half as long as pupa, composed of about 22 slender filaments in three short-petiolate groups, a dorsal one with 10 filaments, a ventral group of eight and a lateral group of four. The short, stout dorsal petiole subtends three long-petiolate pairs and one stouter, shorter petiole itself subtending two pairs. The ventral petiole subtends two groups of three and one long-petiolate pair; the lateral, narrowest petiole subtends four filaments arising close to one another (as in *abdita*). Tergites 2-5 with posterior row of eight long slender anteriorly-directed hooks; tergites 6-8 with fewer, although similar hooks, tergites 6-9 each with an anterior row of minute posteriorly directed spines. Cocoon reduced to a few strands.

Distribution. Muskoka Dist., Renfrew Co. and Frontenac Co., Ontario.

Cnephia emergens Stone

Cnephia emergens Stone, 1952, Proc. ent. Soc. Wash. 54: 80-81 (female, male).

Holotype. Female, Cat. No. 61189, U. S. National Museum.

Type locality. Fairbanks, Alaska; June 19, 1948.

Female. Mouthparts reduced, unsuitable for piercing the skin. A small, brown species with pale hair similar to *C. mutata*. Precoxal bridge incomplete, basisternum as in *mutata*. Costa, dorsal surface of radius and distal half of radial sector, and ventral surface of subcosta and radial sector with dark hairs. Spinules few and not strongly differentiated. Radial sector not forked. Calcipala large, pedisulcus nearly absent. Genitalia as in Fig. 11. Terminal plate of genital fork broadly connected to tergite.

Male. Blackish-brown, with sparse grey pollen and reddish-brown hair. Genitalia similar to those of *mutata*.

Distribution. Alaska (Stone, 1952); east to Baffin Island (Shewell, 1958) south to Big Trout Lake, Patricia Subdist. and Moosonee, Ontario (B.V. Peterson).

Cnephia mutata (Malloch)

Prosimulium mutatum Malloch, 1914, U.S. Dept. Agric., Bur. Ent., Tech. Ser. 26: 20-21, Plate 2, Fig. 18 (female).

Holotype. Female, Cat. No. 15404, U.S. National Museum.

Type locality. Glassboro, New Jersey; March 28, 1910 (C.T. Greene).

Female. A small to medium sized, brown species with greyish-brown pollen and sparse recumbent yellow hair. Precoxal bridge incomplete, lateral corners of basisternum produced as bluntly rounded lobes. Dark hair on costa, dorsal surface of radius and distal one-third of radial sector, and ventral surface of subcosta and radial sector. Spinules present on costa and distal portion of radius. Genitalia as in Fig. 10.

Male. Genitalia as in Fig. 32. Dististyle short, widened slightly distally, with two small, stout, closely set apical spines. Ventral plate small, somewhat triangular, with rounded apex. Paramere small and triangular, weakly sclerotized.

Larva. Abdominal pigment pale pinkish-brown weakly concentrated into transverse bands. Postgenal cleft scarcely differentiated, broad and shallow. Lateral hypostomial teeth moderately elevated, the second lateral tooth of this group relatively enlarged. Head capsule pale yellowish; head pattern pale but discrete. Penultimate segment of antenna darkened, elongate and slender, almost as long as the paler basal portion. Ventral tubercle a single median fold.

Distribution. Alaska (Stone, 1952) south to California (Peterson, 1960), east to Goose Bay, Nfld. (Hocking and Richards, 1952) in the north, and to Alabama (Stone and Jamnback, 1955) in the south.

Keys to the Ontario Species of Simulium (Eusimulium)

Females

1. Claws simple 2

Claws each with a large, thumb-like basal lobe (Fig. 7) . 3

2. Mandible serrate; galea of maxilla with retrorse teeth . . . . furculatum

Mandible and galea of maxilla reduced, with only fine hair apically . . . . baffinense

3. Basal two-thirds of tibiae (integument and vestiture) yellow, contrasting with the distal black portion (integument and vestiture); postscutellum with two patches of gold hair (usually 20 or more hairs in each patch) . . . . aureum

Tibiae not as above, the integument darker basally as well as distally, these dark areas usually connected by a dark strip along the dorsal edge (in teneral specimens), or tibiae brown, grey or black (in rivuli and congareenarum, the tibiae may be rather pale basally, but the vestiture is entirely pale); postscutellum bare (about 10 or fewer hairs rarely present in latipes) 4

4. Pedisulcus long and shallow, its depth less than one-third the width of the segment (Fig. 7a); sensory vesicle of third palpal segment small (Fig. 3b), about one-fourth the length of the segment; second segment of antenna longer and wider than third segment. 5

Pedisulcus short and deep (Fig. 7b), its depth usually one-half or more the width of the segment; sensory vesicle of third palpal segment large, over one-half the length of the segment (Fig. 3a) (except for gouldingi, which has an extensive patch of hair on the katepisternum); second segment of antenna shorter than third segment 9

5. Frons narrow, at its narrowest point about one-tenth or less the width of the head . . . . innocens

Frons wider, at its narrowest point one-fifth to one-eighth the width of the head 6

6. Integument of fore coxa (at least distal half) and basal seven-eighths of femur yellow, contrasting with the adjacent grey of the thorax; posterior margin of terminal plate of genital fork unsclerotized, not folded dorsally 7

Integument of fore coxa grey, not contrasting with the adjacent thorax; integument of femur grey or brown and grey; posterior margin of terminal plate of genital fork folded dorsally, appearing as a sclerotized edge (Figs. 16, 17) 8

7. Length of claw about two-thirds the length of the last tarsal segment; antenna grey; terminal plates of genital fork lacking well-defined, strongly sclerotized areas (Fig. 15); frons usually with concave margins . . . . rivuli

Length of claw about one-half or less the length of the last tarsal segment; basal two segments of antenna usually paler, contrasting with the flagellum; terminal plates of genital fork strongly sclerotized along the anterior edges (Fig. 13); frons widening above, with straight margins . . . . congareenarum

8. Head relatively small, its width to that of the thorax (at the humeral angles) 1 to 1.2; cercus longer than wide . . . . anatinum n. sp.

Head width to that of thorax 1 to 1.1; cercus wider than long . . . . excisum n. sp.

9. Katepisternum with a patch of hair along the dorsal margin (sockets of these hairs visible in rubbed specimens after clearing) 10

Katepisternum bare 11

10. Sensory vesicle of third palpal segment over one-half the length of the segment; patch of hair on katepisternum small, centrally placed (usually with 20 or fewer hairs); abdomen densely covered with silvery hair, in places obscuring the integument laterally . . . . <u>croxtoni</u>

Sensory vesicle of third palpal segment about one-third or less the length of the segment; patch of hair on katepisternum more extensive, extending to the anterior margin; abdomen sparsely covered with golden hair . . . . . <u>gouldingi</u>

11. Precoxal bridge not complete, with a narrow interruption near proepisternum (Fig. 6a) (rarely with a tenuous connection on one or both sides in old specimens (Fig. 6b)); the silvery or white hair of abdomen dense laterally, obscuring the integument, but absent on the black, dorsolateral areas of segments three and four 12

Precoxal bridge complete, strongly sclerotized, narrow (Fig. 6c); hair of abdomen yellow, sparse, not obscuring the integument, dorsolateral areas of segments three and four not usually contrastingly black and bare 13

12. Small species; width of thorax at humeral angles less than 0.9 mm. (0.8 ± 0.07); posteromedial areas of terminal plates of genital fork strongly sclerotized, as dark as the eighth sternite; hair on scutum with a brassy tinge

(similar to quebecense) when viewed under blue-filtered light; hair on stem vein black, or with some white hair, but not entirely white . . . . emarginatum n. sp.

Large species; width of thorax at humeral angles 0.9 mm. or more (1.0 ± 0.1); posteromedial areas of terminal plates of genital fork weakly sclerotized, contrasting with the strongly sclerotized anteromedial angles and lighter than the eighth sternite; hair on scutum white or silvery when viewed under blue-filtered light; hair on stem vein white, or white mixed with black hairs, but rarely all black . . . . euryadminiculum

13. Posterolateral areas of terminal plates of genital fork, at points of attachment to ninth tergite, widened dorsoventrally to form strongly sclerotized, paddle-shaped structures which are most conspicuous in a terminal or lateral view (Fig. 27); scutum with pale brassy hair; a small, common species . . . . quebecense

Posterolateral areas of terminal plates not widened appreciably, not paddle-shaped; hair on scutum variable 14

14. Arms of genital fork almost uniform in width, almost as narrow (1 1/2 times at most) at point of bifurcation as at points of attachment to terminal plates; posteromedial angles of terminal plates widely spaced, the U-shaped cavity enclosed by the arms of the genital fork wider than long (Fig. 23); a small species . . . . . . impar n. sp.

Arms of genital fork narrowing distally, more than twice as wide at point of bifurcation as at points of attachment to terminal plates; posteromedial angles of terminal plates not as widely spaced, the U-shaped cavity enclosed by the arms of the genital fork about as wide as long 15

15. Frons narrow, at its narrowest point about one-ninth the width of the head; posteromedial areas of the terminal plates of the genital fork large, the angles rounded (Fig. 24); hair on stem vein gold (occasionally with a few black hairs); hair on scutum gold; a rather small, uncommon species . . . . aestivum n. sp.

Frons wider, at its narrowest point one-seventh or more width of the head; posteromedial areas of the terminal plates of the genital fork small, usually with acute angles (Fig. 26); hair on stem vein black or nearly so; hair on scutum variable 16

16. Arms of genital fork diverging from stem at about the mid-point of the total length of the genital fork; tubercle on each internal dorsal arm of metasternum small, shallow, with a broad base (Fig. 8b); hair of scutum uniformly pale yellow; a large, early spring species . . . . pugetense

Arms of genital fork diverging from stem at a point about two-thirds of the total length from the anterior end of the stem (Fig. 25); tubercle on each internal dorsal arm of metasternum prominent (Fig. 8c); hair on central portion of scutum golden, contrasting with the paler hair on the anterior and lateral margins . . . . latipes

Males

1. Ventral plate a laterally compressed, median keel that is more than twice as long as broad, basal arms extending laterally (Fig. 54); postscutellum with two patches of gold hair . . . . aureum

Ventral plate flattened dorso-ventrally, about as broad as long, basal arms subparallel, extending anteriorly; postscutellum bare 2

2. Dististyle in ventral view tapering to a pointed apex, with a small, apical spine (Figs. 35, 45) 3

Dististyle rounded apically, with a flattened, triangular flange medially, the small, apical spine directed anteromedially (Fig. 46) 11

3. Dististyle with a rounded, flange-like ridge along the dorsolateral edge, near the mid-point (Fig. 45) . . . . . <u>furculatum</u>

Dististyle tapering uniformly, without a flange-like ridge along the lateral edge 4

4. Body of ventral plate somewhat rectangular in shape, its greatest width being distal to the point of attachment of the basal arms 5

Body of ventral plate triangular to somewhat trapezoidal in shape, its greatest width being at the point of attachment of the basal arms, narrowing distally to the prominent, ventrally recurved lip (Figs. 35-38) 7

5. Ventral plate, in terminal view, broadly V-shaped (Fig. 39); paramere narrow, three or more times as long as wide, without a long apical spine, but with a free spine-like sclerite near distal end . . . . <u>baffinense</u>

Ventral plate, in terminal view, flattened; paramere rectangular, about twice as long as wide, with long terminal spine 6

6\. Distal margin of ventral plate straight in ventral view (Fig. 41) . . . . <u>euryadminiculum</u>

Distal margin of ventral plate broadly concave (Fig. 42) . . . . <u>emarginatum</u> n. sp.

7\. Teeth on parameral arm small, the longest teeth equal to less than one-half the distance from the tip of the basal arm of the ventral plate to the point of its attachment to the paramere; basal arms of ventral plate usually moderately curved medially (Fig. 36); scutum entirely brownish-grey pollinose, hair brown and sparse . . . . <u>excisum</u> n. sp.

Teeth on parameral arm large, the longest teeth equal to three-quarters or more of the distance from the tip of the basal arm of the ventral plate to the point of its attachment to the paramere; basal arms of ventral plate usually parallel or diverging (Fig. 35); central area of scutum a dark, dull brown to black (often obscured by hair), contrasting with the lighter pollinose marginal areas, hair yellow to brown 8

8\. Hair on scutum entirely gold; mesepimeral tuft pale; abdominal hair, especially basal fringe, with pale tips . . . . <u>congareenarum</u>

Hair on scutum entirely brown or brown centrally with gold hair on the antero-lateral areas; mesepimeral tuft and abdominal hair entirely brown 9

9. Pollinosity, particularly of pleuron, grey without a brownish cast; antero-lateral areas of scutum nearly always with some gold hair 10

Pollinosity, noticeable particularly on pleuron, greyish-brown; hair on scutum nearly always entirely brown . . . . <u>rivuli</u>

10. Longest teeth on parameral arm in length about three-quarters the distance from the tip of the basal arm of the ventral plate to the point of its attachment to the paramere . . . . <u>innocens</u>

Longest teeth on parameral arm as long as or longer than the distance from the tip of the basal arm of the ventral plate to the point of its attachment to the paramere . . . . <u>anatinum</u>

11. Katepisternum with a patch of gold hair along the dorsal edge . . . . <u>gouldingi</u>

Katepisternum bare 12

12. Body of ventral plate narrowing distally, in ventral view, the small, central, hirsute lip extending like a tubercle beyond the posterior edge (Fig. 51) . . <u>croxtoni</u>

Body of ventral plate truncate or emarginate distally, in ventral view, the hirsute lip directed ventrally, not extending beyond the posterior edge (Figs. 47-50) . . 13

13. Distal margin of ventral plate, in ventral view, almost truncate, the lip broad and shallow, about one-half the width (measured along the proximal margin at junction of basal arms) of the body of the ventral plate; dististyle relatively short and thick (Fig. 50) . . . . . latipes

Distal margin of ventral plate, in ventral view, concave, the lip narrower (about one-third or less the width of the body of the ventral plate), sometimes projecting into this concavity but not beyond (Figs. 46-49) 14

14. Ventral plate, in terminal view, flattened, the lip weak; ventral hair of lip arising from a triangular area extending almost half-way to the proximal margin of the body; median sclerite uncleft or cleft apically to about one-third of its length; dorsal sclerite three or more times as long as wide (Fig. 49) . . . aestivum n. sp.

Ventral plate, in terminal view, V-shaped, the lip more strongly recurved ventrally; ventral hair of lip arising from a small, oval area, extending about one-quarter of the distance to the proximal margin of the body; median sclerite cleft apically to one-half its length; dorsal sclerite broader, less than twice as long as wide 15

15. Lip of ventral plate, in terminal view, deeper than wide and appearing enlarged or swollen (Fig. 48) . . . . quebecense

Lip of ventral plate, in terminal view, smaller, appearing wider than deep, without evident enlargement or swelling 16

16. Basal arms of ventral plate straight or only slightly bowed inwardly, the distance between their tips greater than the width of the body of the ventral plate (Fig. 47); no additional small spines mesad of apex of paramere; large species . . . . pugetense

Basal arms of ventral plate strongly bowed, the distance between their tips less than the width of the body of the ventral plate (Fig. 46); one to three small spines on aedeagal membrane mesad of apex of paramere; small species . . . . impar n. sp.

Larvae

1. Second annulus of basal portion of antenna subdivided into four or more annuli, the divisions usually marked by white rings (Fig. 57c) 2

Second annulus of basal portion of antenna not subdivided (Fig. 57d) 7

2. Five or more secondary annuli 3

Four secondary annuli 4

3. Antenna darkly pigmented, contrasting with adjacent head-fan (Fig. 66) . . . . *baffinense*

Antenna moderately pigmented, not contrastingly dark (Fig. 64) . . . . *anatinum* n. sp.

4. Median hypostomial tooth shorter than longest lateral teeth; postgenal cleft small, and narrow, its width 1/6 or less the width of the head 5

Median hypostomial tooth longer than lateral teeth; postgenal cleft wider, its width 1/5 or more the width of the head 6

5. Anterior margin of postgenal cleft V-shaped; dorsal-head spots dark brown (Fig. 63); abdomen without two clearly defined longitudinal rows of spots . . . *innocens*

Postgenal cleft square; dorsal head spots pale brown (Fig. 65); abdomen with two dorsal longitudinal rows of reddish spots . . . . *congareenarum*

6. Dorsal head spots brown on an almost transparent background (Fig. 72) . . . . *emarginatum* n. sp.

Dorsal head spots enclosed in a dark pigmented area (Fig. 69) . . . . *euryadminiculum*

7. Ventral tubercles conspicuous, 1/2 to 1/3 the depth of the abdomen below their point of attachment (Fig. 56); antenna usually noticably longer than head-fan stalk . . . 8

Ventral tubercles reduced, less than 1/6 the depth of abdomen below their point of attachment; antenna shorter to slightly longer than head-fan stalk (Fig. 79) . . . . <u>furculatum</u>

8. Postgenal cleft small, usually square, with straight or broadly V-shaped anterior border (rarely slightly rounded), its length (from posterior tentorial pit to anterior margin of cleft) one-fifth or less the length of the head between posterior tentorial pit and hypostomial teeth 9

Postgenal cleft larger, one-third or more the length of the head between posterior tentorial pit and hypostomial teeth, with rounded apex, usually broadest at about the mid-point of its length 12

9. Median hypostomial tooth equal to or shorter than longest lateral tooth; body pigment unicolorous, either green or reddish-brown; antero-lateral head spots not closely approximated to one another (Figs. 67-68) . . . 10

Median hypostomial tooth longer than lateral teeth; body pigment of two contrasting colours, reddish-brown with greenish-grey or pale orange-brown 11

10. Second antero-lateral head spot almost directly . . . . behind first antero-lateral spot; median hypostomial tooth smaller than longest lateral teeth (Fig. 67); body pigment greenish; antenna somewhat darkened . . . . <u>rivuli</u>

Second antero-lateral head spot somewhat lateral to, not directly behind first antero-lateral spot; median hypostomial tooth about equal in length to longest lateral tooth (Fig. 68); body pigment reddish or pinkish-brown; antenna pale . . . . . <u>excisum</u> n. sp.

11. Second antero-lateral spots, postero-median spot and postero-lateral spots enclosed in a darkly pigmented area (Fig. 76); antero-lateral spots not closely approximated; body pigment orange-brown with two longitudinal rows of oval reddish spots . . . . <u>aestivum</u> n. sp.

Dorsal head spots not enclosed in a darkly pigmented area; antero-lateral spots almost confluent (Figs. 77, 80); body pigment of alternating bands of reddish-brown and greenish-grey . . . . <u>aureum</u>

12. Pigment area antero-ventral to eye present, large . . . 13

Pigment area antero-ventral to eye absent, or very small 14

13. Dorsal background pigment of head extended forward beyond bases of antennae as a dark median stripe; length of postgenal cleft one-third or more the distance from posterior tentorial pit to hypostomial teeth (Fig. 78) . . . . <u>croxtoni</u>

Dorsal background pigment not extended beyond antero-median spot; length of postgenal cleft one-quarter or less the distance from posterior tentorial pit to hypostomial teeth (Fig. 75) . . . . . <u>latipes</u>

14. First abdominal segment with two dorsal and two ventral spots of darker, denser greenish pigment contrasting to paler pigment on adjacent segments; head capsule pale, almost colourless on anterior half, contrastingly dark brown basally (Fig. 70) <u>quebecense</u>

Pigment of first abdominal segment not contrastingly darker than that of adjacent segments 15

15. Toothed area of hypostomium relatively narrow, the teeth relatively uniform in size; postgenal cleft tapering apically, widest posteriorly (Fig. 73); a large overwintering species, maturing in early spring . . . . <u>pugetense</u>

Toothed area of hypostomium wider, the median tooth relatively long, the two flanking pairs of teeth relatively small, the remaining lateral teeth raised; postgenal cleft widest near mid-point of its length (Figs. 71, 74); small species maturing in summer 16

16. Length of postgenal cleft one-third or more the distance from posterior tentorial pit to hypostomial teeth (Fig. 71); body pigment pale sand brown. . . . . <u>gouldingi</u>

Length of postgenal cleft one-quarter or less the distance from posterior tentorial pit to hypostomial teeth (Fig. 74); body pigment orange-brown . . . . <u>impar</u> n. sp.

Pupae

1. Respiratory filaments 3, somewhat inflated and arising from a common base . . . . *baffinense*

Respiratory filaments 4 or more, slender 2

2. Respiratory filaments 4 3

Respiratory filaments 6 or more 5

3. Antero-dorsal margin of cocoon with a long, median projection (this may be broken off, but base is usually visible) . 4

Antero-dorsal margin of cocoon without a long, median projection, but a short, convex projection may be present 10

4. Respiratory filaments in two petiolate pairs; the antero-dorsal projection of cocoon long, slender, tightly woven . . . . *latipes*

One pair of respiratory filaments petiolate, the other two filaments sessile or nearly so; the antero-dorsal projection of cocoon shorter, broad and loosely woven except at edges . . . . *rivuli*

5. Respiratory filaments 6, in 3 petiolate pairs 6

Respiratory filaments 8 or more, in 3-4 petiolate groups 7

6. Antero-dorsal projection of cocoon long, slender, petiole of dorsal pair of filaments constricted and somewhat flexible at its point of attachment . . . . *excisum* n. sp.

Antero-dorsal projection of cocoon shorter, broad, loosely woven; petiole of dorsal pair of filaments not constricted at base and inflexible . . . . . . *gouldingi*

7. Respiratory filaments 8; antero-dorsal projection of cocoon short or absent 8

Respiratory filaments 10 or 12; antero-dorsal projection of cocoon very long 9

8. Cocoon loosely woven, with a moderate antero-dorsal projection and usually a thickened anterior rim; dorsal filament diverging at right angles basally from remaining filaments . . . . *croxtoni*

Cocoon tightly woven, with a slight mid-dorsal projection on the thickened anterior rim; filaments moderately divergent in dorso-lateral plane, the dorsal filament not strongly divergent . . . . . *furculatum*

9. Respiratory filaments 10 . . . . *innocens*

Respiratory filaments 12 . . . . *congareenarum*

anatinum n. sp.

10. Dorsal respiratory filament strongly divergent at base from the other three; dorsal pair of filaments on a short petiole, the ventral pair with almost no petiole . . . . <u>aureum</u>

    Dorsal respiratory filament not strongly divergent at base from the other three 11

11. Annuli along basal portion of respiratory filaments, just beyond petiole, numerous and narrow, giving a grey, roughened appearance; ventral filaments with 5-6 annuli per diameter of filament 12

    Annuli along basal portion of respiratory filaments, just beyond petiole, less numerous and wider, giving a shiny appearance; ventral filaments with 2-3 annuli per diameter of filament . . . . <u>emarginatum</u> n. sp.
    <u>euryadminiculum</u>

12. Petiole of ventral pair of respiratory filaments at least 4-7 times as long as petiole of dorsal pair of filaments . . . . <u>impar</u> n. sp.

    Petiole of ventral pair of respiratory filaments at most twice as long as petiole of dorsal pair of filaments 13

13. Respiratory filaments diverging dorso-ventrally, petiole of dorsal pair at most one and one-half times as thick as petiole of ventral pair; tubercles on head and thorax small, regularly spaced, not strongly grouped . . <u>quebecense</u>

Respiratory filaments not diverging, subparallel; tubercles on head and thorax larger, placed in irregular groups . . 14

14. Petiole of ventral pair of respiratory filaments usually longer than, and about one-half as thick as petiole of dorsal pair, arising from a ventro-lateral position less than its own width from the base of the respiratory organ; filaments subparallel in an oblique plane . . pugetense

Petiole of ventral pair of respiratory filaments nearly equal in length to, and about two-thirds as thick as petiole of dorsal pair, arising ventral to it; filaments subparallel in dorso-ventral plane . . . . aestivum n. sp.

ECOLOGY OF THE EUSIMULIUM GROUP

Adult Feeding

The blood-feeding habits of only a few of the Ontario species of Eusimulium are known and it is difficult to make generalizations about them, especially since misidentification has resulted in some confusion, and early feeding records are untrustworthy. Davies and Peterson (1956), Bennett (1960) and Davies, Peterson and Wood (1962) have summarized the available knowledge, and clarified some of the misidentifications.

Only a single Ontario species of Eusimulium, baffinense,is unable to feed on blood, its mouthparts being unsuited for piercing. In the remaining 16 species, the females have well developed mouthparts, and with one exception (furculatum) all have bifid claws. Most species, on emergence, have undeveloped eggs and usually little stored nutrient (Davies, Peterson and Wood, 1962). The presence of the bifid claw has been interpreted as an indication that a species feeds on birds (Shewell, 1955). Only six of these species have been taken in numbers while feeding on birds of several species and in various habitats (Bennett, 1960). Bennett has suggested that the habitat in which the bird occurs is of equal or more importance than the species of bird, in relation to which simuliid species feed on it.

Thus, *latipes*, *quebecense*, *croxtoni* and *aureum* have all been taken on birds in numbers only in the forest canopy, 10 to 30 feet above the ground. Various species of birds, when placed in the canopy, are attacked by these four species of flies.

On the other hand, *euryadminiculum* and *anatinum* have been (+ *S. rugglesi*) taken only from loons and ducks respectively and these only in the vicinity of water. The unusual concentrations of *euryadminiculum* females flying over lakes may be related to their feeding habits (Davies and Peterson, 1957). Many of the records of *latipes*, *croxtoni* and *euryadminiculum* from domestic ducks (Anderson, 1956; Fallis *et al*, 1956) are probably based on various colour variants of *anatinum* which was unknown at that time.

Larval Ecology

Fortunately, larvae of all the Ontario species of *Eusimulium* have been found, often in large numbers. This has permitted a qualitative, and to some extent a quantitative, evaluation of the type of stream inhabitated and of the time and sequence of their development.

Aquatic habitat

The stream in which the larvae develop is probably selected by the ovipositing female, although females of *Eusimulium* have been rarely observed during oviposition (Davies and Peterson, 1956; Davies, Peterson and Wood, 1962). Nevertheless, during the course of this study the larvae of each species were nearly always found in only one type of stream. Therefore, it has been possible to relate the presence and abundance of certain species to features of habitat, such as the width of the stream and water temperature.

The majority of Ontario species of *Eusimulium* are generally confined to small streams, two to three feet or less in width. In these small streams there appear to be only two basic types, eurythermal and stenothermal streams. The eurythermal streams are usually temporary streams draining swamps exposed to the sun, often containing such a small quantity of water that the temperature of the stream approximates that of the air. Thus, during April and May the temperatures in these small streams may fluctuate from below 40°F. to nearly 80°F. during a single 24-hour period, and larval development as a result is usually rapid. Several *Eusimulium* species are commonly encountered in this type of stream, for example, *rivuli*, *excisum*, *innocens*, *anatinum*, *congareenarum*, *croxtoni*, *latipes* and *aureum*. Probably *gouldingi* should be included here as well, but collections of it have been smaller and fewer.

The other type of stream, the stenothermal stream, usually drains a bog or spring source, and remains cold and usually permanent during the summer. Species that appear to be restricted to this type of stream are *aestivum* and *impar*. *Pugetense* and *baffinense* are also found in relatively small streams. The former overwinters as a larva, adults emerging in April; thus its habitat may be considered as a cold, stenothermal stream even though the stream in which it occurs may warm up during the summer. *Baffinense* is confined to arctic and subarctic streams which may not often warm up. Other species, for example, *latipes* and *gouldingi*, are also encountered in stenothermal streams, in association with *aestivum* and *impar*, usually in smaller numbers.

The larvae of *euryadminiculum*, *emarginatum* and *quebecense*, inhabit larger rivers, usually over 10 feet in width. Small larvae of *euryadminiculum* (or *emarginatum*) were taken in October in Algonquin Park. The larvae develop during the winter, pupating in late April and early May, at approximately the time when the eggs of *quebecense* are presumed to hatch. Although two larvae of the last species have been taken in Algonquin Park in October, pupae have only been taken in numbers in late May and early June, and it has been concluded that the majority of the eggs of this species hatch in the spring. Small numbers of larvae and pupae of *latipes*, *croxtoni* and *aureum* have also been encountered in larger rivers, particularly those with islands which form narrow side channels, thus possibly simulating smaller streams for short portions of their length. In addition, the single locality in southern Ontario where *furculatum* has been found is a large river, but in the Patricia district it was found in smaller cool streams draining partly wooded muskeg.

Sequence of development

As was indicated above, the larvae of *euryadminiculum* and *emarginatum* develop together in large rivers during the winter, pupation appears to be almost simultaneous, in late April and early May in Algonquin Park, Ontario. In the same rivers the remaining species, *latipes*, *croxtoni*, *quebecense*, *aureum* and *furculatum* appear later, evidently hatching in the spring.

In small eurythermal streams a definite and annually repeated sequence of development has been observed in each of the streams studied from 1959 to 1962. The results of the 1960 and 1961 collections that were made in a small eurythermal stream typical of this type, located three miles south of Huntsville, Ontario, are summarized in Table I. The data for this stream are presented in preference to those from other streams because this stream supported the largest number of *Eusimulium* species that were found together in one stream.

The first two species to begin pupating in any of these streams in southern Ontario were *rivuli* and *excisum*. These two species seldom occurred together; if both were present one species was invariably much more numerous than the other. *Rivuli* was the only species present in Algonquin Park and was the dominant species in most of the streams on the Precambrian Shield in Ontario. *Excisum* was more numerous farther south, and was the dominant species in the Ottawa Valley and in southern Ontario, south of the Shield. It has, however, been taken as far north as Big Trout Lake, Patricia Subdistrict, Ontario, and Churchill, Manitoba; perhaps it is significant that *rivuli* does not occur here. The northern specimens of *excisum* may eventually prove to be another species, however.

Shortly after *rivuli* and *excisum* have begun pupating in late April at Huntsville, the pupae of *anatinum* begin to appear, but they have always been found in small numbers. In the second week of May, *latipes* reaches its first peak of pupation. At Huntsville in the three years studied, it was the most abundant species and it is possible that *anatinum*, and *innocens* as well, may have been affected by its abundance. In streams in eastern Ontario (Carleton County and Frontenac County), *anatinum* and *innocens* were more numerous however, and it was evident that *innocens* developed and pupated at about the same time as *latipes*, at least a week later than *anatinum*. In the Huntsville region, the last species to appear were *aureum* and *croxtoni* during the third week of May.

In the small, cold, stenothermal streams, pupation of all species is usually delayed until late May or June. Again the first species to begin pupating is *rivuli*, followed about a week later by *latipes*. Later, *aestivum* and *impar* begin pupating in mid-June in Ontario and pupae of *aestivum* were taken in mid-July at Mont Tremblant, Quebec (B.V.P.). The ratio of larvae to pupae indicated that impar is slightly later than aestivum. When gouldingi is present in such cold stenothermal streams, it is also very late, the last species to appear, i.e., in late June and early July in Algonquin Park.

The remaining two species, pugetense and baffinense, probably represent special cases, and are thus treated separately. As indicated above, pugetense overwinters in the larval stage and begins pupating in late March in southern Ontario and in early May at Bagotville, Quebec (D.M.D.). Farther north, at Shefferville, Quebec, exuviae were collected (B.V.P.) in mid-June; these collections show a very early pupation. In western Canada, however, collection dates for pugetense suggest that this species is multivoltine; the eastern and western populations may eventually prove to be different species. Baffinense is found only in the arctic and subarctic, in streams draining muskeg and tundra. Collection records indicate that baffinense along with aureum is one of the last species to appear (Hocking and Pickering, 1954; Davies, Peterson and Wood, 1962).

Present data indicate that most of the species mentioned above are univoltine; however, congareenarum, latipes, aureum and possibly croxtoni are multivoltine. In South Carolina, congareenarum begins pupating in late February and passes through two or more generations before the streams begin to dry up (Jones and Richey, 1956).

In Bruce County, this species has been taken at the outlet of a small shallow lake (only a few inches deep) which tended to be eurythermal. Pupation of congareenarum reached a peak in mid-June and again in mid-July, and it is quite possible that these represented a second and third generation, although in subsequent years attempts to find the species in May were unsuccessful. It has been more difficult to find a pattern in the development of latipes. Collection records suggest that it is multivoltine. However, there are at least two forms or cytological entities involved in this species (Landau in Dunbar, 1962), and one of these may be univoltine.

Dunbar (1958) has shown that aureum, in southern Ontario, is a complex of two cytological entities, both of which are multivoltine and usually occur together in the same stream. His data (1958, p. 25) indicate, however, that both forms are not equally abundant at the same time, form A usually predominating during the summer, and form B predominating in May and September. In northern Ontario and elsewhere, additional siblings have been found (Dunbar, 1959).

PHYLOGENY WITHIN THE EUSIMULIUM-GROUP

In the two previous sections, the morphology of the larvae, pupae and adults of the seventeen Ontario species of Eusimulium was described, and the available knowledge on larval habitat and seasonal development was summarized. In this section, this information is reviewed and condensed to provide a basis for the assembling of the 17 species into six groups. Two additional groups, containing no Nearctic representatives, are added to assist the phylogenetic interpretation. The remaining related Palaearctic species are associated with this core as far as the literature and availability of specimens has permitted.

Morphological and biological similarities among the members of any one group are sufficiently close that separation is usually difficult, and close phylogenetic relationship is assumed. It is often possible to link each of the species in the group one to another in a two-dimensional sequence; the resulting pattern would then resemble a phylogenetic tree as viewed from above, and should, if correct, resemble the linkage diagrams resulting from cytological studies of the giant salivary gland chromosomes of the same species (Basrur, 1959; Dunbar, 1959, 1962). Alternatives, however, are sometimes more possible in morphological than in cytological groupings.

A study of morphological and biological similarities between each of the eight groups of species has permitted the construction of inter-group linkages similar to the inter-specific linkages.

Although fossils are rare and the cytological knowledge is incomplete, it is sometimes possible to speculate on the degree of primitiveness of each of the species groups. Thus, one of them (the rivuli group) bears strong resemblances to several species of Cnephia. The other groups can be linked one to another, the terminal one (the aureum group) showing relationships in only one direction. It is thus assumed that the members of the rivuli-group are themselves descendants of an older and more primitive species, than that which gave rise to the aureum group, and thus are considered first.

Group 1 - The rivuli Group

The following Ontario species - rivuli, excisum, anatinum, innocens and congareenarum are all similar in their morphology and are often difficult to identify. For this reason, their close relationship is assumed and they are assembled together in group 1. Members of this group have the following characters in common that are not all found together in subsequent groups: in the female, the sensory vesicle of the third palpal segment is small, about one-quarter the length of the segment (Fig. 3b), the calcipala is small and

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The larvae have only been found in small streams, usually less than 1 foot wide, often with sluggish flow and considerable emergent vegetation. Only congareenarum is multivoltine; most of the species tend to develop early in the season (Table I). Both anatinum and congareenarum feed on waterfowl, turkeys or other birds, on the ground rather than in the forest canopy (Bennett, 1960; Jones and Richey, 1956).

From western North America, two female paratypes of minus D. & S. (which is known only in the female) have been examined. The sensory vesicle, calcipala and pedisulcus are reduced, and the genital fork resembles other species in group 1, and thus minus probably belongs here. In northern Europe there are three additional species, which, though they have not been studied first hand, can safely be included in this group on the basis of published illustrations. One of these, dogeli Usova (1961) is evidently quite similar to anatinum and congareenarum. The other two are subexcisum Edw. and yerberyi Edw. Grenier (1953) suggested that the latter might be merely a variant of the former, and except for his illustrations of the double and triple hooks at the tip of the pupal abdomen of subexcisum, there is nothing to suggest that subexcisum and yerberyi may not also be included in group 1.

Group 2 - The baffinense Group

S. baffinense has been placed in a separate group because its immature stages strongly resemble those of group 1, but the structure of the male genitalia is quite different, and resembles those of euryadminiculum, discussed in the subsequent group. The only other members of the Eusimulium-group that seem from Rubtzov (1962) to be closely related and are here placed with it, are crassum Rubtzov and arctium Rubtzov. Rubtzov (1962) has also included tsheburovae Rubtzov in this group; it is known only in the male and probably belongs to group 1, or perhaps to *Cnephia*.

The larva of *baffinense* is similar to those of *innocens* and *anatinum* and indicates some relationship between them. Although the lateral hypostomial teeth are not as strongly elevated, the second annulus of the basal portion of the antenna is subdivided, as in *anatinum* and the postgenal cleft is small and square. Likewise, the cocoon with its long median anterior process thickened along the edges is of the same type found in group 1. The respiratory filaments of the pupa, while only three in number, and inflated basally, nevertheless show the basic branching pattern characteristic of most members of group 1, in which the dorsal filament diverges strongly (almost at right angles) from the two ventral filaments, before curving forward to lie under the anterior projection of the cocoon.

The adults, however, show significant differences from those of group 1. The female is evidently autogenous and the mouth parts are reduced and unsuitable for taking a blood meal. The sensory vesicle in the third segment of the maxillary palp is minute and the claws lack the large basal lobe; these reductions may, however, be associated with the loss of the blood-sucking habit. The terminal plates of the genital fork do not show the convoluted, ribbon-like connection with the tergite that is characteristic of females in group 1; instead, the connection is narrower and appears to be less flexible. Nevertheless, the posterior edges of the terminal plates are folded dorsally which is reminiscent of the genital fork of excisum. In the male, the dististyle is similar to that in group 1, slender, evenly tapering and moderately curved, bearing a single apical spine. The ventral plate is broader, the hair sparser and the lip is not strongly ventrally re-curved; instead, the whole ventral plate is keeled medially. The paramere, however, is considerably different from the paramere of group 1. In baffinense, it is long and slender, and the inwardly folded apical portion or parameral arm is present, but the spines that are associated with it in group 1 are not present in baffinense. Instead, each parameral arm appears as a small separate sclerite forming a small finger-like process extending from the ventro-lateral wall of the aedeagus. The dorsal wall of the aedeagus bears a patch of numerous small spines which may be homologous with the long, slender parameral spines of group 1, although they are separated from the parameral arm. They may, however, be a separate development of the many, usually minute spines covering the surface of the aedeagal membrane, possibly functioning in the same manner as the parameral spines of group 1. An important feature is the presence of both a calcipala and a pedisulcus.

Group 3 - The euryadminiculum Group

In Ontario, two very similar species, euryadminiculum and emarginatum are grouped separately because their larval and adult structure, though showing some unique features, bears similarities to that of baffinense, while the pupal structure resembles that of following groups. Both species overwinter as larvae in large rivers - thus differing from other species. Rubtzov (1962) has illustrated two species (annulum Lundström and annuliforme Rubtzov) that apparently may be included in this group. In western North America there is a single species, canonicolum D. & S. also of this group. Shewell and Fredeen (1958) synonymized euryadminiculum with canonicolum , but small morphological differences (Figs. 40, 41) suggest they are not conspecific.

The larvae of the Nearctic members of this group have the second annulus of the basal portion of the antenna subdivided into four secondary annuli. The teeth on the hypostomium, however, are more uniform in size, the lateral teeth not showing to any extent the enlargement characteristic of group 1 and baffinense of group 2. The cocoon is slipper-shaped, but has no anterior median process and the respiratory filaments of the pupa are arranged in two short petiolate pairs rather than in a group of three with one divergent dorsal one as in most members of groups 1 and 2.

In the female, the sensory vesicle of the maxillary palp is enlarged, its length over one-half the length of the segment, and the mouthparts and basal lobe on the claw are well developed. The basisternum is not connected to the proepisternum by a precoxal bridge, a character not found elsewhere in Eusimulium but common outside it. The calcipala and pedisulcus of the hind leg are both well developed. On the abdomen, the hair is dense laterally, but is almost absent from two dorso-lateral patches on segments two and three, a condition not found in baffinense or in members of group 1. The terminal plates of the genital fork are more narrowly connected by an apparently less flexible connection to the tergite. The terminal plates are triangular; the anteriorly directed apodemes are large and conical. In the male, the dististyle is similar to that in baffinense and members of group 1. The ventral plate, however, is unusually wide and flattened, and the ventrally directed lip is nearly absent. Hair is present over most of its surface as in baffinense. The parameres are not elongate as in baffinense, but are scarcely twice as long as wide and each bears a strong apical spine ventral to the junction of the parameral arm. In euryadminiculum, this spine points ventrally, extending over the edge of the ventral plate; it is directed antero-ventrally in emarginatum and anteriorly in canonicolum. The parameral arm as in baffinense lacks spines directly attached to it; instead it forms the dorsal surface of a finger-like projection on the ventro-lateral surface of the aedeagus.

The dorsal patch of spines of baffinense is represented in euryadminiculum by two more laterally placed patches; the spines are fewer and much longer than those in baffinense but they are not associated with the parameral arm. Perhaps emphasis should be placed on the presence of the long apical spine on the paramere; the spine considered to be homologous with it, becomes a prominent feature of the paramere in the four subsequent groups.

Group 4 - The furculatum Group

A single North American species, furculatum, is placed in a separate group because of the peculiar features of the male paramere. Several Palaearctic species, with similar structures are discussed by Rubtzov (1962) as representing the genus Schoenbaueria. Carlsson (1962) includes three additional species. Two of these, pusillum Fries, and the females of annulitarse Zetterstedt were available for study; they are evidently closely related to furculatum and all are included here.

The larvae of furculatum have small ventral tubercles and relatively short antennae. The second annulus of the basal portion of the antenna is not subdivided. The lateral hypostomial teeth are low, not strongly enlarged. The throat cleft, however, is much larger than in the larvae of any species discussed previously.

It is long, widest at the middle, and rounded or pointed apically, as is characteristic of some members of group 5. The cocoon is of the slipper-shaped type, without an anterior process and the respiratory filaments of the pupa which are much the same in the Palaearctic species as in furculatum have a basic branching pattern of three short-petiolate groups of two, three and three filaments each.

In the female, the sensory vesicle, calcipala and pedisulcus are well developed, and the precoxal bridge is present. The claws of furculatum lack the large basal lobe, but a small tooth is present in the female claw of pusillum. The mouthparts are well developed for biting, and furculatum, although its feeding habits are unknown, may attack mammals. The terminal plates of the genital fork are more like some species in the following group in having a rounded postero-median lobe, a low, broad anterior apodeme, and a slender tergal connection.

In the male of furculatum, the dististyle is considerably shortened, the apical spine is directed medially and a dorso-lateral flange-like ridge alters the appearance of the more evenly tapered dististyle in group 3 in which there is only a suggestion of such a structure in euryadminiculum. The ventral plate is not strongly modified, however; it is broad and flattened and the hair, sparser than in group 3,is evenly distributed over much of the surface in furculatum, but confined to a narrow median area in pusillum.

The paramere, rather than being rectangular, however, is somewhat S-shaped, broadened basally between its articulations on the basal arms of the ventral plate and the basistyles. It narrows apically and bends ventrally, the long, slender apical spine folded almost dorsally and lying tightly pressed to the ventrally curved apical portion of the paramere (Fig. 45). This condition is also found among all members of group 5. In *furculatum*, however, in addition, the parameral arm is still present and terminates in a similar but smaller, dorsally folded spine lying parallel and mesad of the apical parameral spine. In addition, two much smaller but similarly constructed spines are mesad of the two larger spines. In *pusillum* only a single extra spine is present, which is longer than the apical spine and arises beside it (Fig. 43). The patches of spines on the dorsal surface of the aedeagus, characteristic of *baffinense* and group 3, are lacking.

Group 5 - The *latipes* Group

The members of this group, the *latipes* group, are numerous and widely distributed in the northern hemisphere. In Ontario there are seven species, *latipes*, *aestivum*, *pugetense*, *quebecense*, *impar*, *croxtoni* and *gouldingi*, that are difficult to differentiate, especially in the female. In addition, *wyomingensis* Stone and DeFoliart occurs in western North America, as well as other undescribed species. Over 35 species from Asia have been described and illustrated by Rubtzov

(1956, 1962) and several additional species occur in Europe, i.e. codreanui Serban, bertrandi Grenier and Dorier, carthusiense G. & D. and armoricanum Doby and David. It is probable that the North American latipes is not conspecific with the true form, and even in Ontario has been shown to consist of at least two siblings (Landau in Dunbar, 1962).

The larvae of the group are much alike and are specifically distinguished by details of the head pattern, the shape of the throat cleft, and colour and distribution of body pigment. The ventral tubercles are well developed, the throat cleft is usually long and usually widest above the base, and the lateral hypostomial teeth are only moderately enlarged. The basal portion of the antenna is usually longer than the head fan stalk, and the second annulus is not subdivided.

The cocoons of the North American species are basically of the slipper-shaped type with a thickened anterior margin. In a few species (e.g. latipes) the margin is extended forward to produce a long anterior process, but this process differs from the anterior process of the cocoons of members of group 1 by being almost completely thickened instead of having only thickened margins. The pupal respiratory organ of most species has four filaments in two petiolate pairs, but a few species, which represent a small subgroup (gouldingi, croxtoni and wyomingensis) have 6 to 8 filaments, the latter resembling in number and branching pattern members of group 4.

In the female, the sensory vesicle of the maxillary palp is well developed (except in gouldingi, in which, though small, it is larger and more elaborate than that in the rivuli group). The calcipala and pedisulcus are well-developed, the claw has a large basal lobe and the precoxal bridge is present. The terminal plates of the genital fork are rather uniform in nearly all the species, making identification difficult. They usually have a rounded postero-median angle and a low, broad anteriorly directed apodeme as in furculatum, and are narrowly connected to the tergite. The anal lobes are almost identical in most species, but are also similar to those in groups 3 and 4.

The dististyle of the male in all the species of this group has a characteristic shape, similar to that of pusillum. The dorso-lateral flange of the dististyle in pusillum and the members of the latipes group is smaller and more dorsally placed than in furculatum, while the medially directed terminal portion is enlarged into a triangular flange bearing the small, stout spine directed antero-medially (which was apical in former groups) (Figs. 46-52). The ventral plate is similar in ventral view to that in group 4, but the lip is usually narrower, sometimes appearing as a protuberance (Fig. 48). The hair is restricted to the region of the lip, however, and it is usually longer and denser than in previous groups. The paramere is similar to that of *furculatum*, being basically triangular with its apex curved ventrally and the long, slender apical spine sharply bent dorsally. No additional spines are present, however, except in *quebecense* and *impar* (and possibly also in some Palaearctic species as illustrated by Rubtzov, 1956) in which one to three minute spines are present mesad of the apex of the paramere. This condition is less developed, but not basically different from that of *furculatum* of group 4 (Figs. 45, 46).

The larvae of the *latipes* group have been found chiefly in small streams, occasionally in medium-sized rivers, especially those that are not turbulent and have islands and narrow side-channels. *Quebecense*, however, is normally found only in such rivers. All the species develop in the spring, except *pugetense*, which over-winters in the larval stage. The adult females of *croxtoni*, *latipes* and *quebecense* have been taken feeding in numbers in Ontario only on birds in the forest canopy (Bennett, 1960).

Group 6 - The *angustitarse* Group

No species resembling *angustitarse* Lundström are known from North America, but Rubtzov (1962) has discussed fourteen Palaearctic species under what he has designated "the *angustitarse* group". One of them, *ruficorne* Macquart, is also found in Africa, and an examination of two of the African species (*nigritarse*

Coq. and *aureosimile* Pomeroy) of Freeman and de Meillon's Group III of Division A (1953) indicate they are related to *angustitarse* (a conclusion shared by Rubtzov, 1962). Other species, also apparently related to *angustitarse* are known from the Oriental region (*aureohirtum*) and Australian region (*ornatipes*).

The male genitalia of *angustitarse* are suggestive of those of members of the *latipes* group. The dististyle shows the characteristic shape in ventral view typical of *latipes*, but the dorsal flange is absent. The ventral plate has a deep median keel, that is entirely haired; in ventral view it resembles to some extent both *latipes* and *pusillum*. The paramere, however, is long, narrow and curved rather than triangular, and the apical spine is long. Mesad of the apical spine is a small round sclerite, surrounded by membranous cuticle (Fig. 53).

The anal lobes of the female of *angustitarse* are shorter than those of members of groups 4 and 5. The long hairs with large sockets are numerous on the antero-medial area, while the postero-medial surface is covered with fine hair; the two surfaces are separated by a membranous area (Fig. 30). The anal lobe shows similarities both to that of *croxtoni* (Fig. 28) and of *aureum* (Fig. 31) being intermediate between them. The anal lobe of *aureosimile* is similar to that of *angustitarse*.

The immature stages do not differ sufficiently from those of the *latipes* group to enable separate characterization. The larvae of some species, i.e. *ruficorne* and *ornatipes*, show a high tolerance of sluggish or even standing water (Freeman and de Meillon, 1953; Mackerras and Mackerras, 1949).

Group 7 - The *alcocki-hirsutum* Group

The 27 African species of Groups I, II and IV of Division A of Freeman and de Meillon (1953) have been placed in a separate group, because the males (judged from figures presented by Freeman and de Meillon and a male specimen of *unicornutum* Pomeroy) show some features suggestive of group 4 and other features of group 6, and on the other hand a study of females of *alcocki* Pomeroy and *neavei* Roubaud indicates their anal lobes to be very similar to those of the *aureum* group (group 8 below).

A distinctive feature of the males of this group is the Z-shaped paramere, in which the ventrally curved portion and apical spine are greatly elongate. Additional apical spines may be present. The paramere resembles an exaggerated version of that found in groups 4 and 6. The ventral plate lacks the narrow deep median keel of *angustitarse*. In *hirsutum* Pomeroy and related species, both ventral plate and dististyle suggest group 4.

The larvae as illustrated by Crosskey (1960) do not seem to have any features distinctive of the group as a whole, although some have an inverse head pattern. The antero-lateral spots are so close to one another (they are usually visible in an inverse pattern) that Crosskey has not differentiated a first and second spot.

Rubtzov (1962a) has proposed two new genera, *Pomeroyellum*, with *unicornutum* as genotype, for Groups I and II of Freeman and de Meillon (1953) and *Meilloniellum*, with *hirsutum* as genotype, for Group IV.

Group 8 - The *aureum* Group

Subsequent to the description of *aureum* in 1824, several authors have described new species (i.e. *bracteatum* Coq. 1898, *angustipes* Edw. 1915, *pilosum* and *utahense* Knowlton & Rowe, 1934, which were later synonymized with *aureum*. Rubtzov (1947) was probably the first to subdivide the species on morphological grounds. Subsequently, Terterjan, Djafarov, Rubtzov and Serban have further subdivided the original *aureum* into several new species (Rubtzov, 1956; 1962).

Dunbar (1958, 1959) was the first to demonstrate cytologically the existence of five sibling species of *aureum* in North America, of which at least three occur in Ontario. Although cytological comparison has evidently not been made, it is probable that none of these are conspecific with aureum of Sweden.

In southern Ontario, form "A" and form "B" of Dunbar (1958) are often found together in the same stream. Morphological separation between the two has only been successful between the larvae (Figs. 77, 80) and the male, and distinguishing features are subtle.

Form "D" has been found in more northern regions of Ontario, while form "C" is known only from Churchill, Man. The remaining form "G" is southwestern (California), and was unavailable for this study.

Of the many Palaearctic representatives of the aureum group, only a few specimens from England and Sweden has been examined, but the remaining species all are sufficiently well illustrated by their authors to assure their inclusion in the aureum group.

The genitalia of the male possess distinctive features which allow ready inclusion into a single group. The claspers are unusual, in that the basistyle is disproportionally much longer and stouter than the dististyle (Fig. 54). The latter, nevertheless, is rounded distally, and the small apical spine is directed mesally. The body of the ventral plate is strongly compressed laterally into a median keel that is more than twice as long as broad, and is entirely covered with setae. It resembles that of angustitarse, except for the lack of the flattened lateral extensions. The parameres resemble those of *angustitarse*, except that they are not articulated closely to the ventral plate.

In most respects the female is like *angustitarse*. The anal lobes, however, are more crescent-shaped (Fig. 31).

The larva, pupa and cocoon are much like those of the *angustitarse* group and they cannot be separately characterized by a consistent feature.

Other Groups

Rubtzov (1962) has included under the genus *Eusimulium*, 30 species which he has divided into three groups. All of the species, as he has illustrated them, have long parameral spines somewhat like those of the *rivuli* group discussed above. None of these species were available for study, but a single North American species, *johannseni* Hart appears similar to some of the species that Rubtzov has associated with *batoense* Edw. The male and female genitalia of *johannseni* are shown in Figs. 22 and 44. This species appears to indicate a relationship between the *Eusimulium*-group and other groups of *Simulium*, some of which have been referred by some authors to *Eusimulium* because of the presence of hair on the basal portion of the radius. These problems are dealt with in the next section.

The foregoing remarks have been a summary and comparison of the morphological structures of the adults and immature stages of the *Eusimulium*-group. Emphasis has been placed on the external genitalia of the male because of the complexity and variability of their structure. The three major components, the clasper, paramere and ventral plate show progressive changes from one group to another, and these three structures are re-illustrated in Fig. 86, using one or two species from each group. A more detailed diagram of the intra- and inter-group linkages is presented in Fig. 87. As was indicated earlier in this section, alternative arrangements also seem possible; only the relationships most probable with the present information are shown in Fig. 87. In such a diagram there can be little indication of the time element, i.e. the relative age of each group.

In formulating relationships between species, a comparison of the cytological and morphological approaches has been mutually beneficial. Concurrently with the present study, Dunbar (1962) examined the gross cytology of most of the pertinent Ontario species. His preliminary groupings were based primarily on the position of the nucleolus, the degree of pairing and other features, and are essentially similar to those arrived at in the course of this study.

PHYLOGENY OF THE FAMILY SIMULIIDAE

In a discussion of the phylogeny of any large and varied group, it seems logical to begin by selecting from the array of known forms, those which appear to be the most primitive. It is usually an easy matter to single out a few forms, which by peculiarities of their morphology and distribution suggest primitiveness. It is more difficult, however, to decide whether these peculiarities are genuinely primitive or whether they represent simplification or loss of specialized structures. Thus, the problem of deciding on truly primitive forms in the Simuliidae has aroused much controversy.

Before the discovery of Gymnopais, the genus Prosimulium was considered more primitive than the remaining members of the family. The reasons behind this are probably associated with the absence of spinules on the wing veins, the lack of a calcipala and pedisulcus, the forked radial sector, the second basal cell and the poorly formed cocoon. Parasimulium was also considered primitive for the above reasons, except for the last two (Stone, 1941), but lack of material has limited study of the genus. After the description of Gymnopais by Stone (1949) in which the head fans of the larva are lacking, Prosimulium was believed to be derived from Gymnopais, and thus Gymnopais was considered to be the most primitive form. This belief was strengthened by the peculiar appearance of the adult of G. dicopticus, in which the legs are long and slender, the adult superficially resembling a chironomid. Still later, Stone and Jamnback (1956) described another genus, Twinnia, in which the larvae lacked head fans. Shewell (1958) in discussing the shape of the head of Gymnopais and Twinnia, drew attention to their similarity with the larvae of the Chironomidae. He also indicated that the adult of Twinnia more closely resembled the adult of Prosimulium than did the adult of Gymnopais. The discovery of the first instar of Prosimulium, in which the head fans were also lacking (L. Davies, 1960), appeared to substantiate the evolution of Prosimulium from forms in which head fans were lacking. The assumption that Gymnopais and Twinnia are the most primitive members of the family is apparently widespread; Grenier and Rageau (1961) in discussing the reduction of head fans in the larva of Simulium oviceps, noted that aside from this reduction and the associated ovoid shape of the head, the remaining structures of the larva and adult indicated that they were more closely related to other species of Simulium of that region and not to Gymnopais or Twinnia. In addition, they implied that no one could possibly think of Gymnopais or Twinnia as not being primitive, and thus the larvae of Simulium oviceps must have assumed its chironomoid appearance secondarily.

If it is possible for the larva of *Simulium oviceps* to assume the chironomoid appearance secondarily,it may be argued that the larva of *Gymnopais* and *Twinnia* has also arrived at this condition secondarily, perhaps by a process of neoteny, i.e. by the retention of first instar features throughout larval life. A study of the labrum of a last instar of *Twinnia tibblesi* does not disclose any structures that might be regarded as reduced head fan structures; internally however, a pair of muscles exists which originate on either side of the mid-line just behind the much larger pair of epipharyngeal muscles. These two slender muscles are each inserted on a slender transparent apodeme that arises from the transparent, membranous lateral wall of the labrum. Their small size, and the unsclerotized nature of the points of insertion suggest that their function is considerably reduced. A study of the labrum of *Gymnopais*, however, is more rewarding. In the lateral walls of the labrum are several sclerites (Fig. 58a) which by their shape and position suggest the torma and related sclerites that are found in the head fans of other species. In addition, one of the small sclerites gives rise to a slender, transparent apodeme, and this small sclerite may thus be identified as the torma. (The specimens were not well enough preserved for distinguishing the insertion of the muscle on the apodeme.)

This evidence, in itself, suggests but does not conclusively demonstrate that the larva of *Gymnopais* and *Twinnia* have lost the head fans secondarily. It could be argued that these muscles and sclerites, that are present in the larva of *Gymnopais* and *Twinnia*, are precursors of the fully developed head fan structure, and thus it is necessary to examine in detail the labral structures of some other Nematocera. In this regard, the larvae of *Aedes aegypti* L., *Dixa* sp. and *Chironomus* sp. were studied. In the larva of *Aedes aegypti* (Fig. 58e), the labrum is developed into a complex of hairs and sclerites that are also used for obtaining food; the morphology of these structures has been interpreted by Snodgrass (1959).

The presence of a slender, transparent apodeme, terminating in a small heavily sclerotized semi-circular bar (the 'stirrup apodeme' of Christophers, 1960) on which is inserted a large bipartite muscle with two points of origin on the cephalic apotome is reminiscent of the torma and its musculature in the black-fly larva. In the mosquito larva, a portion of the torma extends laterally and expands to form a small rounded sclerite, the connective sclerite, which extends almost to the base of the hairs of the mouth brush. In *Cnephia strenua* and *Cnephia tonnoiri*, a similar condition exists in which the connective sclerite arises below the middle of the torma (Fig. 58b). There are two basic differences between the mouth brush of the mosquito and the head fan of the black-fly larva, however; in the black fly, the torma is directed antero-laterally and is rotated almost 180° in contrast to the anteriorly directed, unrotated position of the torma in the mosquito larva; thus the connective sclerite arises from the dorsal surface of the torma in the black fly and from its ventral surface in the mosquito, and the point of the invagination of the apodeme for muscle insertion has undergone a similar change in position from a lateral point of attachment in the mosquito to a mesal one in the black fly. These changes of orientation are apparently also accompanied by changes in the movement of the torma itself with regard to the movement of the mouth brushes. In the mosquito larva, the torma tends to be anchored at both ends, and the lateral position of the apodeme suggests that the whole torma is rotated around its long axis during feeding, rather than a back and forth movement along its axis as in the black fly. This rotation can be simulated both by mechanical pressure on the torma and by pulling the muscles in fixed specimens; both of these operations cause the hairs of the mouth brush to fold inward.

A study of the labrum of the larvae of Chironomus has been less revealing. In these larvae, mouth brushes are absent and a pair of sclerites, called premandibles or messores are present on the ventral surface of the labrum. Snodgrass (1959) has called the messores the tormae, although Gouin (1959) has labelled as tormae the sclerites on which the premandibles are articulated. The messores are capable of relatively complex movement; this is achieved by two pairs of muscles, one dorsal to and the other ventral to their articulation on the torma of Gouin (1959). The situation is further complicated by the presence of a third pair of smaller muscles, each inserted on a long, slender apodome invaginated from a small sclerite in the lateral wall of the labrum antero-ventral to the antenna. Perhaps this is the pair of muscles that Cook (in Snodgrass, 1959) has called the tormal muscles, an interpretation which may eventually prove to be the most acceptable.

Thus it seems that homology between the labral structures of the larva of Chironomus and those of the black fly is not obvious and requires further study and interpretation. Nevertheless, the messores are somewhat reminiscent of the epipharyngeal apparatus of the mosquito and black-fly larva, and it may be that what appears to be a single pair of epipharyngeal muscles in the latter two forms has become divided into two pairs of muscles in the chironomid. In all three of these insects, the epipharyngeal apparatus appears to serve somewhat the same function, that of pushing food into the mouth. In the black fly and mosquito, however, it may also be involved in cleaning food particles from the mandibular brushes after they have collected the food from the mouth brushes or head fans.

Regardless of the homologies between the larvae of these three groups, it would appear that the labrum is a complex structure in at least some larval Nematocera. Mouth brushes of a type similar to *Aedes* are also found in *Dixa*, and are illustrated for a tanyderid larva by Johannsen (1933).

The foregoing discussion is intended to show that black-fly larvae are not the only forms among the Nematocera which possess this type of feeding apparatus. If the mouth brushes of a mosquito are indeed homologous with the head fans of the black fly (Smart (in Dumbleton, 1962) has also suggested they are), one would have to conclude that they were both derived from a similar although perhaps simpler structure, thus one would expect a primitive black-fly larva to be almost as well equipped with head fans as an advanced form, but not without them. Therefore, it may be that *Gymnopais* and *Twinnia* have evolved from *Prosimulium*.

This conclusion and the fact that the mature larvae of the remaining simuliid species all possess head fans (although simplified in a few species (Dumbleton, 1962)) makes it necessary to look for other evidence of primitiveness.

Closer study of the structure of the head fans of many species has revealed that in the larvae of *Prosimulium* spp., *Cnephia tonnoiri* and *C. strenua* of Australia, and *Gigantodax igniculum*, the secondary head fan is of the simple type and many fine hairs are present around the edge of the connective sclerite (Figs. 58b, d). In addition, in the two species of *Cnephia* from Australia, the connective sclerite itself arises from below the middle of the torma. In *Gigantodax* there is a suggestion of this condition, but it is not found in *Prosimulium*. In nearly all these species, the cocoon is shapeless and loosely woven, often containing detritus.

Although the adult structure of all black flies is uniform there are a few features which complement the features in the larvae indicating both primitiveness of and relationship among these three groups. One of these is the structure of the paramere in the male. In *Prosimulium* and *Cnephia tonnoiri*, the paramere is broadly and inflexibly attached at its base to the mid-dorsal extension of the basal edge of the basistyle. This inflexible attachment may represent a primitive condition; the articulation found in most other species may be a secondary development. Thus, the paramere of *Prosimulium*, is reminiscent of, and may even be homologous with the inferior lobe of the male of *Chironomus*. In *Prosimulium* and *Cnephia tonnoiri*, the paramere is rounded apically and no spines are associated with it, but in *Gigantodax* some spines are evidently present (Dalmat, 1955; Wygodzinsky, 1949), but the reduction of the basal arms of the ventral plate and corresponding enlargement of the median sclerite (as shown for several species of *Gigantodax* by Vargas and Diaz Najera, 1951) is similar to that of certain Nearctic species of *Pro-*

simulium, i.e. *gibsoni* Twinn, *decemarticulatum* Twinn and *vernale* Shewell. In the female of other species of *Prosimulium*, the terminal plates of the genital fork are slender and poorly differentiated; this condition is also found in *Cnephia tonnoiri*. The terminal plates of females of *Gigantodax* are unusually large as are those of the three species of *Prosimulium* mentioned above. Other features of the adult of *Prosimulium* mentioned earlier, particularly wing structures, are not shared by all *Cnephia* of Australia and *Gigantodax*, however. *C. fergusoni* Tonnoir lacks spinules on the wing veins but the other Australian *Cnephias* have them (Mackerras and Mackerras, 1949). All lack the pedisulcus, but the calcipala is particularly large in *Gigantodax* and Australian *Cnephia*.

Two other groups that may prove, when better known, to be members of this primitive assemblage are *Parasimulium* and *Paracnephia*. *Parasimulium furcatum* Malloch has a deeply forked radial sector as in *Prosimulium* but has many unique features (Stone, 1941). One species of *Paracnephia* (*harrisoni* F. & de M.) also has a small fork on the radial sector.

The larvae of the remaining simuliid species differ in possessing secondary fan rays of the more complex type (Fig. 58f) but some species have other larval structures that are reminiscent of *Gigantodax*, suggesting an intermediate group, of later derivation. In *Austrosimulium*, a member of this intermediate group, the larvae of some species possess a ring sclerite encircling the posterior ring of hooks as in *Gigantodax* (Fig. 57b). Also in all species of *Austrosimulium*, as in *Gigantodax*, the anterior arms of the anal sclerite have posteriorly directed struts (Fig. 57a) (Mackerras & Mackerras, 1948; Dumbleton, 1960, 1962a). The larvae of some *Austrosimulium* possess ventral tubercles, in common with some species of *Gigantodax*. The wing venation of *Austrosimulium* is essentially like that of *Gigantodax*. The basal cell is small in both groups and the radial sector tends to be fused with the costa for most of its length beyond the end of the radius, especially in the former. In *Austrosimulium*, vein cu-2 is sinuous, while it is straight in *Gigantodax*. *Austrosimulium* spp. possess a well-formed cocoon, and in at least certain species of *Gigantodax*, eg. *G. abalosi* Wygodzinsky, the cocoon tends to show some complexity (in having a floor distinct from the remaining part) while lacking a well-defined anterior margin (Wygodzinsky, 1958).

Other miscellaneous species of *Cnephia* s. lat. show affinities to *Austrosimulium* and *Gigantodax*. Most of these are Holarctic, and include *Cnephia mutata* and *C. emergens* which are closely related to *Stegopterna richteri* End. (*C. mutata* was included in *Stegopterna* by Rubtzov (1961)) and are referred to henceforth as *Stegopterna*. Other Nearctic species of *Cnephia*, i.e. *C. denaria*, *C. abdita*, *C. abditoides* and probably *C. stewarti*, show relations to

Greniera fabri Doby & David and are referred to collectively below as *Greniera*, although they appear to be related to *Stegopterna* as well (*fabri* is intermediate in larval and adult features between *mutata* and *denaria*). A third group, discussed by Dalmat (1955), and by Vargas and Diaz Najera (1957) includes *Cnephia aguirrei* (Dalmat), *C. grenieri* V. & D.N., *C. pachecolunai* (De Leon) and *C. roblesi* (De Leon). These four are associated with *Stegopterna* and *Greniera* only on the basis of illustrations of the genitalia (Dalmat, 1955; Vargas & Diaz Najera, 1948, 1957). *Lutzsimulium* probably also is related to the foregoing species (d'Andretta and d'Andretta, 1948, 1952).

In these species of *Cnephia*, and all of *Greniera* and *Stegopterna*, the male parameres lack spines (or they are extremely small in some species), the ventral plate is square or triangular, covered with hair, and the dististyle is short, evenly tapered with two or three short terminal spines. Other adult structures, however, particularly features of the wing, vary widely; for example, *stewarti*, *fabri* and *denaria* have a forked radial sector, although it is very small, while the other species do not. Spinules are absent in *abdita*, *abditoides* and *denaria*, are poorly differentiated in *fabri* and are few in number in *emergens*, whereas in *mutata* they are more numerous. The calcipala is relatively large in *mutata*, moderate in *emergens*, *fabri* and *grenieri*, but nearly lacking in *denaria*, *abdita* and *abdi-*

toides. In spite of these inconsistencies, it is apparent from the overall structure of the immature and adult stages that relationships do exist among these species, and to *Austrosimulium* as well, and it is concluded that characters of the wing such as the forked or unforked condition of the radial sector, and the presence or absence of spinules on the costa are of reduced value in indicating relationships.

The remaining species of the family fall into two groups, *Cnephia*, in a more restricted sense, and *Simulium*, with many subgroups. A few species of *Cnephia* s. str. (e.g. *pecuaria* (Riley), *dacotensis*, and *invenusta* (Walker)) share some of the features of the earlier groups, i.e. *Greniera*, for example, having the radial sector forked near its apex. All species of *Cnephia* s. str. and *Simulium*, however, have at least one long conspicuous spine on the paramere of the male, and most have a comb-like row of spines. In nearly all species of *Cnephia*, the calcipala is small to minute; in a few species, however, its size approaches the size typical of *Simulium*. The pedisulcus in some *Cnephias* (*dacotensis*, *pecuaria*, *saskatchewana* Shewell and others) is represented by a wrinkled relatively hairless area on the dorsal surface of the hind basitarsus: in other species, however (e.g. *tungus* Rubtzov), the pedisulcus is almost as well formed as in members of *Simulium*.

The larvae of *Cnephia* s. str. lack ventral tubercles, and as a rule the hypostomial teeth are small and little differentiated one from another. A peculiar feature of many species is the elongate postgenal cleft which extends to, or even ahead of, the labio-hypostomial fold. The antennae are usually small, but the larvae are not otherwise peculiarly differentiated from those of *Simulium*. In a few species, the cocoon is poorly formed (i.e. *dacotensis*, *borealis* (Malloch) and *pecuaria*) while in most other species it has a discrete anterior opening usually raised, collar-like, above the surface (boot-shaped). The anterior opening, however, does not have a thickened edge.

The *rivuli* group appears to be intermediate in relation to *Cnephia* s. str., *Simulium* s. lat., and *Stegopterna* and *Greniera*, showing some features of each. Larvae of the *rivuli* group have ventral tubercles, and many of them show strongly elevated lateral hypostomial teeth, small postgenal cleft, and elongate antennae that are characteristic of larvae of *Stegopterna* and *Greniera*. Even the shape of the head and of the head pattern are similar. It is principally this similarity in the larvae of the *rivuli* group and *Greniera* that has strengthened the hypothesis that *Eusimulium* is derived from *Greniera* and *Stegopterna* rather than from *Cnephia* s. str. On the other hand, the male genitalia of the *rivuli* group show resemblances to most species of *Cnephia* s. str., particularly in the structure of the paramere in which there is a comb-like row of long spines. The female genitalia have features in common to both *Cnephia* and *Greniera*; indeed there is little that can be said to distinguish these three groups on the basis of female genitalia. Furthermore, the calcipala is minute in most species, and the pedisulcus is at most a shallow depression on the dorsal surface of the basitarsus. The affinities of the *rivuli* group with the other *Eusimulium* groups have been discussed in the previous section, and have been drawn principally from the similarity of the immature stages of some members of this group with *baffinense*.

The problem of the phylogeny of the remaining groups of *Simulium*, exclusive of *Eusimulium*, is a separate and involved problem, and cannot be fully discussed at this time. The relationship of these other groups to *Eusimulium*, however, may be discussed, but unfortunately owing to the lack of material of several of Rubtzov's (1962) groups (e.g., the *montium* group and the *batoense* group) only an incomplete picture can be drawn. A single North American species which is probably important in this respect is *johannseni* Hart. It has always been placed in *Eusimulium* by North American authors because the basal portion of the radius is haired. The genitalia of both sexes, however, suggest a closer relationship with other *Simuliums*; yet the presence of a minute spine on the paramere itself (Fig. 44) (in addition to the comb-like row) and to some extent the appearance of the female and of the immature stages suggest some features of the euryadminiculum group. In this respect, the absence of a complete precoxal bridge in these species (as well as in Simulium s. str.) may be of significance. An apparently basic difference (one which may prove unimportant in the future, however) is the position of the comb-like row of spines in relation to the parameral arm. In johannseni it is a single row associated with the parameral arm (as in Cnephia s. str., the rivuli group and Simulium s. str.) while in euryadminiculum the spines are in a patch on the dorso-lateral membrane of the aedeagus.

Several other groups of Simulium have the basal part of the radius haired and have thus been placed in Eusimulium at various times. One of these, Wilhelmia, is represented by many species in the Palaearctic and Ethiopian regions. Although it may be distantly related to johannseni, it does not seem to have any closer connections to Eusimulium as it is used in this thesis. Another group of African species with the radius completely haired, exemplified by dentulosum Roubaud, may have affinities with Wilhelmia and possibly be distantly related to Eusimulium, but its position, beyond this assertion, is not evident at present. The parameres of both Wilhelmia and dentulosum have a comb-like row of spines.

In South America, the simuliid fauna seems to be made up almost entirely of indigenous groups of Simulium; they have been classified into several subgenera by Vargas et al (1946). These authors recognized that although many of the Neotropical species had a completely haired radius, they were not related closely to *Eusimulium*, although earlier workers placed them in *Eusimulium* (e.g. Pinto, 1931).

Only one other group of *Simulium* comprising species that have a completely haired radius are found in Australia and the surrounding territory: the genitalia of *S. nicholsoni* M. & M. are not unlike some *Austrosimulium*, although they are probably not closely related to this genus. They appear unrelated to *Eusimulium*, however.

The remaining members of *Simulium* lack hair on the basal portion of the radius. Even these species, however, do not form a homogeneous group; the many Palaearctic species (e.g. *ornatum* Mg.and many others) are closely related to the Nearctic species (e.g. *venustum* Say, *decorum* Wlk. and *corbis* Twinn) and additional Oriental forms (Puri, 1932) and seem unrelated to the Neotropical species mentioned earlier.

A few species, evidently of Neotropical origin, are known also from North America (e.g. species of *Psilopelmia*, *Hearlea*, *Hagenomyia*, *Hemicnetha* and *Neosimulium*) each with many more representatives in Mexico, Central and South America.

The foregoing account has attempted to show that there are three basic phylogenetic levels in the Simuliidae. What appear to be the oldest elements are widely scattered; *Parasimulium* in western

North America, *Paracnephia* in South Africa, another similar group (still referred to *Cnephia*) in Australia, *Gigantodax* in southern South America and the Andes of the remainder of the continent, and *Prosimulium* in arctic and north temperate regions, with limited southern alpine extensions. Superimposed upon this relict fauna is one of intermediate complexity; *Austrosimulium* throughout the southern parts of the Southern Hemisphere, except in Africa, and *Stegopterna* and *Greniera* scattered throughout the Northern Hemisphere. These two main groups are connected by various species probably distributed along the entire Andean chain.

The highest assemblage comprises *Cnephia* s. str. and *Simulium* with many subgroups. Even within this more recent assemblage, however, there appears to be two phylogenetic levels. One assemblage representing an older level consists of *Cnephia* s. str. in the Holarctic region, *Eusimulium* in the Holarctic and Ethiopian regions (with a small extension into the Oriental and Australian regions), *Wilhelmia* in the Palaearctic and Ethiopian regions and many other subgroups of *Simulium* in the Neotropical region, a few extending into North America. The other assemblage, *Simulium* s. str., which is found throughout the Holarctic region, with extensions into the Oriental region and the Neotropical region, appears to be the most recently derived.

These patterns of phylogeny are graphically summarized in Fig. 88.

Darlington (1957) has shown, for each of the vertebrate classes, that their distribution conforms to a pattern. The oldest, relict forms are distributed discontinuously, and are usually present in Australia and Africa, but may occur elsewhere. The permanently isolated nature of the Australian region, and the isolation of South America (and to some extent, Africa) during the Tertiary has allowed the faunas of these areas to develop a high degree of endemism. Even though the Simuliidae are probably capable of dispersal over wider water barriers than are most vertebrates, their zoogeography is not unlike that postulated by Darlington (1957). A notable difference, however, is the strong Antarctic affiliation among Paracnephia, the Australian Cnephias and Gigantodax, noted by Mackerras (1950), which Darlington indicated was often true of insect groups but not of vertebrates. Nevertheless, the present distribution of marsupials, in Australia and South America, was accounted for by original dispersal from Asia and North America, from a once much larger marsupial fauna. The presence of Prosimulium in the north might suggest that the same was true of these relict simuliid species.

A more detailed case may be made for *Eusimulium*. As was shown in earlier sections, the *Eusimulium* group is primarily Holarctic, although it also forms a considerable part of the African fauna. Only a few species appear to be present in the Oriental and Australian regions. As was indicated earlier, the African species show broad relationship to several Palaearctic groups of *Eusimulium* and it is presumed that development in these two regions has taken place simultaneously from some common ancestral stock. This parallel development has probably required a long period; the few species of *Eusimulium* in the Oriental and Australian regions, and *ruficorne*, *nigritarse* and *aureosimile* of the Ethiopian region, show close relationship with Palaearctic species and have probably invaded these regions in relatively recent times. There is, as might be expected, no essential differences between *Eusimulium* fauna of the Palaearctic and Nearctic regions, except perhaps the Nearctic fauna is not quite as diverse and appears to be derived from the Palaearctic fauna. Darlington has also shown this to be true of vertebrate groups. Perhaps the most notable deletion from the Nearctic fauna is the *angustitarse* group, and the presence of only a single species, *furculatum*, from group 4. The Nearctic *Eusimuliums* have extended south only as far as the mountains of Guatemala.

The remaining groups of *Simulium* are more difficult to categorize zoogeographically, perhaps because their phylogeny has not been as fully worked out. The *Wilhelmia* group is perhaps the most interesting because it seems to parallel the *Eusimulium* group in its development in Africa and Asia, although it has not extended into North America. Another distinctive portion of *Simulium*, zoogeographically, are the many groups from South America. Of these, a few species have spread into North America, the majority only into the mountains of western North America, with a pair of closely related species (*pictipes* Hagen and *longistylatum* Shewell) occurring in the east. The remaining *Simuliums* are of the *Simulium* s. str. group and appear to be Holarctic with Oriental and Neotropical extensions. Their development and spread also seems to parallel that of *Eusimulium*.

SPECIATION

The previous sections have been primarily devoted to a comparative study of the morphology, ecology and distribution, both geographically and seasonally. In this section these data form the basis for the development of a hypothesis of speciation.

Controversy over the process of speciation and the definition of species is as old as the theory of evolution itself. Some advancement has been made in understanding and even experimenting with the process of evolution, but the definition of a species remains difficult largely because of the variety of organisms and because the very process of speciation may not be an immediate step. Yet the species problem is, as Dodson (1960) has emphasized, one of the most basic problems of biology and certainly of systematics.

The difficulty in defining species is due partly to the variety among organisms and partly to an insufficient understanding of the process of speciation. This insufficiency is reflected in the current prevalence of at least two schools of thought. The older discipline, called neo-Darwinism, is an outgrowth of Darwin's own philosophy. Darwin (1859) conceived of the process of natural selection working on variability as a mechanism for the change in species, and extended it to explain the production of new species from isolated remnants of parent species. Dobzhansky (1937) was one of the first (Dodson, 1960) to incorporate the accumulated knowledge of heredity into this scheme as a mechanism for creating variability and thus as a basis for the action of natural selection. The crucial step, that of how a new species becomes free of the parent species and begins its separate existence, took place when point mutations had built up in the two different populations after long periods of isolation to the level where hybridization resulted in unbalanced assortment of genes, producing poor viability or sterility in hybrids (Dobzhansky, 1937). This theory is further refined (Sinnott, Dunn & Dobzhansky, 1958) by introducing reproductive isolating mechanisms between the two populations which would keep them separate when they became sympatric again. These authors listed several forms of isolating mechanisms: ecological, seasonal, sexual, mechanical and gametic. These mechanisms reduce mating or fertilization and thus assist alone, or more often in combination, in keeping the two species apart. The process is further assisted by some degree of hybrid sterility or inviability.

Goldschmidt (1940) found this hypothesis of species formation unacceptable. He concluded (p. 396): "Micro-evolution (i.e. raciation), especially geographic variation, adapts the species to the different conditions existing in the available range of distribution. Micro-evolution does not lead beyond the confines of the species, and the typical products of micro-evolution, the geographic races, are not incipient species. There is no such category as incipient species.". Essentially he believed that the production of a new species (and also higher categories) is a single relatively large step involving chromosomal rearrangement, and consequently results in a new genetic system.

Goldschmidt struck at what he considered to be the weak point in the neo-Darwinian theory by attacking the whole concept of the slow accumulation of micro-mutation over a long period of time. He rejected the particulate theory of the gene considering that the chromosome functioned as a unit and that rearrangement within it, now called 'position effect', could also affect the phenotype and that new species were produced in this way. When his arguments and evidence are thoroughly investigated however, it would appear that such chromosomal rearrangements would serve as reproductive isolating mechanisms akin to hybrid sterility on a chromosomal rather than genic level and thus would be one of the requirements of the neo-Darwinian theory as developed above.

Another cytological mechanism that may play a role in speciation is that of the suppression of crossover in a heterozygous paracentric inversion (Rothfels, pers. comm.). It is presumed that the build-up of two different gene sequences could take place in the two different homozygotes because the formation of a chromosomal bridge at meiosis connecting the two centromeres after a single crossover, would render the gamete inviable. This might provide a mechanism causing hybrid sterility provided crossover often occurred in that region of the chromosome. It could not, however, lead to speciation until another isolating mechanism arose, which prevented the production of the inviable heterozygotes.

The evidence obtained in the study of the Ontario species of Eusimulium has revealed two basic points. The first is that most of the species may, on morphological grounds, be associated in pairs. Examples of very similar pairs are: anatinum and innocens, euryadminiculum and emarginatum, quebecense and impar, and aureum A and B. Dunbar (1962) has also shown that latipes and congareenarum each have two sibling species, but sufficient morphological evidence has yet to be found. Other, less similar associations may be found, e.g. excisum and rivuli. Such examples are not restricted to the Eusimulium group; many other examples are known in Prosimulium (e.g. fuscum S. & D. and mixtum S. & D. (Syme and Davies, 1958), and magnum D. & S. and multidentatum Twinn), in Cnephia (e.g. mutata and emergens, and abdita and abditoides), and in Simulium (e.g. venustum and verecundum S. & J., and pictipes and longistylatum).

The second basic point is that the closer the morphological similarity is between two species, the more similar, although never identical, is their ecology and distribution. The evidence is incomplete, but none of it appears to be contradictory.

It appears that the controversy revolves around the problem of which came first, the new race or species, or the isolating mechanism. The neo-Darwinian theory holds that the isolating mechanism or mechanisms arose after raciation had taken place in isolation, thus producing two new separate species which then came together again but remained distinct. This is termed 'allopatric speciation'. Goldschmidt (1940) believed that the species did not arise until after the isolating mechanisms occurred. He chose only chromosomal rearrangement, which he called 'systemic mutation', as an alternative to micro-mutation and evidently considered it to be the only alternative. This hypothesis has merit but has not been generally accepted (Dodson, 1960) because it is hidden in the overall idea of macro-evolution, i.e. "The first bird hatched from a reptilian egg" (Goldschmidt, 1940).

It is evident that reproductive isolating mechanisms play a decisive role in both of these theories of speciation and it is necessary to enlarge on the known mechanisms and to compare them one to another as to their possible effectiveness in the process of speciation. The various isolating mechanisms mentioned above (including ecological, temporal, sexual, mechanical and gametic isolation as well as hybrid inviability or sterility) may play different roles at different times in the process of speciation. The first two mechanisms, ecological and temporal or seasonal isolation, undoubtedly exist and are well documented. In the examples usually cited (Sinnott, Dunn & Dobzhansky, 1958; Ross 1962) however, and probably in many other less studied cases as well, some overlap of both habitat and breeding season does occur and hybridization takes place also. This evidence weakens the argument that these isolating mechanisms could be, in themselves, the primary causes of speciation in the absence of geographic isolation, although their assisting role cannot be disputed.

The remaining isolating mechanisms, sexual (concerning differences in behaviour), mechanical (or structural), gametic, hybrid inviability and hybrid sterility, concern the failure of the reproductive process and deserve special attention. Each of these represents a failure at a different point in the reproductive process, from the meeting of the sexes to the production of fertile offspring, and all have the same end result, i.e. no offspring are produced. It is evident, however, that sexual isolation is in a special category, not only because it is of primary importance, for if it operates, no other mechanism can take effect subsequent to it, but because alternative choices of mates are possible, influenced only by an inherited behaviour pattern. The remaining isolating mechanisms can only operate if and after the wrong choice has been made, they are irreversible and all produce essentially the same result, that of preventing further inheritance. It is axiomatic that some degree of sexual isolation must exist between different species if there are no other isolating mechanisms, otherwise they would not remain different species.

Therefore, the process of speciation must involve, at some point, a change in sexual behaviour of the new form from that of the ancestral form. The present problem is thus to determine whether this change plays an active role in speciation, and how it is implemented, for it is difficult to envisage changes in both recognition and response of both sexes of sufficient magnitude taking place among sympatric forms, that would render more than one individual totally isolated sexually.

The role of mechanical, or structural, isolation (in which the genitalia, especially of insects, are structurally incompatible between two species, thus preventing interbreeding) is probably of negligible importance. Close morphological similarity nearly always includes close similarity in the genitalia of both sexes, particularly in the Simuliidae, and it is difficult to see how the slight differences between the genitalia of similar species could be important in the process of speciation. Even if it did, the result would then be similar to that of hybrid inviability. Gametic isolation in which the gametes, particularly the sperms, fail to bring about fertilization is also, in result at least, similar to that of hybrid inviability.

Hybrid inviability and hybrid sterility has been repeatedly demonstrated both between and within species, particularly in species of plants and insects. Several examples are summarized by Ross (1962). Such cases may be universal among species of sexually reproducing organisms. Essentially, members of the species from widely separate areas of the range show some degree of inter-sterility which is lacking when each is crossed with its neighbouring members. Thus the two distinct inter-sterile populations may exchange genes through intermediate members. Should the range of the species as a whole shrink, as a result of decimation or extinction of habitat, or of other factors, isolated pockets would result and gene exchange would be interrupted. Such range changes involving decimation and expansion have been discussed by Ross (1962) and are probably universal phenomena. If such pockets are left in isolation for long periods of time, divergence would ensue and it can be argued and evidently is assumed by proponents of neo-Darwinism that sterility barriers would, by the disappearance of neighbouring populations, leave the isolated population an incipient species. Many instances are known in North America where such isolated populations on mountain tops and other islands of habitat have been left by retreating glaciation (e. g. the Cyprus hills, Black hills, Ozarks and Riding Mountains). Many of the organisms in these areas (especially insects and plants) have diverged slightly from their parent population in the Arctic or forest regions many hundreds of miles distant, but the existence of sterility barriers has not been recorded. It cannot be denied, however, that this method of isolation can and does account for the production of new species.

Discontinuity is a characteristic feature of the range of probably every widespread organism, if only because the habitat is discontinuous. Among animals, such as certain insects whose immature stages occupy a different habitat than their adults, this tendency to discontinuity will be greatly increased. This discontinuity of range is conceded by all students of population biology, and the realization of inter-sterility among far-flung members is increasing (Ross, 1962).

The hypothesis of speciation, developed here, requires the existence of a fragmented range of one species where inter-sterility in some degree exists between the members of one fragment and the remaining members. If the population of a fragment is small enough, the behaviour associated with sexual recognition may change by genetic drift. Selection for the response from the opposite sex will be immediate. If the change is too great, it will probably be lost. Such a change to be successful must be considered only as a shift in the relative proportions of the components of the total process of sexual selection. These components are known for relatively few animals but in general are fewer and more stereotyped among lower animals, particularly among insects. Nevertheless, they represent several steps involving recognition of the opposite sex by both partners and it is difficult to conceive of any process of sexual selection among insects which depends on only a single step or a single chemical compound. Even in the latter case, small chemical changes in its structure might not fall beyond the olfactory response of all available members of the opposite sex. This change in behaviour need not be so large as to prevent matings with the parent population if and when they become sympatric again, for if hybrid sterility exists, selection for sexual isolation will occur. This has been shown experimentally by Koopman (1950) using two species of Drosophila, between which sexual isolation was weak at low temperatures, and the hybrid males were sterile. Koopman bred the two species together generation after generation, and by eliminating all the hybrids after each generation he artificially imposed an absolute hybrid sterility. In fewer than seven generations, the percentage of hybrids dropped from an initial 20 to 50% to less than 2% and remained low thereafter, fluctuating every few generations back to 10% or less. This experiment demonstrates that the presence of hybrid sterility can cause a rapid increase or reinforcement in the existing sexual isolation.

It was indicated earlier in this section that crossover within a paracentric inversion would lead to inviability of that gamete. If crossover in the inverted region were frequent, gene recombination would thus be suppressed within the inverted segment, leading to the formation of two different gene sequences. If genes controlling sexual behaviour were located within the inverted region, it is conceivable that two different patterns of sexual behaviour might develop sympatrically and it would not be necessary to begin with an isolated fragment.

It is interesting to note that in fully analyzed cases, closely related pairs of species of black flies differ in one or more fixed inversions (in which one sequence is restricted to one species, the other sequence to the other, and heterokaryotypes, i.e. chromosomal inversion polymorphs, are unknown), and that each species has its own peculiar set of "floating" inversions (those in which the homokaryotypic standard sequence, the homokaryotypic inverted sequence and the heterokaryotype all occur in the same population) (Dunbar, 1959, 1962). The two forms A and B of aureum differ by two fixed, as well as several floating inversions.

In an effort to determine whether hybrid sterility (which is presumed to exist) resulted from the existence of the two large paracentric inversions on chromosome I or whether it is caused by genic factors, such as failure of synapsis, hybridization between the two forms was attempted. Mating was circumvented by artificial fertilization of the ripe eggs of a female (believed to be of type A) using sperm from the spermatheca of a gravid and inseminated female (believed to be of type B). Only one trial was possible, but the percentage of fertilization appeared to be as high as that obtained in other trials when sperm from the female's own spermatheca was used. Embryos developed to the "eye spot" stage before diapause occurred. This was broken by keeping the eggs at 35° to 40°F. for at least two months and some of the eggs had developed almost to the point of hatching at the time of writing. The verification of the hybrid nature of the eggs and of the mechanism of hybrid sterility, if any, must await the rearing of these and more eggs similarly obtained in the future.

In a detailed study of six "races" of *Drosophila paulistorum* Dobzhansky and Pavan, Dobzhansky and Pavlovsky (1962) found that the arrangement of floating inversions was different in each "race" and that, with one exception, these "races" were isolated by sexual and sterility barriers. These authors indicated that the work of Ehrman showed that sexual isolation in *D. paulistorum* was determined polygenically, while hybrid sterility was caused by a maternal cytoplasmic mechanism. From these data these authors concluded that sexual isolation and hybrid sterility are the two chief reproductive isolating mechanisms between "races" of *D. paulistorum*. They speculate that "sterility is the older of the two isolating barriers, and that sexual isolation has been built up by natural selection to minimize the reproductive losses which might result from production of sterile hybrids.". Furthermore, they suggest that a "peripheral colony" isolated from the main population by sterility barriers might give rise to an incipient species which could expand its range to become partly sympatric with the ancestral population without interbreeding with it. These authors have thus arrived at a hypothesis of speciation similar to that outlined earlier, using a different approach than that in the present study.

The process of speciation that has been presented in this section from various viewpoints begins with inter-sterility among members of a population of a species of organisms, followed by a change in the sexual behaviour among some of its members, ideally, those forming a small isolated, population fragment. It does not require any new concept or any change that is not also required in the other theories of speciation mentioned above. No mutations either large or small are required and thus it is not necessary to change the point mutation theory, for one may presume that if variation in the sexual behaviour exists, mutations have already occurred. Similarly, long periods of time are not necessarily required and the degree of morphological differentiation or raciation is immaterial. The critical factor is the complementary action of the two mechanisms and may be expressed as a ratio between them. Thus, if hybrid sterility is low, as it evidently is among various groups of vertebrates and plants in experimental circumstances, sexual isolation in nature must be correspondingly greater and thus if changes take place during isolation they must be of greater magnitude before speciation can occur. Although this process requires geographic isolation and hence is allopatric, great distance or relatively enormous barriers, geological or ecological, are not always necessary, for the nearest separate population may not be many miles away.

Other forms of isolation, ecological and temporal, may assist the process but are not necessary to it. Their interaction is probably required later, however; after the two new species have become sympatric, ecological forces of competition begin to operate on them selecting those individuals which tend to avoid the competition by living in a slightly different habitat. And just as sexual selection favoured those which mated conspecifically, it would also tend to select for a different breeding season or place for each of the new forms.

This hypothesis is applicable only to sexually reproducing species. It cannot be applied to uniparental or extinct organisms, and does not conflict with other known mechanisms of speciation in many plants and a few animals, such as polyploidy and translocation. But for the many hundreds of thousands of insect species, many of which are similar and difficult to interpret and a few of which are involved here, it provides criteria for their recognition, and distinction from races or subspecies.

Dodson (1960) and Simpson (1961) have summarized the opinions that have led to definitions of species. Most of them are based on inter-specific sterility and one of the latest and perhaps one of the best has been offered by Mayr (in Simpson, 1961): "a species is a group of actually or potentially interbreeding populations that is reproductively isolated from other such groups". Simpson (1961) in an effort to go beyond this genetic definition has proposed one that is intended to be inclusive of fossils and uniparental organisms as well: "an evolutionary species is a lineage evolving separately from others and with its own unitary evolutionary role and tendencies". It is most appropriate, but while defining species quite well, it does not provide criteria for their recognition. The hypothesis described above does not require the alteration of Mayr's definition but only a further explanation of the terms "inter-breeding" and "reproductively isolated". Thus, interbreeding must be considered in the sense of mating readily with one another even though they do not leave any offspring, and the term "reproductive isolation" must include hybrid sterility as well as any other known mechanisms.

SUMMARY

(1) Rearing and morphological studies have demonstrated the existence of at least seventeen species of the *Eusimulium* group of black flies in Ontario, including five new species (i.e. *aestivum*, *anatinum*, *emarginatum*, *excisum* and *impar*). Each of the Ontario species is described, the adult and last larval stages are illustrated, and keys for the identification of the female, male, mature larva, and pupa are given.

(2) The available knowledge of the blood feeding habits of the adult females is summarized and data on the seasonal occurrence and on the type of stream inhabited by the larva are presented from a comparative point of view.

(3) The morphological and ecological findings are used as the basis for grouping the species and of formulating an interpretation of the phylogeny of these groups in relation to the world fauna of *Eusimulium*.

(4) A brief and tentative interpretation of the phylogeny of the family Simuliidae, based on larval as well as adult structure, is presented, stressing the most probable ancestry of the *Eusimulium*-group. One new species, *Cnephia abditoides*, and four other related forms are described in this connection.

(5) The phylogenetic interpretation of the Simuliidae is integrated with the peculiarities of distribution of the various elements of the family to form a hypothesis of black-fly zoogeography.

(6) Morphological similarities among the Ontario species have indicated that most of them may be associated in pairs, i.e., close structural similarity is accompanied by close, but not identical, features of their ecology and distribution. A hypothesis of speciation is proposed which involves the complementary action of two isolating mechanisms, first, hybrid sterility or inviability followed by a change in sexual behaviour.

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TABLE I

Collections of immature stages of species of <u>Eusimulium</u> from a small eurythermal stream near Huntsville, Ontario, showing sequence of development over two seasons

		1960				1961					
Species	Stage Present	2-V	12-V	19-V	3-VI	18-IV	1-V	10-V	18-V	31-V	6-VI
rivuli	IL		15*			44	61				
	ML	2		3*		1	21	3			
	P	37	3				16	18	1		
	E	3	4				3	32	11	1	
excisum	IL						8				
	ML	1									
	P	7		2			1				
	E									3	
anatinum	IL		1					2			
	ML	3	1	1					1		
	P	21							1	1	
	E	10		3					2		1
innocens	IL			1							
	ML										
	P									1	
	E										
latipes	IL	38	34	9		14	74	>100	>100	19	
	ML	2	80					7	40	33	
	P		192	24				2	7	23	2
	E		54	12	+			2		50	24
croxtoni	IL			2						28	15
	ML			2						3	9
	P		1	1							
	E				+						
gouldingi	IL										
	ML										
	P			6						1	
	E										
aureum	IL		29	16						3	
	ML		1	41						1	
	P			31							1
	E			223	+						

IL - Immature Larvae

ML - Mature larvae, i.e., those with histoblasts of pupal respiratory organ

P - Pupae

E - Exuviae + - present

* - Larval development inhibited by parasitism with mermithid nematodes or microsporidia.

Fig. 1. Map of Ontario showing the Counties and Districts.

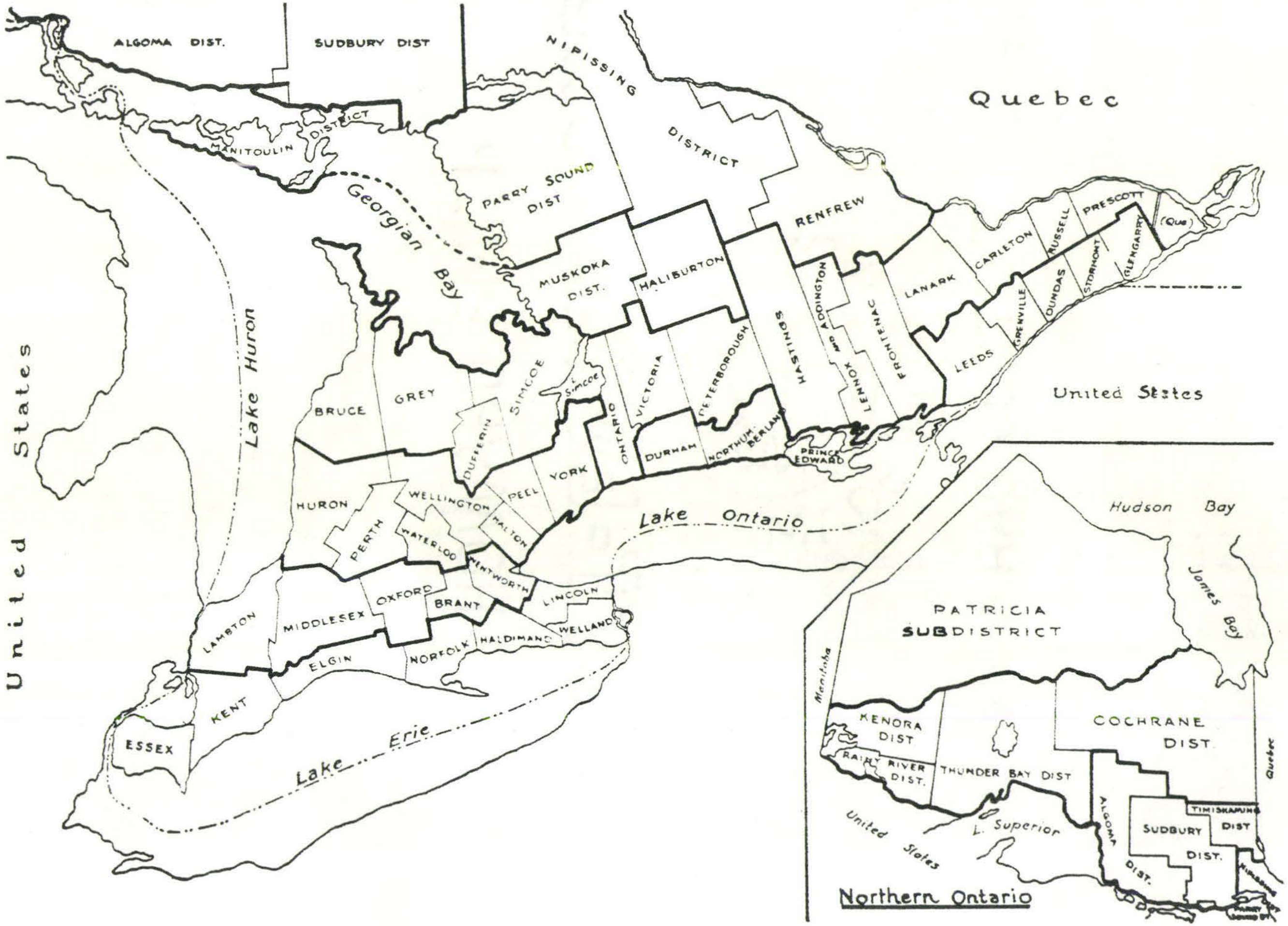

ALGOMA DIST.
SUDBURY DIST
NIPISSING DISTRICT
Quebec
MANITOULIN DISTRICT
Georgian Bay
PARRY SOUND DIST
RENFREW
CARLETON
RUSSELL
PRESCOTT
(Que)
MUSKOKA DIST.
HALIBURTON
LANARK
DUNDAS
STORMONT
GLENGARRY
GRENVILLE
LEEDS
FRONTENAC
LENNOX AND ADDINGTON
HASTINGS
PETERBOROUGH
VICTORIA
ONTARIO
L. Simcoe
SIMCOE
DUFFERIN
GREY
BRUCE
United States
Lake Huron
United States
DURHAM
NORTHUMBERLAND
PRINCE EDWARD
YORK
PEEL
HURON
WELLINGTON
PERTH
WATERLOO
HALTON
WENTWORTH
Lake Ontario
LINCOLN
WELLAND
OXFORD
BRANT
MIDDLESEX
LAMBTON
ELGIN
NORFOLK
HALDIMAND
KENT
ESSEX
Lake Erie
Hudson Bay
James Bay
PATRICIA SUBDISTRICT
Manitoba
KENORA DIST
RAINY RIVER DIST.
THUNDER BAY DIST
COCHRANE DIST.
Quebec
TIMISKAMING DIST
SUDBURY DIST.
ALGOMA DIST.
NIPISSING
PARRY SD. DIST.
United States
L. Superior
Northern Ontario

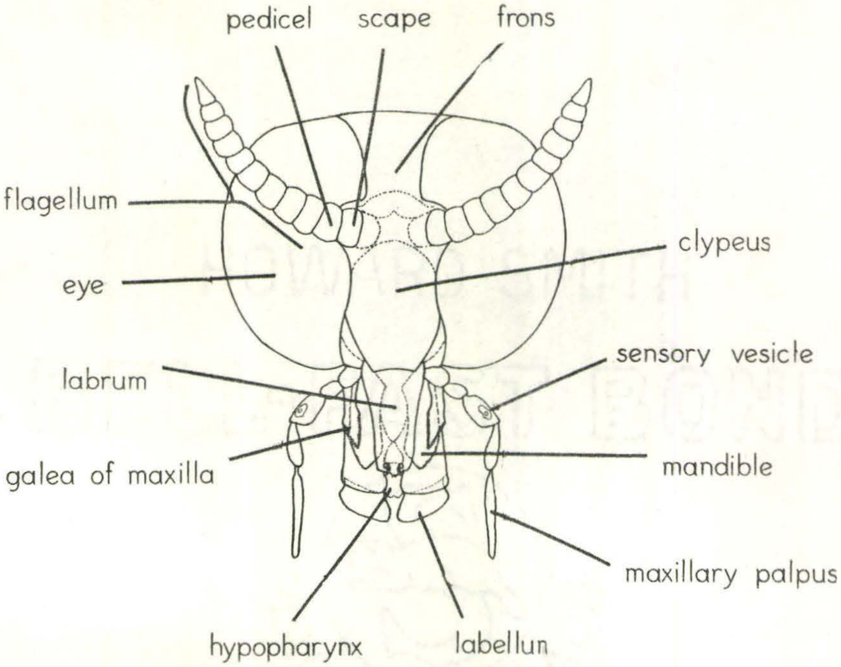
Fig. 1.

Fig. 2. Anterior view of head of adult female of *Simulium*.

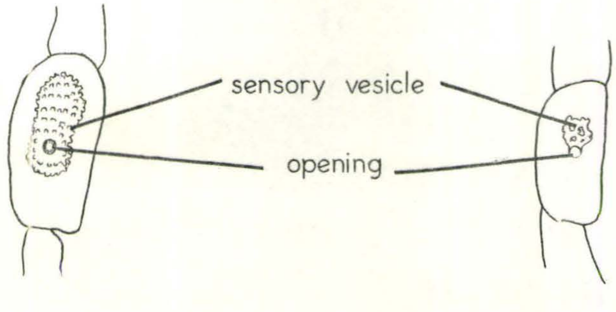
Fig. 3. Anterior view of third segment of maxillary palp of female

a. *S. aestivum*

b. *S. excisum*


pedicel
scape
frons
flagellum
clypeus
eye
sensory vesicle
labrum
galea of maxilla
mandible
maxillary palpus
hypopharynx
labellun

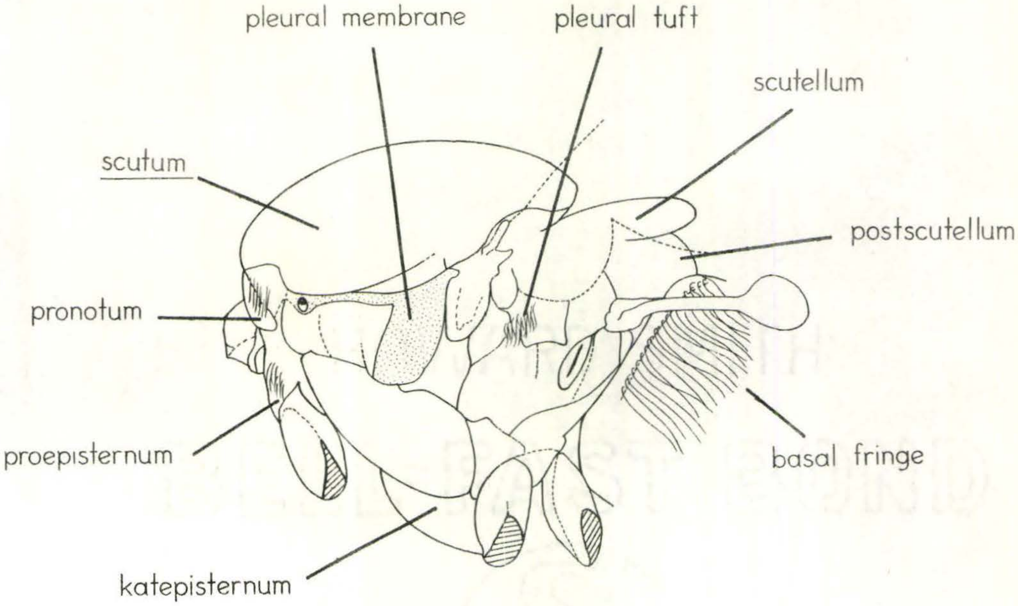
2


sensory vesicle
opening

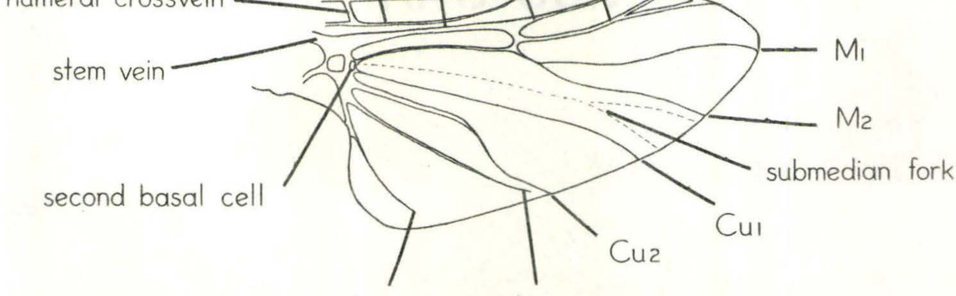
3a 3b

Fig. 4. Left lateral view of thorax of female of *S. euryadminiculum*.

Fig. 5. Dorsal view of right wing of male of *Prosimulium*.


pleural membrane
pleural tuft
scutellum
scutum
postscutellum
pronotum
proepisternum
basal fringe
katepisternum

4


C
Sc
R
R1
Rs
humeral crossvein
stem vein
M1
M2
submedian fork
second basal cell
Cu1
Cu2
An.2
An1

5

Fig. 6a-b. Antero-ventral view of right side of thorax of *S. emarginatum*.

Fig. 6c. Antero-ventral view of thorax of *S. quebecense*.

Fig. 7. Distal portion of right metathoracic leg

a. *S. excisum*

b. *S. latipes*

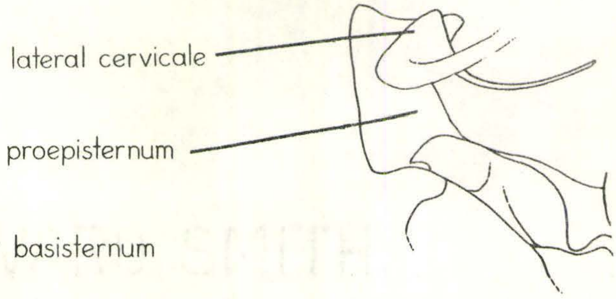
Fig. 8. Internal dorsal arm of metasternum

a. *S. quebecense*

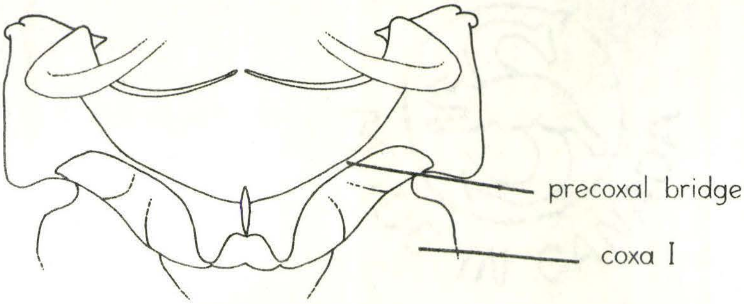
b. *S. pugetense*

Fig. 8c. Metasternum of *S. latipes*.

6a



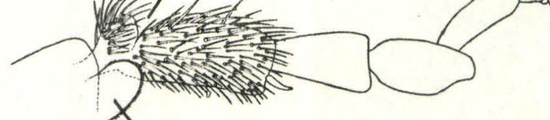
6b



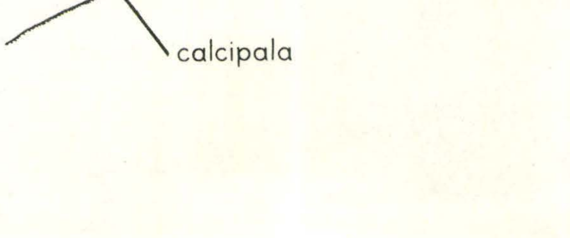
6c

8a

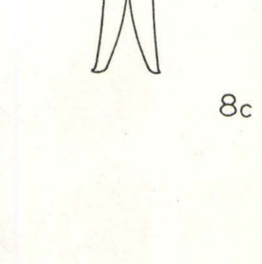
8b.



7a



7b

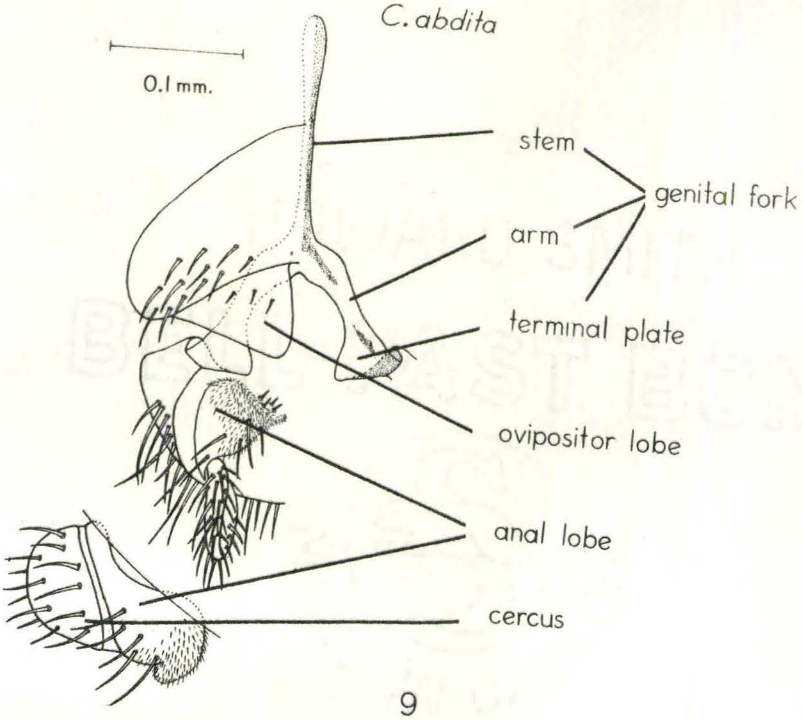


8c

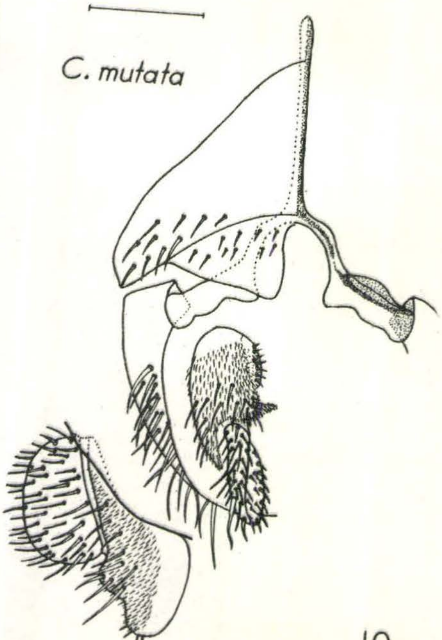
Fig. 9. Ventral view of female genitalia and lateral view of right anal lobe and cercus of *Cnephia abdita*.

Fig. 10. Female genitalia of *C. mutata*.

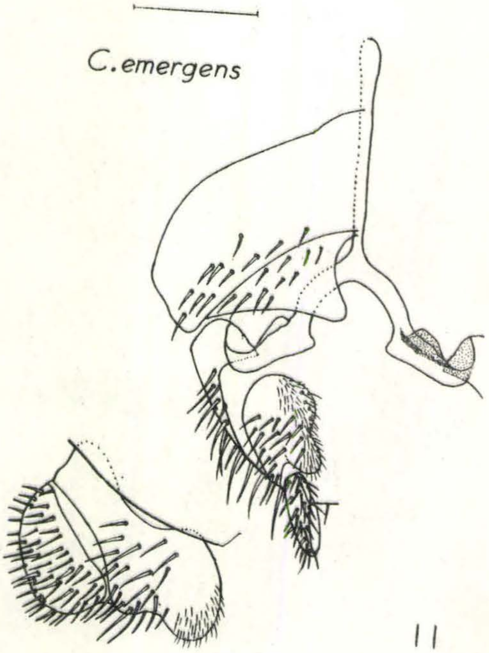
Fig. 11. Female genitalia of *C. emergens*.


C. abdita
0.1 mm.
stem
genital fork
arm
terminal plate
ovipositor lobe
anal lobe
cercus

9


C. mutata

10


C. emergens

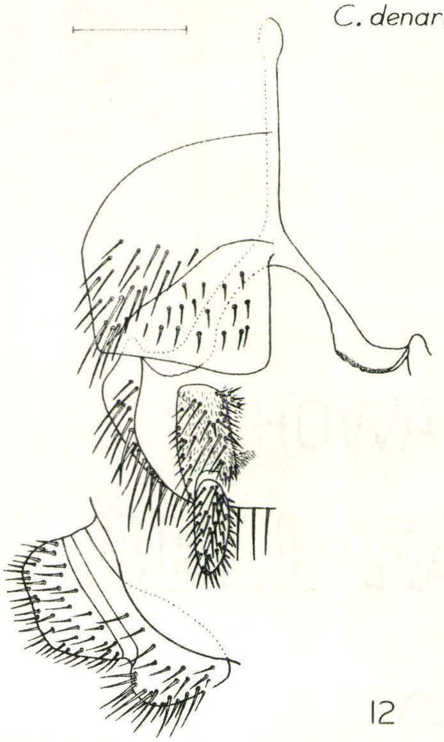
11

Fig. 12. Ventral view of female genitalia and lateral view of right anal lobe and cercus of _C. denaria_.

Fig. 13. Female genitalia of _S. congareenarum_.

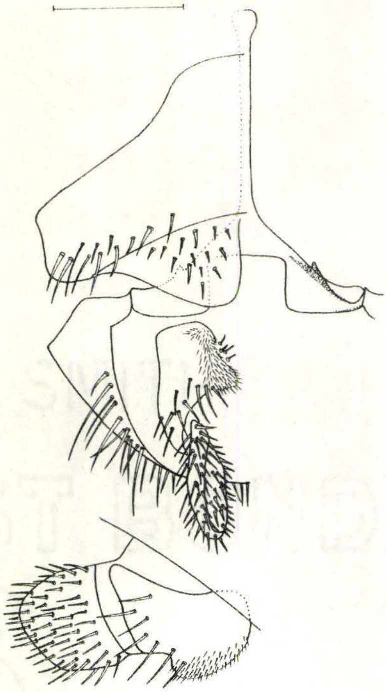
Fig. 14. Female genitalia of _S. innocens_.

Fig. 15. Female genitalia of _S. rivuli_.



C. denaria

12



S. congareenarum

13

S. innocens

14

S. rivuli

15

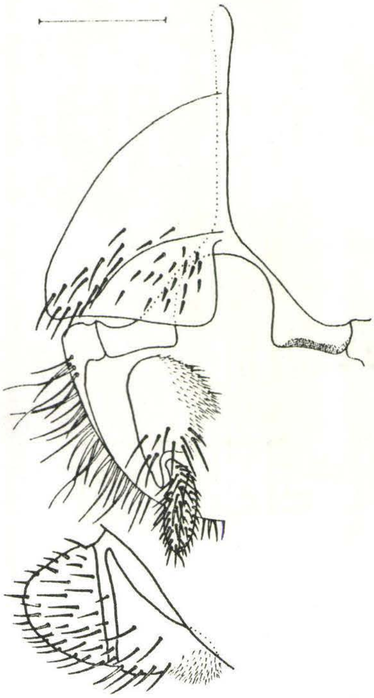
Fig. 16. Ventral view of female genitalia and lateral view of right anal lobe and cercus of *S. excisum*.

Fig. 17. Female genitalia of *S. anatinum*.

Fig. 18. Female genitalia of *S. euryadminiculum*.

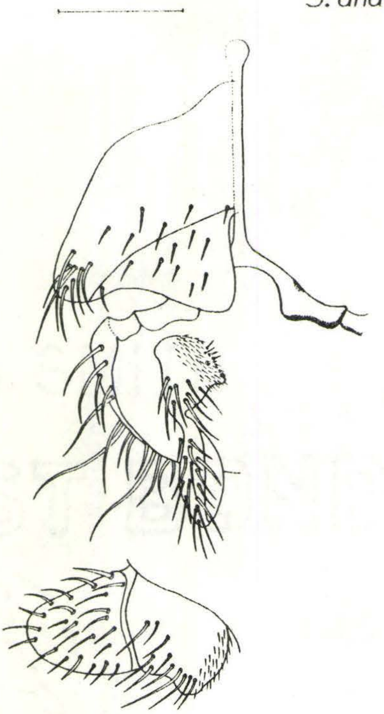
Fig. 19. Female genitalia of *S. emarginatum*.

S. excisum



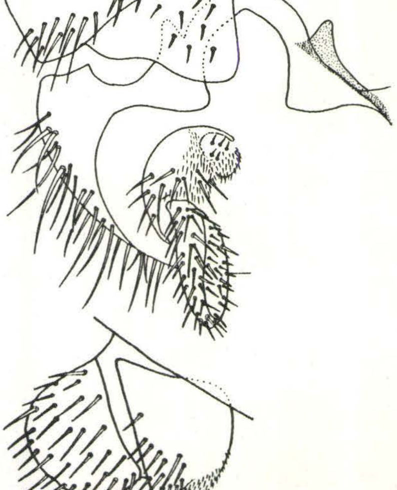
16

S. anatinum



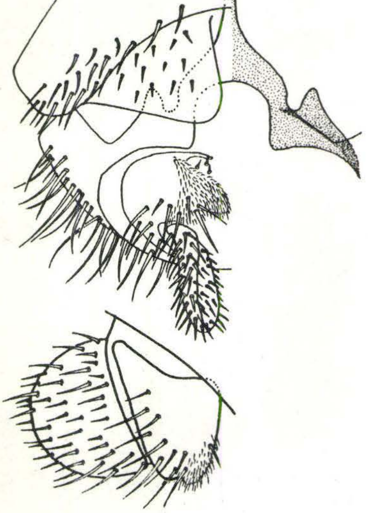
17

S. euryadminiculum



18

S. emarginatum



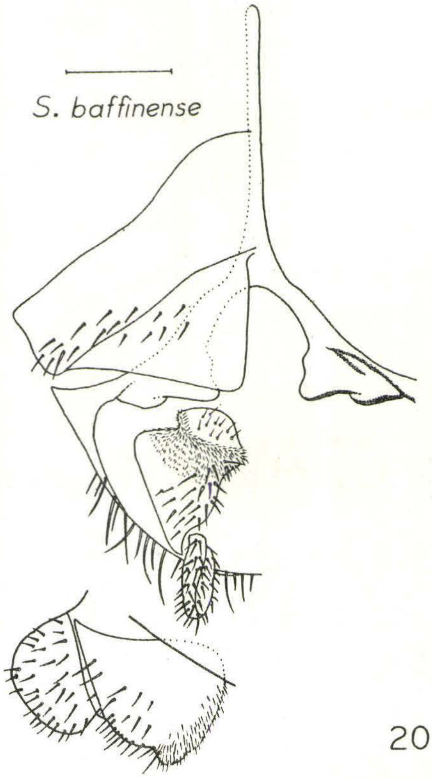
19

Fig. 20. Ventral view of female genitalia and lateral view of right anal lobe and cercus of *S. baffinense*.

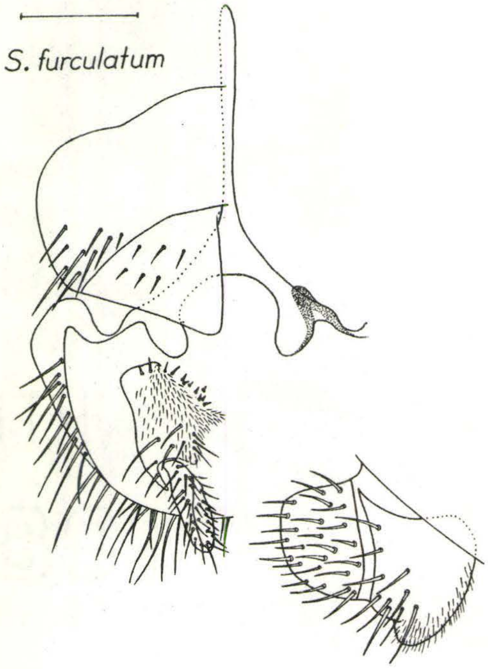
Fig. 21. Female genitalia of *S. furculatum*.

Fig. 22. Female genitalia of *S. johannseni*.

Fig. 23. Female genitalia of *S. impar*.

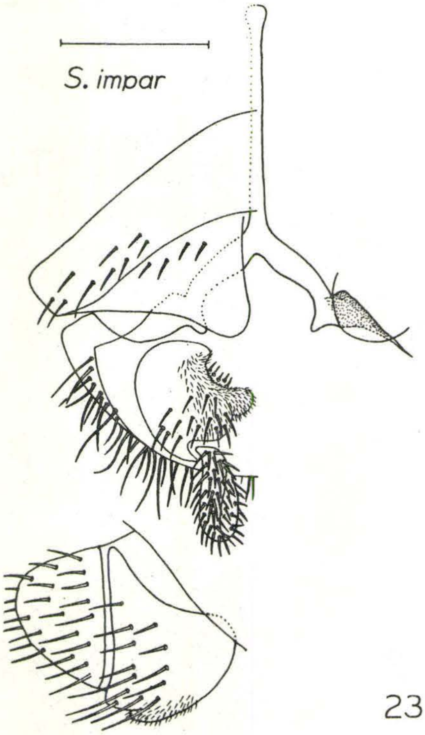


20



21

22



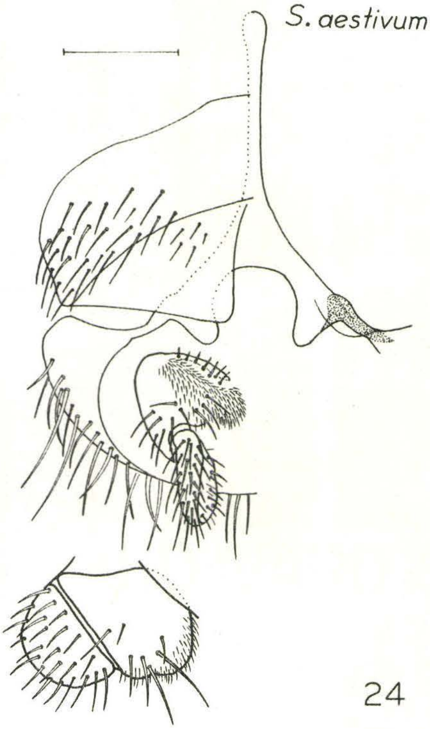
23

Fig. 24. Ventral view of female genitalia and lateral view of right anal lobe and cercus of S. aestivum.

Fig. 25. Female genitalia of S. latipes.

Fig. 26. Female genitalia of S. pugetense.

Fig. 27. Female genitalia of S. quebecense.



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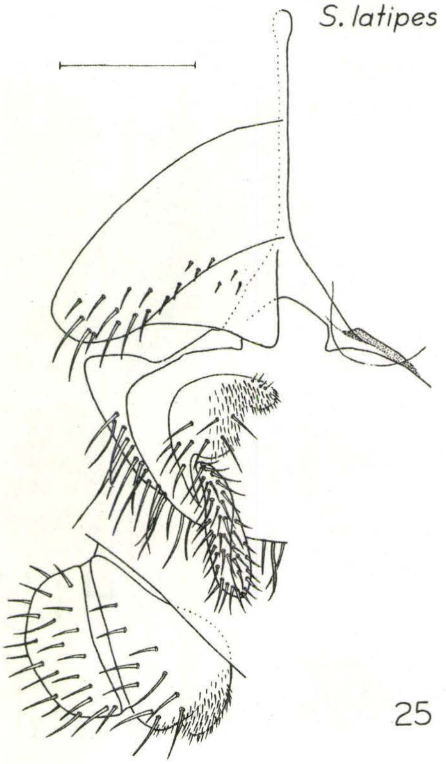
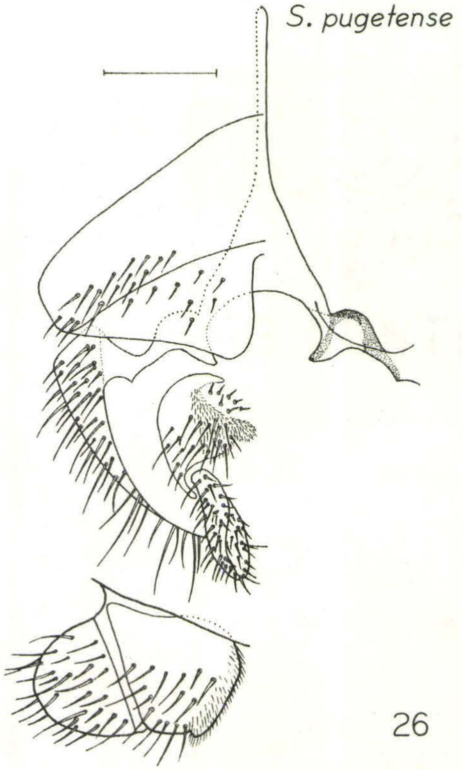


25



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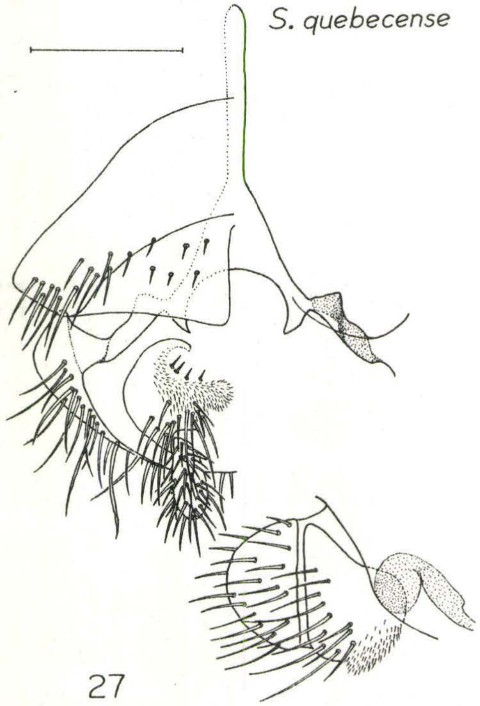


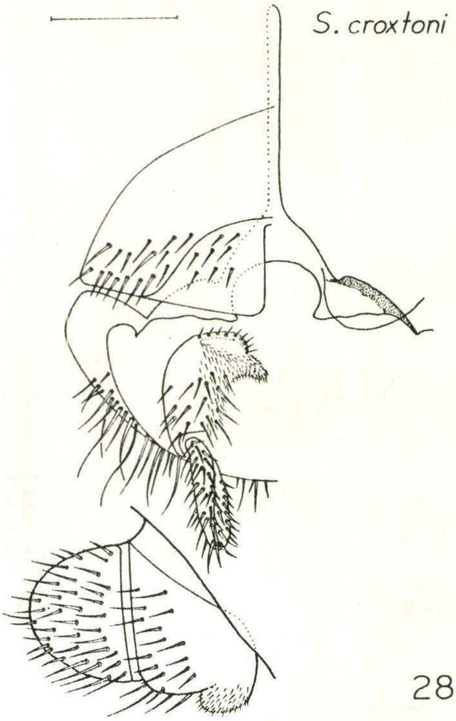
27

Fig. 28. Ventral view of female genitalia and lateral view of right anal lobe and cercus of *S. croxtoni*.

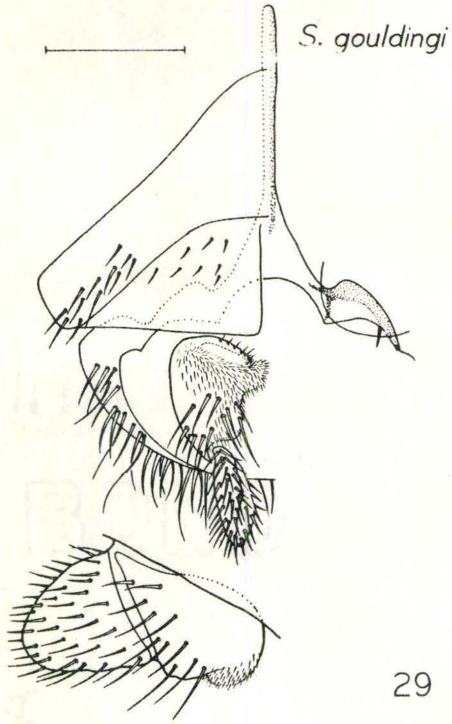
Fig. 29. Female genitalia of *S. gouldingi*.

Fig. 30. Female genitalia of *S. angustitarse*.

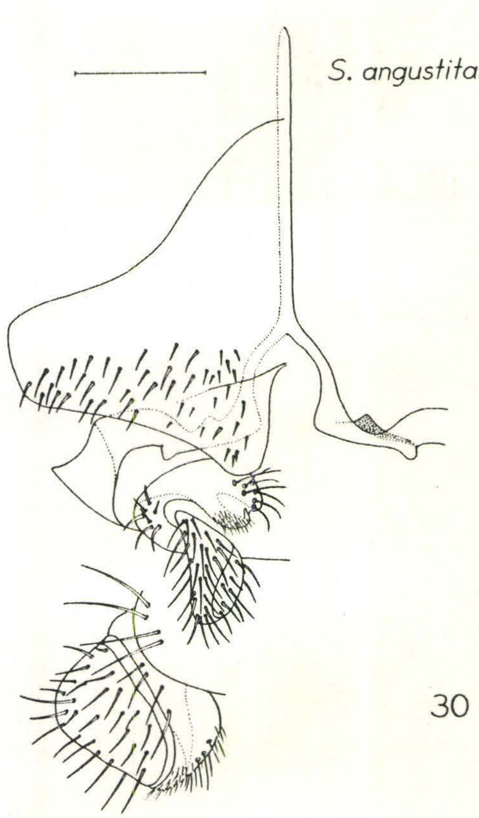
Fig. 31. Female genitalia of *S. aureum* form A.



28



29



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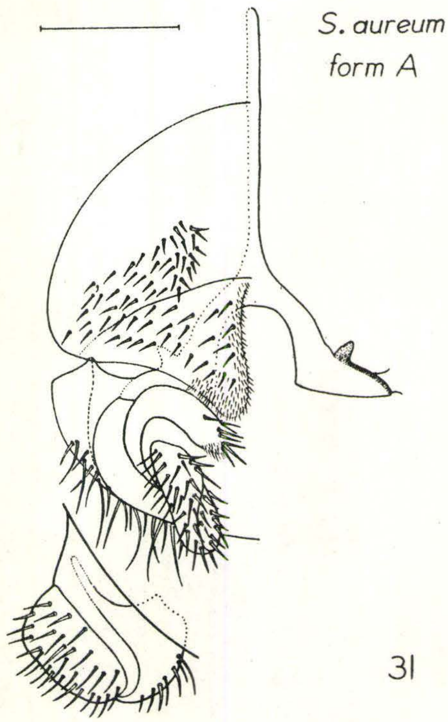
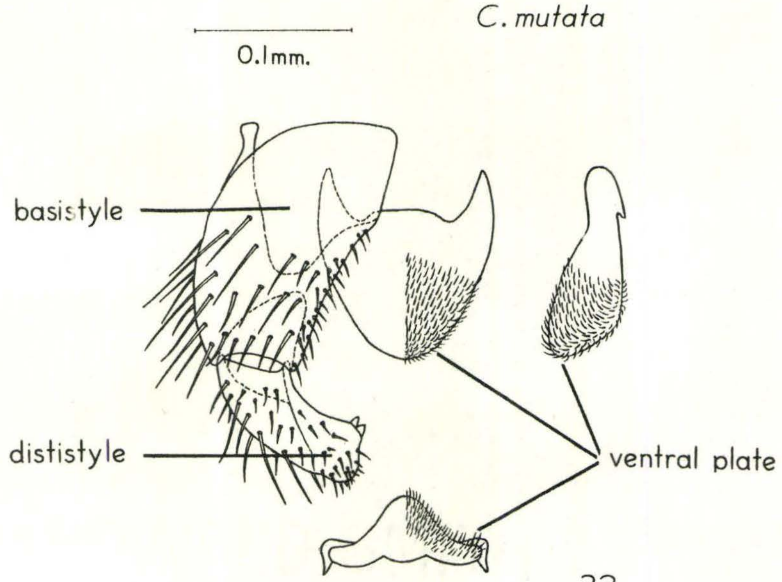


31

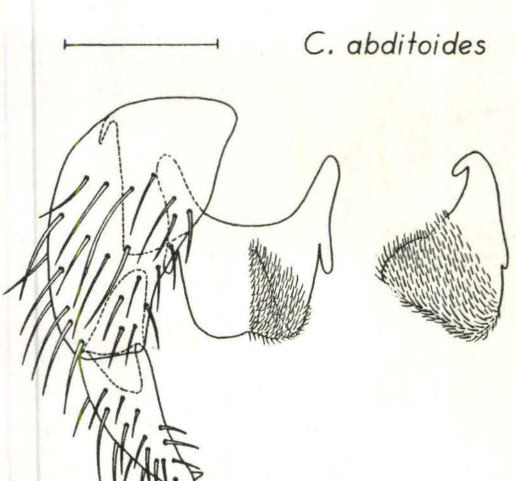
Fig. 32. Ventral view of male genitalia of *C. mutata* showing right clasper and ventral plate in ventral, left lateral and terminal views.

Fig. 33. Male genitalia of *C. abditoides*.

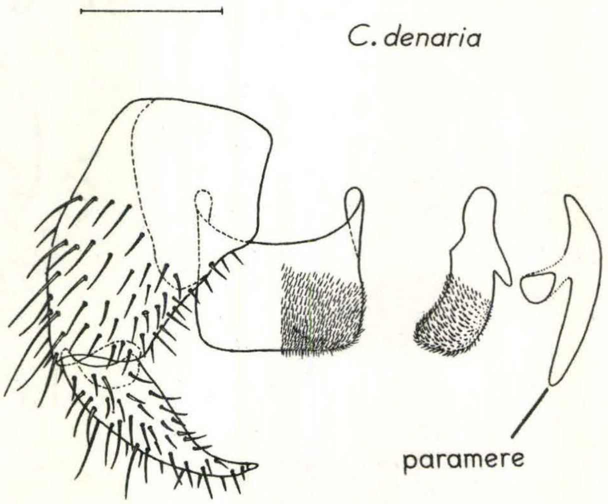
Fig. 34. Male genitalia of *C. denaria* including lateral view of left paramere.


C. mutata
0.1mm.
basistyle
dististyle
ventral plate

32


C. abditoides

33


C. denaria
paramere

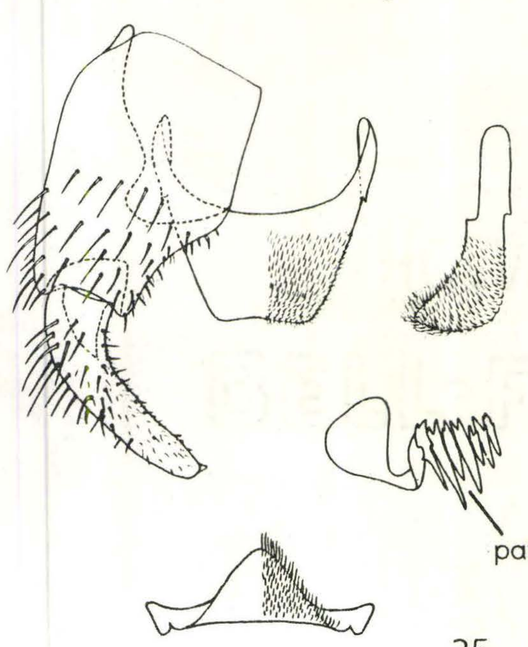
34

Fig. 35. Ventral view of male genitalia of *S. congareenarum* including lateral view of right paramere.

Fig. 36. Male genitalia of *S. excisum* including lateral view of right paramere.

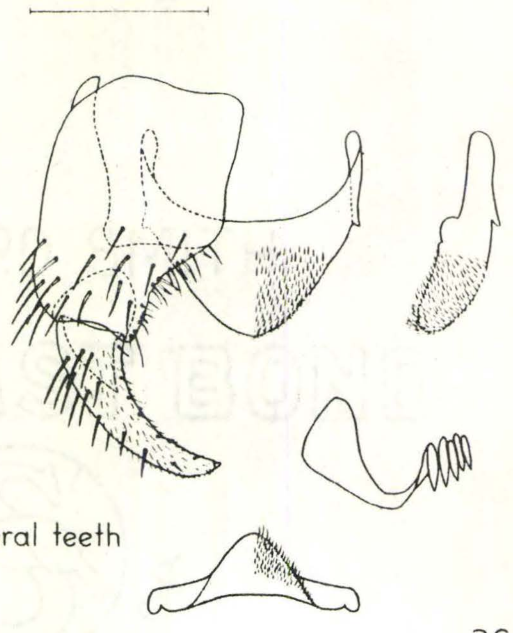
Fig. 37. Male genitalia of *S. innocens*.

Fig. 38. Male genitalia of *S. rivuli*.



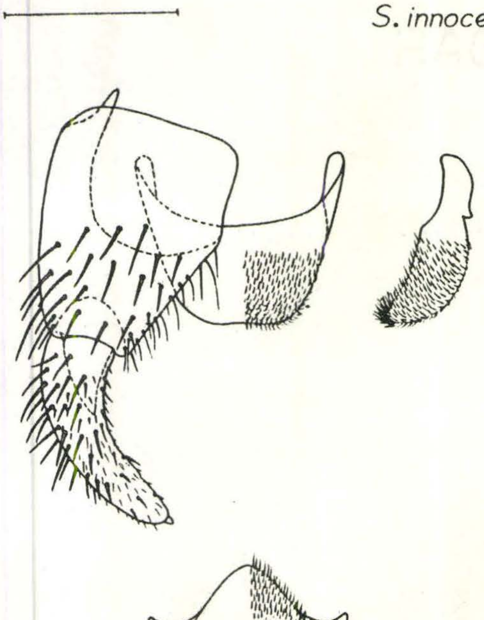
S. congareenarum

35



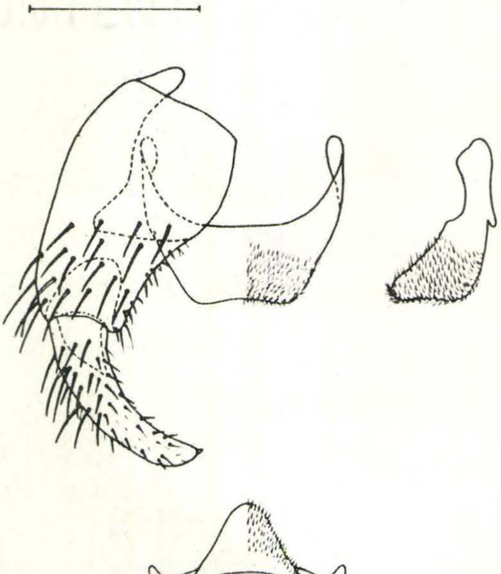
S. excisum

36



S. innocens

37



S. rivuli

38

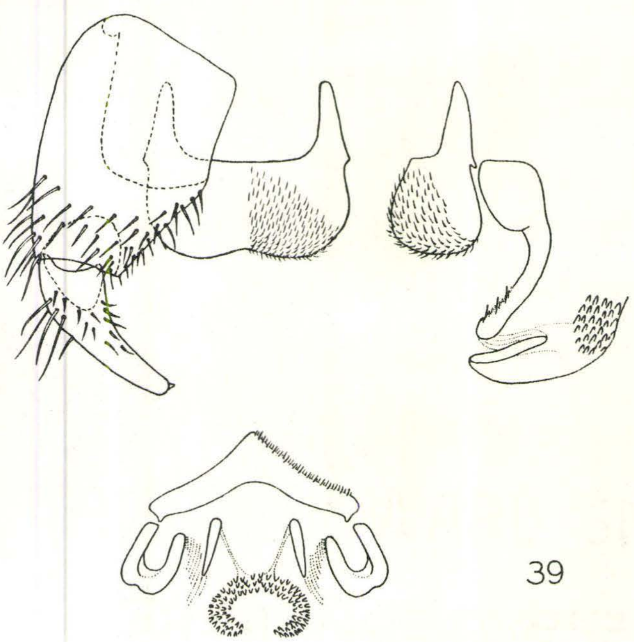
Fig. 39. Ventral view of male genitalia of *S. baffinense* including lateral view of left paramere and terminal view of ventral plate and aedeagus with parameres.

Fig. 40. Male genitalia of *S. canonicolum* (clasper omitted) including ventral, lateral and terminal views of the everted aedeagus.

Fig. 41. Male genitalia of *S. euryadminiculum*.

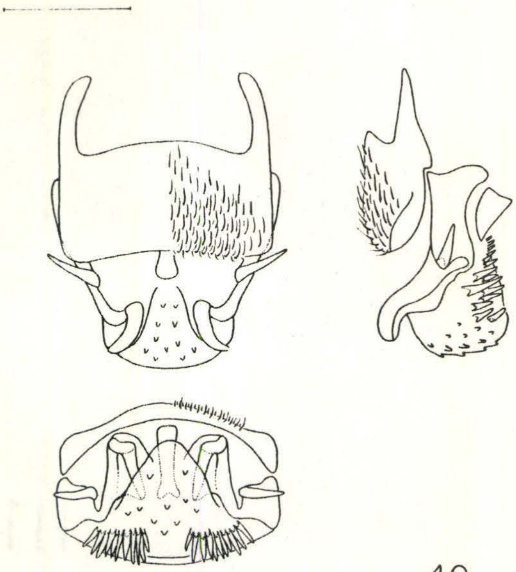
Fig. 42. Male genitalia of *S. emarginatum*.

S. baffinense



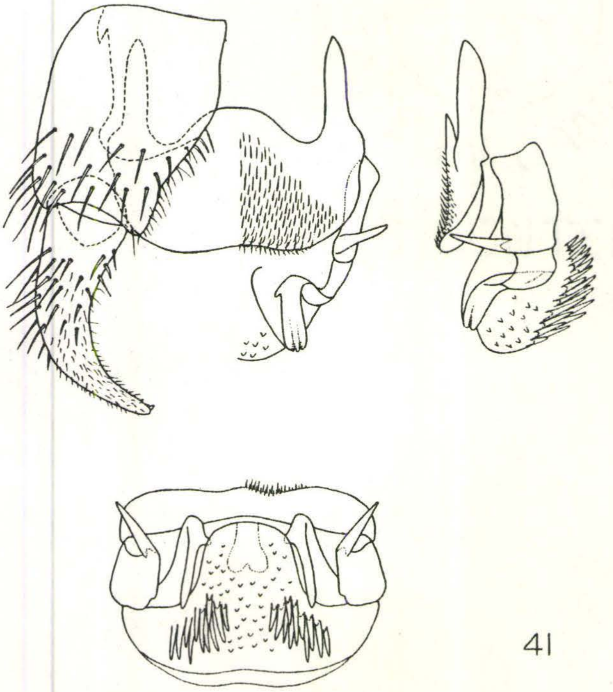
39

S. canonicolum



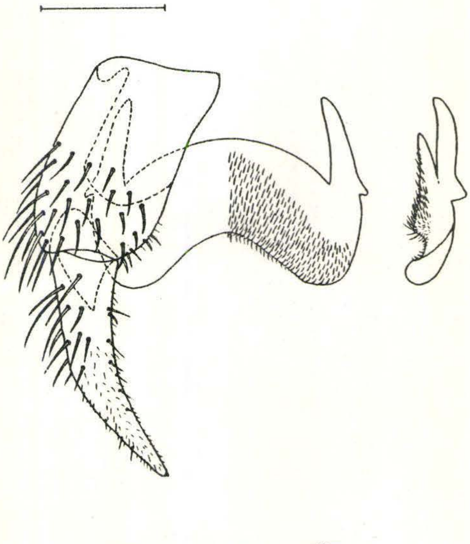
40

S. euryadminiculum



41

S. emarginatum



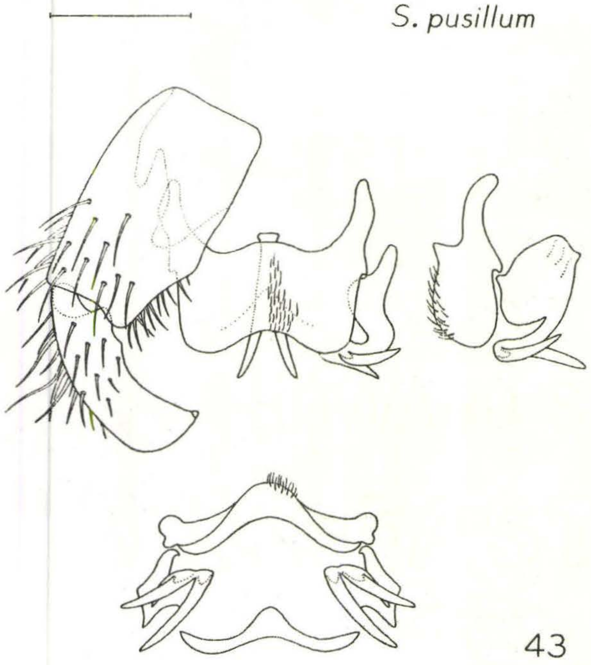
42

Fig. 43. Ventral view of male genitalia of *S. pusillum* including lateral and ventral views of the left paramere and a terminal view of the ventral plate and aedeagus.

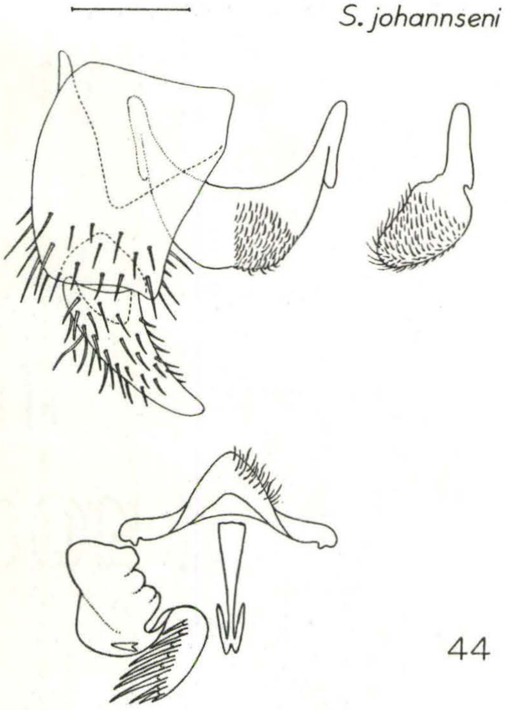
Fig. 44. Male genitalia of *S. johannseni* including a postero-lateral view of right paramere combined with a terminal view of ventral plate and median sclerite.

Fig. 45. Male genitalia of *S. furculatum*.

Fig. 46. Male genitalia of *S. impar*.



43



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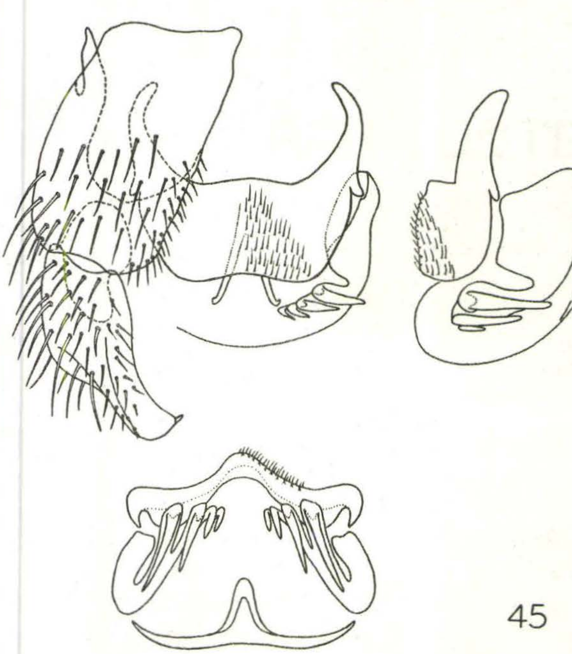
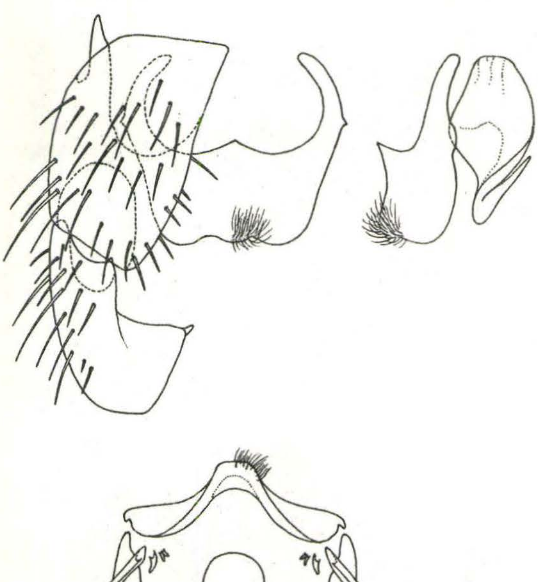


45



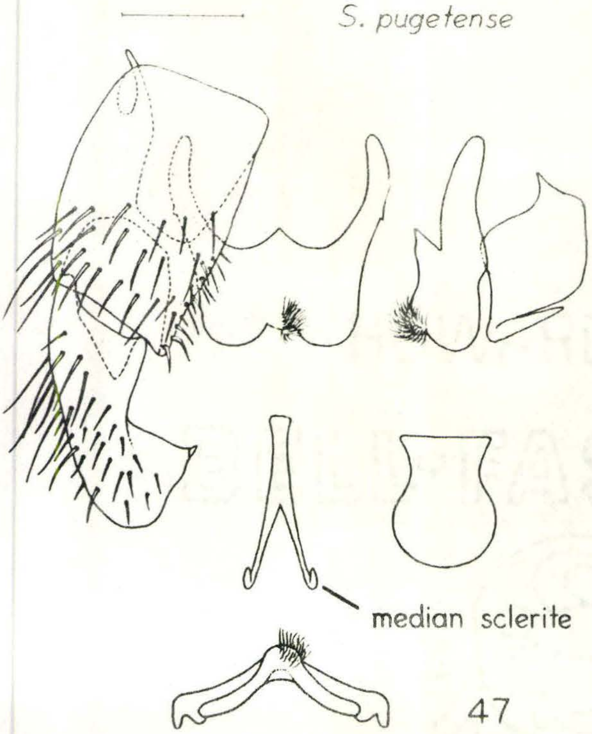
46

Fig. 47. Ventral view of male genitalia of S. pugetense including a left lateral view of ventral plate and paramere, a dorsal view of median sclerite and dorsal sclerite and a terminal view of ventral plate.

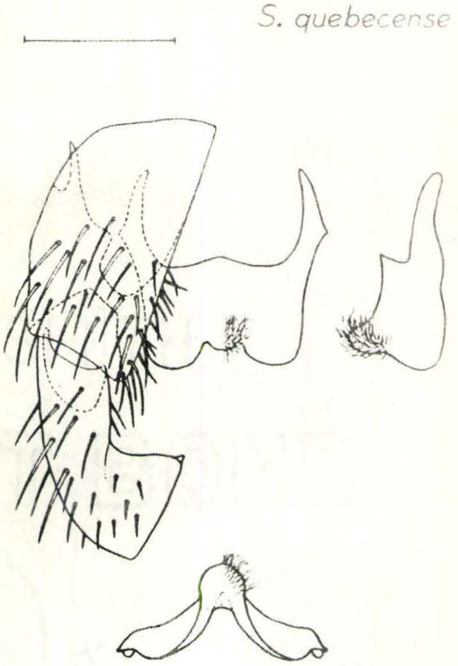
Fig. 48. Male genitalia of S. quebecense.

Fig. 49. Male genitalia of S. aestivum.

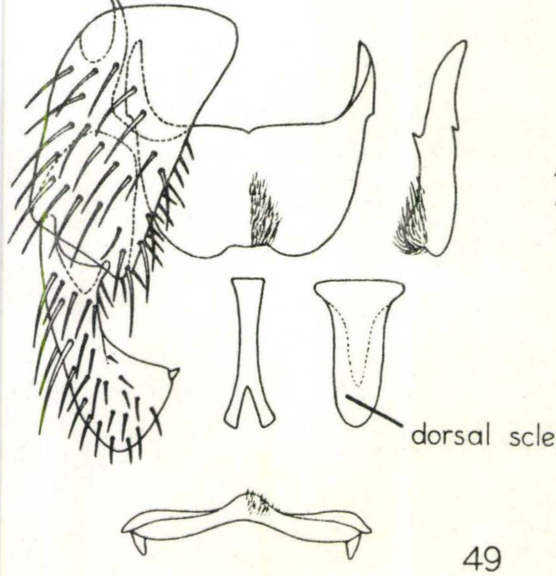
Fig. 50. Male genitalia of S. latipes.


S. pugetense
median sclerite

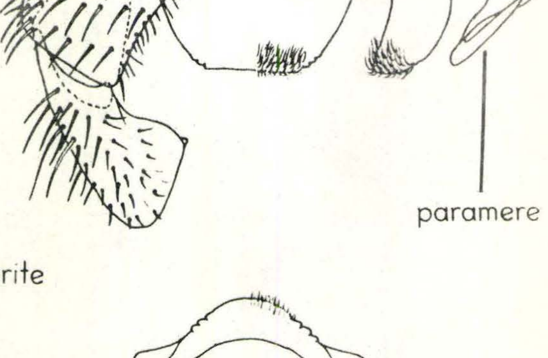
47


S. quebecense

48


S. aestivum
dorsal sclerite

49


S. latipes
paramere

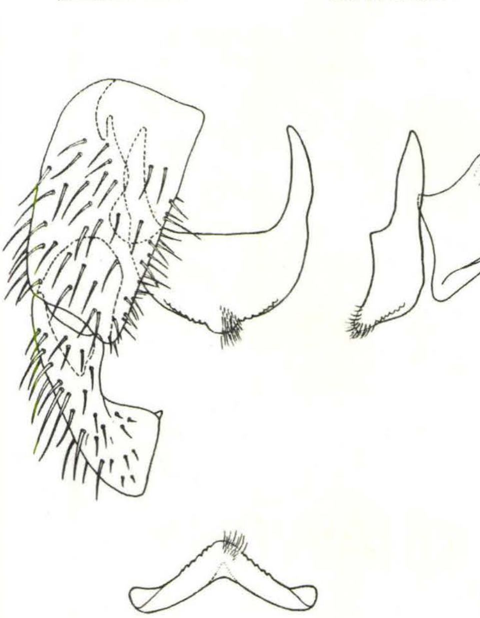
50

Fig. 51. Ventral view of male genitalia of *S. croxtoni* including left lateral view of ventral plate and paramere, and terminal view of ventral plate.

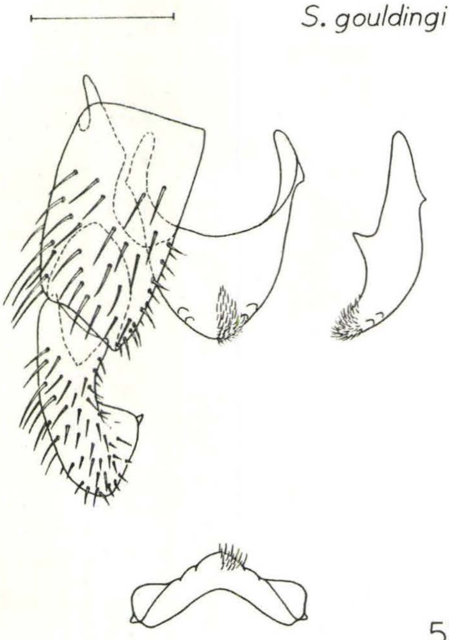
Fig. 52. Male genitalia of *S. gouldingi*.

Fig. 53. Male genitalia of *S. angustitarse* including lateral view of left paramere, and terminal view of aedeagus.

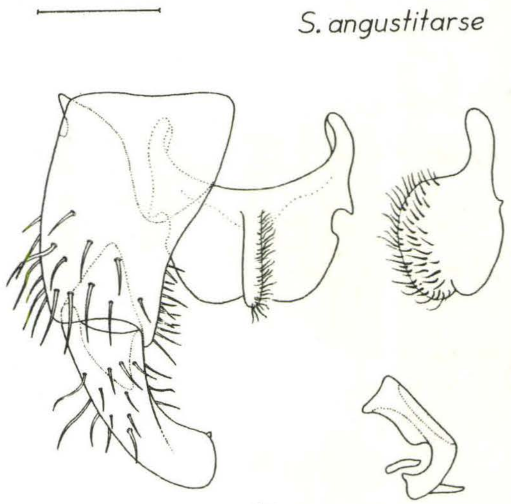
Fig. 54. Male genitalia of *S. aureum* form A, including right lateral view of aedeagus.


S. croxtoni

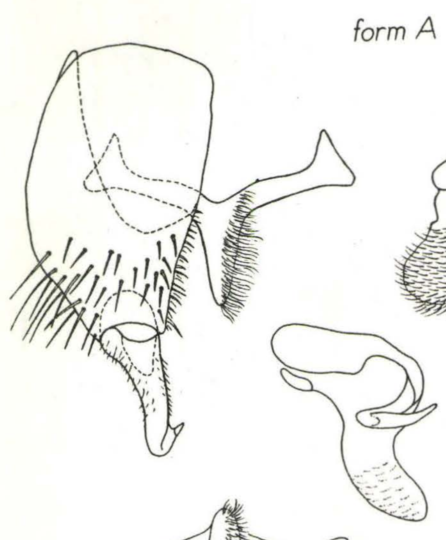
51


S. gouldingi

52

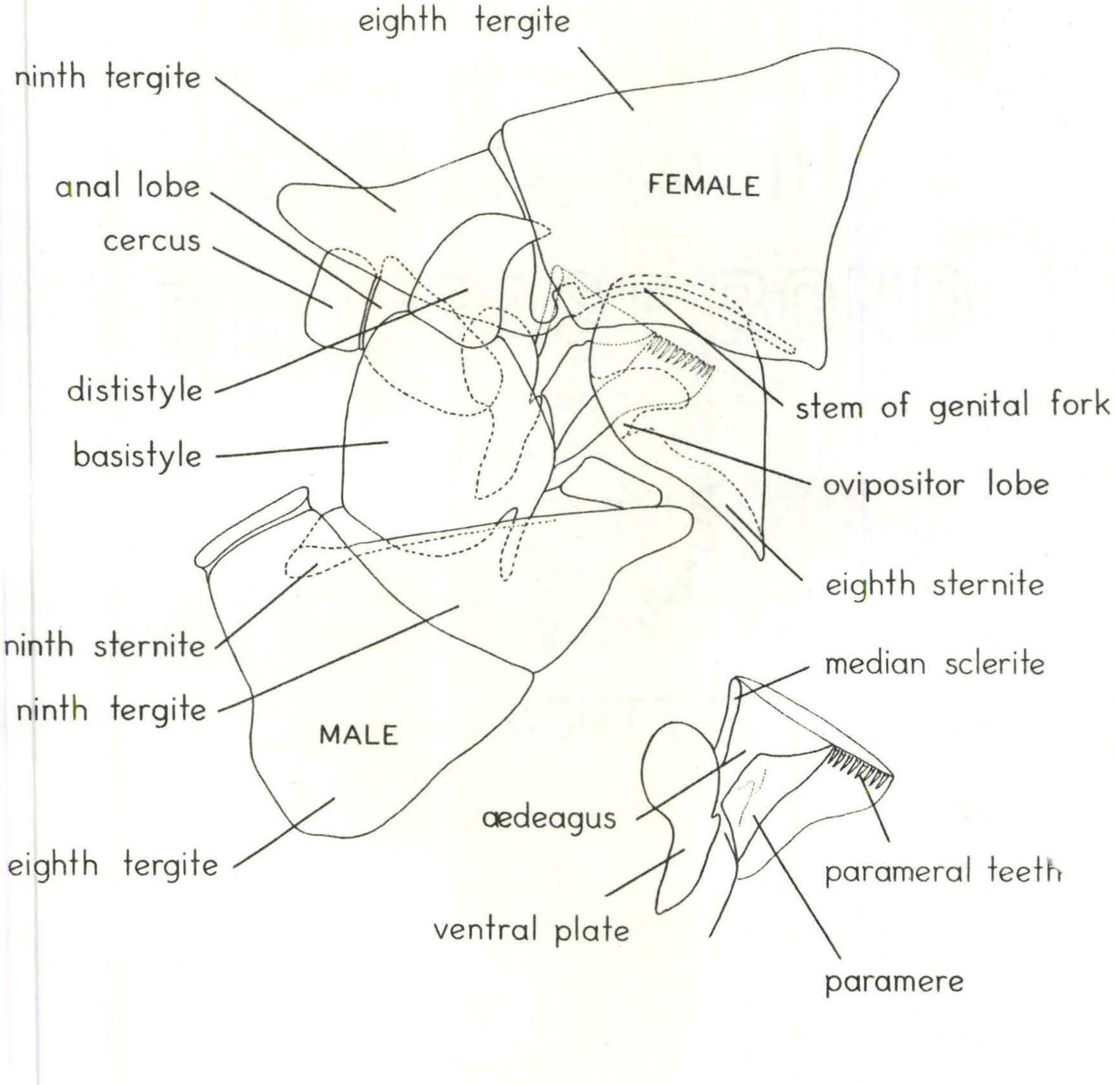

S. angustitarse

53


S. aureum
form A

54

Fig. 55. Right lateral view of coupled genitalia of _C_. _dacotensis_, with separate drawing of lateral view of ventral plate and everted aedeagus.


eighth tergite
ninth tergite
FEMALE
anal lobe
cercus
dististyle
stem of genital fork
basistyle
ovipositor lobe
eighth sternite
ninth sternite
median sclerite
ninth tergite
MALE
aedeagus
parameral teeth
eighth tergite
ventral plate
paramere

55

Fig. 56. Left lateral view of larva of *S. aestivum*.

Fig. 57a. Anal sclerite of larva of *Austrosimulium bancrofti* showing posteriorly directed struts on anterior arms.

Fig. 57b. Anal sclerite of larva of *Gigantodax igniculum* showing ring sclerite encircling posterior ring of hooks.

Fig. 57c. Antenna of larva of *S. baffinense*

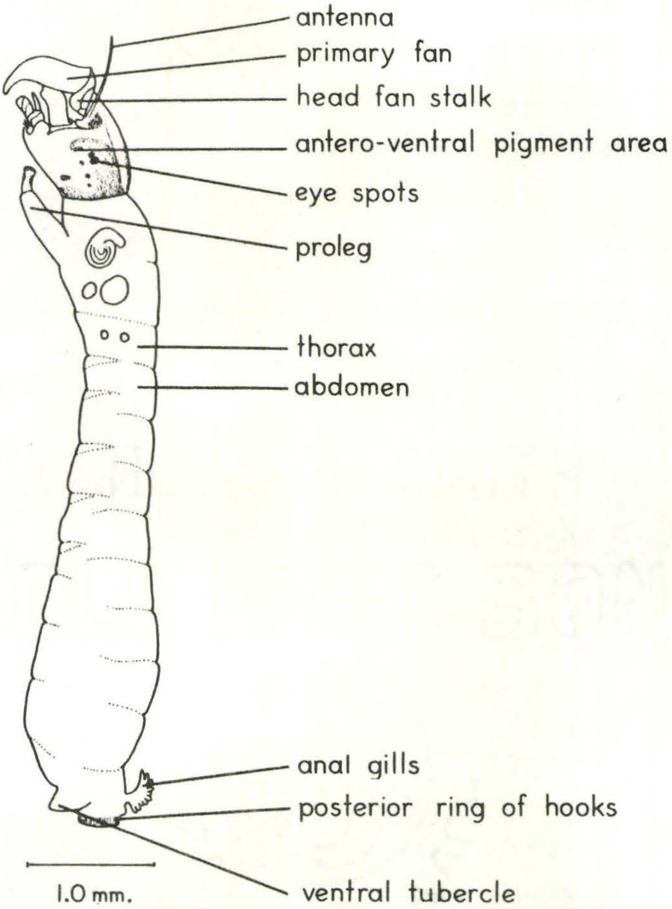
B - basal portion showing primary division into two annuli with the second annulus subdivided into six secondary annuli

D - distal portion (penultimate and terminal segments).

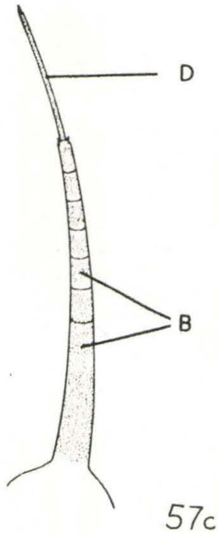
Fig. 57d. Antenna of larva of *S. excisum*

B - basal portion showing two primary annuli, without secondary subdivision

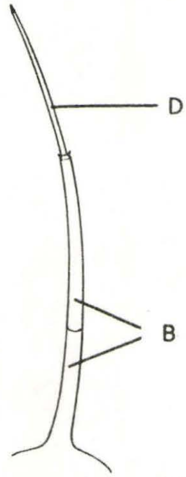
D - distal portion (penultimate and terminal segments).



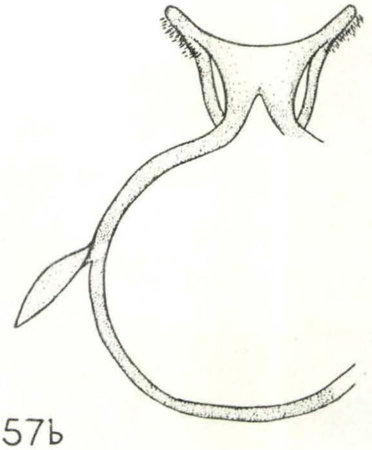
56



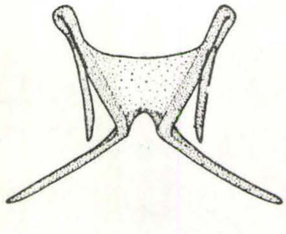
57c



57d



57b



57a

Fig. 58a. Ventro-lateral view of left side of labrum of the larva of *Gymnopais* sp.

Fig. 58b-f. Ventral view of the left feeding organ and associated sclerites of the larva of

b. *Cnephia strenua*

c. First instar of *Simulium pictipes*

d. *Prosimulium fontanum* S. & D.

e. *Aedes aegypti*

f. *S. aureum*

A - apodeme for insertion of tormal muscle

C - connective sclerite

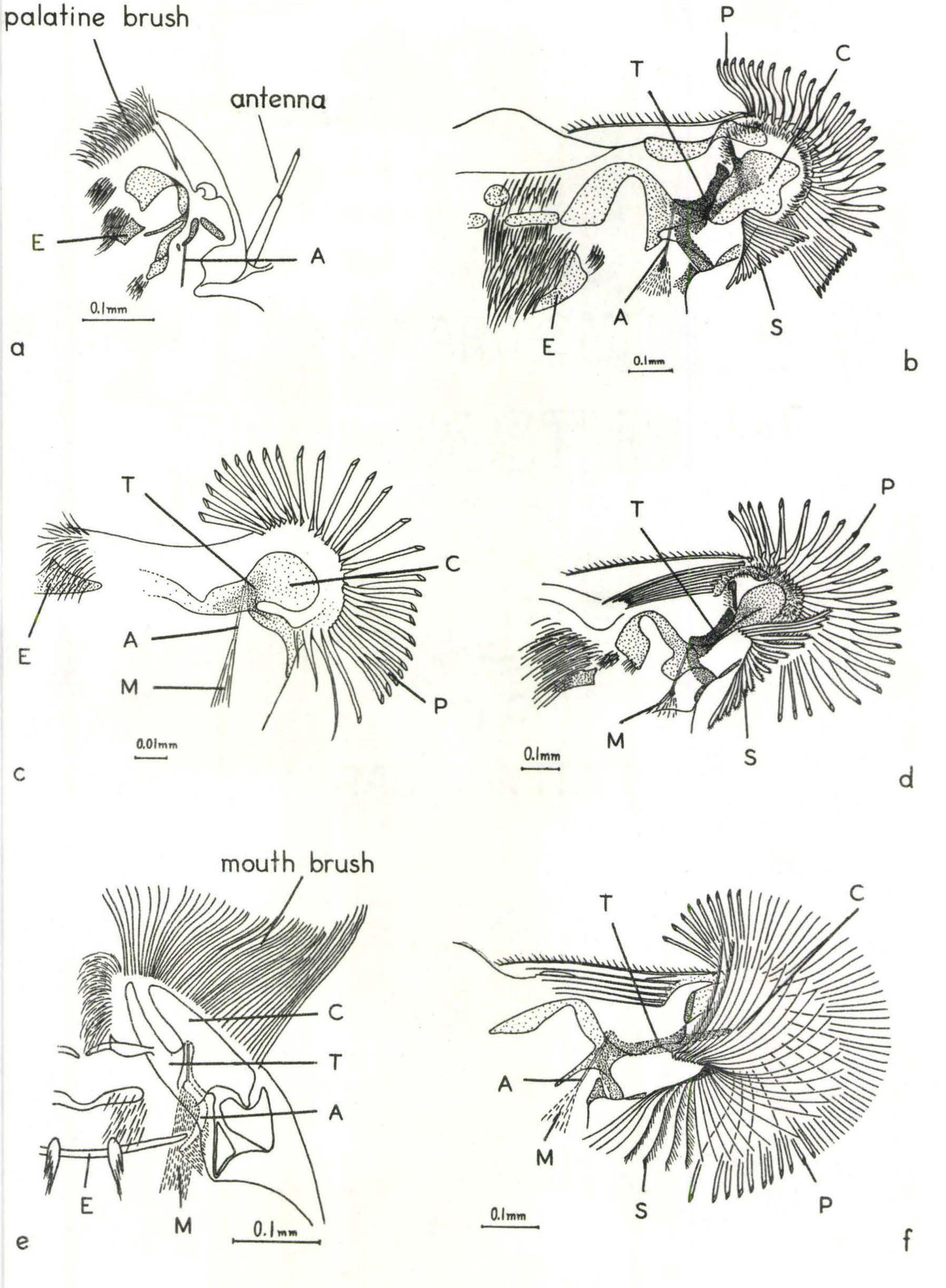
M - tormal muscle

P - primary fan ray

S - secondary fan

T - torma

E - epipharyngeal apparatus


palatine brush
antenna
E
A
0.1mm
a
P
C
T
A
S
E
0.1mm
b
T
C
E
A
M
P
0.01mm
c
P
T
M
S
0.1mm
d
mouth brush
C
T
A
E
M
0.1mm
e
T
C
A
M
S
P
0.1mm
f

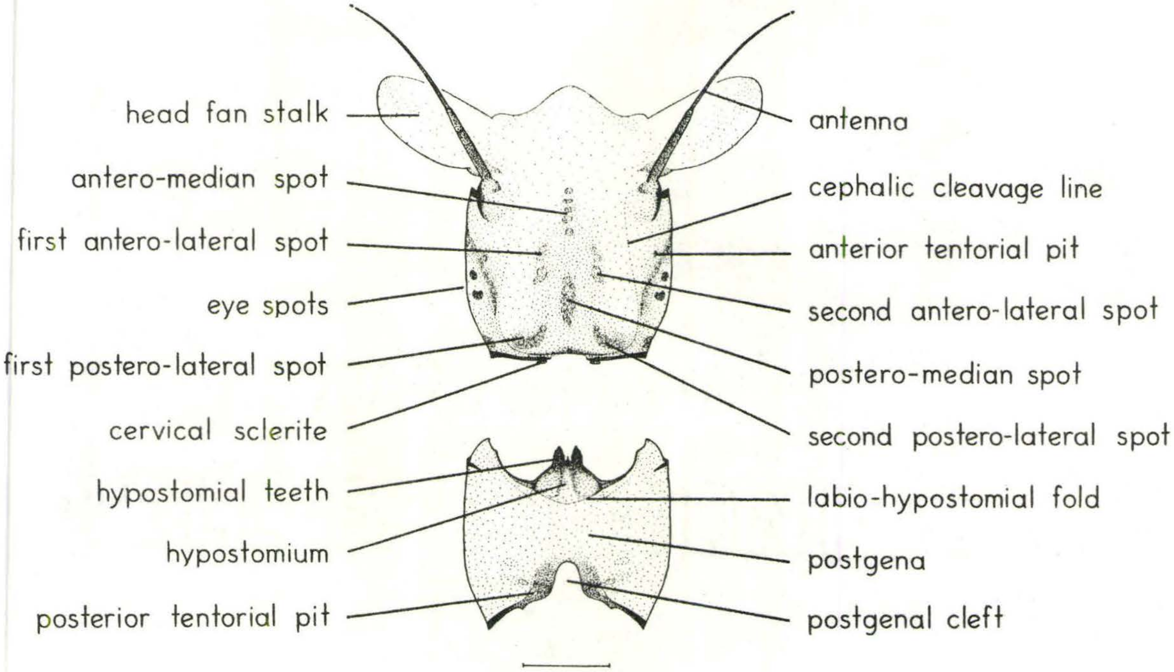
58

Fig. 59. Dorsal and ventral views of the head capsule of the larva of *C. abdita*.

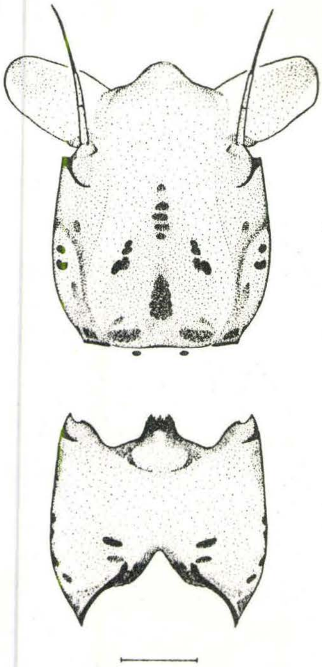
Fig. 60. Larva of *C. mutata*.

Fig. 61. Larva of *C. abditoides*.

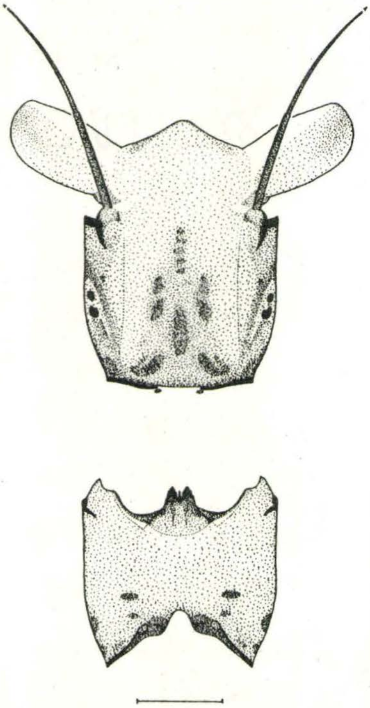
Fig. 62. Larva of *C. denaria*.



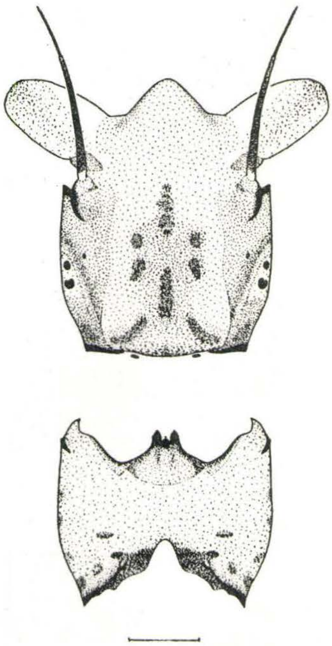
C. abdita 0.25 mm. 59



C. mutata 60



C. abditoides 61



C. denaria 62

Fig. 63. Dorsal and ventral views of the head capsule of the larva of _S._ _innocens_.

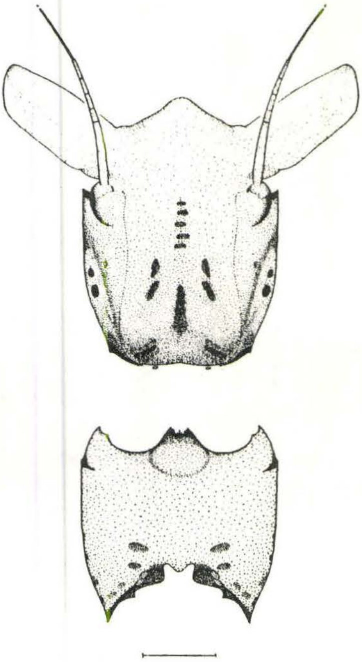
Fig. 64. Larva of _S._ _anatinum_.

Fig. 65. Larva of _S._ _congareenarum_.

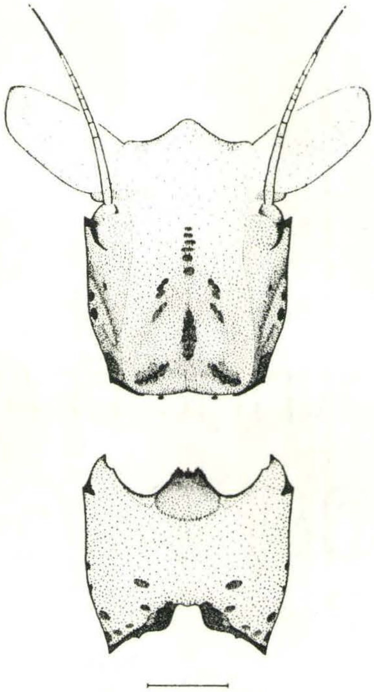
Fig. 66. Larva of _S._ _baffinense_.

Fig. 67. Larva of _S._ _rivuli_.

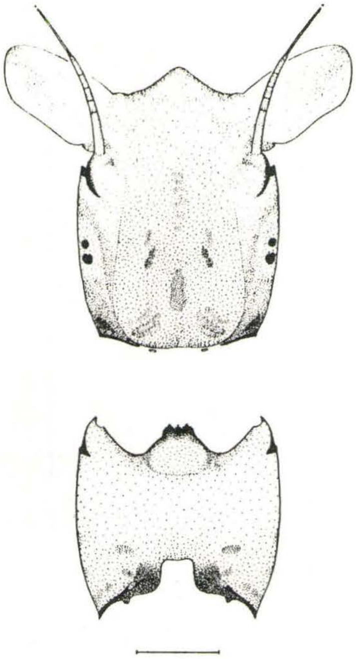
Fig. 68. Larva of _S._ _excisum_.



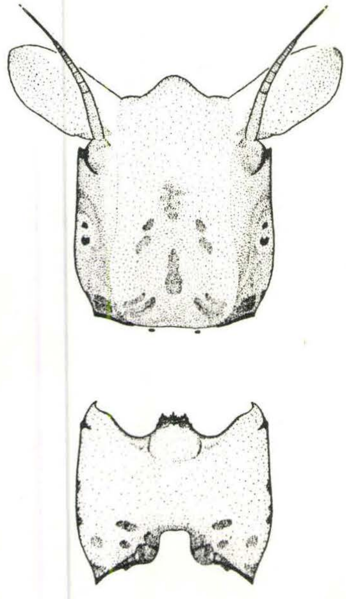
S. innocens 63



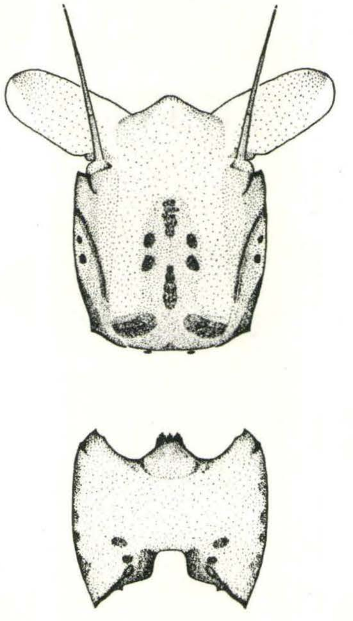
S. anatinum 64



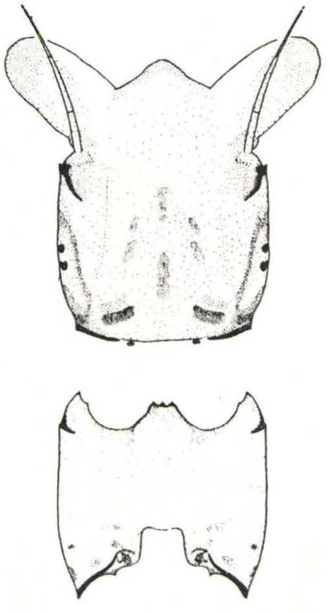
S. congareenarum 65



S. baffinense 66



S. rivuli 67



S. excisum 68

Fig. 69. Dorsal and ventral views of the head capsule of the larva of *S. euryadminiculum*.

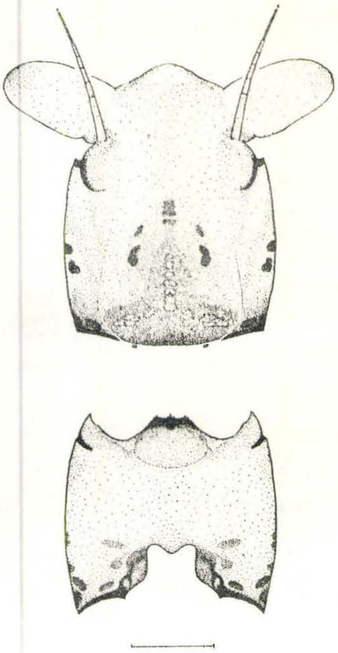
Fig. 70. Larva of *S. quebecense*.

Fig. 71. Larva of *S. gouldingi*.

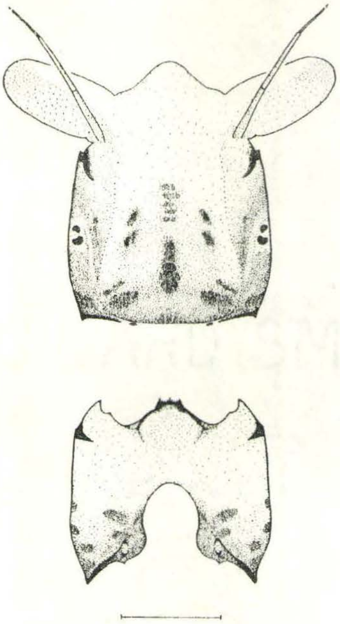
Fig. 72. Larva of *S. emarginatum*.

Fig. 73. Larva of *S. pugetense*.

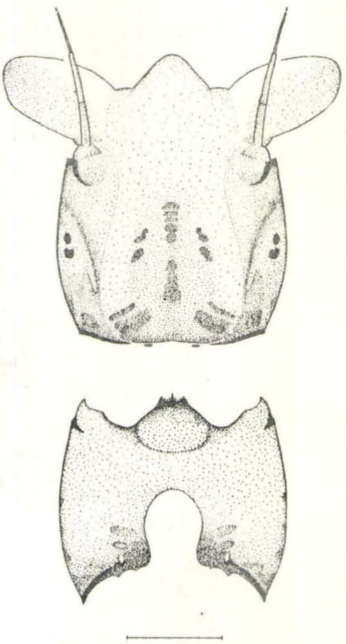
Fig. 74. Larva of *S. impar*.



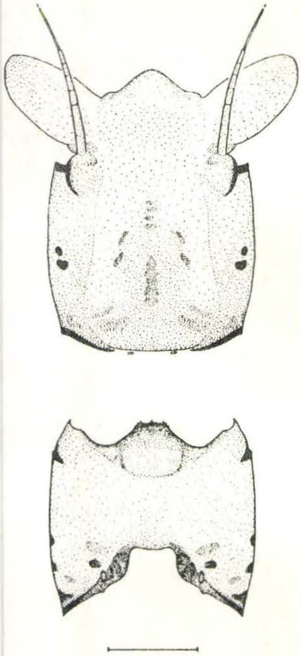
S. euryadminiculum 69



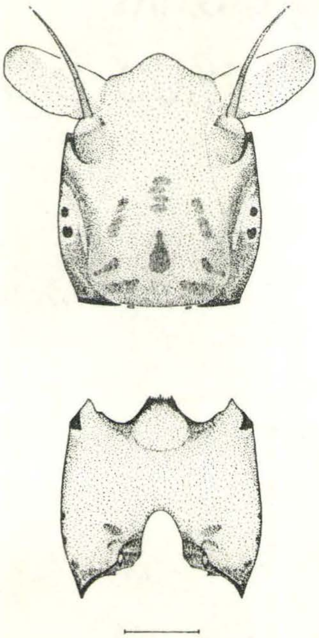
S. quebecense 70



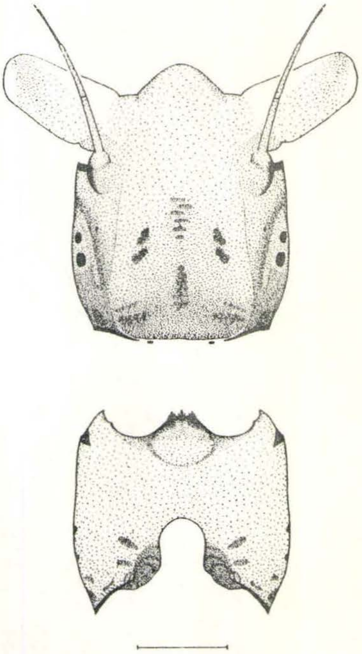
S. gouldingi 71



S. emarginatum 72



S. pugetense 73



S. impar 74

Fig. 75. Dorsal and ventral views of the head capsule of the larva of S. latipes.

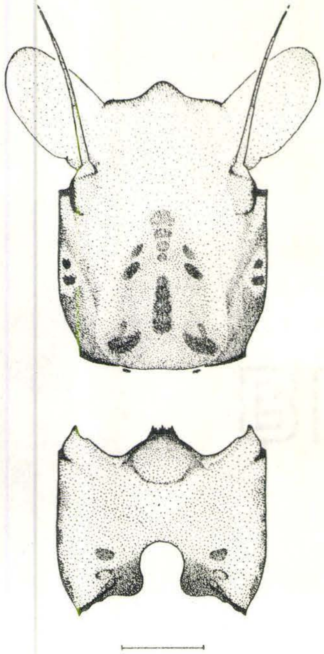
Fig. 76. Larva of S. aestivum.

Fig. 77. Larva of S. aureum form A.

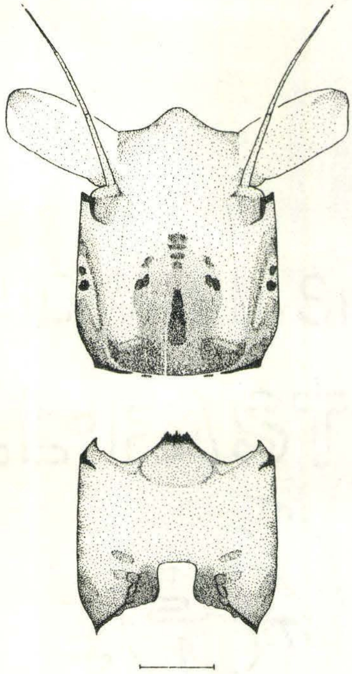
Fig. 78. Larva of S. croxtoni.

Fig. 79. Larva of S. furculatum.

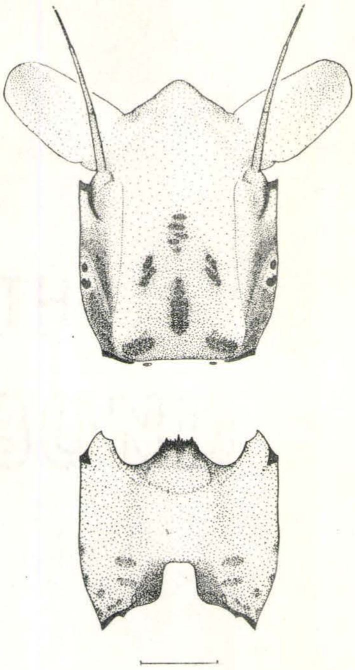
Fig. 80. Larva of S. aureum form B.



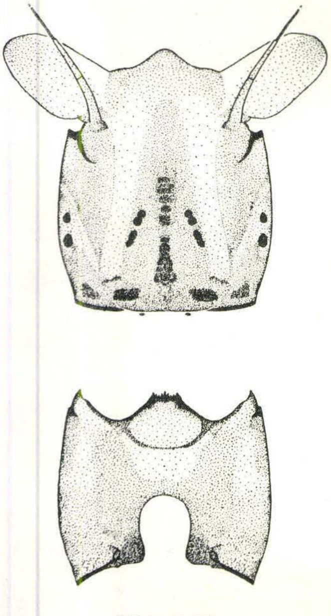
S. latipes 75



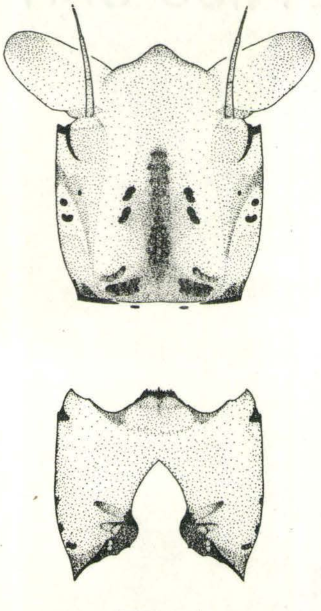
S. aestivum 76



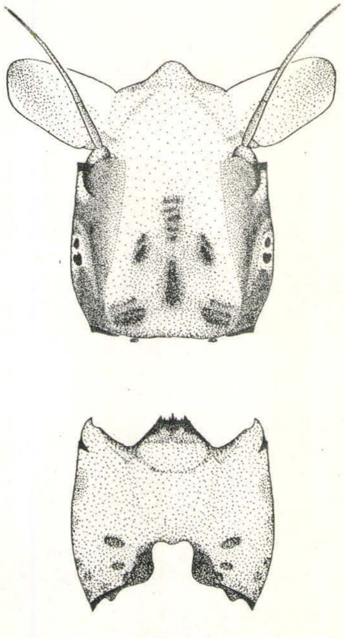
S. aureum form A 77



S. croxtoni 78



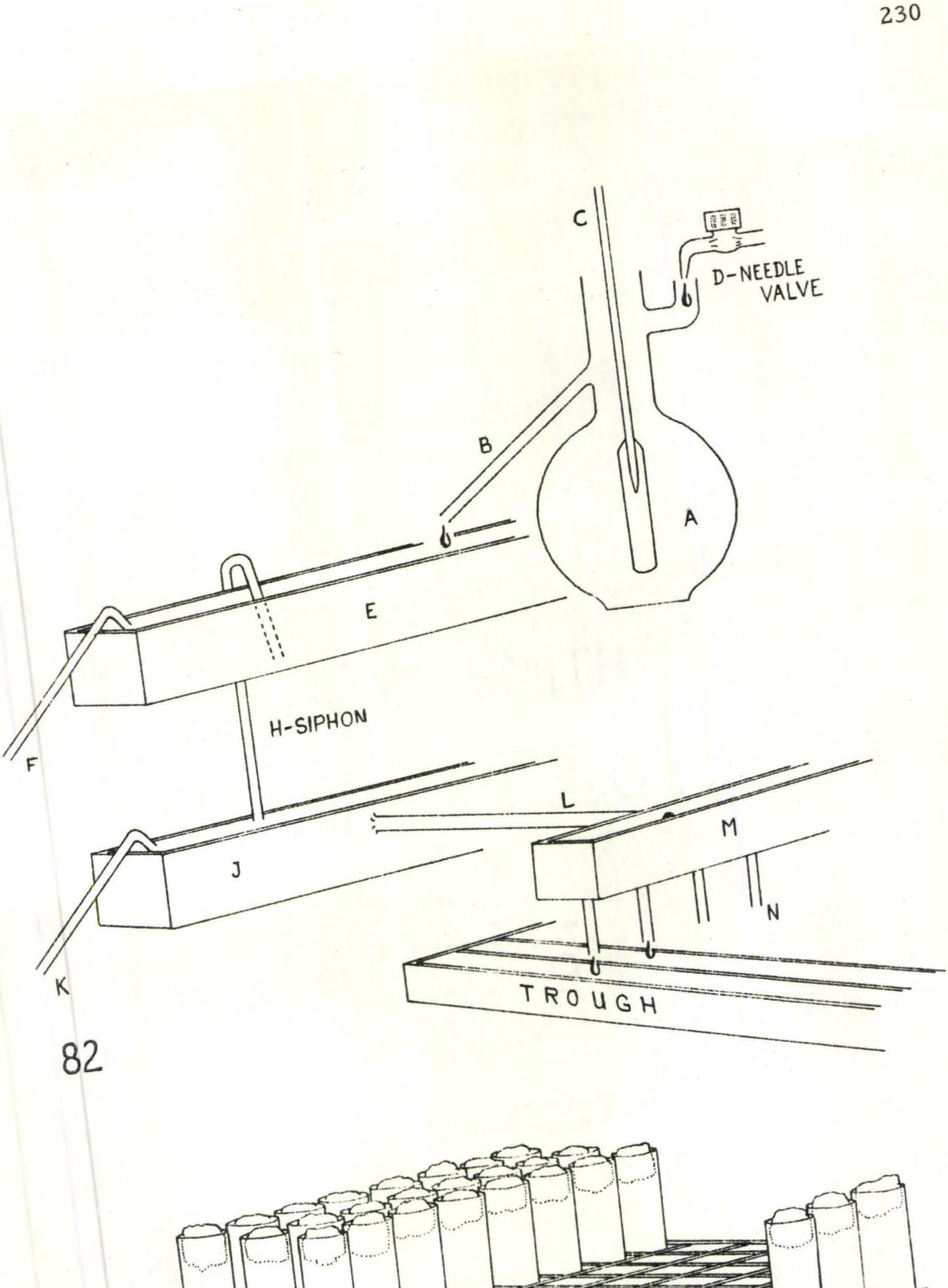
S. furculatum 79



S. aureum form B 80

Fig. 81. Plastic tray for the rearing of individual pupae.

Fig. 82. The components of the apparatus used to convey and dilute yeast suspension to larva in rearing troughs (see text, page 13).



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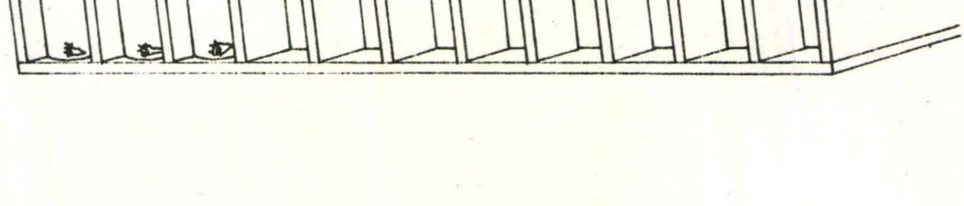

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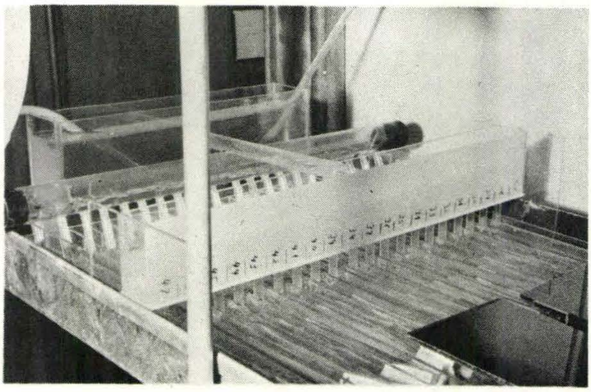
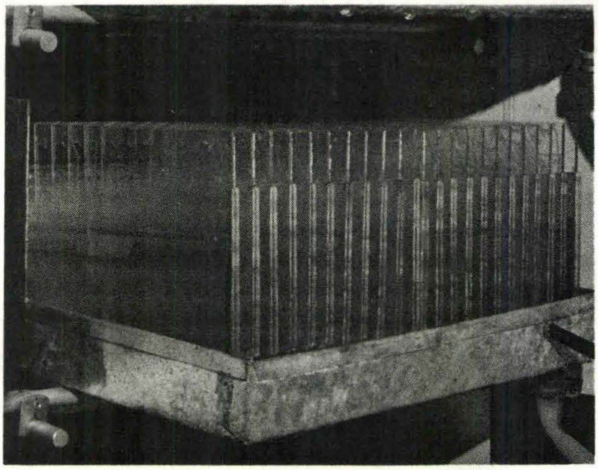
Fig. 83. Upper end of one rack of 21 troughs showing the manifolds for supplying filtered water and diluted yeast suspension to all troughs simultaneously.

Fig. 84. Lower end of one rack of 21 troughs showing deepened terminal reservoir and end wall of stainless steel screen to prevent larval escape.

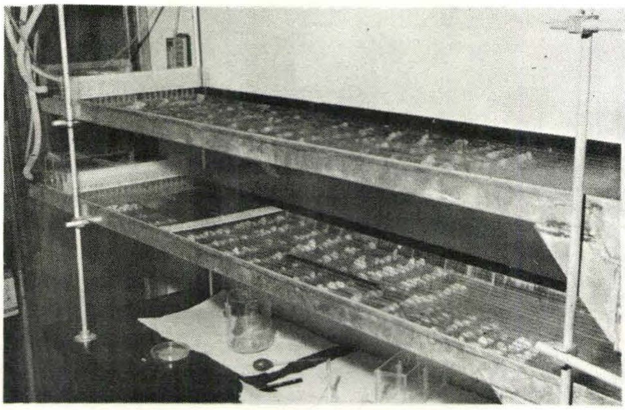
Fig. 85. Two racks of rearing troughs in simultaneous operation.



83

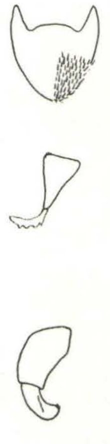


84



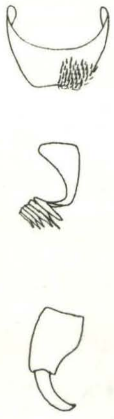
85

Fig. 86. Chart illustrating changes in structure of the ventral plate, left paramere and right clasper of the male of representative species of Cnephia and of groups 1-8 of Eusimulium.



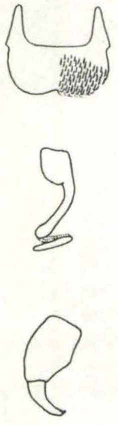
C. mutata

C. denaria



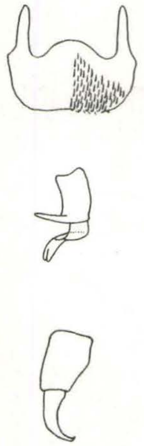
S. rivuli

Group 1



S. baffinense

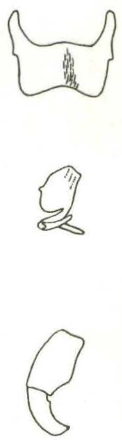
Group 2



S. euryadminiculum

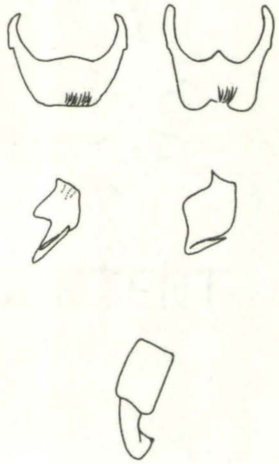
Group 3

S. furculatum



S. pusillum

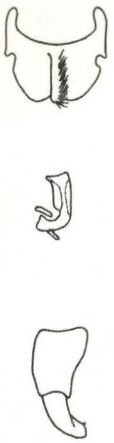
Group 4



S. latipes

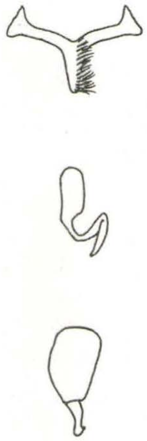
S. pugetense

Group 5



S. angustitarse

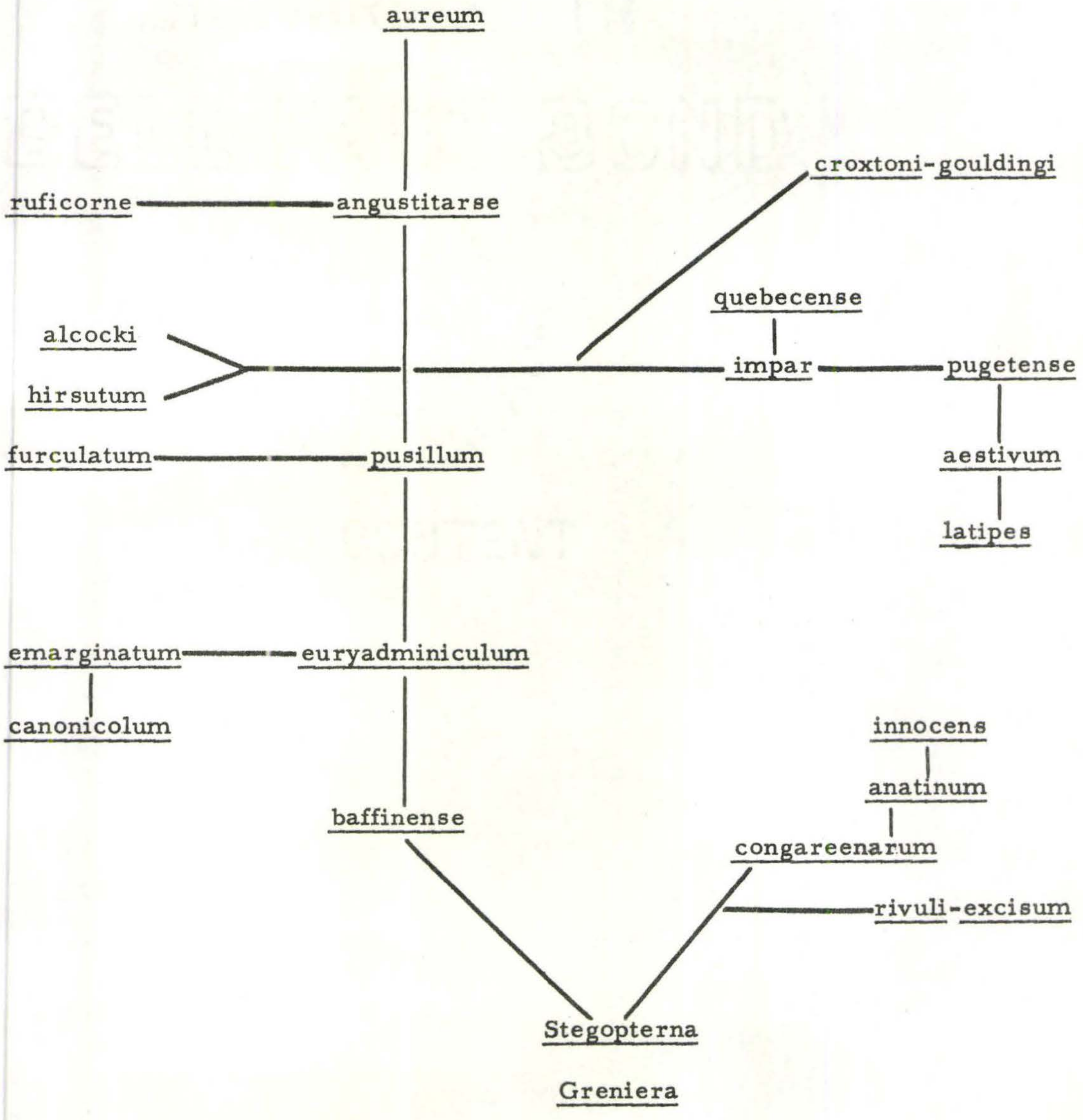
Group 6



S. aureum

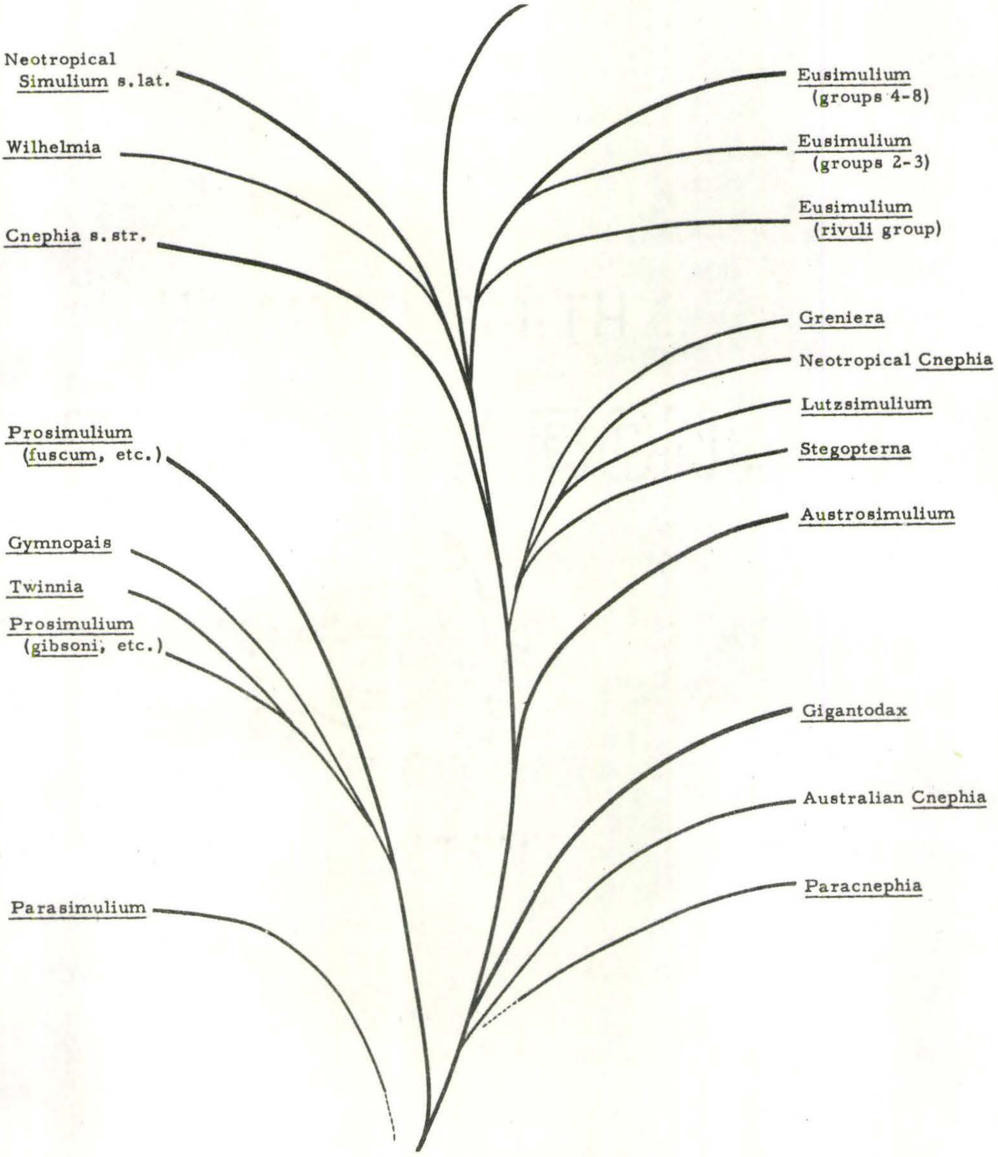
Group 8

Fig. 87. Chart showing phylogenetic relationships among species of the *Eusimulium*-group.


aureum
ruficorne
angustitarse
croxtoni-gouldingi
quebecense
alcocki
hirsutum
impar
pugetense
furculatum
pusillum
aestivum
latipes
emarginatum
euryadminiculum
canonicolum
innocens
anatinum
baffinense
congareenarum
rivuli-excisum
Stegopterna
Greniera

87

Fig. 88. Phylogenetic tree of the family Simuliidae.


Neotropical Simulium s.lat.
Wilhelmia
Cnephia s.str.
Prosimulium (fuscum, etc.)
Gymnopais
Twinnia
Prosimulium (gibsoni, etc.)
Parasimulium
Eusimulium (groups 4-8)
Eusimulium (groups 2-3)
Eusimulium (rivuli group)
Greniera
Neotropical Cnephia
Lutzsimulium
Stegopterna
Austrosimulium
Gigantodax
Australian Cnephia
Paracnephia

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