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## Larval Ecology of Some Lower Michigan Black Flies (Diptera: Simuliidae) With Keys to the Immature Stages

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**LARVAL ECOLOGY OF SOME LOWER MICHIGAN BLACK FLIES (DIPTERA: SIMULIIDAE) WITH KEYS TO THE IMMATURE STAGES<sup>1</sup>**Richard W. Merritt,<sup>2</sup> Douglas H. Ross,<sup>3</sup> and B. V. Peterson<sup>4</sup>**ABSTRACT**

The species composition, succession, and seasonal abundance of immature simuliids occurring in the Rose Lake Wildlife Research Area in lower Michigan are presented. Selected physical and chemical characteristics of streams in the above area were examined and compared in relation to faunal distributions. Comparisons of species differences between permanent and temporary streams were made utilizing the functional group concept based on feeding mechanisms.

Keys and illustrations are presented for the identification of larvae and pupae of four genera (*Prosimulium*, *Simulium*, *Stegopterna*, *Cnephia*) and 19 species of Simuliidae known to occur in lower Michigan. Two species, *Cnephia ornithophilina* and *Simulium vernum*, were recorded for the first time in Michigan.

Few studies have been conducted on the black flies (Diptera: Simuliidae) of Michigan. Wu (1931) studied various aspects of the biology and life history of several *Simulium* species in northern lower Michigan. Laboratory experiments were also conducted on factors influencing larval black fly distribution in streams. She concluded that larvae had a definite requirement for current and that high dissolved oxygen content of the water was not the determining factor for their presence or absence. Gill and West (1955) recorded biological observations on several species of black flies in Michigan's Upper Peninsula. Tarshis (unpubl. data, 1963-1973) and Desser et al. (1978) investigated the role of black flies in waterfowl disease transmission in the Upper Peninsula (mainly Seney National Wildlife Refuge), where the former author recorded 55 species (I. B. Tarshis, pers. comm.). Ross and Merritt (1978) studied the population dynamics of five species of black flies in the Lower Peninsula and their responses to selected environmental factors. They found that stream temperature was the most important physical factor regulating larval black fly population dynamics, determining hatching time and developmental rates.

This study was initiated to: (1) determine the species composition, succession, and seasonal abundance of immature simuliids in the Rose Lake Wildlife Research Area in lower Michigan; (2) examine selected physical and chemical characteristics of streams in the above area in relation to faunal distributions; and (3) provide a standard key to the major genera and species of immature black flies found in Michigan's Lower Peninsula. Prior to this paper, there have been no published keys to Michigan Simuliidae.

**MATERIALS AND METHODS**

Extensive collections of Simuliidae were made at the Rose Lake Wildlife Research Area (RLWRA) from March, 1975, through May, 1977, (Fig. 1, Table 1). This 1350 ha research area in Clinton and Shiawassee counties, Michigan, is located 13 km northeast of the Michigan State University campus. In addition, over 4000 specimens of black flies (mainly *Simulium* spp.) were sorted and identified from stream invertebrate survey collections made throughout the Lower Peninsula during June through September

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Table 2. Characteristics of streams in the Rose Lake Wildlife Research Area.

Stream	Nature Stream Flow	Width	Depth	Substrate(s) <sup>a</sup>	Surrounding Vegetation	Additional Features
Vermillion Creek	Permanent	3-10 m	.1-1.5 m	Stones, submerged wood & trailing vegetation	Lowland brush & woods, & upland woods	Largest stream in the study area.
Mud Creek	Permanent	1.5-5 m	.1-1 m	Stones, gravel & submerged wood & vegetation	Marsh, upland & lowland woods	Source at Site 27; low summer discharge
Site 12	Permanent	1-2 m	.1-1 m	Stones, gravel & trailing grasses	Open meadows	Empties into Vermillion Creek
Sites 1, 2 & 17	Permanent	1-2 m	.15-.5 m	Submerged wood & vegetation	Lowland brush & upland woods	Drains a spring-fed lake
Sites 13, 20 & 21	Temporary	.75-2 m	.1-.75 m	Trailing grasses	Marsh & lowland brush	Drains large lake; completely frozen in winter
Sites 9 & 10	Temporary	1-2 m	.1-.5 m	Submerged wood & vegetation	Marsh & lowland brush	Drains two small lakes
Site 6	Temporary	.3-.5 m	.02-.1 m	Gravel & fallen leaves	Gravel pit (no vegetation)	

<sup>a</sup>Substrates from which immature black flies were collected.

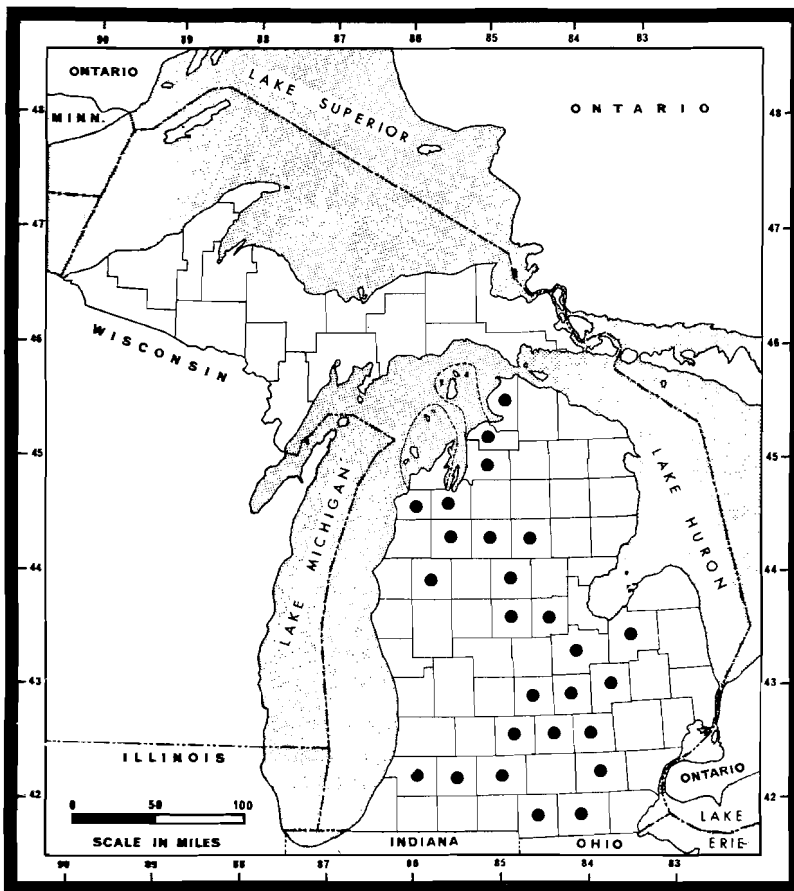


Fig. 2. Distribution of larval black fly collection localities in lower Michigan.

## RESULTS AND DISCUSSION

The 16 species of Simuliidae collected from the RLWRA are listed in Table 1. *Stegopterna mutata* Malloch, *Simulium verecundum* Stone and Jamnback complex, and *S. vittatum* Zetterstedt were the three most widespread and abundant species, while *S. excisum* Davies, Peterson, and Wood, *S. pugetense* Dyar and Shannon, *S. venustum* Say complex, and *S. venum* Macquart complex were collected infrequently. *Cnephia ornithophila* Davies, Peterson, and Wood and *S. venum* were recorded for the first time in Michigan. In addition to those species listed in Table 1, the following species were recorded from other areas of the Lower Peninsula: *Simulium jenningsi* Malloch, *S. luggeri* Nicholson and Mickel, and *S. tuberosum* (Lundström).

The species composition and seasonal occurrence of immature black fly populations in seven creeks of the RLWRA are shown in Figure 3. Life cycle patterns of some species varied among different streams. For example, *Prosimulium fuscum* Syme & Davies, *P. mixtum* and *Stegopterna mutata* overwintered as larvae in Mud and Vermillion Creeks

(which flow under the ice), but did not hatch from eggs until late February at Sites 13, 20 and 21 (which freeze solid in winter) (Fig. 3). Similar observations were made for *S. "verecundum"* and *S. vittatum*, whose occurrence and number of summer generations vary with permanence of the stream (Fig. 3; Mud Creek and Sites 13, 20 and 21).

#### Genus **PROSIMULIUM** Roubaud

Five univoltine species of *Prosimulium* were collected during the study. Low autumn and winter discharge followed by spring flooding from melting snow produced second cohorts of *mixtum* and *fuscum* in 1977 (Ross and Merritt, 1978). Oviposition by *Prosimulium* species occurs in flight when the female taps her abdomen on the water's surface and releases eggs. Eggs settle to the bottom and diapause until autumn or the following spring (Peterson, 1970).

#### Subgenus **PARAHELODON** Peterson

**gibsoni** (Twinn). Overwintering eggs of *gibsoni* hatch in mid-March, and larvae develop rapidly (Fig. 3). Emergence begins four to five weeks later and lasts approximately two weeks. Females, whose mouthparts are not adapted for taking a blood meal, contain mature eggs upon emergence (Davies et al., 1962).

#### Subgenus **PROSIMULIUM** Roubaud

**fuscum** Syme and Davies and **mixtum** Syme and Davies. These species were widely distributed in the study area and always occurred together (Table 1). Their life cycles varied in different streams, but they usually began hatching in mid-November and developed slowly during the winter months (Fig. 3). Larval growth was rapid following snowmelt and increasing water temperatures in late February; synchronous pupation occurred in late March. Adults were collected from late March to early May. Both species fed on deer, elk, and horses, while *mixtum* also engorged on humans. L. Davies (1961) found *fuscum* to be autogenous for the first gonotrophic cycle, with less than 10% of parous females surviving to become biting pests. In contrast, *mixtum* was largely anautogenous, and nulliparous females readily fed on man (L. Davies, 1961).

**multidentatum** (Twinn). The life cycle of this species varied among creeks (Fig. 3). Larvae overwintered in streams which continued to flow beneath the ice and pupation occurred in mid-March. In creeks which were frozen until spring, eggs hatched in late February, and these larvae pupated in early April. Adults were collected as late as 20 April. No data on adult feeding were obtained, although females are capable of taking a blood meal (Peterson, 1970).

**mysticum** Peterson. *P. mysticum* overwintered in the larval stage in lower Michigan, as in Ontario (Mansingh et al., 1972) (Fig. 3). Mature larvae were collected in mid-March and pupated in late March. Adults were captured feeding on deer in late April.

#### Genus **CNEPHIA** Enderlein

**dacotensis** (Dyar and Shannon). Eggs of this univoltine species hatched from late March to mid-April, depending on water temperature during the spring. Larval development was rapid, and pupation occurred six weeks after eclosion (Fig. 3). Emergence took place in May and was concentrated within a few days. Flies mated on streamside objects (e.g., rocks, vegetation, logs, and culverts) soon after emerging, and females oviposited in flight. *C. dacotensis* females possess weak mouthparts and are incapable of taking a blood meal (Krafchick, 1942; Nicholson, 1945). Although Davies et al. (1962) reported that this species was highly parasitized by mermithid nematodes, parasitized larvae were not observed in this study.

**ornithophilia** Davies, Peterson and Wood. Larvae of *ornithophilia* overwintered in large streams such as Vermillion Creek (Fig. 3, Table 2), which flow throughout the winter.

Mature larvae were collected from late February through March and pupation occurred during March and early April (Fig. 3). Eggs of this species did not hatch until March in creeks which froze solid during the winter, and pupation occurred in late April (Fig. 3, Sites 13, 20 and 21). Bennett (1960) reported that *ornithophilis* (under the name *Cnephia* "U") fed on woodland birds (e.g., crow and ruffed grouse) 1.5-7.5 m above the forest floor. This species is capable of transmitting the sporozoan parasite *Leucocytozoon simondi* Mathis and Leger to waterfowl in the laboratory (Tarchis, 1972, 1976).

#### Genus STEGOPTERNA Enderlein

*mutata* (Malloch). Although diploid (bisexual) and triploid (parthenogenetic) forms of this species occur together in Ontario (Basrur and Rothfels, 1959), no attempt was made in the present study to separate them. Second cohorts of this univoltine species were also produced in 1977 as in *P. mixtum/fuscum* (Ross and Merritt, 1978). *S. mutata* overwintered as eggs or larvae, depending on the extent of ice in the stream (Fig. 3). Eggs that produced overwintering larvae hatched in January, and larval growth was slow until water temperatures increased in early March. Pupation occurred from late March through mid-April, and adults were collected from mid-April to early May. Overwintering eggs hatched in March and adults emerged in late April (Fig. 3). Larvae of *S. mutata* were parasitized by *Caudospora brevicauda* Jamnback (Protozoa: Microsporida) with infection rates as high as 20%. Females of this species were collected feeding on penned deer and elk.

#### Genus SIMULIUM Latrielle

##### Subgenus EUSIMULIUM Roubaud.

Species of this subgenus are primarily ornithophilic, feeding on birds in a variety of habitats, and are known vectors of avian blood parasites (Fallis and Bennett, 1958; Bennett, 1960; Anderson and DeFoliart, 1961; Stone, 1964).

*aureum* Fries complex. This multivoltine species complex overwintered in the egg stage and may have two or three generations per year. Eggs hatched in late March and first generation pupae were present in early May (Fig. 3). Eggs, larvae and pupae of other generations occurred throughout the summer until late September (Fig. 3). Engorged females were collected from ruffed grouse exposed 6.0-7.5 m above the forest floor in June (Fig. 1, Site 15; J. N. Stuht, pers. comm.). These findings agreed with Bennett's (1960) data on feeding habits and occurrence of *aureum* in late summer. Some members of the *aureum* complex serve as vectors of *Leucocytozoon bonasae* Clarke, a blood parasite of ruffed grouse (Fallis and Bennett, 1960).

*excisum* Davies, Peterson and Wood. *S. excisum* is a univoltine species which overwinters in the egg stage. Following hatching, larvae developed rapidly in early March and pupation occurred in mid-April (Fig. 3). Bennett (1960) collected females of this species (under the name *S. subexcisum*) engorging on ducks along lake shores, but further studies on its feeding habits are needed (Davies et al., 1962).

*pugetense* (Dyar and Shannon). Larvae of this species were collected only once, in early April at Site 26 (Fig. 1). In Ontario, Davies et al (1962) reported it to be a univoltine species which overwintered in the larval stage and emerged in early spring. Females have bifid claws and mouthparts suitable for blood feeding. Oviposition occurs in spring, and eggs diapause until autumn (Davies et al., 1962).

*vernum* Macquart complex. Larvae of this species complex were collected only once during the study (at Site 27, see Fig. 1). Although *vernum* (as *latipes*) has been previously recorded from North America (Twinn, 1936), its biology is not well known. This species also feeds on birds (Peterson, 1977).



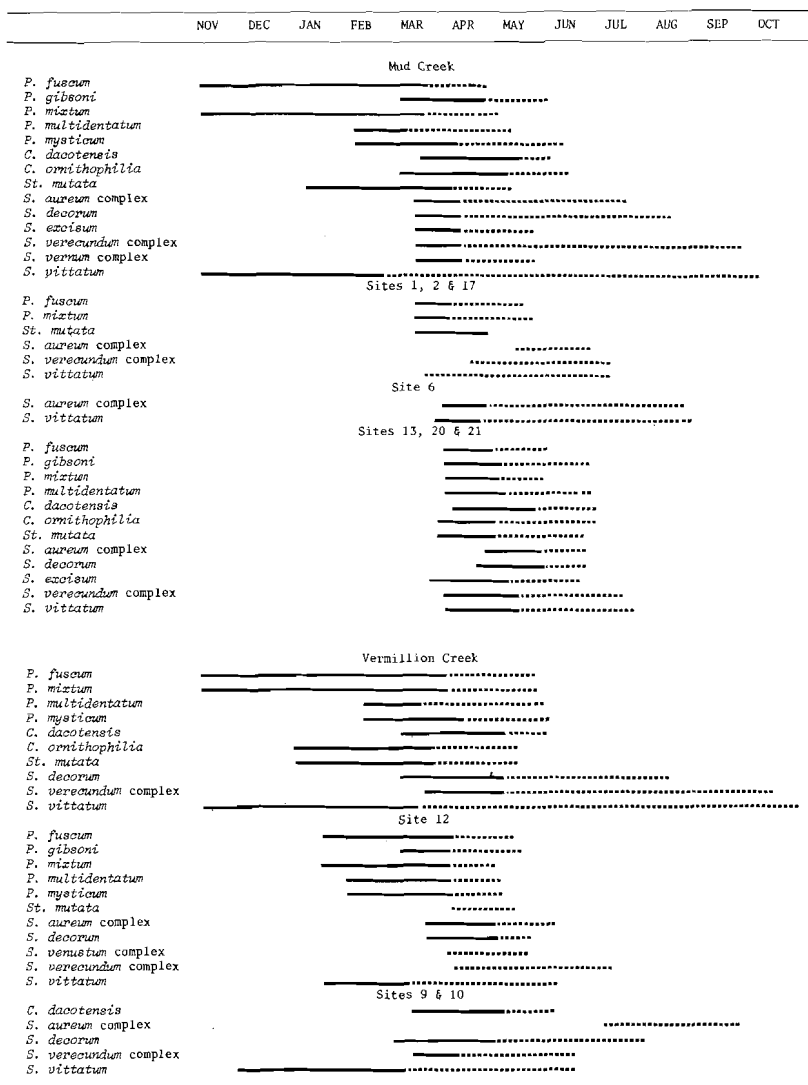


Fig. 3. Seasonal occurrence of simuliid larvae and pupae in seven streams in the Rose Lake Wildlife Research Area. Solid line = larvae; broken line = larvae and pupae.

Subgenus *SIMULIUM* Latrielle.

*decorum* Walker. Overwintering eggs of this multivoltine species hatched in March and the larvae developed rapidly, pupating in mid-April and emerging at the end of April (Fig. 3). Larvae, pupae, and adults of the second generation were collected in mid-July, and a third generation may occur, though it was not observed in this study. Females usually oviposit on streamside objects or vegetation which have water covering or

lapping them, but have also been observed ovipositing in flight, similar to *Prosimulium* spp. (Davies et al., 1962). Although *decorum* females may be autogenous for the first gonotrophic cycle (Davies et al., 1962), they have well-developed mouthparts and have been captured engorging on deer and humans (Davies and Peterson, 1956).

*verecundum* Stone and Jamnback complex and *venustum* Say complex. These two species complexes contain many undescribed species with similar life cycles. *S. "venustum"* was collected only once (at Site 12), while "*verecundum*" was widespread and numerous (Table 1). Both multivoltine species groups overwintered in the egg stage and "*verecundum*" eggs hatched in early March. Pupae and adults of the latter species group were collected in early to mid-April. Four or five generations may occur, since adults were still on the wing in September and pupae were collected in late November (Fig. 3). Females of both species groups lay their eggs in mats on vegetation at or just below the water's surface. *S. "venustum"* is a major pest in Canada and the northern United States (Stone and Jamnback, 1955; Davies et al., 1962), feeding readily on humans, deer, cattle, horses, and even birds (Davies and Peterson, 1956; Teskey, 1960). *S. "verecundum"* is less annoying to man (Stone, 1964).

#### Subgenus PSILOZIA Enderlein.

*vittatum* Zetterstedt. This multivoltine species was the most numerous and widespread simuliid in the study area (Table 1). Eggs of the last summer generation hatched in autumn and larvae grew slowly through the winter (Fig. 3). Pupation began in early March and emergence of this generation occurred in early April. Succeeding generations emerged in mid-June, late July and early September, although some overlap existed (Fig. 3). Oviposition occurs on vegetation and other damp streamside objects, as well as in flight (Davies and Peterson, 1956). *S. vittatum* has been reported to be a major pest of horses and other livestock in some areas of the country (Anderson and DeFoliart, 1961; Townsend et al., 1977). Engorged females were collected from deer, elk and horses in this study. *S. vittatum* is not a serious human pest in this region.

#### SEASONAL SUCCESSION

Data on seasonal succession of black fly species at selected sites are presented in Figures 4-6. Most species occurred at Site 13 during late winter and spring, with eclosion beginning in March following snowmelt (Figs. 3 and 4). *Prosimulium gibsoni*, *Stegopterna mutata*, *Cnephia ornithophilia* and *Simulium* spp. hatched earlier in the month than *Cnephia dacotensis*, since later instars of these species were present when *C. dacotensis* larvae were first collected (Fig. 4; 23 March). First instars of this latter species were the only ones positively identified because the head capsule sclerotization is weaker than that of the other species (Craig, 1974). All eggs of *C. dacotensis* had hatched by 4 April, and pupation of this species and *C. ornithophilia* occurred four weeks later, with adults emerging in mid-May (Figs. 3 and 4). The life cycles of *Prosimulium gibsoni* and *Stegopterna mutata* were also short, requiring approximately six weeks from eclosion to pupation (Figs. 3 and 4). The early peak of *Simulium* spp. was largely *S. excisum*, while the later one was 90 to 95% *S. "verecundum"* (Fig. 4). Larval populations declined rapidly in late May following pupation of a large generation of *S. "verecundum"* (Fig. 4). Discharge also declined and the stream ceased to flow by mid June.

Figures 5 and 6 illustrate the succession of simuliid species in Mud Creek (Site 15) during the 1975-76 and 1976-77 seasons, respectively. Although quantitative sampling did not begin until mid-February, 1976, preliminary collections were made in January and in November, 1975. Data indicated that *Prosimulium mixtum/fuscum* larvae hatched in early to mid-November and were the only black flies present in Mud Creek until January, when *Stegopterna mutata* first appeared (Fig. 6). The latter species was less abundant in 1977 than 1976, possibly due to the microsporidian parasite *Caudospora brevicauda*, which infected 20% of the larvae in 1976, preventing pupation and decreasing egg production. Since the parthenogenetic (triploid) form of *Stegopterna mutata* is more common than the diploid (sexual) form (Davies and Peterson, 1956; Basrur and Rothfels, 1959), a 20%

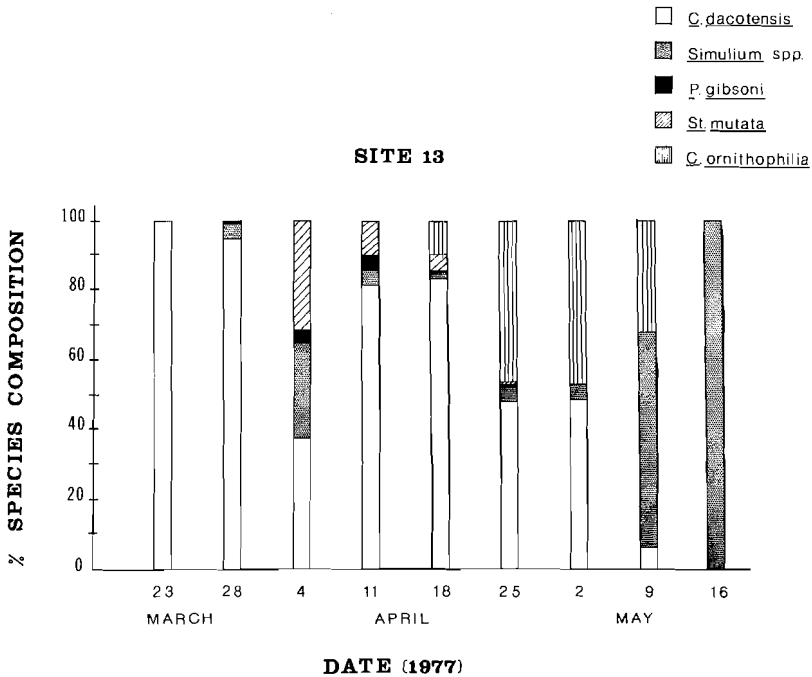


Fig. 4. Seasonal succession of black fly species at Site 13 (1977).

reduction in egg-laying females could have resulted in a smaller population the following year.

The time period that *Prosimulium mixtum/fuscum* and *Stegopterna mutata* populations remained in Mud Creek also varied during the two year study. Larvae of these species were still present in May, 1977, while they had all pupated by early April, 1976 (Figs. 5 and 6). This difference was due to the occurrence of second cohorts of each species during 1977 (Ross and Merritt, 1978). Larvae of the second cohorts did not hatch until early March (1977) and they pupated from mid-April through May (Fig. 6). Data indicated that in lower Michigan, *Prosimulium mixtum/fuscum* and *Stegopterna mutata* usually pupate in late March and early April, respectively.

The succession of *Prosimulium* spp. and *Stegopterna mutata* by *Cnephia* and *Simulium* spp. was similar at Site 13 (Fig. 4) and in Mud Creek (Figs. 5 and 6). Early instars of *Cnephia* and *Simulium* spp. hatched when larvae of the other two genera neared pupation, thus possibly reducing competition for food and suitable habitat. The successional pattern of *Cnephia* and *Simulium* spp. may also be related to other factors. Following ice-out in spring, temperate-zone lakes experience phytoplankton blooms which result in the production of large quantities of diatoms and other algae (Ruttner, 1973). Larval black flies which inhabit lake outlets (e.g., Fig. 2; Site 13 and Mud Creek) would be exposed to a rich food supply (Carlsson, 1967), and may receive some selective advantage over larvae occurring at other times of the year or further downstream. Recently, Carlsson et al. (1977) examined factors influencing black flies inhabiting lake outlets in Sweden and concluded that food quality rather than quantity was responsible for supporting huge larval aggregations of certain species immediately below these areas. *Cnephia dacotensis* has frequently been found in large numbers in lake and pond outlets (Anderson and Dicke, 1960; Davies et al., 1962; Stone, 1964; Gersabeck, 1978), and may

have evolved a life cycle to exploit these food resources. Some species of net-spinning Trichoptera also occur in great abundance at lake outlets and below impoundments (e.g., Chutter, 1963; Wallace and Sherberger, 1974) and different species successfully share habitats and food through different adaptive strategies, such as temporally asynchronous life cycles, different feeding habits (e.g., particle size differences) and/or different microdistributional patterns (Eddington, 1968; Wallace, 1975; Wallace et al., 1977; Malas and Wallace, 1977). Further studies are currently underway on the size, type, and quality of particulate materials ingested by different instars and species of Simuliidae to clarify some of these interspecific relationships.

#### PHYSICAL CHARACTERISTICS OF STREAMS

In a concurrent study the most important physical factor regulating black fly larval development was stream temperature (Ross and Merritt, 1978). It played the major role in determining hatching, pupation, and emergence, and was responsible for the timing and duration of the life cycles of each species. In other areas, temperature has been shown to also affect the number of simuliid species in a stream and the life cycles of their parasites and predators (Ezenwa, 1974; Lewis and Bennett, 1975). Variations in temperature among streams in the study area were negligible and of little use in explaining black fly distribution differences.

Stream discharge also influenced immature Simuliidae. Following prolonged dry conditions, rising water levels flooded unhatched eggs, producing second cohorts of some

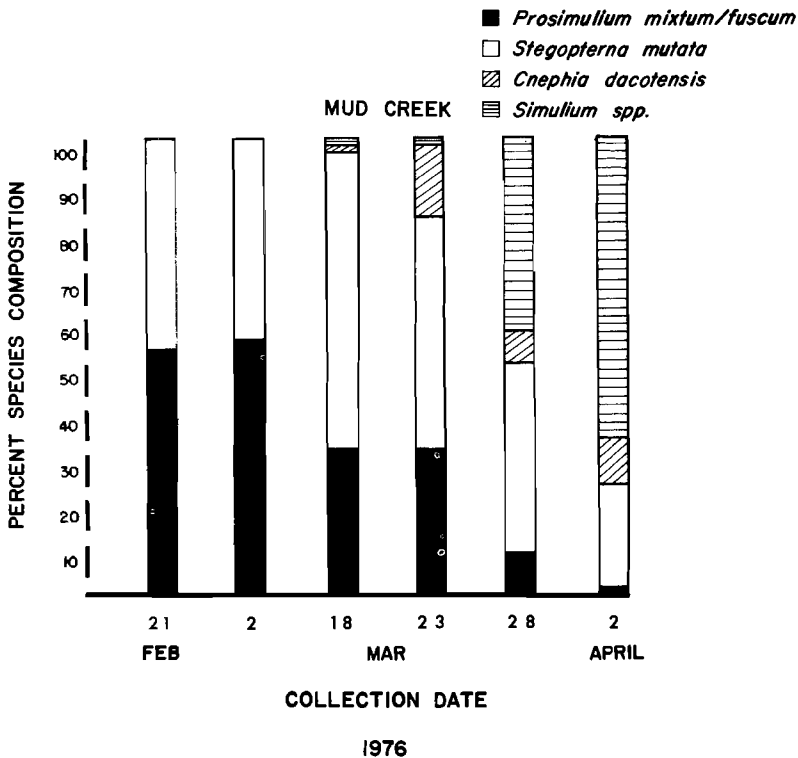


Fig. 5. Seasonal succession of black fly species at Site 15, Mud Creek (1976).

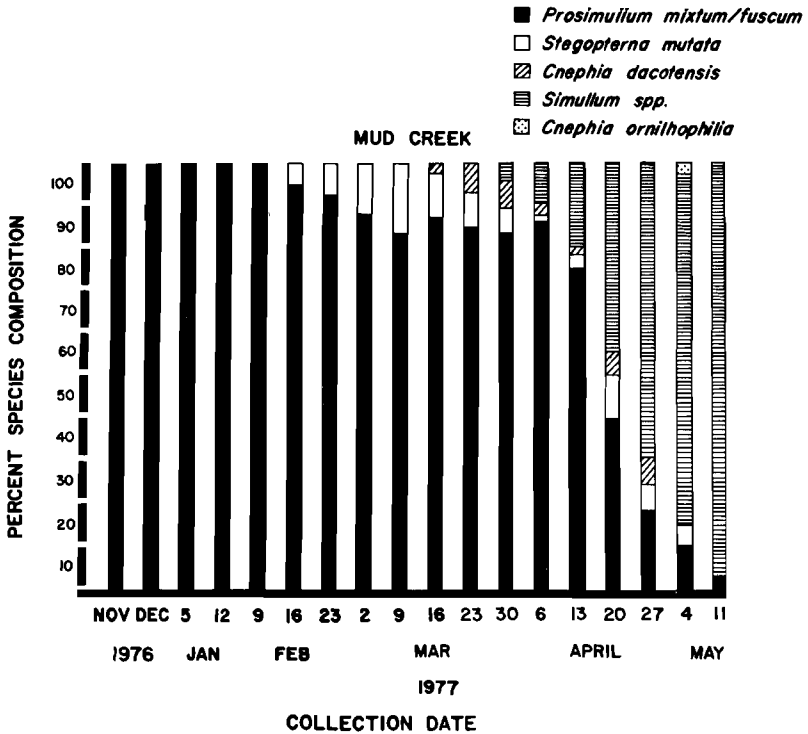


Fig. 6. Seasonal succession of black fly species at Site 15, Mud Creek (1976-77).

univoltine species which typically have only one cohort per generation (Ross and Merritt, 1978). Changes in discharge also affected rates of larval colonization and detachment from artificial substrates, thus influencing estimates of black fly abundance (Disney, 1972; Pegel and Ruhm, 1976; Gersabeck, 1978; Ross and Merritt, 1978). Yearly variations in discharge determined the number of generations of some multivoltine *Simulium* spp. during the summer and early autumn. The nature of stream flow also had important implications, with permanent creeks generally having more species of simuliids than temporary streams (Table 2, Fig. 3).

The number of black fly species inhabiting a stream did not appear to be related to the stream's origin (Figs. 1 and 3, Table 2). For example, Mud Creek and Sites 9 and 10 both drain lakes, yet the former stream contained 14 species of simuliids while the latter had only five (Fig. 3). Contrary to studies by Anderson and Dicke (1960) and Davies et al. (1962) which found substrate preferences among larvae of different species, gravel, stones, wood, and vegetation were utilized by all species collected in the present study. All of these materials were colonized if water velocity was suitable and their surfaces were free of periphyton. Stream depth and width were not related to species distribution, since *Prosimulium mixtum*, *P. fuscum*, *Stegopterna mutata* and other species occurred in both large and small creeks (Fig. 3, Table 2).

#### CHEMICAL CHARACTERISTICS OF STREAMS

Data on the chemical properties of the seven streams showed minor variation between them. All tests for phenolphthalein alkalinity were negative, while methyl orange (bicar-

bonate) alkalinity was generally high ( $< 200 \text{ mg/l CaCO}_3$ ). Water in all streams was hard ( $150\text{-}300 \text{ mg/l CaCO}_3$ ) (Kevem, 1973), and differences among streams were insignificant. Melting snow and rainfall reduced alkalinity and hardness by dilution, as well as nitrate ( $\text{NO}_3$ ) and orthophosphate ( $\text{PO}_4$ ) concentrations. Nitrate and orthophosphate were consistently present at low levels ( $< 1.1$  and  $< 0.02 \text{ mg/l}$ , respectively), indicating a lack of organic enrichment (Kevem, 1973). Dissolved oxygen exceeded  $10 \text{ mg/l}$  (71% saturation) in all streams except at Sites 9 and 10, where it was less than  $6 \text{ mg/l}$  (43% saturation) during the winter. This was caused by the formation of pools of stagnating water under the ice cover. The variability of results from the free carbon dioxide tests made estimates unreliable. Other investigators (Carlsson, 1962, 1967; Chutter, 1968; Ali et al., 1974; Ezenwa, 1974; Lewis and Bennett, 1975) who have measured chemical properties were also unable to correlate differences with simuliid distribution patterns. Grunewald (1972) determined a combination of physical and chemical factors at breeding sites of *Boophtora erythrocephala* DeGeer which were quite distinct from those of other black fly species; however, such success has not been achieved with other simuliids. Chemicals indicative of organic pollution (e.g.,  $\text{NO}_3$  and  $\text{PO}_4$ ) are capable of affecting black fly population abundance and distribution by increasing food supplies. Such enriched streams were found to contain significant quantities of microplankton on which large populations of *Simulium* spp. fed (Chutter, 1968; Ali et al., 1974). More recent studies by Chance (1970, 1977), Kurtak (1973) and Ladle et al. (1977) suggested that the sizes of particulate matter available to filter-feeding black fly larvae in different streams may affect species distribution. Habitat preference and oviposition behavior could also influence species distribution (Rhum, 1971; Lewis and Bennett, 1975).

#### ASSOCIATED AQUATIC INSECTS

The insects collected in association with immature simuliids from seven streams in the study area are listed in Table 3. With the exception of one stream (Sites 13, 20 and 21), the fauna of temporary streams was not as diverse as that of permanent ones (Table 2 and 3, Fig. 3). Although these collections were not complete, equal effort was expended in each stream, and all samples were taken at the same time of year. Thus, some comparisons can be made among creeks. The number of black fly species occurring in each stream showed a significant positive correlation ( $r = .70$ ) with the number of other insect species in the same stream (Fig. 7). This suggested that factors which influence simuliid distribution may also affect the diversity of abundance of other aquatic insects.

To make general comparisons of species differences between permanent and temporary streams in the study area, we have categorized various combinations of taxa into similar functional groups based on feeding mechanisms (Merritt and Cummins, 1978) (Fig. 8). As shown, in both permanent and temporary streams the largest percent of the species recorded were collectors, those groups which are filter or suspension feeders (filters; e.g., Simuliidae, Hydropsychidae) or sediment and deposit feeders (gatherers; e.g., Ephemeridae, Chironomini). Shredders (i.e., herbivores and large particle detritivores) were fewer in number, although more abundant in permanent streams. Predators were equally represented in both types of streams and consisted mainly of Odonata, Hemiptera, and Plecoptera (Table 3). Scrapers of mineral and organic surfaces made up the smallest percent in each stream type, consisting of two genera of heptageniid mayflies (Table 3). Contrary to small first order or headwater woodland streams, which are heavily dependent upon terrestrial contributions of coarse particulate organic matter (particularly leaf litter) (Sedell et al., 1974; Cummins, 1977), streams in this study area were primarily of small lake origin (Fig. 1) and less dependent on direct terrestrial inputs and more on nutrient and detrital input from the lakes. This would account for the predominance of collectors and fewer shredders (Fig. 8). Functional group differences between temporary and permanent streams were not significant except for the greater number of shredders in permanent streams, which could be attributed to a requirement for year-round flow by the dominant species of shredders which were all univoltine. This factor most likely accounted for the greater number of species also found in permanent streams.

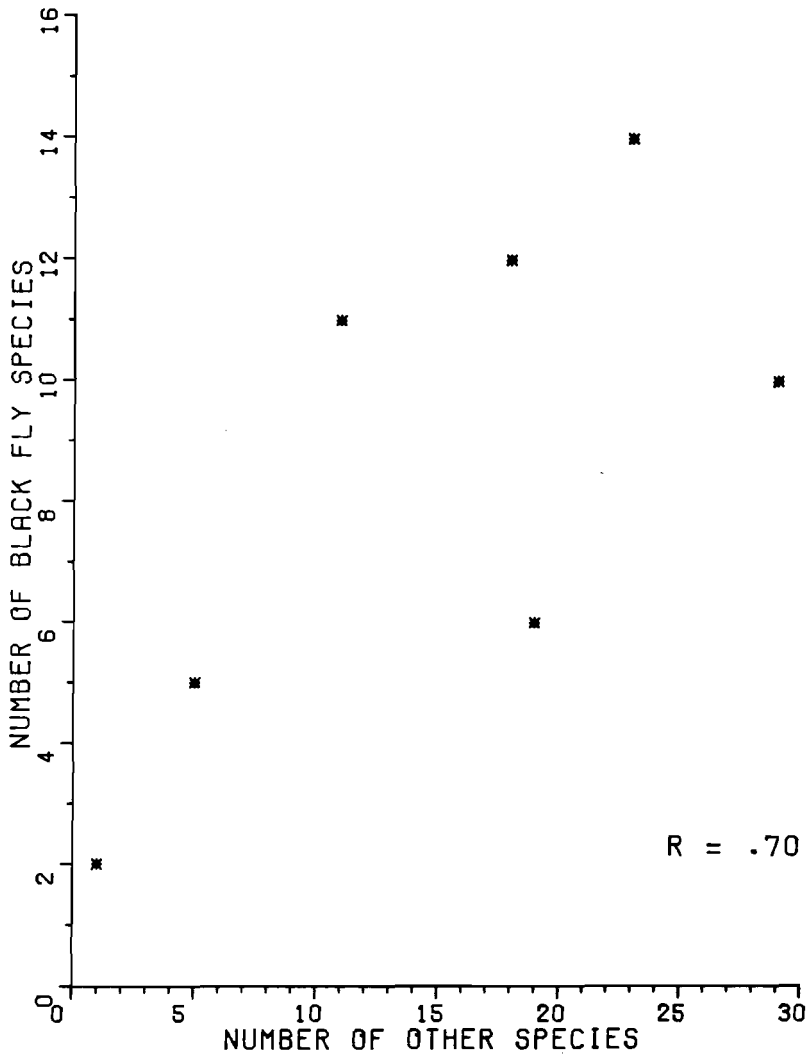


Fig. 7. Correlation between the number of simuliid species and number of other aquatic insect species in seven streams of the Rose Lake Wildlife Research Area.

#### SYSTEMATICS

It is presumed that those readers interested in the identification of immature black flies are familiar with current character terminology. For those not familiar with this terminology the labels on the accompanying illustrations will be of help. For a discussion of larval black fly terminology see Crosskey (1960), Chance (1970), and Wood et al. (1963).

Table 3. Aquatic insect fauna associated with immature black flies in the Rose Lake Wildlife Research Area.

Taxon	Creek						
	Mud Creek	Vermilion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
EPHEMEROPTERA							
Ephemeridae							
<i>Hexagenia</i> sp.		X					
<i>Ephemera</i> sp.							X
Lepthophlebiidae							
<i>Lepthophlebia</i> spp.	X	X		X	X		X
Siphonuridae							
<i>Siphonurus</i> sp.		X					
Baetidae							
<i>Baetis</i> sp.		X			X		
Caenidae							
<i>Caenis</i> sp.							X
Heptageniidae							
<i>Stenonema</i> sp.		X			X		
<i>Stenacron</i> sp.					X		
ODONATA (Anisoptera)							
Aeshnidae							
<i>Boyeria</i> sp.	X	X					
Corduliidae							
<i>Tetragoneuria</i> sp.					X		
Gomphidae							
<i>Gomphus</i> sp.		X					
Libellulidae							
<i>Libellula</i> sp.					X		
ODONATA (Zygoptera)							
Calopterygidae							
<i>Calopteryx</i> spp.	X	X					X
Coenagrionidae							
<i>Enallagma</i> sp.		X					
PLECOPTERA							
Perlidae							
<i>Acroneuria</i> sp.		X					
<i>Perlesta</i> sp.	X	X			X		
Perlodidae							
<i>Isoperla</i> sp.	X			X			X
HEMIPTERA							
Corixidae	X	X		X	X		X



Table 3, Continued

Taxon	Creek						
	Mud Creek	Vermilion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
<b>Notonectidae</b>							
<i>Notonecta</i> sp.		X					
<b>Belostomatidae</b>							
<i>Belostoma</i> sp.	X	X			X	X	
<i>Lethocerus</i> sp.			X				
<b>Pleidae</b>							
<i>Plea</i> sp.					X		
<b>Nepidae</b>							
<i>Nepa</i> sp.					X		
<i>Ranatra</i> sp.	X	X				X	
<b>Mesoveliidae</b>							
<i>Microvelia</i> sp.	X						
<b>Gerridae</b>							
<i>Gerris</i> sp.	X	X	X	X	X	X	X
<b>MEGALOPTERA</b>							
<b>Corydalidae</b>							
<i>Nigronia</i> sp.		X	X				
<b>Sialidae</b>							
<i>Sialis</i> sp.	X			X	X	X	
<b>COLEOPTERA</b>							
<b>Haliplidae</b>							
<i>Peltodytes</i> sp.						X	
<b>Hydrophilidae</b>							
<i>Tropisternus</i> sp.	X						
<b>Dytiscidae</b>							
<i>Agabus</i> sp.		X					
<i>Dytiscus</i> sp.		X				X	
<b>Gyrinidae</b>							
<i>Dineutus</i> sp.		X					
<b>Helodidae</b>							
			X				
<b>TRICHOPTERA</b>							
<b>Hydropsychidae</b>							
<i>Hydropsyche betteni</i> Ross		X					
<i>Hydropsyche</i> spp.	X	X		X			
<i>Cheumatopsyche</i> sp.	X				X		
<b>Limnephilidae</b>							
<i>Limnephilus consocius</i> Walker	X	X		X			
<i>Limnephilus</i> spp.	X	X		X	X	X	
<i>Limnephilus submonilifer</i> Walker		X		X	X		

Table 3, Continued

Taxon	Creek						
	Mud Creek	Vermilion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
<i>Neophylax</i> sp.					X		
<i>Pseudostenophylax</i> sp.	X						
<i>Pycnopsyche</i> sp.	X	X			X	X	
Molannidae							
<i>Molanna</i> sp.		X			X		
Phryganeidae							
<i>Ptilostomis</i> spp.				X	X		
DIPTERA							
Tipulidae							
<i>Tipula</i> sp.	X	X					
<i>Limonia</i> sp.	X					X	
Chironomidae							
Chironomini	X	X	X	X	X	X	
Tabanidae							
<i>Chrysops</i> sp.	X	X		X		X	
Athericidae							
<i>Atherix variegata</i> Walker		X					
Stratiomyidae							
<i>Stratiomyia</i> sp.	X					X	
Empididae							
<i>Hemerodromia</i> sp.	X						

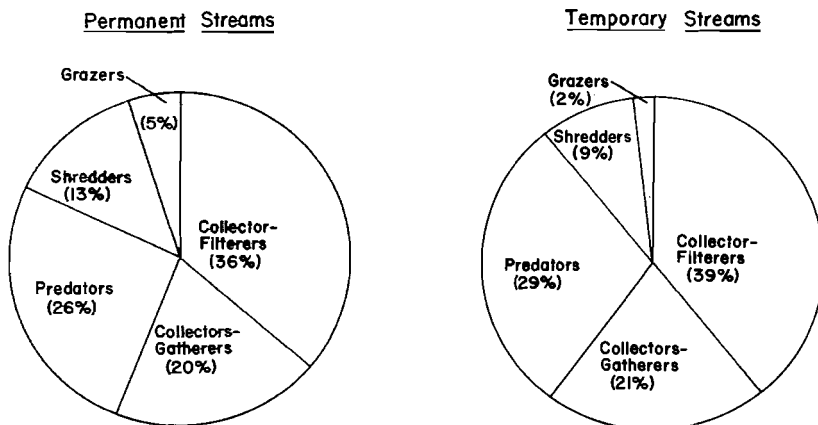


Fig. 8. The relative dominance of different functional groups (% species composition) of aquatic insects in permanent and temporary streams in the study area.

KEY TO GENERA AND SPECIES OF SIMULIIDAE<sup>5</sup>

LARVAE

1. Head capsule with postoccipt nearly complete dorsally, enclosing cervical sclerites (Fig. 3). Basal two segments of antenna pale, contrasting with darkly pigmented distal segments (Figs. 1-5). Median tooth of hypostomium distinctly trifid (Figs. 20-24). Anal gill with three simple finger-like lobes (Fig. 30). Genus *Prosimulium* . . . . . 2
- 1'. Head capsule with postoccipt usually with a broad gap dorsally, not enclosing cervical sclerites (Fig. 6). Basal two segments of antenna at least partially pigmented, not contrasting in color with distal segments (Figs. 6, 8, 11-19). Median tooth of hypostomium single (Figs. 25-27). Anal gill with three simple or compound lobes (Figs. 30-31) . . . . . 6
- 2(1). Lateral plate of proleg a narrow horizontal bar lying parallel to bases of apical ring of hooks (Fig. 9). Anal sclerite subrectangular, anterodorsal and posteroventral arms only weakly developed (Fig. 34). Outer lateral and sublateral teeth of hypostomium of nearly equal height, median tooth lower than lateral teeth (Fig. 20). (Subgenus *Parahelodon*) . . . . . *gibsoni* Twinn
- 2'. Lateral plate of proleg broader, with a well developed vertical portion (Fig. 10). Anal sclerite X-shaped (Fig. 30). Teeth of hypostomium variable, but not exactly as above (Subgenus *Prosimulium*) . . . . . 3
- 3(2'). Antenna conspicuously shorter than stalk of cephalic fan (Fig. 1). Hypostomial teeth as in Figure 21; median tooth rather broad. Maxillary palpus (Fig. 7) about 2.0 times as long as width at base. Abdomen gradually expanding posteriorly . . . . . *multidentatum* Twinn
- 3'. Antenna subequal to (at most only slightly shorter) or longer than stalk of cephalic fan (Figs. 2-4). Hypostomial teeth as in Figures 22-24; median tooth rather slender. Maxillary palpus 2.5-3.0 times as long as width at base. Abdomen rather abruptly expanding at segment 5 . . . . . 4
- 4(3'). Outer lateral teeth of hypostomium higher than sublateral teeth (Fig. 22). First posterolateral head spot usually present; anterolateral head spots relatively small (Fig. 2). Anterodorsal arms of anal sclerite nearly equal in length or only slightly longer than posteroventral arms. Cephalic fan with about 37-46 rays (av. 41) . . . . . *fuscum* Syme and Davies
- 4'. Outer lateral teeth and sublateral teeth of hypostomium nearly equal in height, or outer lateral teeth often lower than highest of sublateral teeth (Figs. 23-24). First posterolateral head spot usually absent; anterolateral head spots relatively large (Figs. 3-4). Anterodorsal arms of anal sclerite considerably longer than posteroventral arms. Cephalic fan with about 27-40 rays (av. 33) . . . . . 5
- 5(4'). Outer lateral teeth and sublateral teeth of hypostomium of nearly equal height; median tooth only slightly higher than outer lateral teeth (Fig. 23). Head capsule yellowish-brown to dark brown, head spots more pale and less distinct (Fig. 3) . . . . . *mixtum* Syme & Davies
- 5'. Outer lateral teeth of hypostomium often lower than highest sublateral teeth; median tooth distinctly higher than outer lateral teeth (Fig. 24). Head capsule pale yellow to medium yellowish brown, head spots darker and more distinct (Fig. 4) . . . . . *mysticum* Peterson
- 6(1'). Hypostomium either with rather uniformly small teeth (Fig. 26), or with teeth clustered in three prominent groups (Fig. 25). Anterodorsal portion of head capsule often strongly convex (Fig. 7). Anal gill with three simple lobes . . . . . 7
- 6'. Hypostomium with median tooth and outer lateral teeth moderately large and subequal in height, and with three smaller sublateral teeth on each side (Fig. 27). Anterodorsal portion of head capsule not noticeably arched nor strongly convex. Anal gill with three simple or compound lobes. Genus *Simulium* . . . . . 9

<sup>5</sup>Figures illustrating the key are contained in Plates I-VIII.

- 7(6). Postgenal cleft narrow, shallow, acutely pointed, an inverted V-shape (Fig. 6). Hypostomial teeth clustered in three prominent groups (Fig. 25). Abdominal segment 9 with a single transverse midventral bulge (Fig. 32) . . . . . *Stegopterna mutata* (Malloch)
- 7'. Postgenal cleft moderately deep, its anterior margin usually rounded (Fig. 8). Hypostomial teeth rather uniformly small (Fig. 26). Abdominal segment 8 simple, without a transverse midventral bulge. Genus *Cnephia* . . . . . 8
- 8(7'). Both rather uniformly and darker greyish-brown to moderately dark brown, with only narrow inconspicuously lighter intersegmental bands. Head capsule darker brown, less contrasting with dark head spots; dorsal head spots surrounded by a distinct fulvous area (Fig. 8). Overall size smaller and more slender . . . . . *dacotensis* (Dyar and Shannon)
- 8'. Body distinctly bicolored, overall more pale, with distinct and rather wide greyish intersegmental bands contrasting with bands of greyish brown to reddish brown. Head capsule lighter brownish yellow, strongly contrasting with dark head spots; dorsal head spots surrounded by at most a faint fulvous area. Overall size larger and broader . . . . . *ornithophilus* Davies, Peterson and Wood
- 9(6'). Abdominal segment 8 with two large ventral tubercles equal to about one-third to one-half depth of abdomen (Fig. 33). Antenna usually distinctly longer than stalk of cephalic fan. Postgenal cleft short, anterior margin subtruncate or rounded but without an anteriorly directed point (Figs. 11-14) (Subgenus *Eusimulium*) . . . . . 10
- 9'. Abdominal segment 8 without ventral tubercles, or these inconspicuous and equal to less than about one-sixth depth of abdomen (Fig. 35). Length of antenna variable. Postgenal cleft rather long, either an inverted U-shape, pointed apically or long and bulbous (Figs. 16-19) . . . . . 13
- 10(9). Hypostomial teeth clustered in three slightly elevated groups. Antennae pale, almost transparent. Head capsule pale, head spot pattern as in Figure 11. Body pigment unicolorous, reddish- or pinkish-brown . . . . . *excisum* Davies, Peterson and Wood
- 10'. Hypostomial teeth more regular, not clustered in three slightly elevated groups. Antenna and head capsule darker with more distinct head spot pattern. Body pigment of two contrasting colors . . . . . 11
- 11(10'). Postgenal cleft widest basally, tapering distally to a rounded or pointed apex (Fig. 12). Toothed margin of hypostomium relatively narrow, the teeth relatively uniform in size. Pigmented area anteroventral to eye absent. Head spot pattern as in Figure 12 . . . . . *pugetense* (Dyar and Shannon)
- 11'. Postgenal cleft smaller, square and of nearly uniform width or widest at about the mid-point of its length, with a straight, broadly V-shaped, or rounded anterior margin (Figs. 13-14). Toothed margin of hypostomium relatively wide, the median and outer lateral teeth distinctly longer than sublateral teeth. Pigmented area anteroventral to eye present but varying in intensity. Head spot pattern as in Figures 13-14 . . . . . 12
- 12(11'). Anteromedian and posteromedian head spots often nearly confluent or with a narrower or less distinct gap between them; a faint but usually distinct infuscation present around head spots extending to slightly beyond outer edge of anterolateral spots (Fig. 13); pigmented area anteroventral to eye usually smaller and more pale. Labrum with setal pattern as in Figure 28. Anal gill consisting of three simple, digitiform lobes . . . . . *aureum* Fries complex
- 12'. Anteromedian and posteromedian head spots with a distinct pale gap between them; infuscation darker and more apparent around lateral head spots resulting in a pale stripe on each side of median spots (Fig. 14); pigmented area anteroventral to eye usually larger and darker. Labrum with setal pattern as in Figure 29. Anal gill consisting of three lobes, each with several small accessory lobes . . . . . *vernum* Macquart complex
- 13(9'). Postgenal cleft subquadrate, apical margin straight or rounded (Fig. 15). Second segment of antenna with a ventral whitish band or spot. Head spot pattern as in

- Figure 15. Anal gill with three simple lobes, these occasionally with minute, secondary bumps (Fig. 30) (Subgenus *Psilozia*) . . . . . *vittatum* Zetterstedt
- 13'. Postgenal cleft either long and bulbous, narrowly rounded or sharply pointed apically (Figs. 16-19). Second segment of antenna more uniformly colored, without a contrasting white band or spot ventrally. Head spot pattern not exactly as above. Anal gill with three compound lobes (Fig. 31) . . . . . 14
- 14(13'). Postgenal cleft long and bulbous in outline, length and width near middle subequal. Antenna conspicuously longer than stalk of cephalic fan (Subgenus *Phosterodoros*) . . . . . 15
- 14'. Postgenal cleft variable in length, but length usually greater than width; an inverted U- or V-shape (Figs. 16-19). Antennal length variable (Subgenus *Simulium*) . . . . . 16
- 15(14). Respiratory histoblast (Fig. 35) with 12 filaments<sup>6</sup> . *luggeri* Nicholson and Mickel
- 15'. Respiratory histoblast with 10 filaments . . . . . *jenningsi* Malloch
- 16(14'). Suboesophageal ganglion and sometimes epidermis in postgenal cleft blackish. Dorsal head spots dark but rather obscure, fulvous area around spots broad (Fig. 16). Cephalic fan usually with fewer than 40 rays. Abdomen blackish . . . . . *tuberosum* (Lundström) complex
- 16'. Suboesophageal ganglion and epidermis in postgenal cleft pale, not blackish. Dorsal head spots pale, fulvous area around spots variable (Figs. 17-19). Cephalic fan usually with approximately 50 rays. Abdomen brownish . . . . . 17
- 17(16'). Infuscation around head spots narrow, not extending beyond inner edge of anterolateral spots, forming an H-shaped pattern (Fig. 17). Antenna not extending beyond tip of stalk of cephalic fan. Arms of anal sclerite narrowly fused medially . . . . . *decorum* Walker
- 17'. Infuscation around head spots wider, extending beyond outer edge of anterolateral spots (Figs. 18-19). Antenna slightly longer than stalk of cephalic fan. Arms of anal sclerite broadly fused medially . . . . . 18
- 18(17'). Lateral plate of proleg lightly sclerotized, faintly visible. Postgenal cleft not bordered by a fulvous band (Fig. 18). Head spot pattern as in Figure 18. Posterior circlet with approximately 66 rows of hooks . . . . . *verecundum* Stone and Jamnback complex
- 18'. Lateral plate of proleg heavily sclerotized, conspicuous. Postgenal cleft bordered by a narrow fulvous band (Fig. 19). Head spot pattern as in Figure 19. Posterior circlet with over 70 rows of hooks (Fig. 35) . . . . . *venustum* Say complex

PUPAE

1. Cocoon an irregular, shapeless sleeve, without a well defined anterior margin (Fig. 36). Terminal abdominal segment with two long dorsal spines . . . . . 2
- 1'. Cocoon usually well developed, variously shaped but with a well defined anterior margin (Figs. 37-39). Terminal abdominal segment with two short dorsal spines or none . . . . . 9
- 2(1). Respiratory filaments 12-14, rarely 16; if 16, dorsal trunk not usually branching 3+5 nor 3+2+3 (Figs. 40, 45) . . . . . 3
- 2'. Respiratory filaments 16 or more, if 16, dorsal trunk branching 3+5 or 3+2+3 (Figs. 41-44) . . . . . 4
- 3(2). Respiratory filaments 12, occasionally 14, arising from two long main trunks which diverge from each other (Fig. 45) . . . . . *Stegopterna mutata*
- 3'. Respiratory filaments usually 14 but sometimes 16, arising from three main trunks that are not strongly divergent (Fig. 40) . . . . . *Prosimulium gibsoni*
- 4(2'). Respiratory filaments 16 . . . . . 5
- 4'. Respiratory filaments more than 16, usually more than 20 . . . . . 7

<sup>6</sup>Character must be observed in late or final instar when respiratory histoblasts are well developed.

- 5(4). Primary trunks of respiratory organ short, noticeably thickened; filaments tapering distally, innermost secondary trunk arising from dorsal primary trunk distinctly longer and more remote from other two secondary trunks (Fig. 41) . . . . . *P. mysticum*
- 5'. Primary trunks of respiratory organ variable but usually longer and not noticeably thickened; filaments more uniformly slender; secondary trunks arising from dorsal primary trunk variable but usually subequal in length and separating from base at subequal distances (Figs. 42-43) . . . . . 6
- 6(5'). Respiratory organ, in lateral view, usually broad, often as wide or wider than long; three primary trunks separating from base so that all are equally visible, lateral trunk not obscuring other two; secondary trunks generally longer than in following species (Fig. 42) . . . . . *P. fuscum*
- 6'. Respiratory organ, in lateral view, usually rather narrow and longer than wide; lateral primary trunk usually more divergent from dorsal trunk than from ventral trunk so that it tends to obscure ventral trunk usually resulting in a distinct >-shaped space between dorsal trunk and other two primary trunks; secondary trunks variable but generally shorter than in above species (Fig. 43) . . . *P. mixtum*
- 7(4'). Respiratory filaments 20-28 (av 24), arising from a short base that immediately divides into three short primary trunks or groups of filaments; entire clump of filaments, viewed laterally, distinctly longer than wide (Fig. 44). Lateral margins of segments 8 and 9 without short curved hook-like setae . . . . . *P. multidentatum*
- 7'. Respiratory filaments variable in number but filaments arising in at least five main groups from a short rounded knob-like base. Lateral margins of at least segments 8 and 9 with short, curved single or sometimes double hook-like setae . . . . . 8
- 8(7'). Respiratory organ, in lateral view, usually broad, often as wide or wider than long; filaments about as long as head and thorax . . . . . *Cnephia dacotensis*
- 8'. Respiratory organ, in lateral view, usually narrower and longer than wide; filaments conspicuously longer than head and thorax . . . . . *C. ornithophilia*
- 9(1'). Anterodorsal margin or cocoon with a long, median projection (this may be broken off, but base is usually evident) (Fig. 38) . . . . . 10
- 9'. Anterodorsal margin of cocoon without a long, median projection, but a short convex protrusion may be present (Figs. 37, 39) . . . . . 11
- 10(9). Respiratory filaments six . . . . . *Simulium excisum*
- 10'. Respiratory filaments four (Fig. 38) . . . . . *S. vernum* complex
- 11(9'). Respiratory filaments four . . . . . 12
- 11'. Respiratory filaments six or more . . . . . 13
- 12(11). Dorsal respiratory filament strongly divergent at base from other three; dorsal pair of filaments on a short petiole, ventral pair with almost no petiole (Fig. 39) . . . . . *S. aureum* complex
- 12'. Dorsal respiratory filament not strongly divergent at base from other three; filaments in two petiolate pairs . . . . . *S. pugetense*
- 13(11'). Respiratory filaments six . . . . . *S. tuberosum* complex<sup>7</sup>  
*S. venustum* complex  
*S. verecundum* complex
- 13'. Respiratory filaments eight or more . . . . . 14
- 14(13'). Respiratory filaments eight, thickened, in three short petiolate pairs, plus two singly. Cocoon, especially anteriorly, loosely woven . . . . . *S. decorum*
- 14'. Respiratory filaments 10 or more. Cocoon tightly woven . . . . . 15
- 15(14'). Cocoon with one-three lateral openings on each side near anterior margin. Respiratory filaments 10 or 12 . . . . . 16
- 15'. Cocoon without lateral openings on each side anteriorly. Respiratory filaments usually 16 but varying from 14 to 17 (Fig. 37) . . . . . *S. vittatum*
- 16(15). Respiratory filaments 10 . . . . . *S. jenningsi*
- 16'. Respiratory filaments 12 . . . . . *S. luggeri*

<sup>7</sup>At present, these species complexes cannot be separated from each other based on pupal characteristics.

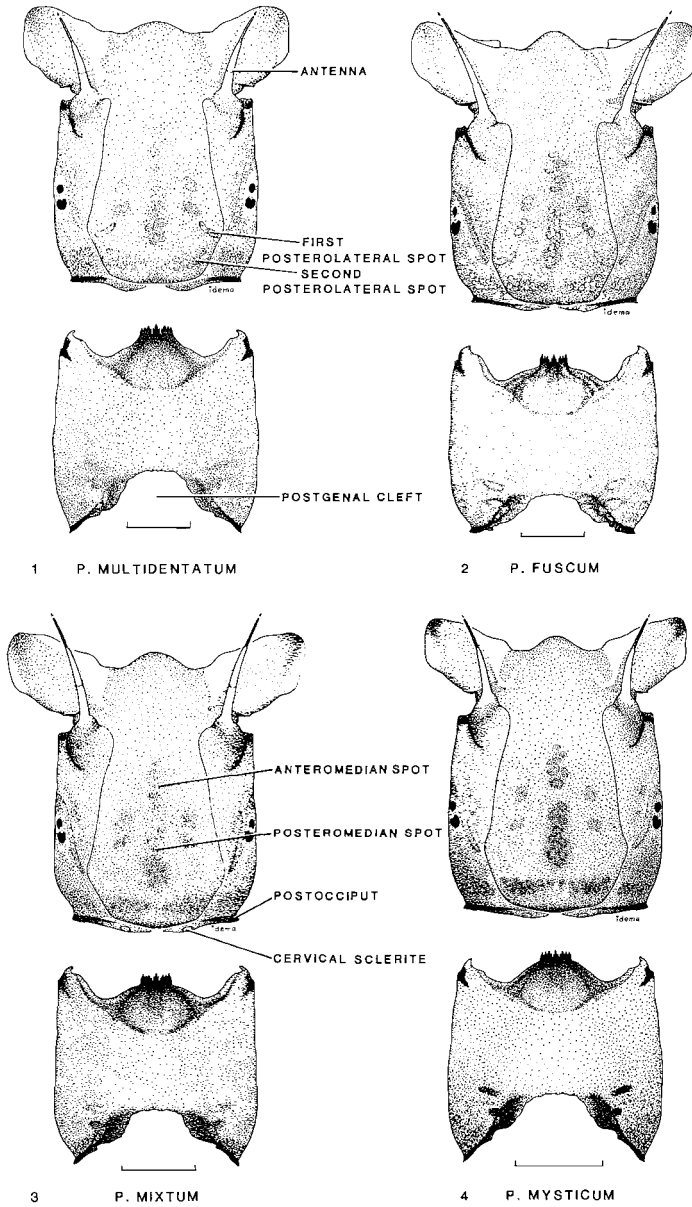
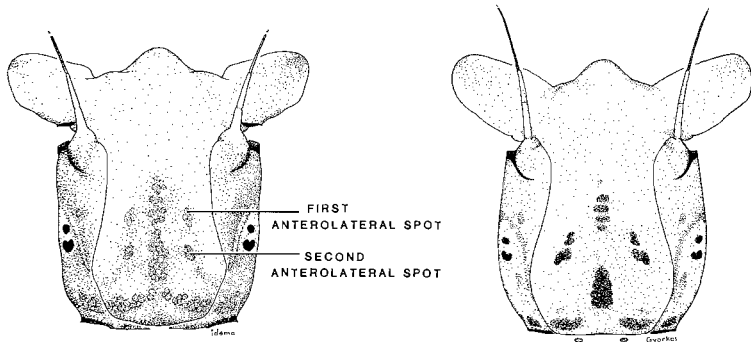
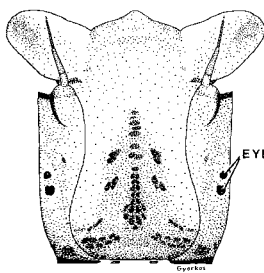


PLATE I

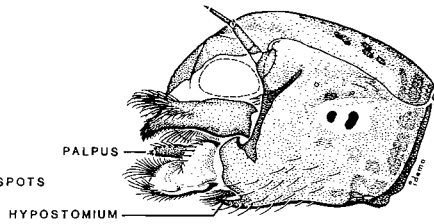


5 P. GIBSONI

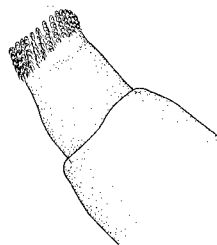
6 S. MUTATA



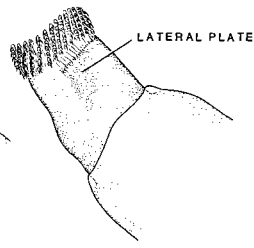
8 C. DACOTENSIS



7 C. DACOTENSIS



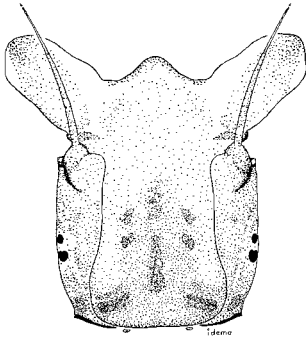
9 P. GIBSONI



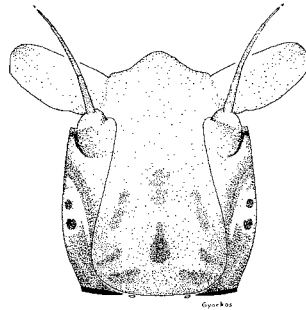
10 P. SP.

PLATE II

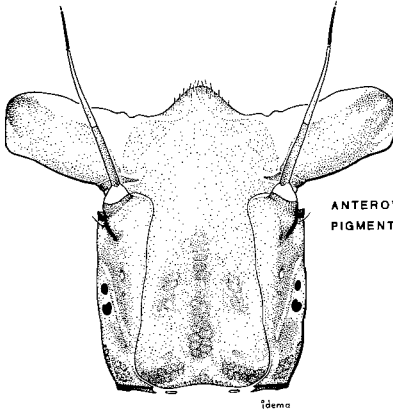
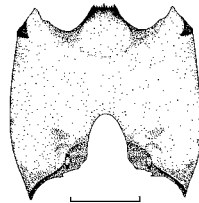
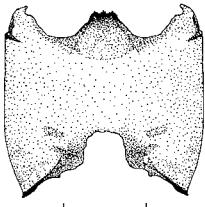




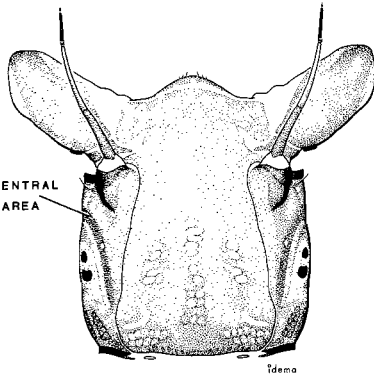
11 S. EXCISUM



12 S. PUGETENSE

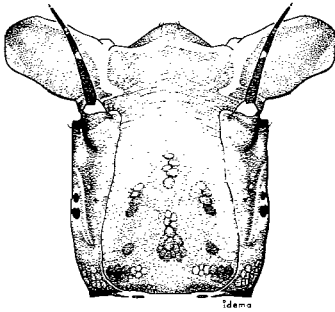


13 S. AUREUM

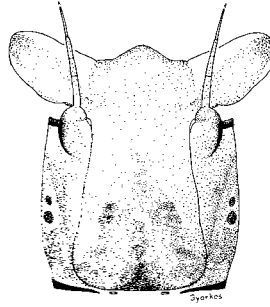


14 S. VERNUM

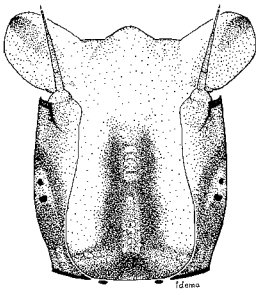
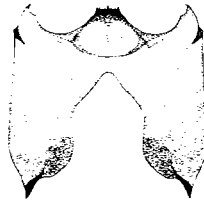
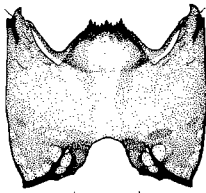
PLATE III



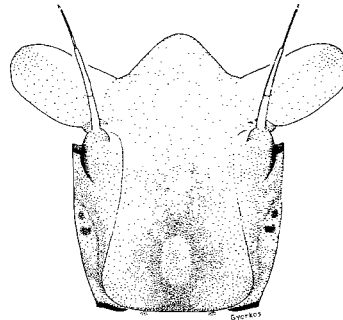
15 S. VITTATUM



16 S. TUBEROSUM



17 S. DECORUM



18 S. VERECUNDUM

PLATE IV

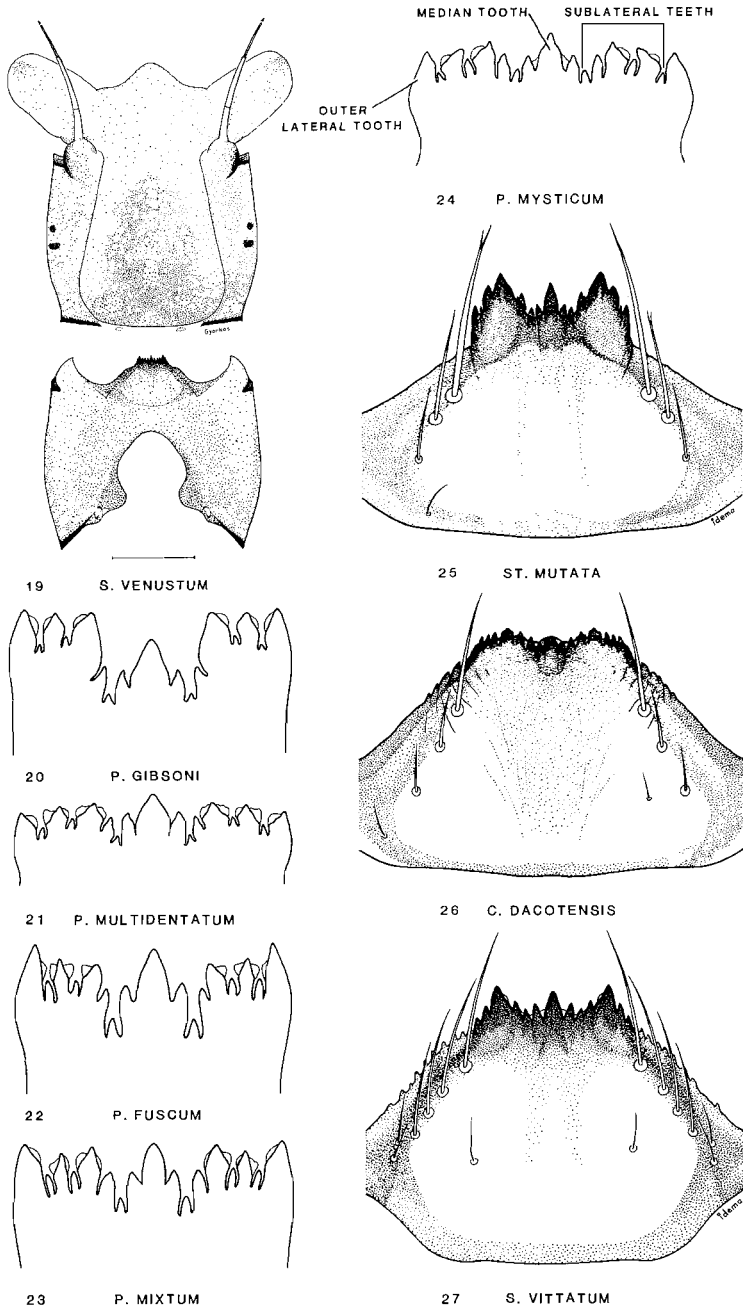
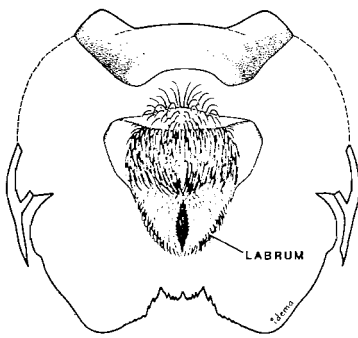
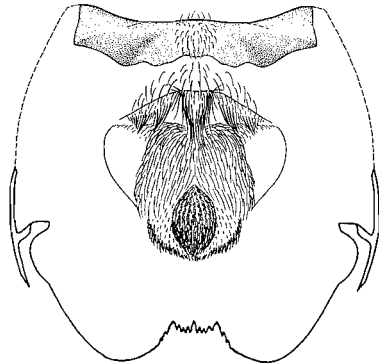


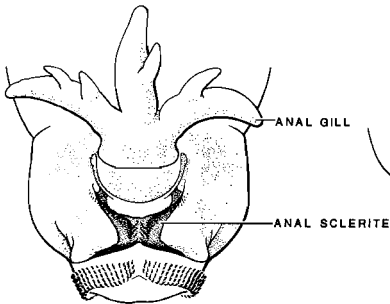
PLATE V



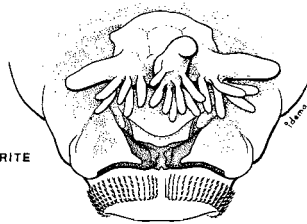
28 S. AUREUM



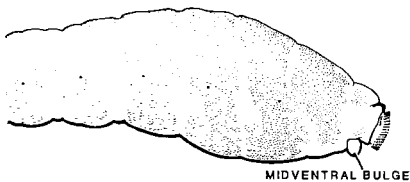
29 S. VERNUM



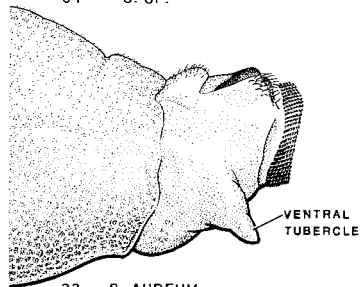
30 S. VITTATUM



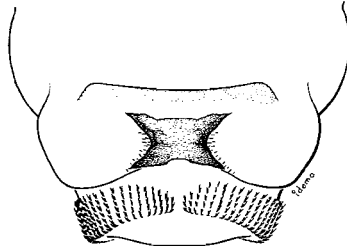
31 S. SP.



32 ST. MUTATA

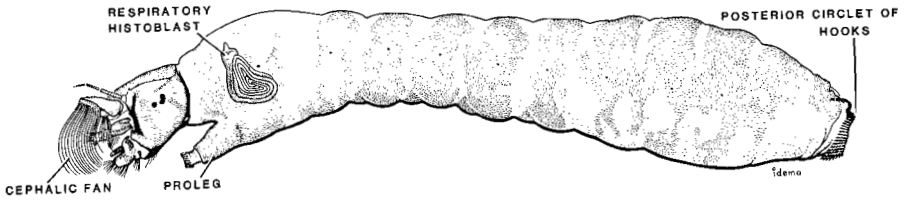


33 S. AUREUM

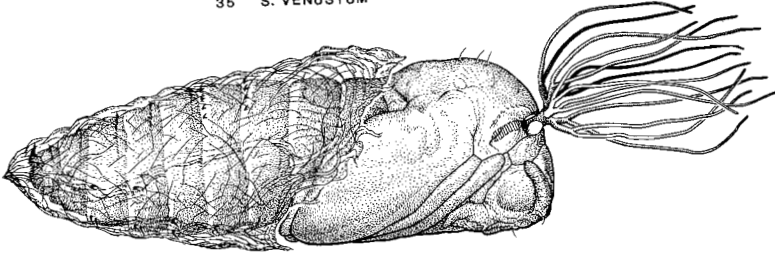


34 P. GIBSONI

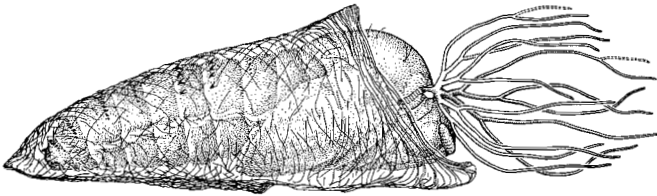
PLATE VI



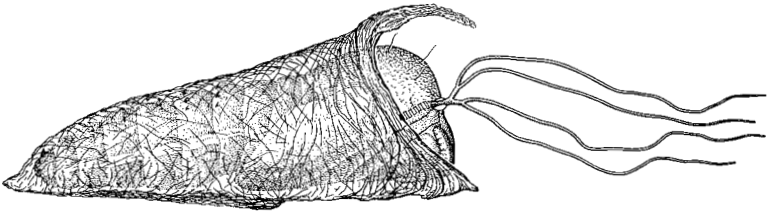
35 S. VENUSTUM



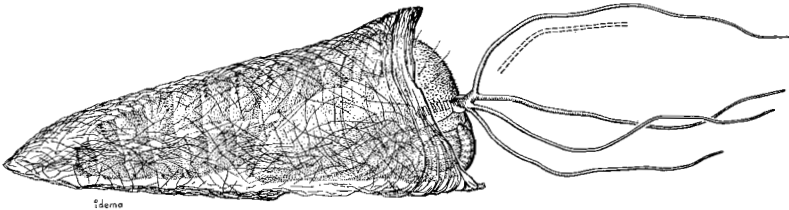
36 PROSIMILIUM SP.



37 S. VITTATUM

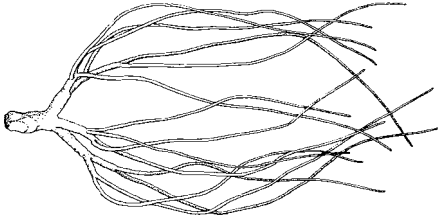


38 S. VERNUM

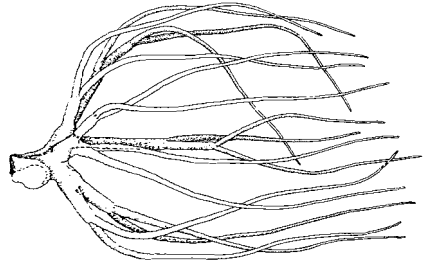


39 S. AUREUM

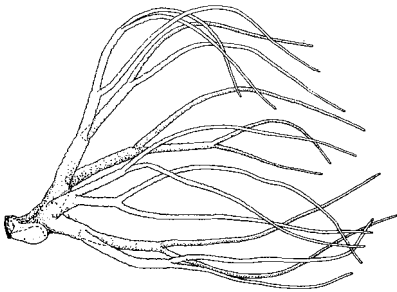
PLATE VII



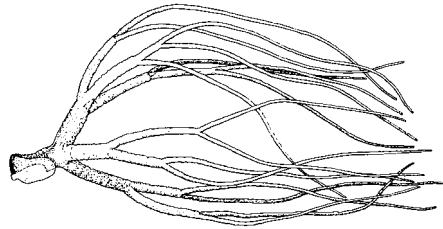
40 P. GIBSONI



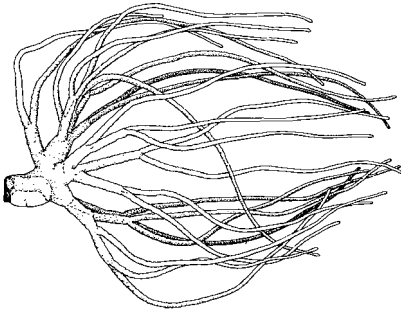
41 P. MYSTICUM



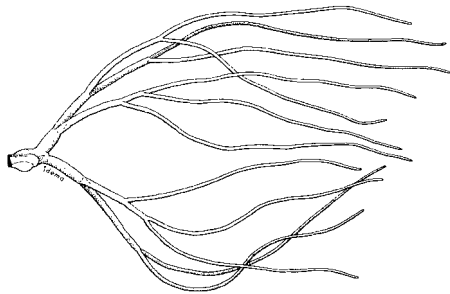
42 P. FUSCUM



43 P. MIXTUM



44 P. MULTIDENTATUM



45 ST. MUTATA

PLATE VIII

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