DOCTORAL DISSERTATION SERIES

TITLE Limnological Relations of Insects to PLANTS of the Genus Potamogeton

AUTHOR Clifford Osburn Berg

UNIVERSITY Of Michigan DATE 1949

DEGREE Ph.D. PUBLICATION NO. 1185

UNIVERSITY MICROFILMS
ANN ARBOR · MICHIGAN

LIMNOLOGICAL RELATIONS OF INSECTS TO PLANTS OF THE GENUS POTAMOGETON

by

Clifford O. Berg

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy, in the University of Michigan

1949

Committee in Charge:
Professor Paul S. Welch, Chairman
Associate Professor Frank E. Eggleton
Professor George R. LaRue
Professor A. Franklin Shull
Professor Wm. Randolph Taylor

CONTENTS

CONTENTS

LIMNOLOGICAL RELATIONS OF INSECTS TO PLANTS OF THE GENUS <u>POTAMOGETON</u>

INTRODUCTION

Much remains to be learned concerning the limnological role of the aquatic flowering plants. In the absence of adequate studies of the direct dependence of certain animals upon them, some investigators have regarded these plants only as cover in which some fresh-water animals live. Thus Shelford (1918) proposed, "One could probably remove all the larger plants and substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations". Wesenberg-Lund (1915) and Welch (1935) support the view that the aquatic flowering plants are food for animals.

A limited amount of data is available on relations of certain vertebrate animals to aquatic flowering plants. McAtee (1939), Martin and Uhler (1939), Bellrose (1941), and others have shown the importance of these plants as food of waterfowl. The literature contains records of the finding of plant material in the stomachs of fishes, but these records are fragmentary and do not warrant the conclusion that most fishes feed regularly on aquatic plants. A far richer invertebrate fauna, of which insects constitute an important part, is directly, intimately, and in some instances probably obligatorily related to these plants. Some important American contributions to knowledge of these invertebrate relations are those of Hart (1895), dealing with certain aquatic insects; Welch (1914a, 1914b, 1916, 1924), chiefly on insects of the yellow water lily; Claassen (1921), dealing with Typha insects; Frohne (1938, 1939a, 1939b, 1939c, 1939d), on insects of certain emergent hydrophytes; and Hoffman (1940a, 1940b, 1940c), concerning the Northern Michigan Donaciinae.

The work on which this paper is based was done in Cheboygan, Emmet, and Presque Isle Counties, Michigan, during the summers of 1939, 1940, 1941, 1946, 1947, and 1948, and in Washtenaw and Livingston Counties, Michigan, during the academic years 1939-40, 1940-41, 1941-42, 1945-46, and 1946-47. In Cheboygan County, practically all lakes and rivers and many smaller bodies of water were visited, and the more advantageous stands of vegetation regularly examined. Collections were also made at approximately regular intervals in Ocqueoc Lake, Presque Isle County, and Carp River, Emmet County. In Southeastern Michigan, plants examined were collected chiefly in Whitmore Lake, Washtenaw and Livingston Counties; Third Sister Lake, Washtenaw County; and Huron River, Washtenaw County.

I am obligated to Professor Paul S. Welch, under whose guidance this study was made. I am also indebted to the following specialists for identifications: the late E.T. Cresson, Jr., formerly of The Academy of Natural Sciences of Philadelphia; H.W. Capps, R.A. Cushman, A.B. Gahan, P.W. Mason, C.F.W. Muesebeck, P.W. Oman, and H.K. Townes, all of the United States National Museum; C.E. Hoffman, the University of Arkansas; O.A. Johannsen, Cornell University; Sherman Moore, Detroit, Michigan; G.T. Riegel, Eastern Illinois State College; H.H. Ross, the Illinois State Natural History Survey; and F.M. Snyder, Orlando, Florida.

LIMNOLOGICAL RELATIONS

Plants and Areas Studied

The plants considered in this paper are *Potamogeton alpinus* Balbis, *P. amplifolius* Tuckerm., *P. epihydrus* Raf., *P. filiformis* Pers., *P. foliosus* var. *macellus* Fernald, *P. Friesii* Rup., *P. gramineus* L., *P. illinoensis* Morong, *P. natans* L., *P. nodosus* Poir., *P. Oakesianus* Robbins, *P. pectinatus* L., *P. praelongus* Wulfen., *P. pusillus* L., *P. Richardsonii* (Benn.) Rydb., *P. Robbinsii* Oakes, and *P. zosteriformis* Fernald. The nomenclature of Fernald (1932) is followed for the linear-leaved species, and that of Ogden (1943), for the broad-leaved species.

The difficult problem of identifying species of *Potamogeton* is well known. I was aided by use of the University of Michigan herbaria. Specimens in the herbarium of the University of Michigan Biological Station, Cheboygan, Michigan, will enable future workers to check my identifications.

The genus *Potamogeton* constitutes a very important element of aquatic vegetation. In the region studied, it is the richest in species of all genera of submerged flowering plants. This group is prominent also because of the large size and great numbers of individuals, and their almost universal occurrence. Oosting (1932) wrote that the genus is so variable and adaptable that some species may be found in almost any aquatic habitat in Michigan.

Distributional data for the species of Potamogeton studied are summarized in Table 1. The terms "abundant", "common", "rare" refer to relative abundance of different species within each body of water.

Bodies of water often differ markedly with respect to the species of Potamogeton which they support. The floral composition also varies in different regions within the same water. The three bogs contained representatives of a single species, P. Oakesianus, found only in these bogs. P. natans was found in all waters examined except these bogs. Six species were found in more than half of all stations regularly visited. One species was collected in only one body of water.

Specimens of Potamogeton were sometimes collected in waters other than those listed. Prominent among these are Black Lake, Burt Lake, Crooked River, Maple River, and Straits of Mackinac in the extreme northern part of the Lower Peninsula of Michigan. Virtually all types of habitats in which plants of the genus occur in this region were considered.

TABLE I

Areas Studied and Species of Potamogeton Collected

Areas in which Potamogeton were collected	alpinus	amplifolius	epihydrus	filiformis	foliosus	Friesii	gramineus	illinoensis	natans	nodosus	Oakesianus	pectinatus	praelongus	pusillus	Richardsonii	Robbinsii	zosteriformis
	Species of Potamogeton collected in each area																
Emmet County:																	
Carp River		c			c				r	c					c	c	c
Cheboygan County:																	
Bessey Creek						c	r		c			c			c		c
Black River		c		r		a	c	r	a			a	c	c	c	r	c
Cheboygan Creek		c	c						c								
Douglas Lake		c		c		c	c	c	c			c	c		c		c
Indian River		c		r		c	c	r	c			c	c	r	c	a	c
Livingston's Bog											c						
Munro Lake		c		c			c		c				r				
Nichols' Bog											a						
Nigger Creek	a					c			c			c					
Sedge Pools		r				c	c		a			c		c	c		r
Smith's Bog											a						
Presque Isle County:																	
Occqueoc Lake		r	c		r	c	c		c			c	c		c		c
Livingston and Washtenaw Counties:																	
Whitmore Lake		c				c	r		c	r		c	c		c	c	c
Washtenaw County:																	
Huron River		a				r	r	c	a	c		c	r		c		c
Third Sister Lake		a					c		a								c
Totals	1	11	2	4	2	9	10	4	13	3	3	9	7	3	9	4	10

(numbers of areas in which the various species were collected)

r: rare c: common a: abundant

Insects

In the region studied, Potamogeton species support a large and heterogeneous fauna of insects which are intimately and in some instances perhaps obligatorily related to the living plants. Although some species of this fauna are found associated with aquatic plants of several different genera, others, which seem to occur only in plant structures peculiar to Potamogeton of certain species, may be dependent on these plants. Thirty-two species having direct nutritive, protective, or respiratory relations to plants of the genus Potamogeton are listed in Table 2. In addition to the identified species listed, Odonata (Zygoptera and Anisoptera) unidentified beyond suborder and representing an unknown number of species hatched from eggs found within these plants.

Insects feed upon living Potamogeton in many ways. Specimens representing 2 species of Homoptera suck the fluids from plant tissues. Several caddis larvae and chrysomelid beetles gnaw the stem, root, or flowering peduncle. Aquatic caterpillars, leaf beetles, and certain caddis larvae defoliate them. Several chironomid larvae and 6 ephydrid larvae mine the leaves and stems.

As already observed by Wesenberg-Lund (1915), Frohne (1938), and others, it would appear that most aquatic phytophagous insects are far less restricted than terrestrial ones in their selection of food plants. Certain caddis larvae,

TABLE II

Insects whose Relations to Potamogeton were Studied

	Order and Family	Genus and Species	Potamogeton Affected	Portion of Plant Affected
1.	Homoptera Aphiidae	Rhopalosiphum nymphaeae (L.)	natans nodosus	Floating leaves
2.	Homoptera Delphacidae	Megamelus davisi Van Duzee (?)	natans	Floating leaves
3.	Coleoptera Chrysomelidae	Haemonia nigricornis Kirby	illinoensis natans Richardsonii	Stems, stipules, roots, leaves, petioles
4.	Coleoptera Chrysomelidae	Donacia cincticornis Newman, variety (?)	alpinus amplifolius gramineus natans Richardsonii	Roots, leaves
5.	Coleoptera Chrysomelidae	Donacia hirticollis Kirby	alpinus amplifolius epihydrus natans Richardsonii	Roots, stipules, stems, leaves
6.	Trichoptera Phryganeidae	Ptilostomis sp.	amplifolius	Leaves
7.	Trichoptera Leptoceridae	Leptocella albida Walker	amplifolius gramineus praelongus Robbinsii	Leaves, stems, stipules, petioles
8.	Trichoptera Leptoceridae	Triaenodes injusta (Hagen)	amplifolius Friesii Richardsonii Robbinsii	Submerged leaves
9.	Trichoptera Leptoceridae	Triaenodes marginata Sibley	alpinus	Submerged leaves

TABLE II (continued)

	Order and Family	Genus and Species	Potamogeton Affected	Portion of Plant Affected
10.	Trichoptera Leptoceridae	*Triaenodes aba* Milne	*amplifolius*	Submerged leaves
11.	Trichoptera Leptoceridae	*Triaenodes tarda* Milne	*amplifolius*	Submerged leaves
12.	Lepidoptera Pyralididae	*Nymphula icciusalis* Walker	*natans*	Floating leaves
13.	Lepidoptera Pyralididae	*Nymphula obscuralis* Grote	*amplifolius* *natans* *praelongus* *Richardsonii*	Submerged leaves
14.	Lepidoptera Pyralididae	*Nymphula badiusalis* Walker	*amplifolius* *natans* *praelongus* *Richardsonii* *zosteriformis*	Submerged leaves (rarely on floating leaves)
15.	Lepidoptera Pyralididae	*Nymphula allionealis itealis* Walker	*natans*	Floating leaves
16.	Diptera Chironomidae	**Cricotopus flavipes* Johannsen	*amplifolius* *epihydrus* *illinoensis* *praelongus* *Richardsonii* *Robbinsii*	Submerged leaves
17.	Diptera Chironomidae	**Cricotopus elegans* Johannsen	*amplifolius* *natans* *nodosus*	Floating leaves
18.	Diptera Chironomidae	*Cricotopus trifasciatus* (Panzer)	*amplifolius* *natans* *nodosus*	Floating leaves

* Species description based on specimens reared during this investigation.

TABLE II (continued)

Order and Family	Genus and Species	*Potamogeton* Affected	Portion of Plant Affected
19. Diptera Chironomidae	*Polypedilum* *(P.) illinoense* (Malloch)	*natans*	Floating leaves
20. Diptera Chironomidae	#*Polypedilum* *(P.) ophioides* Townes	*natans*	Floating leaves
21. Diptera Chironomidae	*Polypedilum* *(Pentapedilum)* *sordens* (van der Wulp)	*amplifolius* *gramineus* *natans* *Richardsonii* *Robbinsii*	Stems, petioles, leaf midribs
22. Diptera Chironomidae	*Glyptotendipes* *(Phytotendipes)* *lobiferus* (Say)	*amplifolius* *gramineus* *Robbinsii*	Stems, petioles, leaf midribs
23. Diptera Chironomidae	#*Glyptotendipes* *(G.) dreisbachi* Townes	*amplifolius* *gramineus* *natans* *nodosus* *praelongus* *Richardsonii* *Robbinsii*	Stems, petioles, leaf midribs
24. Diptera Chironomidae	*Tanytarsus* *(Endochironomus)* *nigricans* (Johannsen)	*amplifolius* *gramineus* *illinoensis* *Richardsonii*	Submerged leaves
25. Diptera Cordyluridae	*Hydromyza* *confluens* Loew.	*alpinus*	Roots
26. Diptera Ephydridae	*Notiphila* *loewi* Cresson	*alpinus* *pectinatus* *Richardsonii*	Roots

\# Species description based partly on specimens reared during this investigation.

TABLE II (continued)

	Order and Family	Genus and Species	Potamogeton Affected	Portion of Plant Affected
27.	Diptera Ephydridae	Hydrellia cruralis Coquillett	alpinus amplifolius epihydrus foliosus gramineus illinoensis natans nodosus praelongus Richardsonii zosteriformis	Submerged leaves (rarely in floating leaves)
28.	Diptera Ephydridae	Hydrellia pulla Cresson	amplifolius gramineus Richardsonii	Submerged leaves
29.	Diptera Ephydridae	*Hydrellia luctuosa Cresson	alpinus amplifolius natans Richardsonii zosteriformis	Submerged leaves (rarely in floating leaves)
30.	Diptera Ephydridae	*Hydrellia bergi Cresson	natans Richardsonii zosteriformis	Stems, petioles
31.	Diptera Ephydridae	*Hydrellia ascita Cresson	alpinus amplifolius epihydrus foliosus illinoensis Oakesianus Richardsonii	Submerged leaves
32.	Diptera Ephydridae	Hydrellia caliginosa Cresson	praelongus	Submerged leaves

* Species description based on specimens reared during this investigation.

for instance, seem to show no choice either for species of plant or type of plant structure eaten. In the laboratory, some devour both plant and animal matter, terrestrial or aquatic, living or dead, exhibiting no apparent preferences.

Although some other insects infest Potamogeton of several species, they always attack certain types of plant structures and do not occur on species which lack them. A chironomid larva mines in thin, flaccid, submerged leaves, It was found in such leaves of 6 species of Potamogeton, but was not encountered in other portions of these plants, nor in any of the species lacking such leaves. Two other chironomids feed in thick, coriaceous, floating leaves of 3 species of Potamogeton, but neither was found in other tissues of these plants, nor in any species which lacks floating leaves. The gill-less caterpillar, Nymphula icciusalis, eats floating leaves, and was bred only from a floating-leaf Potamogeton. Although the gill-breathing caterpillars discussed here usually feed on broad, submerged leaves, they also attack the floating ones. Specimens representing 2 species were reared from larvae and pupae found on P. natans, which has no broad submerged leaves.

Under the heading of protective relations, only those insects which spend some stage of their life cycle within the tissues of Potamogeton are considered. Insects which simply seek cover among these plants, rest upon them, feed upon their epiphytic growth, or maintain other less essential relations to these plants were not studied. Damsel flies and dragonflies of several species insert their eggs into floating leaves and flowering peduncles. Three chironomids pass their larval and pupal stages in burrows in the stems. Defoliating caterpillars and certain caddis larvae live in cases made from pieces of leaf. Leafmining midges and ephydrids are sheltered by the epidermal layers between which they work.

It is believed (Müller, 1922; Varley, 1937) that certain insects, including Donacia (Chrysomelidae) and Hydrellia and Notiphila (Ephydridae), obtain oxygen for respiration from the intercellular gas spaces of hydrophytes. Although Hoffman (1940c) has demonstrated experimentally that some Donaciinae can exist for 21 days in aquaria without plants provided the water contains sufficient dissolved oxygen, he does not deny that the larvae may use oxygen from air spaces of aquatic plants in nature. In the absence of positive evidence, I tentatively adopt the view apparently held by the majority of investigators, namely, insects whose tracheal systems terminate in hollow spines which are usually found inserted in plant tissue probably get oxygen from plants, and when such insects are isolated from contact with oxygenated, freely circulating water they may be dependent on plants for sufficient oxygen to maintain life.

Hymenopterous parasites of insects directly related to Potamogeton are recorded in Table 3. Insect host and plant species from which parasites were reared are both specified. In view of the fact that 56 per cent of the species recorded by Frohne (1938) from emergent hydrophytes are parasitic, it is noteworthy that parasitic species constitute only 22 per cent of this Potamogeton fauna. The lower incidence of parasitism among insects of this group may be due in part to relative inaccessibility in their submerged habitat.

Marked differences in susceptibility to insect parasitism are apparent within this fauna. Of the ten parasitic species, nine infest flies of the ephydrid genus Hydrellia. No insect parasites were found infesting the midges, beetles, and caddis flies.

Including parasites, the total number of species of insects found on each plant is as follows: P. alpinus, 13; P. amplifolius, 25; P. epihydrus, 6; P. filiformis, 0; P. foliosus, 2; P. Friesii, 1; P. gramineus, 10; P. illinoensis, 5; P. natans, 23; P. nodosus, 6; P. Oakesianus, 3; P. pectinatus, 1; P. praelongus, 10; P. pusillus, 0; P. Richardsonii, 18; P. Robbinsii, 6; P. zosteriformis, 7.

The relatively small sizes of faunas harbored by narrow-leaved species of Potamogeton seem to be due largely to their lack of anatomical structures essential or at least desirable for the support of certain insects. Defoliating caterpillars and caddis larvae can obtain more abundant and more succulent food and better materials for casemaking from broad-leaved plants. Insects which mine or channel in broad submerged or floating leaves could not thrive in the very narrow-leaved species of Potamogeton. These defoliators, leaf miners, and leaf channelers constitute about 60 per cent of the insects found directly related to Potamogeton. Krecker

TABLE III

Hymenopterous Parasites of Insects Related to *Potamogeton*

	Order and Family	Genus and Species	Insect Host	*Potamogeton* on which Found
1.	Hymenoptera Diapriidae	*Trichopria columbiana* (Ashmead)	*Hydrellia cruralis* *H. bergi* *H. luctuosa* *H. pulla*	*alpinus* *amplifolius* *epihydrus* *gramineus* *natans* *praelongus* *Richardsonii*
2.	Hymenoptera Pteromalidae	Unidentified	*Hydrellia cruralis*	*amplifolius*
3.	Hymenoptera Braconidae	*Ademon niger* (Ashmead)	*Hydrellia cruralis* *H. bergi* *H. ascita*	*alpinus* *amplifolius* *natans* *praelongus* *zosteriformis*
4.	Hymenoptera Braconidae	*Chorebidea* sp. 1 (species not described)	*Hydrellia cruralis*	*amplifolius* *epihydrus* *gramineus* *nodosus* *praelongus* *Richardsonii*
5.	Hymenoptera Braconidae	*Chorebidea* sp. 2 (not described)	*Hydrellia bergi*	*natans*
6.	Hymenoptera Braconidae	*Chorebidella* sp. (not described)	*Hydrellia cruralis* *H. ascita*	*alpinus* *amplifolius* *Oakesianus*
7.	Hymenoptera Braconidae	*Dacnusa* sp. 1 (not described)	*Hydrellia bergi*	*natans* *zosteriformis*
8.	Hymenoptera Braconidae	*Dacnusa* sp. 2 (not described)	*Hydrellia luctuosa*	*alpinus* *zosteriformis*
9.	Hymenoptera Braconidae	*Dacnusa* sp. 3 (not described)	*Hydrellia ascita*	*alpinus* *Oakesianus*
10.	Hymenoptera Ichneumonidae	*Cremastus* sp.	*Nymphula icciusalis*	*natans*

(1939), who listed P. pectinatus as having a denser animal population than P. zosteriformis (as "P. compressus"), included insects and other invertebrates which simply seek cover among these plants. His figures are based on comparative numbers of animal specimens found on ten-foot lengths of the plants examined.

RELATIONS TO WATER

The insects studied in this investigation are adapted for life in water in diverse ways and to varying degrees. In some species, certain stages of the life cycle are passed in aerial or terrestrial habitats.

Eggs of the species considered in this paper develop in several media. Those of the Coleoptera, Trichoptera, Lepidoptera, and Chironomidae occur beneath the surface of the water, usually attached to leaves, stems, or stipules of the food plant. Eggs of the aphid occur only on fruit trees, exposed to the air. Odonata eggs are inserted into Potamogeton leaves, stems, and flowering peduncles where they are surrounded by plant tissues. Those of the hymenopterous parasites are embedded in animal (host) tissues.

Larvae of most of the species considered here are able to remain constantly submerged. Larvae of Trichoptera, Chironomidae, and 3 species of Nymphula are provided with gills by means of which they can obtain dissolved oxygen from the water. Those of the Ephydridae and the Donaciinae are equipped with sharp, hollow spines with which they can penetrate plant tissue and presumably acquire oxygen from the intercellular gas chambers. Although the aphid, delphacid, and gill-less caterpillar are air breathers, they are able to live submerged for considerable lengths of time, extracting oxygen from the air which envelopes their hydrofuge bodies. Since larvae of parasitic Hymenoptera live surrounded by animal tissues, the microhabitats of aquatic species are quite similar to those of species which infest terrestrial hosts. It is reasonable, therefore, that parasitic larvae of terrestrial and aquatic Hymenoptera do not necessarily differ greatly in their adaptations, and it is not surprising that some genera (including both Trichopria and Dacnusa) contain both terrestrial and aquatic species.

Larvae of the Pyralididae, Ephydridae, and Donaciinae have little or no ability to swim, and some of the smaller ones are quite helpless when they become caught in the surface film. The species of Triaenodes (Trichoptera: Leptoceridae) swim well, and some species of Chironomidae are fair swimmers.

Nearly all of these larvae subsist on plant tissue ingested at or beneath the water's surface. Stem-burrowing midge larvae live principally on plankton, which they capture in a remarkable manner.

Midge pupae and caddis fly pupae, which breathe by means of gills, are truly aquatic. Although the pupae of other species encountered also are normally submerged, the medium immediately surrounding them is gaseous. Moth pupae and ephydrid pupae studied in this investigation die if they are dissected from their cases or puparia and placed in direct contact with the water.

Various types of aquatic adaptations characterize adult insects of this fauna. Moths, midges, ephydrids, and aphids have considerable ability to rest on the surface film, and some are so hydrofuge that they avoid becoming wet even if submerged. The damsel flies, dragonflies, caddis flies, parasitic Hymenoptera, and some Donaciinae submerge voluntarily to oviposit. Parasitic Hymenoptera were observed repeatedly to remain beneath the surface of the water for intervals of more than half an hour, and Hoffman (1940b: 263) stated that 2 of the species of Donaciinae concerned in this investigation, _Haemonia nigricornis_ and _Donacia hirticollis_, spend almost their entire adult lives submerged. Adult Hymenoptera discussed here are fairly good swimmers.

HIBERNATION

Most of the insects infesting submerged portions of plants which remain green throughout the winter pass this season as larvae on their food plants beneath the ice. Caddis larvae and stem-burrowing midge larvae are quite active throughout the winter. The caterpillars, ephydrid larvae, and certain Donaciinae larvae (Hoffman, 1940b: 270) become more or less quiescent. Specimens of _Chorebidea_ sp. and of _Ademon niger_ pass the winter in their host larvae. Insects which infest floating leaves occupy some other habitat during the winter, often passing this season in inactive stages of their life cycles. The aphid _Rhopalosiphum nymphaeae_ returns to its primary host, the plum tree, and hibernates there as a winter egg. According to Kettisch (1936-37: 200) Cricotopus trifasciatus, a midge whose larva channels in floating leaves, hibernates as an egg attached to a stem or stipule of its food plant.

FORMS OF INJURY

Plants of the genus Potamogeton suffer various types of injuries due to infestation by insects. Roots are gnawed by Donaciinae larvae and punctured by their respiratory spines. The stems of these plants, besides being gnawed by larvae of Trichoptera and Donaciinae, have mines of Hydrellia larvae, burrows of chironomid larvae, and punctures of probosces, ovipositors, and respiratory spines. The principal types of injuries to leaves are channels, mines, patches of surface abrasion, skeletonization, series of small holes, mass defoliation, and punctures of various types. As used here, mines are excavations made between the epidermal layers and progressively lengthened as the larva feeds. Burrows are short excavations between the epidermal layers sheltering larvae which do not feed primarily on plant tissue. They open at each end by means of a hole gnawed through the epidermis. They are extended only at infrequent intervals as larvae grow and require more room.

LOCAL DISTRIBUTION

Striking differences were observed in local population densities of this insect fauna. Relatively few insects were found on Potamogeton collected in unsheltered areas of large and medium sized lakes. Plants found in small lakes, bogs, and sheltered coves of larger lakes harbored denser populations, and the highest populations of this fauna were found on the Potamogeton growing in rivers, creeks, and beach pools. This pattern of local distribution may be caused chiefly by effects of wind and wave action on insects in the adult stage. It would not seem that most insects are likely to oviposit among plants growing in open, unsheltered water except during calm weather. If moderate wind and wave action occurs at any time between the dates of emergence and oviposition, most adults which emerge in these situations are apt to be driven either to the cover of foliage growing on the shore or into the rough water where they may be drowned. The accessibility of Potamogeton growing in creeks, river margins, and beach pools to insects sheltered amidst terrestrial foliage is probably the main factor accounting for higher infestation of these plants than those of the same species which grow in open, unprotected areas of lakes.

DATA ON LIFE HISTORIES

Odonata

It is well known that damsel flies (Zygoptera) and certain dragonflies (Anisoptera) normally insert their eggs into plant tissues. This habit was often observed in Cheboygan County, Michigan, where damsel-fly naiads hatched from eggs found in flowering peduncles and stems of Potamogeton amplifolius, P. gramineus, P. illinoensis, P. natans, P.

pectinatus, and *P. Richardsonii*, and where other eggs partially inserted into floating and submerged leaves of *P. natans* produced dragon-fly naiads. All damsel-fly eggs were completely covered by plant tissue, but those of the dragonflies were exposed in varying degrees. Since these naiads are carnivorous and not intimately related to the plants, they were not reared.

Rhopalosiphum nymphaeae (Linnaeus) (Homoptera: Aphididae)

The life cycle of *Rhopalosiphum nymphaeae* is so well known that it is not necessary to present a detailed account of it here. These aphids live on plum and related fruit trees as primary hosts, often doing considerable damage. In summer, winged migrants fly to any of a wide variety of aquatic plants including *Nymphea*, *Nuphar*, *Alisma*, *Sagittaria*, *Potamogeton*, *Ranunculus*, *Typha*, and *Lemna*, which serve as secondary hosts. Wilson and Vickery (1918) list 49 species of plants on which specimens have been found. On these plants the aphids often live partially or completely submerged. They are hydrofuge, and all of the submerged specimens observed in this study were enclosed in gas bubbles. Aphids of this species often spoil the appearance of ornamental aquatic plants in green houses and lily ponds. The several generations which are produced during spring and summer are made up entirely of ovoviviparous, parthenogenetic females. In autumn, winged individuals migrate to the primary hosts, where males are produced, mating takes place, and the females lay overwintering eggs.

Representatives of this species were collected on the floating leaves of *Potamogeton natans* growing in Nigger Creek, Cheboygan County, Michigan, on August 6, 1941. They also infested some *Nuphar* and *Sagittaria* near the mouth of this creek. Additional specimens were taken from the floating leaves of *P. natans* in Indian River, Cheboygan County, on August 9, and from floating leaves of *P. natans* and *P. nodosus* growing in Lake Mendota, Dane County, Wisconsin, on August 29, 1941. Specimens of all 3 lots were identified as *Rhopalosiphum nymphaeae* by P. W. Mason of the United States National Museum. Other aphids presumably belonging to the same species were found on floating leaves of *P. amplifolius* and *P. natans* in Whitmore Lake, Washtenaw and Livingston Counties, Michigan.

Megamelus davisi Van Duzee (?) (Homoptera: Delphacidae)

Species of *Megamelus* (Delphacidae; formerly Delphacinae, Fulgoridae) are known to feed on aquatic plants of several genera. Au (1941) reported that one species is a serious pest of *Nymphaea* in Hawaii, and P. W. Oman stated (personal correspondence) that specimens of *M. davisi* in the collection of the United States National Museum are recorded as destroying "*Castalia odorata*".

On June 28, 1942, Delphacidae were found on floating leaves of *P. natans* in Third Sister Lake, Washtenaw County, Michigan. Not prepared to collect nor preserve these insects, I managed to save only one perfect specimen. This was identified by Oman as a female Megamelus, presumably davisi Van Duzee.

Since a considerable number of these insects were concentrated in this bed of Potamogeton, and since they appeared to have their probosces inserted in the plants, it seems probable that a significant nutritive relationship exists between P. natans and M. davisi.

Donaciinae (Coleoptera: Chrysomelidae)

Hoffman (1940a, b, c) presented considerable information concerning the morphology, biology, and limnological relations of the Northern Michigan Donaciinae. Observations made in this investigation substantiate many of his statements and extend the list of known food plants of certain species.

The only Potamogeton on which Hoffman (1940c: 268, 272) found larvae and pupae of Haemonia nigricornis was P. natans. Although most of my specimens were also collected on P. natans, some larvae were taken on P. illinoensis (Sedge Pools, Douglas Lake, Michigan, July 3, 1941), and other larvae and pupae were found on P. Richardsonii (Indian River, Cheboygan County, Michigan, August 9, 1941).

I found cocoons of Donacia hirticollis on the 3 species listed by Hoffman, P. natans, P. Richardsonii, and P. amplifolius, and also on P. alpinus (Nigger Creek, Cheboygan County, June 20, 1940) and on P. epihydrus (Ocqueoc Lake, Presque Isle County, Michigan, July 13, 1941). An egg mass identified by Hoffman as that of D. hirticollis was also found on the P. epihydrus listed above.

Hoffman (1940c: 263, 272) took larvae, pupae, and adults of an undetermined species of Donacia on P. natans. He identified specimens collected in this investigation with those mentioned in his paper (personal correspondence), and stated that they represent a variety of D. cincticornis. They differ from the typical D. cincticornis in morphology of adult and of egg mass, and in food plants, habits, and seasonal behavior.

D. cincticornis var. seems to be the most abundant form of Donaciinae which feeds on Potamogeton in this region. Besides being taken on P. natans, the food plant recorded by Hoffman, specimens of this species were found on P. alpinus (Nigger Creek, Cheboygan County, June 20, 1940), P. amplifolius (Black River, Cheboygan County, July 15, 1940), P. Richardsonii (Black River, July 15, 1940) and P. gramineus (Black River, July 15, 1940).

Egg masses of this variety are found very commonly on the lower sides of floating leaves of P. natans. These masses are similar in position and general arrangement to those of the typical D. cincticornis, D. proxima, and D. palmata. Each is located near a small hole cut through the leaf by the female beetle. The eggs are arranged in 2 semicircles, one just outside the other, extending approximately half way around the hole.

Larvae of this variety are similar in appearance to those of the typical _D_. _cincticornis_. Actively feeding larvae were found repeatedly on subterranean portions of the stems of _P_. _natans_, and once on corresponding structures of _P_. _alpinus_.

Cocoons of this form, containing mature larvae, pupae, and adults, were collected on subterranean stems of _P_. _natans_, _P_. _Richardsonii_, _P_. _amplifolius_, and _P_. _gramineus_.

Trichoptera

Although some caddis larvae are carnivorous and some are herbivorous, others seem to eat plant and animal matter indiscriminately. Lloyd (1921: 16) referred to the Phryganeidae as omnivorous plant feeders and stated that the first to pupate in an aquarium are often eaten by their fellows. Muttkowski (1918) wrote that caddis larvae readily change from a phytophagous to a sarcophagous diet. Evidence corroborating these statements was found in the course of this investigation.

Since certain caddis larvae readily eat a wide variety of materials in aquaria, it is difficult to determine what constitutes their food in nature. The substances eaten by these captive larvae are not necessarily their only natural foods. Usually reliable means of determining natural foods are difficult to apply to these larvae. While plant tissues are often recognizable in fecal pellets and in stomachs of freshly captured larvae, it is usually impossible to identify species of Potamogeton from these small fragments. Since larvae of Phryganeidae feed primarily at night, it would be very difficult to observe their feeding in nature.

While it is difficult to determine the natural diets of these general feeders, it is even more difficult to judge the extent to which these larvae depend on each plant. No species of Potamogeton is essential for the life, growth, and well being even of larvae known to feed principally upon it, if there is available a sufficient amount of any other material upon which the larvae can subsist. Lloyd (1921: 29) wrote of Phryganea larvae, "Apparently the larvae feed upon green tissue because of their habit of living among living plants.. .... rather than through any choice of appetite. In aquaria, among a mixture of living and dead plants, they displayed no preference for either sort."

The list of Trichoptera given in this paper probably does not include all the species in this region which will, under certain circumstances, eat Potamogeton. Each caddis larva listed could probably thrive without some of the species of Potamogeton listed as food plants; others possibly could live quite normally without any Potamogeton.

Ptilostomis sp. (Phryganeidae)

Larvae belonging to the genus Ptilostomis were collected repeatedly on Potamogeton amplifolius growing in Third Sister

Lake, Washtenaw County, Michigan. Larvae of this genus are poorly known. Since adults were not reared, specific identification of these specimens is impossible.

Larvae of Ptilostomis sp. use Potamogeton leaves both for food and for case-making material. Apparently these larvae have nocturnal habits. The morning after they were collected they were placed in aquaria with a few whole leaves of Potamogeton amplifolius. That evening the leaves were still whole and undamaged. The next morning, however, many bits of leaf were cut away. A small portion of the leaf tissue which was removed had been added to the larval cases, and it is evident that much of it had been eaten. Repetition of this experiment for 5 days, changing leaves each morning, consistently gave results indicating that the larvae carry on their activities principally at night. This observation supports the statement of Lloyd (1921: 16) that larvae of the Phryganeidae in general carry on their activities chiefly at night.

In order to test statements in the literature that phryganeid larvae tend to be omnivorous, these specimens were offered various types of food. They ate leaves, stems and stipules of Potamogeton, leaves of Populus, and bodies of Chironomidae and Tubificidae, exhibiting little if any preference whether these tissues were living, quite freshly killed, or partly decomposed.

Leptocella albida Walker (Leptoceridae)

Larvae of Leptocella albida were collected frequently on leaves of Potamogeton amplifolius, P. gramineus, P. praelongus, and P. Robbinsii. They are abundant in Third Sister Lake and Whitmore Lake, Washtenaw County, Michigan, and were also collected in Ocqueoc Lake, Presque Isle County. Specimens of this species pupated readily in the laboratory, and many adults were obtained.

In Whitmore Lake their tapered, slightly curved cases are made almost entirely of marl, chiefly the encrusting form found on Potamogeton leaves, held together with silk. Since cases of L. albida taken in most situations are composed principally of sand grains, these larvae cannot be regarded as dependent normally on Potamogeton for their case-building material. It may be that marl is used only because there is no exposed sand available in certain areas of Whitmore Lake.

Larvae of L. albida were observed to eat submerged leaves, stems, stipules, and petioles of several species of Potamogeton in aquaria. A common type of injury due to these larvae is consumption of leaf blades and smaller veins, leaving coarsely skeletonized leaves. Similarly damaged plants, harboring these larvae, were found in Whitmore and Third Sister Lakes.

Specimens kept in aquaria during winter showed less and less appetite for leaves, but gnawed many excavations in the stems. Their fecal pellets were composed mainly of brown plant material, probably stem and stipule tissue. They ate tubificids eagerly and evidently indulged in some cannibalism. Empty larval cases and pieces of larval head capsules and appendages were frequently found in the aquarium.

Triaenodes injusta (Hagen) (Leptoceridae)

Larvae of Triaenodes injusta were found commonly in Third Sister Lake and in Huron River, Washtenaw County, Michigan. They utilize submerged leaves of Potamogeton amplifolius and P. Robbinsii for food and for case-making material. Pupation and emergence occurred in laboratory aquaria, and several adults of each sex were reared.

Larvae of Triaenodes seem to be more completely phytophagous than the other genera of Trichoptera considered in this paper. Fresh fecal pellets of specimens just brought in from the field are made up almost entirely of green leaf tissue. They fed eagerly on green leaves in laboratory aquaria and were never seen to eat animal matter in any form, even when the plant food was sparse. They eat leaf tissue in a manner similar to that of Leptocella albida, taking leaf blades and finer veins and leaving the larger veins.

Triaenodes marginata Sibley (Leptoceridae)

Larvae of Triaenodes marginata were collected repeatedly in Nigger Creek, Cheboygan County, Michigan, where they were feeding on the submerged leaves of Potamogeton alpinus.

Their methods of feeding and case making are similar to those of *T. injusta*. Like the latter, they seem to be completely phytophagous, apparently eating no animal matter even when the supply of plant food was seriously curtailed. Larvae of this species pupated readily in the laboratory, and several imagoes were obtained.

Triaenodes aba Milne (Leptoceridae)

A single specimen of *Triaenodes aba* was collected on *Potamogeton amplifolius* in Third Sister Lake, Washtenaw County, Michigan, and reared on the submerged leaves of this plant. In food habits and case building, it seems to be quite similar to *T. injusta* and *T. marginata*.

Triaenodes tarda Milne (Leptoceridae)

A larva of *Triaenodes tarda* was collected on *Potamogeton amplifolius* in Huron River, Washtenaw County, and reared on the submerged leaves of this plant. In appearance and habits, this larva is similar to those of other *Triaenodes* species herein discussed. Like them, it seems to be a true herbivore.

Nymphula (Lepidoptera: Pyralididae)

Although the aquatic Lepidoptera have been regarded with interest for a long time much remains to be learned concerning their metamorphosis and biology. More than two hundred years ago Reaumur (1736) wrote a surprisingly thorough paper on the habits and adaptations of *Nymphula nymphaeata*. Other European zoologists (Buckler, 1876a, 1876b, 1877, 1881; Jeffrey, 1877; Müller, 1892; Miall, 1895; Willem, 1907; Berg, 1941; and others) have contributed to the knowledge of nymphuline caterpillars, and in this country Packard (1884), Hart (1895), Forbes (1910, 1923), Miller (1912), Welch (1916, 1922, 1924), and Welch and Sehon (1928) have investigated these insects and published information concerning them. Many taxonomic papers have been written in which new species and varieties of Nymphulinae are described, and many notes have been printed in journals of agriculture and economic entomology reporting the depredations of certain nymphuline caterpillars on cultivated aquatic and semiaquatic plants and outlining methods for controlling them. The species of economic importance include *Nymphula depunctalis*, the "rice caseworm" of India, Assam, Malaya, and the Dutch East Indies; *N. vittalis*, which often causes serious damage to rice in Japan; and *N. nymphaeata*, reported as injurious to rice in Italy and to cultivated water lilies in England.

Some of the European papers cited above record species of *Potamogeton* as food plants of *Nymphula* larvae. All species of *Nymphula* previously reared from *Potamogeton* in this country except *N. obliteralis* Walker were also encountered in this study. Hart (1895) reared *N. obliteralis* (as "*Hydrocampa obliteralis*") from *P. natans* in the Illinois River, and his records may form the basis for statements by

Forbes (1910, 1923) that N. obliteralis larvae feed on Potamogeton. My failure to find this species may be due to limitations of its range. Welch (1915) does not include N. obliteralis in his list of the Lepidoptera of the Douglas Lake region.

In spite of the long standing interest in this group, some of the larvae remain completely unknown, and good characters for distinguishing some of the known species have not been found. Forbes (1910, 1923) presented preliminary keys to some of the nymphuline caterpillars of the Northeastern States. Since larvae of some species were unknown, his keys are incomplete. He separated the gilled species from one another chiefly on relative numbers of gill filaments. Unfortunately, numbers of filaments may vary among corresponding gills of various individuals in a brood, among successive segments of a given specimen, and even between the right and left sides of a given segment. Numbers of filaments also increase as the larva grows older, and a description based on a certain instar does not necessarily apply to any other instar.

It would be desirable to find specific characters among the sclerotized parts of the larvae. These structures would seem less likely to change drastically from one instar to the next, and have the great additional advantage of being well preserved and easily studied in exuviae as well as in larvae. However, a preliminary examination of larval sclerites, made during this investigation, failed to reveal any good characters for specific determination. Although the chaetotaxy of several sclerites and the shape of certain others is complex enough to seem capable of considerable variation, these structures apparently vary about as much among individuals of a given species as between the closely related species Nymphula badiusalis and N. obscuralis.

Since reliable characters for distinguishing immature stages were not found, the species in this investigation are determined only in adult specimens, mature pupae in which the wing markings of the future adult have become evident, and eggs and larvae of known ancestry.

Nymphula icciusalis Walker

Information concerning the immature stages of Nymphula icciusalis has been presented by several investigators. Welch (1916) reviewed the earlier papers as follows: "Packard ('84, p. 824) figured a larva, which he supposed to be N. icciusalis. Forbes ('10, pp. 225-6) reared a single larva through to maturity and reported close correspondence of data with those of Packard, but made no mention of the eggs or early larval instars. Miller ('12, pp. 127-134, 245) made some observations on this species, described some of the activities of the larvae, made slight mention of the pupa and of the eggs, and described the full grown larva in considerable detail." He described eggs and first instar larvae in detail, contributed information concerning oviposition and development of eggs, and discussed feeding and case-making activities of the young larvae. Forbes (1923) wrote of this species, "Caterpillar in an oblong case on Potamogeton, sedge, Lemna, Menyanthes, and other aquatic plants, Cocoon sometimes anchored under water. Moth in August. Common everywhere, flying over the water and along the shore of ponds."

In this investigation, N. icciusalis were reared from mature larvae and pupae collected on floating leaves of P. natans in Cheboygan County, Michigan. Larvae and pupae were not collected on any other species of Potamogeton, but some of their cases were composed partly of P. Friesii, P. gramineus, P. Richardsonii, and Vallisneria leaves. Adults emerged in July and August.

Other adults were collected in the vegetation surrounding the Sedge Pools, Douglas Lake, Michigan throughout July and during the first half of August, 1941. Some of these specimens were females which either mated in the breeding cages or had mated before they were captured. They laid masses of light gray or whitish, elliptical eggs on the lower surfaces of floating P. natans leaves very near their margins, as described by Welch (1916: 181-82). These egg masses, which fit the description given by Welch, were deposited without exception during the night. Eggs frequently overlap in the compact masses. Those of some masses averaged 0.45 by 0.60 mm., the size previously reported (Welch, 1916).

Others were larger, one mass of 22 averaging 0.50 by 0.67 mm. Dying females often deposit diffuse masses of eggs on the upper sides of floating leaves. A high percentage of such eggs usually fails to develop.

Eggs of N. *maculalis* Clemens increase in size during development (Welch, 1916), but it seems that this phenomenon has not been reported for N. *icciusalis*. Evidence that eggs of the latter species also increase in size during development was obtained from a mass of 46 eggs deposited on the night of August 5-6, 1941. When these eggs were measured 5.5 days later they averaged 0.588 mm. long. Just before hatching, 6 days after these measurements were taken and 11.5 days after oviposition, they averaged 0.614 mm. long. This increment of 0.025 mm. is only about 0.25 as great as that (0.099 mm.) reported by Welch (1916) for N. *maculalis* eggs. Perhaps it would be larger if the first set of measurements had been taken just after the eggs were laid, as his were.

In one instance, eggs of N. *icciusalis* which were laid in breeding cages in the laboratory hatched 6.5 and 7.5 days later. Those deposited on the night of July 20-21, 1941, and those laid the following night all hatched during the day, July 28. The average egg period seems to be closer to Welch's figure of 10-11 days. The unusual speed of development of these eggs may have been caused by the extreme heat during the period between oviposition and hatching. The temperature of surface water in Douglas Lake rose from 69° F. on July 20 to 84° F. on July 28. Undoubtedly the increase in temperature of water in my small rearing dishes was even greater than that of surface lake water. The appearance of these eggs changed rapidly in the few hours just preceding hatching. In the morning the larvae within were motionless, and only their ocelli and tips of their mandibles were darkened. Dark color had appeared in the head capsules and prothoracic shields early in the afternoon, and the larvae were wriggling about with the mandibles in motion, beginning to break the egg membranes and escape.

The first instar larva agrees well with Welch's description and illustration (1916), but head capsules of the specimens I measured are slightly larger. Welch gave 0.25 mm. as maximum diameter of head of the newly hatched larva. My specimens, measured 7 days after hatching, had maximum head widths of 0.27 and 0.28 mm. The body lengths of newly hatched larvae average about 1.4 mm.

As stated by Welch, cases are made from pieces of leaf soon after hatching. When alternately discarding and replacing the 2 pieces which make up sides of the case, the larva cuts larger and larger pieces of leaf. Except for increase in size, there appears to be no significant change in the case nor in method of case construction throughout larval life.

Duration of first larval instar in aquaria is approximately 7-8 days, and the first molt occurs when larvae are about 2.2 - 2.8 mm. long. Twenty larvae from a single egg mass were killed in hot water, transferred into alcohol and measured 7 days after hatching. Thirteen of these had head capsules with maximum widths of 0.27 - 0.28 mm., and body lengths of 1.8 - 2.7mm. It seems that these 13 specimens were still in first instar. The other 7 larvae had head capsules 0.37 - 0.40 mm. wide, and body lengths of 2.2 - 3.2 mm. These probably had recently undergone their first molt and were then in the early part of their second instar.

Twelve other larvae from the egg mass mentioned above were killed in hot water, transferred to alcohol, and measured 9 days after the first 20, and 16 days after hatching. Maximum head widths of these 12 were 0.32, 0.33, 0.33, 0.35, 0.36, 0.38, 0.38, 0.39, 0.40, 0.43, 0.45, and 0.52 mm. The first 11, which had body lengths of 2.6 - 3.4 mm., are tentatively assigned to second instar, although their head widths range both above and below those of that instar killed 9 days earlier. The specimen with head capsule 0.52 mm. wide was 4.2 mm. long and probably was in third instar. The larvae remaining were lost, and no additional data are available.

Duration of each larval instar is evidently quite variable among individuals from a single egg mass. Sizes of head capsules usually vary only slightly in first instar larvae from a single egg mass, but the range of sizes increases in each successive instar, and it becomes more difficult to recognize instars from dimensions only in older larvae. Perhaps limited space and food supply and other failures to duplicate the natural environment account for smaller average sizes of laboratory reared specimens than larvae of corresponding instars collected in nature.

Specimens of N. icciusalis on P. natans remain near the surface among the floating leaves throughout all larval instars. In contrast to N. maculalis (Welch, 1916), there is no significant change in food nor in method of feeding during the larval stage, and no migration to various parts of the plant.

N. icciusalis may be host to certain parasitic Hymenoptera. A teneral adult specimen identified by R. A. Cushman as Cremastus sp. (Ichneumonidae) was found within an icciusalis pupa case, together with normal exuviae of the host larva and empty exoskeleton of the host pupa.

Nymphula badiusalis Walker

Although Nymphula badiusalis is common throughout the Northeastern States, its immature stages apparently have remained unknown until now. Forbes (1923) wrote of this species, "Moth in August. Early stages unknown. Common north of West Virginia and Illinois." Then he listed localities in New York State in which it has been collected. Welch (1915) included the species in his list of Lepidoptera of the Douglas Lake region, Northern Michigan.

In this investigation, N. badiusalis were encountered more commonly than any other Nymphula on Potamogeton. Specimens were collected in Cheboygan, Presque Isle, and Washtenaw Counties, Michigan, and in Dane County, Wisconsin. Adults were reared from larvae and pupae found most commonly on thin, submerged leaves of P. amplifolius, P. praelongus, P. Richardsonii, and P. zosteriformis, but they were also found amidst and evidently feeding upon the coriaceous floating leaves of P. natans. Their cases were constructed primarily from leaves of the food plants listed, but they also included leaves of P. gramineus, P. nodosus, Vallisneria, and in one instance an aspen leaf.

An almost complete life cycle of this species was observed in the laboratory. Specimens collected as mature larvae and kept in aquaria in which P. amplifolius was growing pupated, emerged, mated, and laid eggs. The larvae which hatched from these eggs molted twice but died while still in the third larval instar.

Activities of the full grown larva follow the general pattern discussed by various investigators for other Nymphula caterpillars. Cases are made, in a manner similar to that of N. maculalis (Welch, 1916), from 2 oval pieces of leaf fastened together with silk. The larva extends its anterior end from the case to feed on Potamogeton leaves and its posterior end to eject feces. Periodic vibratory movements similar to those of N. maculalis (Welch and Sehon,

1928) produce a current of water through the case, thus renewing the supply of oxygenated water.

Before pupating, the mature larva usually attaches one end of its case to a Potamogeton stem, below the water's surface, at such an angle that it resembles a stipule. Then it completely closes the case and lines it throughout with closely woven silk, managing somehow to exclude water from within the silken lining. Although pupal cases are similar to larval cases in external appearance, the former differ in being completely closed, more firmly sealed, and filled with gas.

Since pupal cases are not transparent, pupae were removed from their cases in order to observe their development. Naked pupae which were placed in water half an inch deep developed normally until almost time for emergence, then all died. Young pupae are translucent yellow throughout. Later, as the scales of the future adult develop, pupae become opaque, predominantly white, but showing gradually more and more distinctly the wing markings of the future adult. At this stage, pupae of the various species encountered in this investigation could be positively identified by comparing their wing markings with those of identified adult specimens. A mature pupa which had developed apparent wing markings of N. badiusalis was removed from the water, and placed on a strip of paper suspended in moist atmosphere less than an inch above the water surface in a closed rearing bottle. Two days later, the adult female emerged normally. Following this experience, all pupae were removed from water and placed in moist air as soon as their wing markings became clearly discernible, where a high percentage of them emerged normally. Less than half of the young pupae which were removed from their cases and placed directly in air lived long enough to produce adults. If they were not placed in moist atmosphere, they died apparently from dessication; if they were, many died from infection with mold. The best procedure found for observing the development of pupae is removal of young pupae from their cases into shallow water and transfer to moist air when their wing markings become well developed.

Since the opacity of larval and pupal cases makes observation of pupation difficult, exact duration of the pupal stage was not determined. Emergence of a moth 16 days after the pupa was removed from its case shows that in some instances at least the pupal stage may last at least 16 days.

Although adults of N. badiusalis were not found in nature until June, specimens taken as larvae on March 24 and kept in aquaria at room temperature pupated and emerged as early as April 21. It seems that emergence normally occurs only during the evening or night. Most new adults were discovered during early morning examinations of rearing cages. None ever appeared during the course of the day until 8:25, 8:37, and 8:55 P.M., Eastern Standard Time, when freshly emerged adults with unexpanded wings were found. Emerging moths leave the larval and pupal exuviae in their cases.

Adult N. badiusalis were collected by sweeping the vegetation at the north shore of Douglas Lake, Michigan, in late June, July, and August. No emergence heights were noticed during this time. Adults were found in much greater abundance resting in the nettle and Polygonum which encroached on the west shore of University Bay, Lake Mendota, Wisconsin, on August 29, 1941. All 26 Nymphula collected there were N. badiusalis.

Mating evidently occurred several times in cylindrical screen rearing cages (7 by 12 inches) in the laboratory, but it was observed on only one occasion. A female which was discovered freshly emerged at 8:25 P.M., May 5, 1942, was found mating with a 2- or 3-day old male at 7:15 the following morning. They stood on a vertical side of the rearing cage facing in opposite directions, with only the tips of their abdomens in contact and their wings outspread. The female once moved a few steps forward, dragging the male behind her. At 9:00 A.M., 10:45 A.M., and 11:45 A.M. they were observed thus united in the same position, where they presumably remained in copula for at least 4.5 hours. At 2:15 P.M. they had separated. Following this mating, the female laid 489 eggs, most of which ultimately hatched.

This moth oviposited 25 to 35 hours after emergence and about 9.5 to 19.5 hours after being last observed in copula. She laid 441 eggs, 421 of which hatched, during the night (between 9:20 P.M. and 7:05 A.M.) of May 6-7. These eggs were laid in masses of 39, 100, 121, and 171 just within the margin on the under side and a group of 10 on the upper side of a piece of paper towel, the only floating object in the breeding cage.

It seems that females of N. badiusalis normally oviposit only at night. The one being discussed laid no eggs during daylight hours of May 7, but deposited a mass of 23, 22 of which proved fertile, just beneath the edge of a floating paper towel between 9:20 P.M., May 7, and 7:05 A.M., May 8. She did not oviposit until evening on May 8, but laid a well-arranged group of 18 just beneath the edge and a dispersed mass of 7 on the upper side of the floating paper towel between 9:40 P.M., May 8, and 7:15 A.M., May 9, when she floated dead on the water. Embryos failed to develop in 8 of the 25 eggs deposited during her last night.

Oviposition by a female which emerged in a breeding cage during the night of July 11-12, 1941 was observed on July 13 at 9:15 P.M. When discovered on the morning of July 12, this specimen was placed in the cage of a male which had been caught with a net the preceeding day. There was no oviposition until 9:00 P.M., July 13, when the female was resting on the center of a floating leaf. A few minutes later she moved about on the water surface, apparently supporting part of her weight by resting tarsi on the surface film and part by constantly fluttering the wings. At 9:15 she was discovered sitting on the edge of a floating P. natans leaf with abdomen extended into the water and evidently bent back so that its tip was in contact with the lower surface of the leaf. The wings were extended similar to those of a well spread specimen. Except for occasional movements a bit to one side, the moth sat motionless for at least the next 20 minutes, when there was a 25 minute interruption in my observations. At 10:00 she had left this leaf and was sitting in a similar position on a second one. Examination of the first leaf revealed a normally placed mass of 120 eggs near its margin on the lower surface. Then the moth's entire abdomen appeared above water and it was apparent that oviposition had ceased. A minute later she moved across the water in the manner described above and flew up along the screen side of the cage. There was no further oviposition during that night. A normally placed mass of 73 eggs was found beneath the second leaf. These 193 eggs all hatched.

Information on eggs of N. badiusalis was obtained from numerous egg masses laid in breeding cages and from others collected in the field. These masses are normally laid on the lower surface of a floating Potamogeton leaf, near its margin. The eggs are arranged in rows, usually 4, which are slightly curved, with the concave side toward the leaf margin. Occasionally contiguous egg masses form a band extending nearly or quite the entire perimeter of the leaf near and roughly parallel to its margin.

Eggs are elliptical, slightly flattened, about 0.38 - 0.44 mm. wide and 0.53 - 0.60 mm. long. When first laid they are nearly opaque yellow throughout, showing no signs of internal differentiation.

Weak, partly disabled, or dying females sometimes deposit eggs on the upper sides of floating leaves. The female observed ovipositing wetted her wings on the following day and seemed to be unable to fly. That night she laid 2 masses of 52 and 54 eggs respectively, on the upper surface of a _P. natans_ leaf, all but 2 of which proved fertile. The following night she deposited masses of 43, 14, 8, 8, and 2 eggs on the upper surfaces of leaves, but 24 eggs failed to develop.

Percentage of viable eggs gradually decreased as each of the females discussed above approached the end of her egg laying period. This was true of all _N. badiusalis_ which oviposited in the laboratory.

The period from oviposition to hatching varied from 7.5 to 11.5 days in eggs laid in breeding cages. Within limits embryonation is accelerated by increased temperature. In eggs which hatch 11.5 days after oviposition, the first vague signs of internal differentiation usually appear when they are 5.5 days old. There is a narrow, curved, poorly defined region of slightly greater transparency near the center of each egg. In 6.5 day eggs these portions, the developing bodies of larvae, are more transparent and more clearly differentiated from the surrounding opaque yellow yolk. They are wider, longer, more definite in outline, and each is in the form of a sigmoid curve. In 7.5 day eggs eye spots are visible close to the more blunt end of each larva, which is always toward the end of the egg nearer the leaf margin. As each larva grows within its egg membranes it curves into an oval position with its head in contact with its posterior end. The ocelli and tips of the mandibles turn black, and lighter pigment develops in the head, prothoracic shield, and intersegmental grooves.

Newly hatched larvae are grayish cream color with brown heads and prothoracic shields. Maximum width of head capsules is about 0.28 mm.; total body length, 1.2 or 1.3 mm. They begin at once to make cases from *Potamogeton* leaves and to eat leaves in the same manner as that of mature larvae. In aquaria they used leaves of *P. amplifolius*, *P. natans*, *P. praelongus*, and *P. Richardsonii* for food and for case-making material.

Larvae of *N. badiusalis* pass the winter on food plants which live beneath the ice. Specimens were collected during all 12 months. Those taken in winter became active and resumed feeding as soon as they were warmed up to laboratory temperature.

Nymphula obscuralis Grote

It seems that everything published on the biology and immature stages of *Nymphula obscuralis* is based on the original research of Hart (1895, as "Paraponyx obscuralis"), who reared adults from larvae and pupae collected on Vallisneria and Potamogeton in the Illinois River. He described and figured the larva and pupa, discussed habits of the former, and presented data on seasonal aspects of this species. Dyar's descriptions of larva and pupa (1906) are abridgements of those of Hart. Since Forbes (1910) did not list this larva among those which he had collected, his statements (1910, 1923) that it lives on Vallisneria and Potamogeton would seem to be based on contributions of Hart.

Although previous authors have listed only 2 of their food plants, larvae of N. obscuralis feed on aquatic plants of several different species. After having reared 3 specimens, Hart (1895) concluded, "The favorite food of the larva of P. obscuralis is the leaf of Vallisneria spiralis, and it has also been found upon Potamogeton nutans". I have reared adults from larvae and pupae found in Cheboygan and Washtenaw Counties, Michigan, on P. amplifolius, P. natans, P. praelongus, P. Richardsonii, and Nuphar advena. Specimens collected as pupae and confined in breeding cages emerged, mated, and laid fertile eggs, but the larvae which hatched from these eggs lived for only a few days.

Activities of the full grown larva are similar to those of other Nymphula caterpillars. Cases are made, like those of N. badiusalis, by cutting an oval piece of leaf from a food plant and fastening it loosely with silk to the attached portion of the leaf or to another leaf so that the larva is concealed between the two. Later it usually cuts the attached side along approximately the same outline as the oval piece, thus obtaining a case which it can move about by protruding the anterior end, crawling at will with the thoracic legs, and pulling the case along. Shelters made of 2 or 3 whole leaves such as those described by Hart (1895) were not seen. It seems that such retreats must be used by larvae deprived of their cases, only as a temporary expedient until new ones can be cut out.

Construction of the pupal case is similar to the process described above for *N. badiusalis*. Like the latter, *N. obscuralis* was observed to attach its case to a stem so that it resembles a stipule. Detached pupal cases floating as those described by Hart were not observed.

Fewer specimens of *N. obscuralis* were encountered than of *N. badiusalis*, and less information was obtained concerning pupae of the former species. Young pupae are translucent yellow throughout and quite similar in appearance to those of *N. badiusalis*. Mature pupae can be identified quite readily because wing markings of the future adult become very distinct before emergence.

In rearing cages, new adults were discovered in the morning, and it seems that emergence normally occurs predominantly if not exclusively during the evening or night.

At least 1, probably 2, females of *N. obscuralis* mated in screen rearing cages in the laboratory. A male was discovered August 14, 1941, in a breeding cage containing a living female first seen the previous morning. The following morning a second female was found in this cage. After the older female had been isolated on August 16, normally placed egg masses were found in both cages. Unfortunately, the eggs in one cage were accidentally destroyed, and their fertility remains in doubt.

Oviposition by the younger female mentioned above was observed on August 21 at 9:45 P.M. No difference was detected between this process and the oviposition of N. badiusalis. Like the latter, moths of N. obscuralis also stand near the edge of a floating leaf with wings outspread, thrust the abdomen into the water and back beneath the leaf, and deposit their egg masses on its lower surface near the margin. It seems that females of N. obscuralis oviposit only at night.

Egg masses of this species appear quite similar to those of N. badiusalis. They are laid on the lower surface of a leaf, near its margin, usually arranged in 4 rows which are almost parallel to the leaf margin. Eggs are shaped and colored like those of N. badiusalis, but seem to average a little larger. The 32 measured were 0.43 - 0.50 mm. wide and 0.56 - 0.63 mm. long. While the yellow eggs of N. badiusalis and N. obscuralis are easily recognized among the whitish ones of N. icciusalis, I found no reliable way of distinguishing them from each other until the embryo has started to develop.

The developmental period of eggs laid in the laboratory was 11.5 - 15.5 days. Eggs deposited August 21 hatched before those laid August 18. The first sign of internal differentiation was barely noticeable in some eggs only 1.5 days old. These contained C-shaped embryos slightly more transparent than the surrounding yolk. In 3.5 day eggs each embryo was longer and spirally coiled through about 540° with the more attenuated posterior end at the inside of the coil. The embryo of N. badiusalis at a corresponding stage of development is in the shape of a sigmoid curve and lacks this spiral coiling. In 4.5 day eggs the embryo was unchanged in size and form but differed in having distinct, pigmented ocelli. Later, the developing larva partially uncoils and assumes the form of an oval with head in contact with posterior end. Like the larva of N. badiusalis, it becomes heavily pigmented on ocelli and mandible tips and lightly pigmented on head, prothoracic shield, and intersegmental grooves before hatching.

Newly hatched larvae are similar in color, shape, and dimensions to those of N. badiusalis. They did not thrive in aquaria supplied with leaves of P. praelongus, and little information about them was obtained.

Larvae of N. obscuralis pass the winter in a somewhat torpid condition on food plants which live beneath the ice.

Such larvae become active and resume feeding when they are warmed up to laboratory temperature. A specimen taken as a mature larva on March 24, 1942, and kept in an aquarium in which *P. amplifolius* was growing behaved normally, pupated, and finally emerged on April 24.

Nymphula allionealis itealis Walker

It seems that the immature stages and food plant of *Nymphula allionealis itealis* remain unknown. Welch (1915) reported the species from the Douglas Lake region, Michigan.

A single specimen of *N. allionealis itealis* was obtained during this investigation. The larva or pupa was taken, together with several specimens of other species of *Nymphula*, on *P. natans* collected July 9, 1941 in the Sedge Pools, Douglas Lake, Michigan. The adult emerged in a breeding cage July 28. The case of this specimen was made from *P. natans* leaves.

Chironomidae

In this section the nomenclature of Townes (1945) has been followed for all species within the scope of his monograph, with the exception that the well-known family name "Chironomidae" is retained in favor of the less familiar "Tendipedidae". Johannsen's nomenclature (1937a, 1942, 1943) is followed for the subfamily Orthocladiinae.

Because of conflicting published statements, it seems advisable to review the literature before undertaking a discussion of the Chironomidae which feed upon *Potamogeton*. Frost (1924: 31-32) wrote: ". . . none of the Chironomidae are true leaf miners . . . because they do not work between the two epidermal layers of the leaves . . . *Cricotopus sylvestris* Fabr. and *Chironomus brasenae* Leathers, are the only known species of Chironomidae which feed on living plant tissue. The others all attach themselves to the leaves by means of silk, and feed on algae and diatoms which may come their way."

It seems that Frost overlooked the fact that Thienemann (1909: 146-8) and Gripekoven (1914: 135-6, 209-14) had described the habits of a true leaf miner, *Cricotopus brevipalpis*, and the possibility that subsequent investigations might reveal other leaf miners among undescribed Chironomidae or among described species whose larvae were unknown. Several herbivorous species have been recorded in addition to the 2 listed as "the only known species . . . which feed on living plant tissue". Among those whose habits have been known for many years might be mentioned *Tanytarsus quadripunctatus* (Malloch) (as "*Chironomus albistria*", Needham, 1908), *Chironomus nymphaeae* Willem (Willem, 1908), *Cricotopus trifasciatus* (Panzer) (as "*C. limnanthemi* Kieffer", Willem, 1910), several species of *Tendipes* and *Cricotopus* discussed by Gripekoven (1914), and the species of "*Chironomus*" and "*Tanytarsus*" listed by Moore (1915). Finally, in stating that all other Chironomidae have the same habitat, mode of attachment and food, Frost has overlooked the free living, predaceous Tanypodinae; those larvae which burrow in living plants, Spongilla and Plumatella tissues, and bark (Gripekoven, 1914: 133-5, 141-2); the littoral, sublittoral and profundal muck dwellers; those Diamesinae, Orthocladiinae and others which build cases on the rocks in intertidal zones and swift-flowing streams; the larvae which live within bodies of snails (Barnard, 1911); the Symbiocladius and Spaniotoma larvae which live attached to May-fly and stone-fly nymphs (Claassen, 1922; Johannsen, 1937a); the terrestrial species which live in moss, rotten wood, potatoes, dung, and humus, some of which feed on root hairs and have become known as greenhouse pests; and others.

It is convenient to classify the chironomid larvae which are intimately related to plants of the genus Potamogeton into 3 groups according to their food habits, although some differences exist within these groups.

Group 1 comprises the true leaf miners, which make linear mines between the 2 epidermal layers of the leaves. These larvae apparently do not spin silken tubes within their mines, which they extend almost continuously as they feed on mesophyll tissue. Two of the species included in this group were not known prior to this study, and other authors have not recognized this assemblage. Besides Cricotopus brevipalpis Kieffer, the biology of which was presented by Thienemann (1909) and Gripekoven (1914), it contains C. elegans Johannsen and C. flavipes Johannsen, whose habits are reported here. Inasmuch as the excavations made by these larvae are the only ones which are comparable in position, extent, and function with those of the terrestrial insect leaf miners, it seems appropriate to restrict the term "mine" to designate only this type of excavation.

Group 2 embraces those larvae which subsist on leaf tissues, feeding on one epidermis and the mesophyll layer but leaving the other epidermis intact. Insofar as these are larvae which live in channels produced by their feeding activities, this assemblage equals Gripekoven's "Gruppe 2, oberflächlich Minierer", and Leather's Group IV. These larvae live in silken tubes, spun within the channels of all channeling species and laden with detritus. <u>Polypedilum ophioides</u> Townes, a leaf eater which does not produce nor occupy well defined channels, is included in this group because it subsists on tissues of upper epidermis and mesophyll. Channeling species included in this assemblage are <u>Cricotopus</u> <u>trifasciatus</u> (Panzer) and <u>Polypedilum</u> <u>illinoense</u> (Malloch), the larval habits of which are discussed here, and several species previously reported from <u>Potamogeton</u> and other hydrophytes, such as <u>Cricotopus</u> <u>sylvestris</u> (Fabr.) (Frost, 1924), a few species of <u>Cricotopus</u> reported by Gripekoven (1914), and <u>Polypedilum</u> <u>braseniae</u> (Leathers) (Leathers, 1922). Since the word "channel" clearly denotes superficiality of position, it seems preferable to such terms as "mine", "half-mine", and "burrow" to designate the usual type of excavation made by larvae in this group.

Group 3 contains the **net-spinning** plankton eaters, most of which live in short burrows just beneath the epidermis of stems or leaves. These excavations, which rarely exceed twice the lengths of their occupants, are oriented longitudinally in the plant tissue, and they open at both ends, usually by means of roughly circular holes gnawed through the epidermis. A tube of closely woven silk lines each burrow throughout, and a conical silken net of relatively open weave is usually stretched across it just behind the larva.

Each specimen of this group produces a current through the burrow by dorsoventral undulations of the body. Some investigators have ascribed only a respiratory function to these currents, maintaining that the chironomid subsists primarily on spermatophyte tissue. It has been demonstrated for at least 9 species, however, that the larva of each feeds on plankton filtered from the water as it passes through the conical net.

Periodically, each larva turns about in the burrow, devours net and contents, weaves a new net, again reverses its position, and resumes rhythmic undulations of the body which produce a current through the burrow and into the net.

Not all specimens of this group live in stem burrows. Some silken tubes are spun in folds or rolled edges of leaves, and previous investigators have reported them on or within several types of substrata other than tissues of hydrophytes. Wherever they live, chironomids of Group 3 subsist largely on plankton and detritus filtered from the water by their silken nets. Most of them, which consume little if any Potamogeton tissue, are included as dependent on these plants for protection rather than for food.

This assemblage seems to be comparable with Gripekoven's "Gruppe 1", and with Leather's Group I. It includes Glyptotendipes lobiferus (Say), Glyptotendipes dreisbachi Townes, Polypedilum sordens (Wulp), and Tanytarsus nigricans (Johannsen), whose biologies are discussed here; Microtendipes pedellus (De Geer) and Tanytarsus obediens Johannsen, observed and reported by Leathers (1922); and Glyptotendipes glaucus (Mg.), Glyptotendipes imbecillis (Walk.), and Polypedilum tritum (Walk.), recorded by Burtt (1940).

Several additional species which probably belong to this group have been discussed by Willem (1908), Thienemann (1909), Goetghebuer (1913), Gripekoven (1914), and Wesenberg-Lund (1943). However, it will not be certain that these larvae exhibit all characteristics listed for Group 3 until their food habits have been adequately investigated. Considerable information might be obtained by studying them and other chironomid larvae, including plant burrowers, burrowers in other substrata, and nonburrowing species, using the simple techniques employed here to observe feeding habits.

The burrows made by these larvae are of the type described for Group 3. Like larvae of Group 3, larvae of these species also produce currents through their burrows by means of dorsoventral undulations of their bodies. Although plankton nets within the burrows were not known and the remarkable sequence of feeding activities was not understood, the descriptions of larval activities presented by Willem (1908: 698) and Gripekoven (1914: 137) would fit larvae of Group 3 very well. Willem (1908: 698) actually stated that larvae living in such situations feed on plankton which is brought into their burrows by the currents which they produce.

Characterizations of this group by Gripekoven (1914: 140) as a "typischen Miniergruppe" and by Wesenberg-Lund (1943: 524) as "die typischen Blattminierer" evidently are incorrect. The habits of these larvae differ from those of typical insect leaf miners in 3 fundamental respects. Their excavations do not increase in length at a rate even approximating that of the typical leaf miners, which subsist on plant tissue and are constantly lengthening their mines as they feed, crawling forward, and leaving old mines of considerable length behind them. They live in dead and decomposing portions as well as in living parts of the plants. Burrows of some species are often found in several types of substrata other than aquatic plants, and some attach their silken tubes superficially without making any excavation.

A mining larva which subsists principally on tissues of the plant which shelters it must either extend its excavation at approximately regular and frequent intervals as it feeds, or often abandon it and make new excavations. In Thienemann's illustration (1909: Fig. 19), reprinted by both Gripekoven (1914) and Wesenberg-Lund (1943), the sum of the lengths of 13 Tanytarsus stratiotes burrows is less than twice the sum of the lengths of the larvae occupying them. Yet not one empty burrow is shown. Evidently, burrows which are extended only as their occupants grow and require more room, as seems to be the case in this group, function more as havens of refuge and seclusion than as typical food mines. It follows that larvae which occupy such burrows must have an important source of food other than the tissues of plants in which they live.

Leathers (1922: 9) reported on one of the species known to live in or on substrata other than tissues of living plants. He stated that, besides occurring in nearly all the submerged aquatics, the "burrows of Chironomus [Glyptotendipes] lobiferus may be found on floating logs, at the bottoms of ponds, or attached to stems, stumps, and other perpendicular surfaces." Tendipes gripekoveni Kieffer, which Townes (1945) considers identical with G. lobiferus, is recorded by Gripekoven (1914: 166-8) as occurring in aquatic plants of 4 genera including, "alten abgestorbenen Stücken von Scirpus lacuster," and, "in alten Eichenrinde...und..in Stöcken von Plumatella fungosa." While a plankton eating species would appear capable of living in or on a variety of substrata, it is difficult to conceive of any true leaf miner altering its food habits so drastically as life in these different substances would seem to demand.

Considering the facts mentioned above, it seems that no useful purpose can be served and much confusion and misunderstanding may result from continued reference to these species as "leaf miners". As an alternative, the term "burrower" is suggested. This term has the advantage of applicability to species which make or adopt short, protective excavations in any type of substratum, thus obviating the necessity of classifying any species in 2 or more groups simply because it lives in a variety of substrata.

Larvae of Tanytarsus nigricans (Johannsen) construct their silken tubes between rolled or folded leaves and seem to subsist partly on plankton and partly on leaf tissue. Since the plankton is obtained by producing a current through the silken tube in which a cone-shaped net filters out the particulate matter, and since the larva exhibits the typical sequence of feeding activities mentioned above, this species is placed in Group 3, although it differs from most of the group in lacking the burrowing habit.

METHODS

Larvae of Groups 1 and 2 were brought into the laboratory in the leaves in which they were feeding, and kept in culture dishes about 220 mm. in diameter and 70 mm. high.

Fresh leaves were supplied as needed, and aeration was maintained either by continuously bubbling air or by a continuous flow of aerated water through the culture dishes. The latter method, since it removed all dissolved and particulate wastes, and held the temperature at a constant, moderate level, kept the cultures fresher and was more successful. This method, however, required that a cylinder of copper screening be placed within the culture dish, emerging slightly above its rim, to keep the leaves from flowing out with the overflowing water. Larvae migrating from one leaf to another were frequently lost even when a screen cylinder of fairly fine mesh was used.

In order to observe larval activities, a single leaf was often removed from the culture dish and placed in a finger bowl or petri dish on the stage of a dissecting microscope. Larvae of Group 2, the leaf channelers, were studied almost entirely with reflected light. *Cricotopus flavipea* larvae, which mine in thin, transparent leaves, are more easily observed with transmitted light. Since larvae of *C. elegans* mine in thick, nearly opaque leaves, they are not clearly visible unless a piece of the epidermis covering them is removed.

Two methods were used to rear these Chironomidae. When positive association of larva, pupa and adult stages was required, nearly mature pupae, with their last larval exuviae still adhering to their bodies, were carefully removed from their mines or channels and placed individually in test tubes. These tubes, each containing less than 10 cc. of water, were loosely stoppered with cotton and placed in a shallow tray in inclined positions providing maximum surface exposure to aerate the water. A stream of tap water which flowed continuously through the tray kept the temperature quite constant. In order to allow the skeleton of the imago to harden properly, a tube was not disturbed until at least 24 hours after emergence. At that time, the adult was usually resting on the cotton, and the larval and pupal exuviae were easily recovered from the water. These exuviae were dehydrated, mounted in balsam or clarite, and labelled. The adult was killed, pinned, and labelled with the same number.

It was found, however, that mass rearing resulted in less trouble and less mortality. This method was used whenever a collection was known to contain only 1 species, or when association of larva, pupa and adult stages of all species involved was already positively established. When pupation began to occur in a culture, a kitchen strainer was inverted over the dish, forming a canopy of fine mesh screening. A large size which fitted snugly around the rim of the culture dish worked especially well. A tube supplying aerated water was introduced through a small hole in the screening. Adult midges rested on the inside of this canopy and were collected by removing the water tube and introducing the tube of an aspirator in its place. Although these adults were kept alive until their skeletons were hardened, they were usually removed when first noticed and transferred to a dry container. Those left within the canopy frequently fell into the water and were drowned.

Stem-burrowing larvae were brought into the laboratory in pieces of plant stems and kept in battery jars or small aquaria. These species are quite resistant to the toxic effects of decay products, and were easily maintained in the laboratory if aeration was supplied by bubbling air through the vessels. When pupation began, battery jars containing these chironomids were placed in screen rearing cages, the aeration tube being introduced through a small hole in the screen. By providing 2 cages for each battery jar and shifting the jar from one to the other each morning, it was possible to make sure that no adult was killed until it was at least 24 hours old and the exoskeleton was well sclerotized. The first morning after emergence had begun, the jar was removed from cage 1 without disturbing the freshly emerged adults resting on the screen and placed in cage 2. The following morning, adults in cage 1 were killed and pinned, and the battery jar was shifted back into it without disturbing the adults in cage 2. When individual rearing was necessary, pupae were removed from their burrows and allowed to emerge separately in test tubes in the manner described above.

Larvae of Tanytarsus nigricans were brought into the laboratory in plants whose folded or curled leaves sheltered their silken tubes. Like other species of Group 3, they proved quite hearty and required no more attention then that an air bubbler be provided in their battery jar or aquarium. Individual and mass rearings were conducted in the same manner with this species as with other species of Group 3.

Certain special techniques were required in order to study the feeding activities of Group 3 larvae. Their positions in the plants would naturally suggest that they probably subsist mainly on spermatophyte tissue. Stomach analysis, however, showed little or no Potamogeton tissue, the recognizable material being chiefly plankton. The question of how this plankton is obtained could not be answered without securing better visibility of the larvae than was possible in their natural burrows.

Modification of a technique suggested by Leathers (1922:4;Fig. 26, p. 56) afforded excellent visibility of larval activities. Several capillary glass tubes, slightly larger than the mature larvae, were cemented side by side to a rectangular glass cover slip. A similar cover slip was then cemented to the exposed sides of these capillary tubes. This preparation was placed in a watch glass filled with water, together with several larvae which had been removed from their burrows. Within a few hours, most of the larvae had spun their silken tubes within the capillary glass tubes. They could then be studied with a microscope by both transmitted and reflected light, or the preparation containing them could be removed from the watch glass and placed in a miniature aquarium mounted in a lantern slide projector (Berg, 1948), in order to demonstrate larval activities by projecting images of the larvae onto a screen.

The silk of which the cone-shaped nets are constructed is quite transparent and invisible in its natural condition even in these glass preparations. Leathers (1922: 5) reported that Ehrlich's acid hematoxylin stains this substance, but this stain cannot be used on living material. Addition of a suspension of powdered carmine or ultramarine blue to the water passing through the net gives it a coating of colored particles. Its existence, shape, position and the fact that larvae devour it and its contents then become evident. The carmine is only partially dissolved by digestive enzymes. Both carmine and ultramarine blue, which does not dissolve to any noticeable degree, are easily recognized even in small quantities in fecal pellets. Their passage through the transparent bodies of the larvae can be traced readily, and they give a reliable index of progress of particulate material through the digestive tract. The larvae suffered no apparent ill effects from ingesting these stains, but they did not eat nets which were too heavily loaded with either substance.

Cricotopus elegans Johannsen

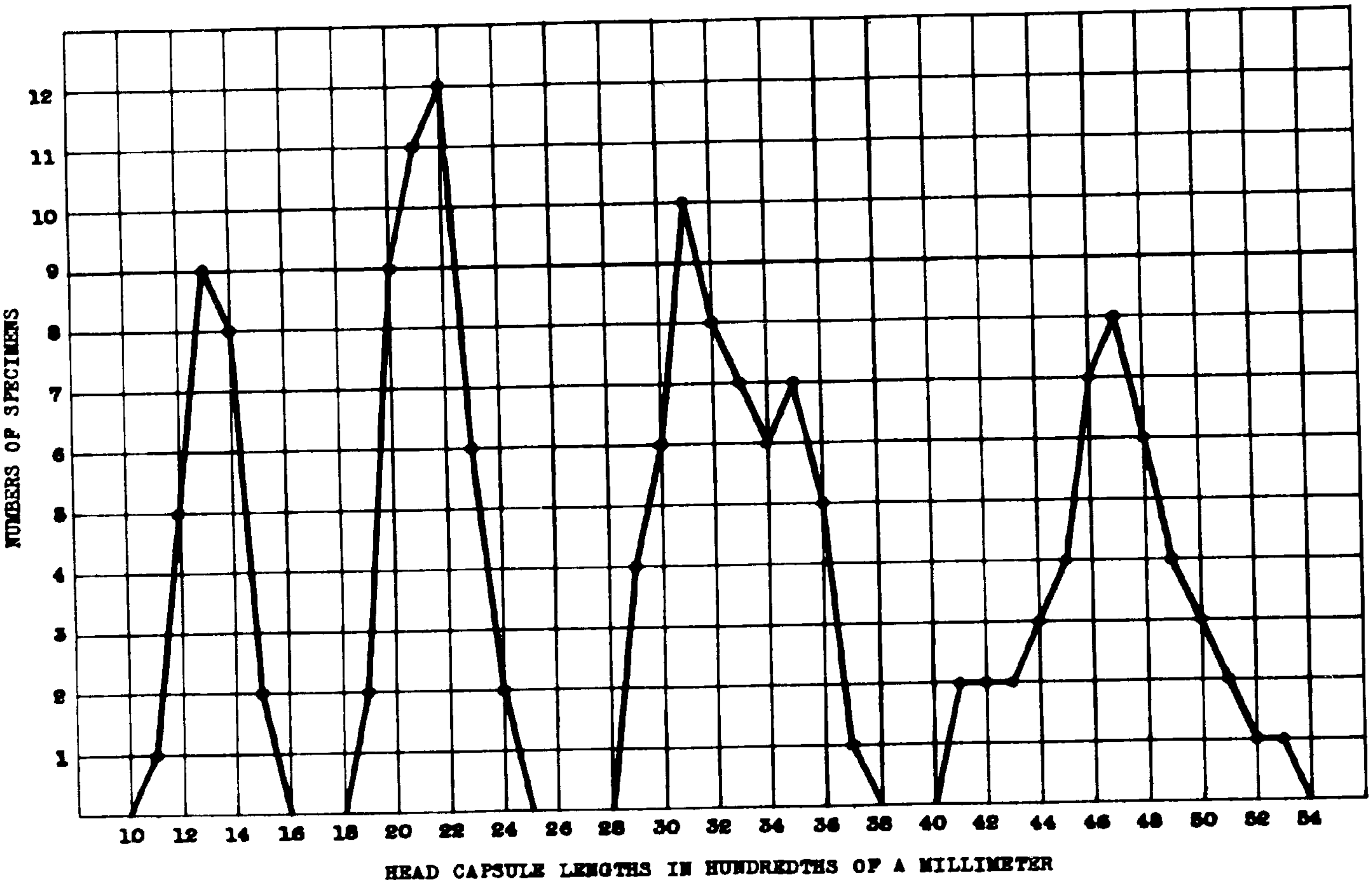
It appears that the only published reference to *Cricotopus elegans* is the original description of larva, pupa and adult stages (Johannsen, 1943), which was based upon specimens I collected and reared in this investigation.

C. elegans was encountered, May through October, in Livingston, Presque Isle, and Washtenaw Counties, Michigan. During most larval instars, specimens of this species mine in the coriaceous floating leaves of *Potamogeton amplifolius*, *P. natans*, and *P. nodosus*.

Measurement of the head capsules of 166 *C. elegans* larvae (Graph 1) shows that they belong to 4 distinct size groups composed of 25, 42, 54, and 45 individuals, respectively. The specimens measured were collected while they were in first or in second size group, then reared in culture dishes in the laboratory. Larvae which shed head capsule exuviae of size group 1 had heads of group 2. Changes from second to third and from third to fourth size group were also observed. Larvae with heads of group 4 invariably pupated at their next molt. It appears quite evident, therefore, that these 4 size groups correspond to the last 4 larval instars.

Eggs were not obtained and larval instars could not be positively identified by observation of hatching and all subsequent molts. Branch (1923) and Sadler (1935) have observed complete life cycles of "*Chironomus cristatus* Fabr."

and *Tendipes tentans* (Fabr.) (as "*Chironomus tentans* Fabr."), respectively. They stated that each includes only 4 larval instars and that head capsule sizes for all specimens of a given instar are relatively uniform. For convenience in referring to instars of *C. elegans* represented by the 4 size groups, they may be numbered first, second, third, and fourth, if it is assumed that this species has the same number of larval instars as "*C. cristatus*" and *T. tentans*. The possibility that an unobserved instar may precede the one represented by size group 1 must be recognized, and the tentative



Graph 1. Distribution of *Cricotopus elegans* larvae according to lengths of head capsules.

nature of these instar numbers should be borne in mind.

According to Graph 1, mean lengths of larval head capsules along the median line from posterior rim to tip of extended labrum are 0.132 ±0.0022, 0.214 ±0.0010, 0.326 ±0.0015, and 0.467 ±0.0024 mm., for first, second, third, and fourth instar larvae, respectively. Ranges in head lengths within the 4 groups are 0.05, 0.06, 0.09, and 0.13 mm.

Increments of growth between means of successive size groups are not a constant percentage of the smaller mean, as might be expected on the basis of Dyar's Law, but gradually decrease. The increment between means of size groups 1 and 2 is 62 per cent of the mean of group 1; that between means of groups 2 and 3 is 52 per cent of the mean of group 2; and the increment between means of size groups 3 and 4 is 43 per cent of the mean of group 3.

Johannsen (1943) included no figures in his description of immature stages. Since all specimens sent to him were faded by preservation in alcohol, he does not mention color patterns characteristic of living material.

Mandible, antenna, and labial plate of the mature larva are shown in Plate I, Figures 1-4. Since the latter normally is quite convex, it is impossible to see all of its teeth from any angle unless the plate is flattened as shown in Figure 4.

Coloring of the larva during late first, second, third, and early fourth instars is unusual and distinctive. The head is dark brown. Pro- and mesothorax are pale stramineous.

Metathorax and first abdominal segment contrast sharply with these, being much darker with considerable violet color mixed with brown. Violet pigment gradually fades through the next 3 abdominal segments, which are predominantly brown. Posterior to these, olivaceous pigment arises and gradually increases, and in the last 3 segments this bluish olive color almost completely covers the brown.

Older fourth instar larvae, excluding their dark brown head capsules, and young pupae are pale stramineous throughout. Older pupae show more and more definite markings as color patterns of future adults develop within. Posterior end of the pupa is shown in Plate I, Figure 5.

Each leaf infested by larvae of C. elegans usually harbors several specimens, the number of young larvae per leaf tending to be higher than that of older specimens. More than 20 first instar larvae often riddle a leaf with an irregular network of crisscrossing mines. It is uncommon, however, to find more than 3 third instar larvae in one leaf. Since all young larvae present in a group of several leaves floating close together usually are concentrated in only 1 or 2 of the leaves, it seems likely that eggs are deposited in masses on or near Potamogeton leaves, that newly hatched larvae tend to enter the nearest, most desirable, or most accessible leaf, and roam for short distances in search of fresh food as they grow older.

When leaves in which they were collected become brown and waterlogged, second instar larvae all abandon them within a few hours and start new mines in neighboring leaves. Their exuviae are left in the mines. Young third instar larvae often make another short migration, after which they immediately enter fresh leaves.

Later in the third larval stadium, many specimens forsake their food leaves and swim about for a few hours, often settling on sides or bottom of the rearing dish, before reentering the plant. Eventually, many of them start mining in submerged petioles, stems, and midribs. Fourth instar larvae in laboratory rearing dishes are usually found in these situations. Most specimens which remain in leaf blades throughout the third larval stadium leave this habitat early in the next stadium, swim about for some time, and enter one of these thicker portions of the plant. In the laboratory, 2 specimens remained in leaf blade mines during their entire larval lives and pupated there. The facts that last instar larvae were not found in the field and that older larvae in the laboratory abandon the plant and seem to hesitate for a few hours before reentering it may indicate that they do not normally live on Potamogeton during this stage.

Pupation takes place in the mine, and the pupa remains there until it is mature and ready for the final molt, about 2.5 days later. Periodic vertical undulations of its body presumably cause some circulation of water in the mine and renew the supply of oxygen. When ready to leave the mine the pupa greatly increases the force of these movements and tears the plant epidermis. Then it swims up to the surface of the water, where the adult emerges. The pupal exuviae float freely on the water, but those of the last larval instar remain in the mines.

Since young larvae of C. elegans work within the leaf and leave both epidermal layers intact, they are true miners. Late in the third stadium, when larvae become greater in diameter than the thickness of leaves, those which continue to live in leaf blades begin to gnaw away the lower epidermis. From then on, they live not as true miners, but as channelers which are protected from above and at the sides by leaf tissue and from below by their detritus-laden silk tubes.

Cricotopus flavipes Johannsen

Larva, pupa and adult stages of Cricotopus flavipes were described and figured (Johannsen, 1942) from specimens collected and reared in this investigation.

C. flavipes was encountered in Cheboygan, Presque Isle, and Washtenaw Counties, Michigan, in June, July, and August. The larva makes linear mines in the thin submerged leaves of Potamogeton amplifolius, P. epihydrus, P. praelongus, and P. Richardsonii.

Since all immature specimens sent to Johannsen were preserved in alcohol, he wrote nothing concerning natural colors of living material. Except for the light brown head capsule, larvae of all instars observed are entirely pale yellowish green. Pupae are of the same color when young, but show colors and markings of the future adult more and more distinctly as they grow older.

The larva of C. flavipes is strikingly modified for its particular mode of life. The leaves in which it mines are considerably thinner than the smallest diameter of the larva. In order to enter the very limited space between the layers of leaf epidermis and excavate the thin mesophyll layer, the anterior end of the larva's head must be much narrower than the rest of its body. The head capsule is wedge-shaped, its lateral compression becoming more and more pronounced toward the anterior end. Certain structures of the head have unusual shape, size, and orientation. The labial plate is so strongly convex ventrally that its most lateral teeth are invisible in ventral view unless it is forcibly flattened (Johannsen, 1942: Figs. 3 and 4). The mandibles and premandibles are quite stout; the antennae, very minute.

Due to extreme compression of the head capsule anteriorly, bases of the mandibles almost touch each other. Thus it is impossible for tips of the mandibles to move in a nearly lateral plane, converging toward each other as they swing backward, in the manner which is almost general among larvae of nemocerous Diptera. Mandibles of C. flavipes move in a plane only a few degrees from the vertical.

Assuming that the leaf is in normal position, the larva lies on its side when it mines. Regardless of leaf position, however, the larva is oriented with its sides in contact with the 2 epidermal layers. It extends both mandibles, one dorsal to the other, into the mesophyll tissue at the end of the mine and moves the head ventrally through an arc of about 120 degrees. At the end of this stroke the mandibles descend, one after the other, entering the narrow channel formed by the concave dorsal surface of the labial plate. The head then swings dorsally back to the starting position, where the mandibles are again extended and another working stroke is started. After making about 10 strokes in one direction, the larva backs for a distance of a few millimeters from the end of the mine, rolls over, crawls forward again, and makes a similar number of strokes in the opposite direction.

Mines of C. flavipes are readily distinguished from those of any Hydrellia species which might occur in the same leaves. Since this species removes all tissue between the epidermal layers, the mined area is left quite transparent and almost entirely without chlorophyll. This lack of color and the curved marks left by the mandibles, in groups which alternate regularly from side to side, are diagnostic when contrasted with the relatively uniform pale green color of Hydrellia mines. Mines of this species also differ in their tendency to be located near and parallel with the leaf margin.

All C. flavipes larvae found in leaf mines were in either last or next to last larval instar, and there is good reason to believe that younger larvae have a different mode of life.

On January 28, 1942, some larvae which appear to be C. flavipes in antepenultimate larval instar were found in longitudinal excavations in the stems of P. Robbinsii which was living beneath the ice in Whitmore Lake, Washtenaw County, Michigan. These larvae had the wedge-shaped heads, minute antennae, markedly convex labial plates, and other structures characteristic of C. flavipes. Since I was unable to rear them, the tentative identifications of these specimens are based upon their great similarity to larger larvae of C. flavipes.

Besides providing evidence concerning the mode of hibernation of C. flavipes and the form and habitat of its younger larvae, the discovery mentioned above supplies indications that these young larvae may utilize a type of food which is quite unusual among mining insects. Each mine that was opened contained quantities of algae which were identified by Wm. Randolph Taylor as Nostoc, Anabaena, Tolypothrix, Oscillatoria, Schizothrix, and Rhopalodia. These algae appeared to be alive and in good condition. Since each mine opened to the exterior by at least one hole through the epidermis, it is possible that the larvae brought small pieces of living filaments into the mines, and that the algae were growing as rapidly as they were being eaten. Unfortunately, no recognizable material was found in the stomachs of freshly killed larvae.

Measurement of head capsules of 70 C. flavipes larvae, including the small larvae mentioned above, shows that they belong to 3 distinct size groups composed of 12, 17, and 41 individuals, respectively. The dimension used is the length along median line from posterior rim to tip of extended labrum. Heads in the smallest size group, all larvae collected in stems of P. Robbinsii in winter, were 0.22 - 0.24 mm.; average, 0.23 mm. Those in the next group, evidently the penultimate larval instar, were 0.33 - 0.38 mm.; average, 0.35 mm. Those of the largest size group, which is known to represent the last larval instar, were 0.50 - 0.60 mm.; average, 0.55 mm.

Transformations to last larval instar and to pupa occur in leaf mines, and exuviae of the last 2 larval instars are often recovered there. The pupa remains in the mine for a period of about 2.5 days, at the end of which it is mature and ready for the final molt. Then, by beating its body vigorously in a vertical plane, it breaks through the thin leaf epidermis and comes up to the surface of the water. Here the adult emerges, leaving the pupal exuviae floating on the water surface.

Cricotopus trifasciatus (Panzer)

Cricotopus trifasciatus was described (as Chironomus trifasciatus) in 1813. Immature stages were described by Johannsen (1905, 1937a), Willem (as "Cricotopus limnanthemi", 1910), Goetghebuer (as "C. limnanthemi", 1914), Gripekoven (as "C. limnanthemi" and "C. Willemi", 1914), Malloch (1915a), and Kettisch (1936-'37). Diagnostic characters of egg, larva and pupa stages are illustrated in these papers.

The biology of C. trifasciatus was first reported by Willem (1910), who found the larvae channeling in upper surfaces of floating leaves of Limnanthemum nymphoides at Gand in Belgium. Later, Gripekoven (1914) found the larvae feeding on leaves of Potamogeton natans and Polygonum amphibium at Eifel, Germany. Kettisch (1936-'37), who found the larvae feeding on the floating leaves of P. natans at Lunz, Austria, discussed the biology and metamorphosis in detail. Thienemann (1933) reported it from Eifel: Schalkenmehrener Maar, mining in P. natans. Johannsen (1937a) stated that the species has a wide distribution in Europe and North America and that the larvae ". . . perhaps normally, mine in the leaves of the pond lily". It is evident from the foregoing account that trifasciatus feeds on the leaves of several species of aquatic plants.

In contradiction to these observations, Miller (1941: Table 14) has included this species with those "living below the thermocline". Although he did not find the larvae in his dredgings of profundal bottom materials, he captured 159 emerging adults in tent traps set over deep water and less than a dozen in similar traps set over shallow water among floating vegetation (personal correspondence). It is possible that the pupae migrate out to deep water when they leave the plants just before emergence.

C. trifasciatus was encountered in Cheboygan, Livingston, Presque Isle and Washtenaw Counties, Michigan. Larvae were found, May through August, channeling in the coriaceous floating leaves of Potamogeton amplifolius, P. natans, and P. nodosus.

Larvae enter the leaves from either the upper or the lower side, subsisting on one epidermal layer and the mesophyll tissue, but usually leaving the other epidermis intact. In a few instances in which the larvae had attacked leaves from their upper surfaces, the leaves were skeletinized so that only the veins remained. Once the leaf channel is formed, the larva is protected on 3 sides by leaf tissue, and on the other side by its detritus-laden silk tube, within which it is effectively concealed.

The larva frequently extends the anterior end of its body out of its silken tube and eats away the leaf tissue in irregular patches near the sides of its channel. When feeding outside its channel the larva gnaws approximately as deep as in extending its channel, usually leaving the further epidermis intact. In some instances, however, the portion of a leaf near an old channel is completely skeletinized.

Pupation occurs in the larval channel, and the pupa remains there until it is almost ready for the final molt. Dorsoventral undulations of its body periodically renew the supply of oxygenated water in the channel. From 1.5 to 3 days after pupation, these movements become more vigorous, and the pupa frees itself, leaving the last larval exuviae in the channel. It swims into open water, where the adult emerges, leaving the pupa exuvia floating freely on the surface.

Mating and oviposition of *C. trifasciatus* were described by Kettisch (1936-'37). According to her, specimens of this species pass the winter as eggs attached to stems and stipules of *P. natans*.

I found (as reported by Kettisch, 1936-'37) that the speed of development of eggs, larvae and pupae tends to increase with rising temperatures.

Polypedilum (*Polypedilum*) *illinoense* (Malloch)

Polypedilum illinoense was described (as *Chironomus illinoensis*, Malloch, 1915a) from adults collected by sweeping vegetation along the bank of a creek at Carbondale, Illinois. Townes (1945) presented taxonomic, distributional, and seasonal notes, and placed it in the genus *Polypedilum*.

Apparently the immature stages of *P. illinoense* have not been described. The only published indication of their habitat seems to be that of Miller (1941: Table 14), who included them with "species living below the thermocline", on the basis of having collected emerging adults in tent traps set over deep water. Larvae of a closely related species, *P. braseniae* (Leathers) channel in the leaves of *Brasenia schreberi* and *Nymphaea odorata* (Leathers, 1922).

Larvae of *P. illinoense* were encountered, May through

October, in Cheboygan and Washtenaw Counties, Michigan, feeding on the floating leaves of Potamogeton natans.

The mature larva of P. illinoense is pale red or orange, about 5.5 - 6.5 mm. long. The larval antenna, labial plate, paralabial plate, and mandible are illustrated in Pl. II, Figs. 5-7. Facts that the large blade on basal segment of antenna exceeds the apex of distal antennal segment, and that median pair of teeth on the labial plate are almost or quite as long as second lateral pair help to distinguish it from larvae of closely related species.

The pupa is faintly pigmented throughout. One of its most reliable distinguishing characters is the form of the comb on posterolateral angle of eighth abdominal segment (Pl. II, Fig. 8).

In habits and biology these larvae are very similar to those of P. braseniae (Leathers, 1922) and Cricotopus trifasciatus, discussed above. All channel in floating leaves, feeding on one epidermis and the mesophyll tissue, either leaving the other epidermis intact or skeletonizing the leaf. This species often attacks the leaf on its lower surface. Sometimes they feed in their channels; often they gnaw away irregular patches of tissue adjacent to them.

Pupation occurs in silken tubes in the leaf channels, and the pupae remain there until several hours before their final molt. Then, by vigorous dorsoventral undulations of the body, they slip completely out of their last larval exuviae, out of their silk tubes, and into the open water, where they swim about near the surface for a few hours before the adult emerges.

Miller's recovery of teneral adults in tent traps set over deep water (1941) may indicate that pupae which develop in littoral weed beds of lakes normally swim out into the limnetic zone after leaving their leaf channels. It is difficult to conceive of any larva combining such totally unrelated habits as to live and feed sometimes on green, floating leaves and sometimes below the thermocline, as listed in Miller's Table 14, feeding on the limited materials available for food in the hypolimnion.

<u>Polypedilum</u> (<u>Polypedilum</u>) <u>ophioides</u> Townes

The description (Townes, 1945) of <u>Polypedilum</u> <u>ophioides</u> is based in part on specimens reared during this investigation. Nothing has been published concerning its immature stages and biology.

In this study, mature larvae of <u>P</u>. <u>ophioides</u> were encountered in late June and early July in the Sedge Pools, Douglas Lake, Michigan, where they were feeding on floating leaves of <u>P</u>. <u>natans</u>.

The mature larva is pale red, about 5.5 - 6.0 mm. long. Its antenna, labial plate, paralabial plate, and mandible (Pl. II, Figs. 1-3) furnish valuable characters for recognition. Larvae of this species can be distinguished from those of the closely related <u>P</u>. <u>illinoense</u> by the shorter median pair of teeth on labial plate, the shorter large blade on basal segment of antenna, and by other characters illustrated.

The young pupa is very faintly colored throughout. Later the thorax and appendages are stramineous, abdomen pastel green, and compound eyes of the future adult appear as conspicuous black spots.

Position in relation to the leaf and feeding habits of this species differ from those of other larvae included in my Group 2, which live in well defined channels in leaves, extending them as they feed. Larvae of _P_. _ophioides_ produce no distinct channels but feed by gnawing away the upper epidermis and mesophyll tissue in irregular patches. Some correlation may exist between the fact that these larvae lack the seclusion and protection afforded by such channels and the fact that they were found only in rolled lateral edges of young leaves, not exposed on flat leaf surfaces in the position of _P_. _illinoense_ and _C_. _trifasciatus_ larvae.

Pupation occurs in the leaf rolls, and exuviae of the last instar larva remain there. The mature pupa leaves this habitat about 2 days later, and swims out into open water, where emergence of the adult takes place.

Glyptotendipes (_Phytotendipes_) _lobiferus_ (Say)

Glyptotendipes _lobiferus_, which was described as "_Chironomus_ _lobiferus_", is a relatively well known species, the immature stages of which have been described by Johannsen

(1905: 233; 1937b: 37), Malloch (1915a: 430), Leathers (1922: 7-17), and Branch (1931: 154). Of the several papers dealing with its biology, Gripekoven (1914, as "*Chironomus gripekoveni* Kieffer"), Leathers (1922), Fellton (1940), and Lindeman (1941, 1942) are especially informative. Townes (1945: 136) elevated the subgenus *Glyptotendipes* to generic rank, cited literature dealing with this species (1945: 142-44), and presented notes on identification and distribution.

I found *G. lobiferus* in Third Sister Lake and Whitmore Lake, Washtenaw and Livingston Counties, Michigan. Some larvae were taken from burrows in stems of *P. amplifolius*, and *P. gramineus*; others were found in silken tubes in rolled or folded leaves of these species and of *P. Robbinsii*.

Some doubt may exist concerning the identity of my specimens. Fourth lateral labial teeth of these larvae are considerably smaller than those illustrated for *lobiferus* by Johannsen (1937b, Fig. 119). Johannsen (Fig. 118) shows 8 spines in the comb at posterolateral corner of eighth abdominal segment of pupa, but on my specimens these combs are composed of only 3-6 spines. According to Johannsen (1937b: 37), the mace-like processes at bases of pupal abdominal tergites 2-6 have lengths of 0.18, 0.21, 0.25, 0.29, and 0.53 mm., respectively. In 12 pupae collected in Third Sister Lake these relative lengths averaged 18: 20: 23: 27: 40. The mace-like process on abdominal segment 6, the width to length ratio of which averaged 9: 18, is considerably shorter than the one illustrated by Johannsen (Fig. 131), in which this ratio is 9: 24. Although Townes wrote (personal correspondence) that my adult specimens "are atypical in being smaller and darker than usual and in having the scar on the sixth tergite much shorter than usual", he stated that these characters are subject to some variation and identified the specimens as G. lobiferus.

The remarkable feeding method employed by larvae of Group 3, that of capturing plankton in silken nets spun across the ends of their tubes, is mentioned above. The conical net is spun within and anchored to the silken lining of the burrow near one end, with its apex directed distally and its open end nearer the larva. The spinning motion consists of rapid extensions and retractions of the larva's anterior end as it slowly rotates, ostensibly to attach strands of the open end at points all around the circumference of the silk tube. After counting these extensions and retractions, Leathers (1922) concluded that the net is composed of 42 - 44 longitudinal ribbons or sheets. He discussed silk production and the mechanism of spinning in considerable detail.

The larva turns about after spinning its net, and makes rhythmic dorsoventral undulations of the body, like swimming movements of a leech, which progress backward from the head. Since the body is anchored by posterior prolegs to silken lining of the burrow and cannot move forward, these undulations force a current backward over the body and gills and into the open end of the net immediately behind.

After continuing these movements for a few minutes, the larva quickly reverses its position in the tube by bringing its head back along the ventral side of its body. Then it rotates the anterior end rapidly from side to side, cutting or tearing the delicate strands at the open end of the net near their attachment to heavier strands of the permanent silk tube. Continued rotation closes and twists up the net, and the larva, with thoracic prolegs aiding the mouth parts, stuffs net and contents into its mouth.

A short rest period often intervenes between eating the old net and spinning the new one, and the larva sometimes makes a vigorous current-producing motion of short duration during this interval. The purpose of this motion was unknown until I noticed that defecation occurs only during this time, and fecal pellets are forcibly ejected from the tube by this current. Since these pellets are thus carried some distance away from the tube, they are rarely brought in again by food currents, although these enter via the opening through which the pellets are expelled.

Defecation is similarly integrated into the sequence of feeding activities of all other species of this group herein discussed, and this is probably true of all net-spinning plankton eaters. If defecation were indiscriminate, most of the fecal pellets would be caught in food nets.

Since these larvae normally defecate only during the relatively short period that their bodies are reversed from their usual positions in the tube, the statement of Willem (1908: 698) concerning "Chironomus sparganii Kieffer" seems highly questionable. He wrote, "Généralment, la larve est orientée la tête vers le haut, disposition que favorise l'evacuation des excréments par l'orifice inférieur". Although Leathers' suggestion (1922) that "Chironomus sparganii" is identical with "C. lobiferus" may be wrong, the former evidently belongs with lobiferus in Glyptotendipes (Phytotendipes) and probably feeds in the same ways. Willem's description and illustration of the pupa of sparganii include characters found only among species of Glyptotendipes (Phytotendipes), but he figures the labial plate of the larva as quite distinct from that of G. lobiferus larvae. His description of larval activities seems to be a discussion of net spinning, turning, current producing, and other movements of a net-spinning plankton eater written without knowledge of the food net and the sequence of feeding activities associated with it. If this is true, usual orientation of larvae with heads upward indicates that feces are usually evacuated from the tubes via the upper openings, the fecal pellets being carried upward by the strong current produced by the larva just after defecation.

To determine the approximate time spent in each of the major food-getting activities, 4 larvae were timed with a stop watch. Intervals spent spinning nets were 12 - 42 seconds; average of 13 records, 25 seconds. Intervals during which currents were produced through each net were 2 - 9 minutes; average of 12 intervals, 3 minutes 51 seconds. After reversing their positions in the tubes, they loosened and swallowed the loaded nets in 7 - 40 seconds; average of 13 records, 19 seconds. One larva was slower than others in all 3 of these activities; another performed all 3 in the shortest time recorded for each. The times given by Leathers (1922) for these 3 activities are less than half a minute, 10 minutes, and 6 seconds, respectively.

The larvae found sheltered by Potamogeton tissues lived in silken tubes either in stem burrows or in young leaves which were still tightly rolled. Since water could circulate freely through each leaf roll, usually entering and leaving by means of 2 holes gnawed through all leaf layers approximately the same distance apart as holes opening into stem burrows, and since larvae removed from such leaf rolls spun their silken shelters within capillary glass tubes and there exhibited the characteristic sequence of feeding activities described above, it seems probable that these larvae, like those living in stem burrows, subsist primarily on plankton and detritus strained from the water by their silken nets. When leaves once occupied by these larvae mature and unroll, they present a characteristic appearance, with 2 or more parallel, transverse rows of small holes, all holes of a row being approximately the same distance apart.

G. lobiferus larvae live in many different situations and feed by several methods. Leathers (1922: 9) stated that the larva "is capable of living in a loose mud burrow and of collecting and eating its food directly from the surface of the accumulated debris about it, but this is not its most characteristic method of feeding when living in competition with other species". Larvae observed in capillary glass tubes augmented the food obtained from plankton nets by ingesting particulate matter collected both within and without their silken tubes. They frequently fed off inner surfaces of their silk tubes on materials which entered with currents they produced. Less often, a larva would extend the anterior end of its body to browse about and possibly forage on periphyton and other materials nearby.

Pupation occurs within the larval silk tube, and the pupa remains there until the adult is well formed within. Then it breaks out by vigorous dorsoventral undulations and swims about at the water surface for a short time preceding emergence. The observed pupal period was 1.5 - 2.5 days, the shorter records having been obtained when the temperature was higher.

As reported by Fellton (1940) reared and unmated females sometimes lay sterile eggs. Females which were reared and kept alone in test tubes sometimes deposited eggs during the night, about 72 hours after emergence. According to the descriptions of Branch (1931) and Fellton (1940), these masses were of normal shape, but none of the eggs hatched.

G. lobiferus larvae pass the winter in *Potamogeton* stem burrows and rolled leaves beneath the ice. When they are collected and brought into a warm laboratory they are quite active, and many feed by means of silken nets. The majority of specimens collected in January, February, March, and April were in last larval instar. These pupated and emerged 10 - 25 days after they were brought in.

Glyptotendipes (Glyptotendipes) dreisbachi Townes

Glyptotendipes dreisbachi was described by Townes (1945), who designated material reared in this investigation as part of the paratypic series. Apparently nothing further has been published concerning this species, and the immature stages have not been described.

Specimens of *G. dreisbachi* were encountered in Cheboygan, Livingston, and Washtenaw Counties, Michigan. Larvae were found throughout the year in burrows in the stems, petioles, and leaf midribs of *P. amplifolius*, *P. gramineus*, *P. praelongus*, *P. Richardsonii*, *P. Robbinsii*, and some aquatic plants of other genera.

The mature larva of *G. dreisbachi* is pale reddish orange, about 8-10 mm. long. Antenna, labial plate, paralabial plate, and mandible (Pl. I, Figs. 6-9) present characters of value in recognition. Although the convex labial plate appears in ventral view (Fig. 9) to have only 9 teeth, were of normal shape, but none of the eggs hatched.

G. lobiferus larvae pass the winter in *Potamogeton* stem burrows and rolled leaves beneath the ice. When they are collected and brought into a warm laboratory they are quite active, and many feed by means of silken nets. The majority of specimens collected in January, February, March, and April were in last larval instar. These pupated and emerged 10 - 25 days after they were brought in.

Glyptotendipes (Glyptotendipes) dreisbachi Townes

Glyptotendipes dreisbachi was described by Townes (1945), who designated material reared in this investigation as part of the paratypic series. Apparently nothing further has been published concerning this species, and the immature stages have not been described.

Specimens of *G. dreisbachi* were encountered in Cheboygan, Livingston, and Washtenaw Counties, Michigan. Larvae were found throughout the year in burrows in the stems, petioles, and leaf midribs of *P. amplifolius*, *P. gramineus*, *P. praelongus*, *P. Richardsonii*, *P. Robbinsii*, and some aquatic plants of other genera.

The mature larva of *G. dreisbachi* is pale reddish orange, about 8-10 mm. long. Antenna, labial plate, paralabial plate, and mandible (Pl. I, Figs. 6-9) present characters of value in recognition. Although the convex labial plate appears in ventral view (Fig. 9) to have only 9 teeth, it actually has 13. A ventrolateral view (Fig. 7) shows 2 small teeth near the lateral border which are not visible in ventral view. This labial plate differs from that of most Glyptotendipes larvae in having the median tooth considerably smaller than the first laterals.

The pupa is about 6-8 mm. long. Its respiratory organs bear many white thread-like filaments. The second abdominal tergite has a row of small hooks along the posterior margin. Abdominal tergites 3-6 each have a median basal, spiked, mace-like process (Pl. I, Figs. 10-13) typical of Glyptotendipes pupae. The comb at posterolateral angle of eighth abdominal segment (Pl. I, Fig. 14) contrasts with those of most species in the genus in being reduced to 2 (sometimes 3) spines.

Although specimens of G. dreisbachi were encountered more commonly than those of any other chironomid species herein discussed and many adults were reared, attempts to get mating in the laboratory were unsuccessful just as they were with other species of Chironomidae. Since fertile eggs were not obtained and the complete life cycle was not observed, my information concerning larval instars is based only upon existence of distince size groups of larval head capsules and upon observed transitions of larvae from one group to another. Measurement of 117 head capsules shows that they belong to 3 distinct size groups composed of 21, 37, and 59 specimens, respectively. Median lengths of these head capsules from posterior rim to tip of extended labrum are 0.20-0.24 mm., average 0.22 mm.; 0.31-0.40 mm., average 0.35 mm.; and 0.52-0.62 mm., average 0.58 mm. Since observed molts of smaller larvae always resulted in acquisition by the larva of a head capsule in the next larger size group and observed molts of the largest larvae always resulted in pupation, it seems quite evident that these 3 size groups correspond to the last 3 larval instars.

Larvae of G. dreisbachi, in all 3 instars encountered, exhibit the complex sequence of feeding activities characteristic of the net-spinning, plankton-eating species which are here placed in Group 3. It seems that these feeding habits are widespread among larvae of this genus. Those of 3 other Glyptotendipes species also are known to capture their food in silken nets (Leathers, 1922; Burtt, 1940), and those of still others (Willem, 1908; Gripekoven, 1914; Goetghebuer, 1919) live in similar burrows and probably feed in this manner.

Several larvae were timed with a stop watch to determine lengths of time spent spinning food nets, producing currents through them, and eating them. Nets were spun in 20-58 seconds; average of 28 records, 36 seconds. Intervals spent producing a current through each net ranged from one minute 48 seconds to 8 minutes 20 seconds; average of 23 observations, 3 minutes 8 seconds. Animal plankters temporarily trapped in a food net though not entangled in its strands were sometimes observed to escape, but the larva's speed in turning about in the burrow and consuming the loaded net reduces loss of this type to a minimum. Nets were eaten in 8-45 seconds; average of 26 records, 20 seconds.

Many interruptions occur in the sequence of feeding activities associated with use of plankton nets. When a large particle enters the burrow, the larva usually ceases its rhythmic undulations at once, then makes several vigorous and rapid beats in a posterior-to-anterior direction, producing a strong counter current which generally ejects the particle. Since the conical net immediately collapses and closes, relatively little of its contents is swept out by these currents. If the particle is not thus expelled, the chironomid crawls forward and nips viciously at it. This action usually proves quickly effective against intruding larvae and other living animals, but fecal pellets may still adhere to the silken lining of the tube. When the larva cannot dislodge such materials with its mandibles and eject them either by vigorous counter currents or by carrying them to the entrance in its mandibles, it leaves these substances in the burrow but isolates them from the open tube by spinning a patch of silken lining over them.

Counter currents are also produced by larvae which turn about to eat their food nets but find them very heavily loaded with carmine or ultramarine blue. A larva which has torn such a net loose and stuffed about half of it into the mouth often ejects it a considerable distance from the burrow by releasing it while producing a strong posterior-to-anterior current.

Other alterations of the normal pattern of feeding activities have no apparent causes. After producing a current through the net one chironomid turned about in the burrow, immediately spun a new net, then broke through it, ate the old net and its contents, spun another net, and resumed the normal sequence of activities. On another occasion a larva turned about, spun a new net within the old one, then turned back and produced a current through both nets. This larva left the outer net the next 2 times it turned about to eat and replace the inner one, but ate both nets the third time it turned toward them.

A larva sometimes eats the net, neglects to spin a new one, then turns about and produces a current through the burrow. When the larva turns back again it usually eats a bit of debris which adheres to the silk tube approximately where the net would normally be, and, again neglecting to spin a net, often turns and repeatedly produces currents through the burrow with no special provision for straining out the plankton. While some debris adheres to the silk tube, this is far less efficient than a plankton net for retaining food particles. After turning about a few times without spinning any net a larva often spins one in the end of the tube opposite from that in which nets had been placed before. Subsequent activities of the larva are all reversed in direction from previous ones, and food currents enter and excrement is ejected through the opening opposite that previously used.

By introducing suspensions of materials having different colors, the particles of which were caught in food nets and eaten, information on the speed of progress of particulate material through the alimentary tract was obtained. Two drops of a carmine suspension were released near the glass capillary tube in which a larva was producing a current through the net. The larva ate the net which was coated with these particles, and the next 2 nets which were left uncolored. The fourth net was given a coating of ultramarine blue, after which 2 more nets were left uncolored before carmine was released to color the seventh. As long as 2 nets were left uncolored between each release of stain, undissolved particles of stains mixed together very little in the intestine and most fecal pellets contained only one color.

Five larvae of G. dreisbachi living in glass tubes so close together that all were visible in the field of a dissecting microscope were fed alternately on carmine and ultramarine blue and watched for 3.5 hours. Undissolved particles of these stains passed through the alimentary tracts of 4 larvae in 35-124 minutes; average of 34 records, 69 minutes. Although the fifth larva seemed to go through the motions of spinning several times, most particles of stain passed completely through the tube, and it was evident that this larva spun no net during the period of observation. Since this specimen fed at frequent intervals on particles of debris and stain adhering to the silk tube, it was practically impossible to keep account of when certain particles were eaten and to recognize them again in fecal pellets. During these observations I noticed that these larvae defecate, as those of G. lobiferus, only after eating the old net, before spinning the new one. They defecated at intervals of 7-19 minutes; average of 23 records, 12 minutes.

Marked differences in the activities of these larvae were apparent. One consistently ate nets and spun new ones faster and nearly always produced swifter currents for shorter periods of time than the average of the other 3. Two of the 4 larvae which spun nets continued to place them in the same ends of their tubes throughout the period of observation. One larva changed the position of the net and reversed the direction of its activities once; the other, twice.

A few larvae were observed through a dissecting microscope while enlarging their stem burrows. A specimen which had extended one end of its burrow about 5 mm. beyond the opening was evidently trying to make a new hole there. The mouthparts were clearly visible through the thin but yet unbroken epidermis. Labrum and mandibles all worked against the labium, which was moved relatively little. When observations were resumed after a short interruption a new opening was discovered where the mouthparts had been seen at work, and the old hole was sealed shut with silk. Suspended carmine flowed rapidly into the new opening and collected in a conical shape behind the larva. When the chironomid turned about it apparently found the net too heavily loaded with stain. It attempted to tear the net loose and to force it from the burrow by vigorous posterior-to-anterior undulations. Finally giving up these attempts, the larva moved its head to and fro across the net, apparently spinning a patch of silk over it, and left it there.

Larvae removed from their burrows and placed in a watch glass with some freshly cut pieces of stem excavated new burrows in 8-24 hours. These larvae always entered the stem via some cut edge, then made 1 or 2 holes through the epidermis from the inside.

Some larvae were killed soon after making new burrows, and their stomach contents were analyzed by means of the sulphuric acid-iodine test for cellulose, to determine whether they had ingested Potamogeton tissue. Stomach contents were mixed with 1 or 2 drops of concentrated sulphuric acid on a glass microscope slide, and a drop of potassium iodide solution saturated with iodine was stirred into the mixture. The dark blue color indicating the presence of cellulose appeared, and microscopic examination revealed that this color was produced in regular rows of rectangles which were easily recognized as fragments of spermatophyte tissue in which the natural pattern of cell walls remained intact. Stomach contents of larvae selected at random from old burrows showed little if any spermatophyte tissue when subjected to the same test.

Specimens of G. dreisbachi pass the winter as larvae, practically all of which are mature, in burrows in the stems of plants living beneath the ice. Apparently they remain more or less active throughout this season. All winter specimens which were observed, even those noticed before the collection had warmed up to laboratory temperature, were quite active. Specimens collected in winter and kept in aquaria at laboratory temperature pupated and usually began to emerge 11 days after they were collected.

My earliest record of pupae in nature is based upon 3 specimens included with many larvae collected at Third Sister Lake, Washtenaw County, on April 30, 1941. Emergence usually occurs in southern Michigan between May 15 and May 25, and most burrows in plants collected in late May and early June are empty.

Small larvae were taken in burrows in stems, petioles and leaf midribs of P. praelongus growing in Indian River, Cheboygan County on June 29, 1941. Since head capsules of the 11 specimens which were immediately killed and measured all belonged to the smallest size group (0.20-0.24 mm.) mentioned above, it seems that most or all specimens in this collection were in an early larval instar. These larvae grew slowly in laboratory aquaria. Although 5 specimens examined on July 10 had head capsules in the intermediate size group, 5 others still had heads in the smallest group. Ten more larvae were killed and measured on July 17, and their heads also were divided evenly between these 2 size groups. All heads from specimens killed in the laboratory on August 7 and from others collected at Indian River on August 9 were in the intermediate group (0.31-0.40 mm.). None had molted and attained the last larval instar when they were examined again on August 21.

Larvae collected in Washtenaw County in September and October had head capsules in the intermediate and the largest size groups. A specimen in penultimate larval instar was taken in Third Sister Lake on November 3, but nearly all specimens found that late in the season were in last larval instar. It would seem from the facts mentioned above that G. dreisbachi has only one brood per season in Michigan.

The pupal period lasts 2-4 days, and the pupae remain within larval stem burrows during most of this time. Emergence occurs during the night. Mature pupae which had left their stem burrows were often seen swimming at the surface of the water, but such observations were invariably made at night.

Polypedilum (Pentapedilum) sordens (Wulp)

Polypedilum sordens was described (as Tanytarsus sordens) from the Netherlands in 1873. It seems that very little has been published concerning its biology, and that the immature stages are unknown. Townes (1945: 61-62) placed the species in *Polypedilum*, cited literature dealing with it, and presented notes on its identification and distribution.

I found *P. sordens* in Third Sister Lake, Washtenaw County, and Whitmore Lake, Washtenaw and Livingston Counties, Michigan. Larvae were collected from burrows in stems of *P. amplifolius*, *P. gramineus*, *P. natans*, *P. Richardsonii*, and *P. Robbinsii*. A few were taken in rolled or folded leaves of all these plants except *P. natans*. Burtt (1940) reported that a closely related species, *Polypedilum* (*Pentapedilum*) *tritum* (Walker), is also a stem-burrower which feeds on plankton strained from the water by means of a silken net spun within the burrow.

Larvae and pupae of *P. sordens* are easily distinguished, even with low magnification, from those of the 2 *Glyptotendipes* species I found in similar stem burrows. Mature larvae of all 3 species are pale red-orange, those of *P. sordens* about 6.5-8.5 mm. long, while larvae of *Glyptotendipes* are larger. The head capsule of *P. sordens* is depressed and bears only one group of ocelli on each side. Heads of the *Glyptotendipes* species are globoid and have 2 distinctly separate ocelli groups on each side. Pupae of *P. sordens* are 5-6 mm. long. They lack the conspicuous macelike processes found on abdominal tergites of *Glyptotendipes* pupae.

Characters which will help to distinguish P. sordens larvae and pupae from those of closely related species are illustrated on Plate II, Figures 9-12. Larval antenna (Fig. 11) has the ring organ near base of first segment. Labial plate (Fig. 10) bears 16 teeth of fairly uniform length, with median pair somewhat heavier than others; paralabial plates are strikingly long and narrow. Comb at postero-lateral angle of eighth abdominal segment of pupa (Fig. 12) is composed of 4 heavy spines and many smaller ones.

Since I was not able to observe the whole life cycle of P. sordens, my information on larval instars is incomplete. Measurement of 81 larval head capsules shows that they belong to 3 distinct size groups composed of 13, 21, and 48 individuals, respectively. The dimension used is median length from posterior rim to tip of extended labrum. After shedding head capsule exuviae of the smallest size group, larvae had heads belonging to the intermediate one. Changes from intermediate to largest size and from largest larvae size to pupa were also observed. Evidently these 3 size groups correspond with the last 3 larval instars. Probably an unobserved instar precedes that represented by the smallest recorded size group. Heads in these 3 size groups are 0.18-0.20 mm., average 0.19 mm.; 0.31-0.36 mm., average 0.33 mm.; and 0.46-0.62 mm., average 0.54 mm.

Like other larvae of Group 3, those of P. sordens subsist partly on plankton and detritus strained from the water by their silken nets and partly on materials gathered outside or inside their tubes without using any net. Stomach analysis of specimens taken from burrows usually reveals a preponderance of plankton organisms; larvae living in tubes on leaves often contain more periphyton than plankton. The stomach of one collected on a leaf of P. Robbinsii at Whitmore Lake, February 22, 1942, contained at least 25 diatoms, a piece of filamentous alga, and 4 small fragments of spermatophyte tissue.

Various operations in the sequence of feeding activities were timed with a stop watch. Food nets were spun in 17-50 seconds; average of 16 observations, 33 seconds. The interval during which a current was produced through the net was one minute 20 seconds - 4 minutes 3 seconds; average of 17 records, 2 minutes 24 seconds. After turning about in their tubes, larvae ate nets and their contents in 8-18 seconds; average of 13 observations, 13 seconds.

Speed of passage of particulate material through the alimentary tract was determined in the manner described for G. dreisbachi, by alternately introducing different colored stains which were caught in food nets and eaten. Each stain-loaded net produced a colored mass, the progress of which could be watched through the partly transparent body of the larva. Since all particles of a given mass were eaten simultaneously and since these masses retained their identity with very little mixing of different colored particles within the intestine, the interval that each particle was retained could be determined quite accurately.

Particulate material passed through the alimentary tracts of 3 larvae in 33-77 minutes; average of 26 records, 57 minutes. It may be significant that the shortest intervals were always the first ones, when the intestines were relatively empty. As each alimentary tract filled due to bulk of the stains, speed of passage through it gradually decreased. Apparently these stains did not harm the chironomids seriously and permanently; all 3 specimens later pupated and emerged. During these observations, I noticed that the larvae defecated at intervals of 9-16 minutes; average of 18 records, about 11 minutes, or approximately every third time they turned and ate their nets.

It may be that larvae of _P_. _sordens_, particularly those of earlier instars, are less able than those of _G_. _lobiferus_ and _G_. _dreisbachi_ to penetrate tough epidermis of living plant stems. Burrowing larvae of the 2 smaller size groups mentioned above were almost always found in dead, partly decomposed stems, which they may have entered either by gnawing through softened epidermis, by penetrating the stem through breaks in the epidermis, or by occupying burrows vacated by _Glyptotendipes_ larvae.

Specimens removed from their burrows and left in a fingerbowl with freshly cut pieces of living _P_. _amplifolius_ stem entered the stem in several instances, but invariably did so through a cut end, then penetrated the epidermis from within. Once inside the stem it would seem that they could exert more pressure on the epidermis because they can push back against parenchyma as they drive the mouthparts forward. Leathers stated that *G. lobiferus* enter *Typha* stems only through cuts or breaks, and can penetrate the very tough epidermis of that plant only from within. However, burrows of both *G. lobiferus* and *G. dreisbachi*, opening through the epidermis at both ends, are commonly found in living *Potamogeton* stems. Evidently these larvae readily penetrate the living epidermis of *Potamogeton* from either side.

Like other Chironomidae herein discussed, *P. sordens* pupate within larval silk tubes and remain there until mature, then swim about near the water surface for a few hours preceding emergence. In those instances in which both pupation and emergence were witnessed, the pupal stage lasted 1.5-2.5 days.

Unmated females laid masses of sterile eggs about 3 days after emergence.

Larvae of *P. sordens* pass the winter on or within tissues of *Potamogeton* beneath the ice. Specimens representing the last 3 instars occur in January and February collections, but fewer larvae of the smaller instars are collected toward spring.

My record of a reared specimen which emerged on May 3 (Townes, 1945: 62) bears little or no relationship to the natural seasonal aspects of this species. Specimens collected in late winter or early spring as last instar larvae and kept in a warm laboratory pupated and emerged 8-24 days later. Although I have reared adults in March and April as well as early May, they usually do not appear in nature in Washtenaw County until late May or early June.

Tanytarsus (*Endochironomus*) *nigricans* (Johannsen)

Tanytarsus nigricans was described (as "*Chironomus nigricans*") by Johannsen (1905: 219), who included descriptions and illustrations of the larval and pupal stages. Immature stages have also been described by Malloch (1915a: 234) and Johannsen (1937b: 34). Notes on its biology were presented by Richardson (1921: 42; 1925: 381, 418), Bill (1932: 68), Townes (1938: 172), Miller (1941: 35, 45, 61, 63), and Lindeman (1942: 435-6). Townes (1945: 64-5) placed the species in *Tanytarsus*, cited literature concerning it, and presented notes on its identification and distribution.

I collected *T. nigricans* in Huron River and Third Sister Lake, Washtenaw County, and in Black River, Cheboygan County, Michigan. Larvae and pupae were found in folds or in rolled edges of floating and submerged leaves of *P. amplifolius*, *P. gramineus*, *P. illinoensis*, and *P. Richardsonii*.

To some extent at least, the larvae obtain food by use of a net as described above for larvae of Group 3. On one occasion, all 18 larvae in a rearing dish were feeding in this manner. Like larvae of *G. lobiferus* living in rolled edges of leaves, *T. nigricans* larvae usually gnaw holes through all leaf layers at the ends of their silk tubes. These holes allow free circulation of water through the tubes, and the larvae may obtain some nourishment by swallowing the leaf tissue which they remove. Leaves once occupied by these larvae have a characteristic appearance when they mature and unroll, bearing many small holes geometrically arranged in transverse rows. Most of the leaf injury of this type probably is caused by T. nigricans. Larvae on flat unrolled leaves often live within a roll of leaf epidermis which they presumably peel from the mesophyll layer beneath it.

Habits of these larvae differ in some ways from those of other species in Group 3. They seldom if ever occupy stem burrows. They obtain much of their food, including substantial quantities of Potamogeton leaf tissue, by foraging outside their tubes. Even while using food nets, T. nigricans larvae apparently eat some material besides that caught in the nets. They move the mouth parts almost continuously while producing currents through their tubes and seem to catch and devour a portion of their food directly.

Near the silken tubes of T. nigricans larvae, patches of leaf area which are white, devoid of chlorophyll, and sometimes completely skeletonized result from consumption of leaf tissue in these areas by the larvae. Application of the sulphuric acid-iodine test for cellulose (mentioned previously) to stomach contents and fecal pellets of larvae almost always resulted in production of the positive dark blue color. This color was often so well localized that it constituted a differentiating stain, revealing portions of undigested cell walls which were still arranged in normal patterns and clearly recognizable as spermatophyte leaf tissue.

Pupation occurs within the larval silk tube, and the pupa stays there until almost ready for the final molt. Then it leaves this refuge and swims about near the water surface for a short time preceding emergence.

Lindeman (1942: 436) suggested that _T_. _nigricans_ overwinters in the egg stage in Cedar Bog Lake, Minnesota. There is reason to believe, however, that larvae of this species pass the winter beneath the ice in Third Sister Lake. Larvae in last instar were abundant there during September, October, and November, 1941, and other mature larvae were collected there on March 30, 1942, about 2 weeks after the ice on the lake had melted.

Emergence occurred at Third Sister Lake on May 3, 1942. On that date adult _T_. _nigricans_ were flying near the lake shore, and others emerged in a pail of _P_. _amplifolius_ while enroute from the lake to the laboratory. Adults may be reared in the laboratory during seasons when no emergence occurs in nature. Many were reared in connection with unsuccessful attempts to get mating in the laboratory during December, 1941.

Hydrellia (Diptera: Ephydridae)

It appears that the genus Hydrellia has been reported from all zoogeographic regions except the Neotropical. Cresson (1932) published taxonomic notes on 32 species from such widely separated regions as Australia, Formosa, South Africa, Europe, and North America, and his subsequent descriptions include two species from Hawaii (Cresson, 1936). Becker (1926) discussed 35 European species and presented a bibliography of papers on the biology and immature stages of some of them. Cresson (1944) gave distributional notes and keys to 35 Nearctic species, and the taxonomy presented by him is followed in this paper.

All Hydrellia larvae of known habits are phytophagous. Those of most species mine in leaves and stems of aquatic plants, but others attack terrestrial plants, especially the grasses. Some larvae, such as those of H. griseola Fallen (De Ong, 1922, as H. scapularis Loew; Wilke, 1924; Körtung, 1931) and H. nasturtii Collin (Marchall, 1903, as H. ranunculi Haliday; Collin, 1928; Taylor, 1928; Vaysiere, 1933) mine in the leaves of grains and water cress and sometimes assume economic importance. Hendel (1926), Hering (1935-'37), and Hennig (1943) reviewed the knowledge concerning immature stages of European Hydrellia.

The larvae of 5 European species of Hydrellia are known to live on Potamogeton. Thienemann (1916) reported Hydrellia chrysostoma Meigen from P. lucens and H. nigripes Meigen from

P. crispus. Müller (1922) found *H. nigripes* mining in both *P. lucens* and *P. perfoliatus*. Brocher (1910) reared *H. modesta* Loew from an unspecified species of *Potamogeton*, and Thienemann (1916) found what was possibly the same species mining in the leaves of *P. natans*. Hering (1930) described *H. potamogeti* from material "aus Minen an Potamogeton erzogen", and (1935-'37) also reported *H. chrysostoma*, *H. nigripes*, and *H. fascitibia* v. Roser from *Potamogeton*. Wesenberg-Lund (1943) reported *H. modesta* from *P. natans*.

Very little has been published concerning immature stages of North American *Hydrellia*. Malloch (1915b) figured the puparium and posterior part of the larva of *H. griseola* var. *scapularis* Loew, and reported that the larva mines in *Panicum*. From a single specimen, Johannsen (1935) described the puparium of *H. griseola* var. *hypoleuca* Loew, but was unable either to distinguish it from that of variety *scapularis* or to name the food plant. Johannsen also described briefly a puparium believed to be that of *H. cruralis* Coquillet, and illustrated parts of the larva of *Hydrellia* sp. None of the scattered references to the occurrence of Nearctic *Hydrellia* larvae in *Potamogeton* (Moore, 1915; Frost, 1924; Cresson, 1934, 1944; Johannsen, 1935) specifically identifies both the fly and its food plant.

In the present investigation more than 800 specimens of *Hydrellia* were reared from larvae and pupae found in *Potamogeton*. These flies represent 6 species, of which *H. cruralis*

Coquillet, *H. pulla* Cresson, and *H. caliginosa* Cresson were known before this study was undertaken, and *H. bergi* Cresson, *H. ascita* Cresson, and *H. luctuosa* Cresson have been described since from specimens which I reared.

Eggs which were observed, those of *H. bergi*, *H. cruralis*, and *H. pulla*, are elongate, cylindrical, measuring approximately 0.5 x 0.15 mm. All have irregular longitudinal furrows in the chorion, and each possesses a bell-shaped projection bearing the micropyle near one end.

Mature *Hydrellia* larvae examined in this study, those of *H. ascita*, *H. bergi*, *H. cruralis*, *H. luctuosa*, and *H. pulla*, are similar in some respects. All are approximately cylindrical and tapered toward both ends. In the third (last larval) instar, they range from 2.5 x 0.5 mm. to 6.0 x 1.0 mm. All are metapneustic, the only spiracles being slit-like openings near the tips of two sharp, hollow spines at the posterior ends of their bodies. Larvae are usually found with these spines inserted into plant tissue. Presumably they obtain oxygen from the intercellular gas spaces of plants by this means. The sclerotized anal plate, bearing a median longitudinal anal slit, is on the ventral surface a short distance anterior to these spines. On the ventral surface, anterior to the anal plate, there are eight well defined and conspicuous spinulose areas used in locomotion (the "creeping welts" of authors). Anterior to them, 3 less prominent spinulose areas become progressively smaller and more diffuse toward the anterior end. The pharyngeal skeletons are relatively simple, and each bears a single mouth hook. This condition may not be constant for the genus, since Williams (1938) refers to the "pair of mouth hooks" of H. williamsi, and Wesenberg-Lund (1943) mentions the "Paar kleinen Mundhaken" of H. modesta. Anterior spiracles apparently are lacking. A pair of 3-jointed sensory projections (the "antennae" of various authors) are borne near the anterior end of the body. Below these, just anterior to the mouth hooks, there is a pair of single-jointed tubercles which may also have a sensory function. All larvae possess some spinules or setae in addition to those on the creeping welts, but their sizes, numbers, and distribution patterns differ in larvae of different species.

Puparia of all species reared are light brown, subcylindrical, shorter and thicker than the larvae. They are 2.4 - 4.5 mm. in length and 0.7-1.5 mm. in maximum breadth. Vestiges of the larval respiratory spines, anal plates, creeping welts, and setal patterns are evident, and each puparium contains a larval pharyngeal skeleton and mouth hook. Puparia of H. ascita, H. bergi, and H. caliginosa differ from the other 3 species in being narrower and more elongate, tapering slowly and gradually toward the posterior end, and having the respiratory spines terminal. Puparia of H. cruralis, H. pulla, and H. luctuosa are more compact and taper more abruptly to their posterior ends. Their respiratory spines are subterminal, and their anal plates are more or less concave posteriorly. Emerging Hydrellia open their puparia by pushing off an anterodorsal portion including the terga of approximately the 3 thoracic segments. No corresponding ventral portion is detached nor even loosened as in the case of emerging muscoid flies.

Newly emerged flies of these 5 species are hydrofuge, and they experience little difficulty in getting up through the surface film. They crawl up on some floating or emergent object and rest there for about 5 minutes, meanwhile brushing their bodies, especially their wrinkled wings, with their feet. Then the wings expand rapidly, reaching full size in about 45 seconds. They remain soft and useless for a few minutes after expanding. Adult flies alight and walk on the surface film without getting wet.

All Hydrellia mines encountered in this study are linear, and they contain no conspicuous frass. Those in leaf blades are usually near the midrib and parallel **with** it.

Key to Larvae and Puparia of Hydrellia Which Infest Potamogeton in Michigan

A. Larva relatively broad, maximum breadth about 16 per cent of length, shape similar to that of H. cruralis (Pl. III, Fig. 8); puparium (Pl. V, Figs. 1, 4, 5) fairly compact, with respiratory spines subterminal; dorsal setae at least in intersegmental grooves of all abdominal segments, apparent with low power of compound microscope; pharyngeal skeleton (Pl. IV, Figs. 1, 4, 5) with relatively long, narrow shank, dimension between its ventral projections at least 2.3 times the breadth midway between projections.

B. Small species, mature larvae less than 4.8 mm. long; puparium (Pl. V, Fig. 1) 3.5 x 1.1 mm. or smaller, tapered more gradually posteriorly than anteriorly, posterior margin of anal plate only slightly concave; dorsal setae abundant, generally dispersed, in irregular transverse rows; pharyngeal skeleton (Pl. IV, Fig. 1) pigmented throughout, with dorsal rods opaque black..............................H. luctuosa.

BB. Larger species, mature larva more than 4.8 mm. long; puparium (Pl. V, Figs. 4, 5) 3.5 x 1.0 mm. or larger, ovoid, abruptly tapered at both ends, posterior margin of anal plate strongly concave; dorsal setae fewer, concentrated in or near intersegmental grooves; pharyngeal skeleton (Pl. IV, Figs. 4, 5) less extensively pigmented, with dorsal rods colorless.....C

C. Mature larva (Pl. III, Fig. 8) leaf green; puparium (Pl. V, Fig. 4) constricted between segments laterally, giving it scalloped appearance; dorsal abdominal setae confined to narrow bands in intersegmental grooves; pharyngeal skeleton (Pl. IV, Fig. 4) usually colored as shown, rarely almost as light as that of H. pulla..H. cruralis.

CC. Mature larva grayish cream color; puparium (Pl. V, Fig. 5) without scalloped appearance, little if any constriction between segments; bands of dorsal abdominal setae wider, composed of distinct transverse rows; pharyngeal skeleton (Pl. IV, Fig. 5) always very sparsely pigmented..... ....H. pulla

AA. Larva relatively narrow, maximum breadth about 9 per cent of length, shape similar to that of H. bergi (Pl. III, Fig. 1); puparium (Pl. V, Figs. 2, 3) elongate, tapered gradually to posterior end, with respiratory spines terminal; most abdominal segments usually without dorsal setae; pharyngeal skeleton (Pl. IV, Figs. 2, 3, 6) with relatively short, stout shank, dimension between its ventral projections less than 2.3 times the breadth midway between projections...................................D

D. Larger species, puparium (Pl. V, Fig. 3) usually more than 3.7 mm. long; pharyngeal skeleton (Pl. IV, Fig. 3) with distinct hump above cheliform spot, opaque black pigment continuous from cheliform spot posteriorly to dorsoventral fork, ventral rods longer than portion anterior to dorsoventral fork; mouth hook stout. Miner in stems and petioles but not in leaf blades...................................H. bergi

DD. Smaller species, puparium (Pl. V, Fig. 2) usually less than 3.7 mm. long; pharyngeal skeleton (Pl. IV, Figs.

2, 6) without hump above cheliform spot, usually lacking opaque black pigment behind cheliform spot, ventral rods no longer (usually considerably shorter) than portion anterior to dorsoventral fork; mouth hook narrower. Miners in leaf blades only..............E

E. Dorsal setae lacking on all abdominal segments except first 2 and last; pharyngeal skeleton (Pl. IV, Fig. 2) with only diffuse pigment behind cheliform spot...................H. ascita

EE. Dorsal setae at least in intersegmental grooves of all abdominal segments; pharyngeal skeleton (Pl. IV, Fig. 6) with opaque black pigment continuous from cheliform spot posteriorly to dorsoventral fork. Rare on Potamogeton in Michigan. Larva not observed...............H. caliginosa

Hydrellia cruralis Coquillet

The literature contains 5 records of Hydrellia larvae mining in Potamogeton which probably refer to H. cruralis. Moore (1915), working near Ithaca, New York, found the leaves of P. amplifolius mined by Hydrellia larvae. Frost (1924) cited Moore's work and stated, "Hydrellia n. sp. . . . mines in the leaves of P. amplifolius". Johannsen (1935) identified a single specimen presumably reared by Moore as Hydrellia cruralis. Johannsen suggested, however, that this specimen might have been incorrectly labelled, and this record remains in doubt. Cresson (1934) reported specimens of this species reared from Potamogeton sp. by Miss Gertrude Auxier, at Marlington, West Virginia. Cresson (1944) wrote of H. cruralis, "A relatively common northern species and which has been bred from pondweed in Michigan." While not so stated, it seems probable that this last record is based on material reared in this investigation and sent to Cresson for identification on September 1, 1940, March 18, 1941, and October 27, 1941.

During this study, H. cruralis was encountered more frequently than any other species of Hydrellia. Immature specimens were collected in Cheboygan, Emmet, Presque Isle, and Washtenaw Counties, Michigan. Larvae and pupae were found in the leaves of Potamogeton alpinus, P. amplifolius, P. epihydrus, P. foliosus, P. gramineus, P. illinoensis, P. natans, P. nodosus, P. praelongus, P. Richardsonii, and P. zosteriformis. In order of decreasing extent of infestation, the species which harbored the greatest numbers of H. cruralis were P. amplifolius, P. Richardsonii, P. praelongus, P. gramineus, P. illinoensis, and P. nodosus.

Egg: (Pl. III, Fig. 5) Elongate, cylindrical, rounded at both ends; 0.5 - 0.6 x 0.12 - 0.17 mm.; central yolk mass opaque, cream color or faintly yellow; peripheral translucent zone wider at both ends; chorion delicately sculptured with irregular longitudinal furrows; micropyle terminal with lips flared, bell-shaped.

First Instar Larva (living): Cylindrical and tapering abruptly at both ends; length 0.8 - 1.5 mm.; color uniform throughout; at first cream color, later becoming greenish; creeping welts relatively large, conspicuous; pharyngeal skeleton 0.15 - 0.19 mm. long, lightly pigmented throughout, darkly pigmented in same areas as those of third instar pharyngeal skeleton.

Second Instar Larva (living): Shape unchanged except creeping welts relatively less conspicuous; length 1.5 - 3.0 mm.; color, leaf green; pharyngeal skeleton 0.27 - 0.29 mm. long, color pattern same as that of third instar pharyngeal skeleton.

Third Instar Larva (living): (Pl. III, Fig. 8) Length 3.0 - 5.5 or 6.0 mm.; breadth 0.7 - 1.0 mm. ; color usually green, but variable, tends to match color of leaf; ventral setal pattern similar to that of puparium (Pl. V, Fig. 4); dorsal setae in transverse rows confined to intersegmental furrows; setae dispersed laterally; each creeping welt fusiform, bearing 8-13 irregular transverse rows of spinules (Pl. III, Fig. 6); anal plate ovoid; anal and postanal regions armed with spinules which become heavier and often double posteriorly; terminal respiratory spines set on small papillae; anterior end (Pl. III, Fig. 7) supplied with paired, 3-segmented inferior tubercles, single median mouth hook, and post-oral tuft of fine hairs; pharyngeal skeleton (Pl. IV, Fig. 4) 0.40 - 0.62 mm. long, usually dark anteriorly as shown, but rarely almost as light as that of H. pulla (Pl. IV, Fig. 5), slight hump above cheliform black spot.

Puparium: (Pl. V, Fig. 4) 3.5 - 4.5 x 1.1 - 1.5 mm.; transparent golden brown; ovoid, subcylindrical, with laterally distinct intersegmental furrows giving puparium scalloped appearance; setal pattern as shown and as discussed for larva; anal plate crescent shaped with rounded ends; respiratory spines subterminal; pharyngeal skeleton (Pl. IV, Fig. 4) as described for third instar larva; pupa within greenish, becoming olivaceous gray shortly before emergence.

Eggs are deposited on or in the emergent portions of food plants. They are usually laid side by side in compact masses one layer deep, with all eggs of a mass oriented in the same direction. Apparently the female attempts to lay eggs in a concealed or protected situation. In breeding cages, most of the eggs were inserted into exposed intercellular air spaces in broken midribs of leaves and into torn openings in old mines. Others were found on strips of paper hanging over the water, on floating leaves, and, in a few instances, floating unattached. The oviposition which was observed was always at the surface of the water. In nature, egg masses were found in folds of leaves, in curled stipules, and on stems.

Within limits, speed of development increases with rising temperature. After one to five days of embryonation the completely formed larva is visible through the egg shell. The active pharyngeal skeleton is particularly apparent.

From 2 to 7 days after the egg is laid, the larva cuts a slit in one end of the egg shell and emerges. It bores directly into the leaf and begins to mine in the mesophyll between the upper and lower epidermis. In 2 or 3 days the larva has grown to a length of 1.5 mm., and the first molt occurs. The exuviae, including the pharyngeal skeleton, are left in the mine.

Mines of *H. cruralis* in thin, submerged leaves of *Potamogeton* are equally visible from either side, and are most readily seen by examining the leaves with transmitted light. Mines in coriaceous floating leaves are just within the lower epidermis and are visible only from the lower side by use of reflected light.

The larva selects fresh food. If the leaf in which it is mining dies, it cuts through the epidermis, migrates to a greener leaf, and starts a new mine. Six second instar larvae which were mining in a leaf that had begun to turn brown entered a fresh, green leaf within 12 hours after it had been supplied.

That selection of newer, greener leaves also occurs in nature is evident from repeated observations on *Potamogeton Richardsonii*. A lower leaf often has a mine which contains the cast exoskeleton of the first instar larva. The mine in the leaf immediately above it contains exuviae of the second instar larva. The next leaf is mined but empty, and the fourth leaf contains the mature larva or the puparium.

Under laboratory conditions, the duration of the second instar is about 5 - 8 days; that of the third instar, approximately 10 - 18 days. Then the mature larva usually takes a position where the mine is in contact with the midrib. The respiratory spines are inserted into the midrib, the body is contracted to assume the proportions of the puparium, and the body wall sclerotizes in this position. Two days later, the greenish pupa is visible within the transparent brown puparium. Ten - 14 days usually elapse between cessation of larval movement and emergence of the adult. During unusually hot weather, a group of adults once emerged only 8 days after cessation of larval movement.

Emergence and early activities of the adult, observed during daylight hours ranging from 10:00 A.M. to 5:00 P.M., are as described for all 5 species in the introductory section. Young flies, prodded to test their avoiding reactions 15 minutes after emergence, escaped only by walking and by darting an inch or two. Since they could be forced to fall, it is evident that they could not fly effectively. This would seem to indicate that flies emerging in rough water must suffer considerable hazard of drowning. Twenty-five minutes after emergence they flew readily and well.

The adult feeds on Potamogeton leaves, chewing small holes in them. Scotland (1934) and Williams (1938) reported similar habits in closely related species of Ephydridae. However the fly is not exclusively phytophagous. They often dismember and devour the bodies of other flies which die in the rearing bottle.

The reared flies mated within 24 hours after emergence, and laid eggs within 24 hours after mating. The life cycle was completed several times in the laboratory. It had a duration of 32 - 53 days; average of 24 records, 41 days.

In nature, the first adults of the season seem to appear at about the 24th of May in Washtenaw County, Michigan and can be found continuously until approximately the middle of October. Thus, at least 3 generations per season are possible. However, no distinct emergence heights were observed. It seems that all stages of the life cycle may be found on any date during late spring, summer, and early autumn. A single plant from a summer collection may harbor eggs, larvae of all three instars, pupae, and empty puparia.

Larvae of H. cruralis were collected throughout the winter in green leaves of P. amplifolius, the winter form of which was described by Moore (1915) as follows: "In P. amplifolius the tip ends of the branches function as propagative structures . . . . These structures appear in the autumn developing only at the tips of branches. The internodes are short and thick and densely packed with starch. At the end there are a few partially unfolded leaves which continue to grow slowly or, at least, remain green all winter. These rapidly expand when the roots develop in the spring and the entire structure forms an effective and rapid means of propagation."

When other leaves of the food plant turn brown and begin to disintegrate in autumn some larvae migrate to these propagative structures and enter the new leaves. They become less and less active as the water cools, finally reaching a state of quiescence. Specimens representing all 3 larval instars were found thus hibernating in plants beneath the ice, but no other stages of the life cycle were collected during the winter. Specimens collected as larvae in midwinter and placed in an aquarium at laboratory temperature soon became active, resumed feeding, pupated, emerged, mated, and laid fertile eggs. In one instance, the larvae which hatched from such winter eggs were also reared to maturity.

Müller (1922), failing to find the young larvae of H. flavicornis, speculated on where and how young Hydrellia larvae live. Williams (1938) watched the development of a single laboratory-hatched specimen of H. williamsi, but to date very little is known concerning the biology of young Hydrellia larvae of any species.

Observations on laboratory-hatched and wild specimens of H. cruralis indicate that failure to find first and second instar larvae of Hydrellia in nature is probably due chiefly to the great difficulty involved in seeing them. They match the color and optical density of leaves so perfectly that it is very difficult to find them even by carefully examining each leaf with a dissecting microscope. After the larva has been located by detecting movements of its minute pharyngeal skeleton and mouth hook it usually takes a few more seconds of careful scrutiny to distinguish the outline of its body.

The problem is further complicated in fresh winter collections because the torpid larvae make no movements which might disclose their presence. Within 24 hours after winter collections have been brought into the laboratory some larvae can usually be found actively mining in the rolled lower regions of partially opened leaves. Careful examination usually results in finding only a small fraction of the larvae present, however, and it seems advisable to keep all winter collections in aquaria at room temperature for 3 weeks before making a final check for the presence of *Hydrellia*.

Some *P. amplifolius*, collected under ice 12 inches thick at Third Sister Lake, January 9, 1941, was carefully examined after it had stood in a warm laboratory for 24 hours. Four actively mining larvae of *H. cruralis*, 3 in third and 1 in second instar, were found and put into a rearing bottle. The examined plant material was placed in an aquarium which was freshly made up with tap water and kept at laboratory temperature. On January 29, 20 days after the collection was made, a reexamination of the growing plants revealed 11 third instar larvae and 23 puparia of H. cruralis.

Hymenopterous parasites of 5 species were reared from puparia of H. cruralis. The braconids Ademon niger (Ashmead) and Chorebidea sp. 1, and the diapriid Trichopria columbiana (Ashmead) were encountered occasionally to commonly during their respective seasons. Single specimens representing Chorebidella sp. and an unidentified genus of the family Pteromalidae were also obtained.

Hydrellia pulla Cresson

Johannsen (1935) stated that Moore had reared a specimen of Hydrellia pulla from Potamogeton near Ithaca, New York. The only other published note concerning the biology of this species appears to be that of Cresson (1944), who wrote, "A scarce northern species, associated with pondweed". This record was probably based partly on Johannsen's published statement, and partly on material reared in this investigation and sent to Cresson for identification on September 1, 1940, March 18, 1941, and October 27, 1941.

Specimens of this species were collected in Cheboygan and Washtenaw Counties, Michigan. Larvae mine in the leaves of Potamogeton amplifolius, P. gramineus, and P. Richardsonii.

Egg: (Pl. I, Fig. 4) General shape like that of H. cruralis except for greater thickness, and end opposite micropyle is pointed; 0.57-0.65 x 0.18-0.22 mm.; central yolk mass opaque, grayish brown color of variable intensity; surrounded by narrow translucent zone; longitudinal sculpturing of chorion more vague and obscure than on H. cruralis eggs; terminal micropyle projection longer than that of H. cruralis.

First Instar Larva (living): Cylindrical and tapering abruptly at ends, with creeping welts conspicuous, protruding; length 1.0-1.8 mm.; color grayish cream throughout; apparently 12-segmented; pharyngeal skeleton 0.18-0.22 mm. long, darkly pigmented in same areas as those of third instar pharyngeal skeleton, with diffuse pigment throughout all other regions.

Second Instar Larva (living): Color and shape unchanged except creeping welts less conspicuous; length 1.8-3.5 mm.; pharyngeal skeleton 0.28-0.35 mm. long, with color pattern same as that of third instar larva (Pl. IV, Fig. 5).

Third Instar Larva (living): Color and shape unchanged, the latter like that of H. cruralis (Pl. III, Fig. 8); length 3.5-6.6 mm.; breadth 0.8-1.1 mm.; ventral setal pattern similar to that of puparium (Pl. V, Fig. 5); transverse rows of dorsal setae tend to concentrate toward intersegmental furrows, but more dispersed than on H. cruralis; setal rows curved and running in various directions laterally; posterior end similar to that of H. cruralis, (Pl. III, Fig. 6) with terminal respiratory spines short, anal plate ovoid, but no heavy, double spinules on postanal region; anterior end shaped like that of H. cruralis, with 3-segmented antennae, one-segmented inferior tubercles, single median mouth hook and postoral tuft of fine hairs; pharyngeal skeleton and mouth hook (Pl. IV, Fig. 5) light colored, and lacking hump above cheliform black spot, pharyngeal sclerite 0.50-0.65 mm. long.

Puparium: (Pl. V, Fig. 5) 3.5-4.5 x 1.0-1.5 mm.; transparent light brown; ovoid, subcylindrical, lacking distinct intersegmental furrows and scalloped appearance of <u>H</u>. <u>cruralis</u>; setal pattern as shown and as discussed for larva; anal plate slightly concave posteriorly with bluntly rounded ends, and not so crescent shaped as on <u>H</u>. <u>cruralis</u>; respiratory spines subterminal; pharyngeal skeleton (Pl. IV, Fig. 5) as described for third instar larva; pupa light colored, appearing yellowish brown through brown puparium, then turning darker and becoming almost black shortly before emergence.

Eggs were found in nature during June, July, and August on floating or emergent portions of food plants. They are usually laid, like those of <u>H</u>. <u>cruralis</u>, side by side in compact masses one layer deep, often in such concealed situations as folds of leaves, ends of old mines, and in sheathing stipules. In the laboratory, they were laid on emergent parts of the food plant, free on the water surface, and stuck to the side of the rearing bottle.

Embryonation is accelerated by increased temperature. From 2 to 4 days after oviposition, the active larva becomes visible through the egg membranes. The eggs hatch in 4 to 6 days.

The newly hatched larva enters a leaf and begins to mine at once. In 4 to 8 days it has grown to a length of about 2.2 mm., and the first molt occurs. Six to 10 days later, the larva molts again. The exuviae, including pharyngeal skeletons, of the first two instars are left in the mine.

Remarkable concentrations of Hydrellia sometimes result from the larva's tendency to migrate into younger, greener leaves. Three young leaves of P. amplifolius collected May 3, 1942, at Third Sister Lake, Washtenaw County, Michigan, contained 8, 10, and 12 puparia, respectively. Each plant was composed of several tattered, brown leaves formed the previous autumn and one or two new green ones. Mines in the old leaves were empty, the larvae having migrated into the new leaves.

Under laboratory conditions, the duration of third instar is approximately 8-15 days. Then the larva usually extends the mine into contact with the midrib and parallel with it, inserts the respiratory spines into the midrib, and contracts the body to assume the size and shape of the puparium. The body wall sclerotizes, and 2 days later the light colored pupa is visible within the puparium. Ten to 15 days usually elapse between cessation of larval movement and emergence of the adult.

It may be that emergence, which was observed repeatedly through a dissecting microscope, is hastened by radiations from the microscope lamp. A remarkably high percentage of emergences were witnessed when compared with the percentage of time that puparia were under observation. In this process there are intervals of activity and of rest. The imago grips the wall of the puparium with all 6 tarsi and pushes forward until an anterodorsal portion of the puparium ("dorsocephalic cap" of authors) is detached and the fly crawls out.

Newly emerged adults are unable to fly until a few minutes after their wings have expanded. Young, flightless adults of *H. pulla* avoid the heat and intense light of the microscope lamp by crawling onto the shaded sides of available objects. Adult flies in the rearing bottle exhibited the activities described in the general section and for *H. cruralis*.

Laboratory reared *H. pulla* mated and laid eggs within 48 hours after emergence. Life cycles observed had a duration of 34-55 days; average of 7 records, 43 days.

Seasonal aspects of *H. pulla* are similar to those reported above for *H. cruralis*. Adults are found in Washtenaw County, Michigan, continuously from late May through early October. No emergence heights were observed. This species passes the winter as a torpid larva in the leaves of its food plants.

Apparently *H. pulla* is much less susceptible to parasitism than any other species of *Hydrellia* studied in this investigation. Although *H. pulla* was often observed closely associated with *H. cruralis*, the 2 braconid parasites *Chore-*

bidea and *Ademon*, so frequently reared from the latter, were never encountered in puparia of the former.[1] The only species of parasite reared from puparia of *H. pulla* was the diapriid *Trichopria columbiana* (Ashmead).[2]

Hydrellia luctuosa Cresson

Hydrellia luctuosa was described (Cresson, 1942) from specimens which I reared during this study. It appears that the only other published note on this species is that of Cresson (1944), who wrote, "A rare species from Michigan, reared from pondweed". It seems probable that this record was based solely upon the type series which was reared during the summer of 1941 and sent to Cresson during October of

---

1. Seven puparia of *H. pulla* and 5 puparia of *H. cruralis* were found in a single leaf of *P. amplifolius* collected in Third Sister Lake, Washtenaw County, Michigan, May 3, 1942. There was no case of parasitism among the 80 *H. pulla* puparia in this collection, but 12 of the 71 *H. cruralis* puparia harbored braconid parasites.

2. It is evident that *Hydrellia* may be used as food by fishes. The stomach of a bluegill (*Lepomis macrochira*) caught by R.C. Ball in Third Sister Lake, August 13, 1940, contained 7 puparia all of which I examined and identified as *H. pulla*. In another bluegill stomach, puparia of both *H. pulla* and *H. cruralis* were found.

that year.

Specimens of H. luctuosa were collected in several localities in Cheboygan County, Michigan. In the order of preference, the food plants of this species seem to be Potamogeton alpinus, P. zosteriformis, P. Richardsonii, P. amplifolius, and P. natans, infestation of P. amplifolius and P. natans being relatively uncommon.

Egg and first instar larva unknown.

Second Instar Larva (living): 2.0-3.2 mm. long; relatively stout; grayish cream color; pharyngeal skeleton similar to that of third instar larva (Pl. IV, Fig. 1) in shape and color, 0.26-0.31 mm. long.

Third Instar Larva (living): Shape and color unchanged, similar to those of H. pulla; about 4.2 x 0.6 mm.; ventral setal pattern as shown for puparium (Pl. V, Fig. 1); dorsal and lateral setae abundant, in irregular transverse rows, generally dispersed; pharyngeal skeleton (Pl. IV, Fig. 1) slender, heavily pigmented, 0.40-0.48 mm. long.

Puparium: (Pl. V, Fig. 1) Transparent brown; 2.7-3.6 x 0.7-1.1 mm.; taper toward posterior end more abrupt than that of H. bergi and H. ascita, not so abrupt as H. cruralis and H. pulla; respiratory spines subterminal; setal pattern as shown and described for larva; enclosed pharyngeal skeleton (Pl. IV, Fig. 1) as described for larva.

The eggs were not found in nature, and attempts to secure them from reared flies were unsuccessful.

The larvae mine in the mesophyll layer between the upper and lower epidermis of thin submerged leaves. When, rarely, they mine in floating leaves they work just within the lower epidermis and are visible only from the under side.

Little is known about the seasonal behavior of H. luctuosa. Puparia appeared in nature as early as July 3 in 1941, and both larvae and puparia could be found throughout July and August.

H. luctuosa is parasitised by the diapriid Trichopria columbiana, and by the braconid Dacnusa sp. 2.

Hydrellia bergi Cresson

Hydrellia bergi was described (Cresson, 1941) from specimens reared in this investigation. The only other published reference to this species seems to be that of Cresson (1944), who wrote, "Not a common species, and known only from Michigan, where it has been bred from pondweed". This record of Cresson is probably based upon the type series which was sent to him on September 1, 1940, and upon another lot of specimens sent for identification on October 27, 1941.

Specimens of H. bergi were collected in Cheboygan, Presque Isle, and Washtenaw Counties, Michigan. Larvae and pupae were extracted from longitudinal mines just beneath the epidermis of stems, quill-like submerged leaves, and petioles of Potamogeton natans, but were not found in leaf blades. A few larvae were also collected from mines in stems of P. Richardsonii and P. zosteriformis.

Egg: (Pl. III, Fig. 3) Elongate, cylindrical, with ends more nearly truncate than those of H. cruralis and H. pulla; 0.6-0.7 x 0.17-0.20 mm.; longitudinal sculpturing of chorion very evident on exposed side of egg, but obscure on attached side; micropyle inconspicuous, subterminal, on exposed side.

First Instar Larva: (known from exuviae only) Pharyngeal skeleton and mouth hook shaped and colored like that of third instar larva (Pl. IV, Fig. 3); pharyngeal sclerite 0.16-0.18 mm. long.

Second Instar Larva (living): Shape similar to third instar larva (Pl. III, Fig. 1), relatively narrower than that of H. cruralis; length 1.5-3.0 mm.; color greenish yellow; pharyngeal skeleton similar to that of third instar larva except for small size; pharyngeal sclerite 0.25-0.27 mm. long.

Third Instar Larva (living): (Pl. III, Fig. 1) Relatively narrower and more elongate than that of H. cruralis, H. pulla, and H. luctuosa; 5.2 x 0.58 mm.; color predominantly greenish yellow, with intestinal contents often showing through as a deep brown, surrounded by yellow orange area; ventral setal pattern similar to that of puparium (Pl. V, Fig. 3); setae generally distributed over dorsal and lateral surfaces of pseudocephalic segment (Pl. III, Fig. 2); posteriorly, dorsal and lateral setae occur only in bands in intersegmental furrows; the bands gradually become narrower posteriorly, the last one which completely girdles larva being in furrow between first and second abdominal segments; on following segments setae almost solely ventral, except on last, which is completely girdled by somewhat larger spinules; anterior end provided with structures illustrated and discussed under H. cruralis; pharyngeal skeleton and mouth hook (Pl. IV, Fig. 3) relatively stout, with definite hump above cheliform spot, the posterior boundary of which is obscured by concentration of black pigment; pharyngeal sclerite 0.42-0.52 mm. long; posterior end more gradually tapered than that of H. cruralis, with relatively longer respiratory spines; anal plate ovoid.

Puparium: (Pl. V, Fig. 3) 3.5-4.5 x 0.8-1.0 mm.; transparent light brown; distinctly more elongate and more gradually tapered posteriorly than that of H. cruralis, H. pulla, and H. luctuosa; respiratory spines terminal; anal plates ovoid with no concavity of posterior margin; setal pattern as shown and as described for larva; enclosed pharyngeal skeleton and mouth hook as figured and described for larva; pupa light colored at first, then developing pigment in compound eyes, then in body generally, becoming predominantly black before emergence.

Eggs of H. bergi were deposited in the laboratory on stems of P. natans and attached to the side of the rearing bottle. In nature a similar egg mass was found attached to a stipule of P. natans. Unfortunately, none of these eggs hatched, and no information was obtained concerning embryonation, hatching, nor the newly hatched larva.

In biological aspects, larvae of H. bergi seem quite similar to those of H. cruralis and H. pulla. Since the stems in which they mine are thick and opaque, these larvae cannot be found by examination of plants with transmitted light. Some mines can be located because the epidermis covering them appears somewhat collapsed, and larvae were found only after opening such mines. Puparia can often be detected without dissection of plant tissue because the epidermis over them bulges outward and the dark color of mature pupae is often visible through the epidermis.

Just before pupation the larva provides for emergence of the adult by cutting a U-shaped incision in the epidermis of the stem. A similar provision is made by the larva of Hydromyza confluens Loew (Needham, 1908; Welch, 1914a), a scatophagid species which pupates in petioles of the yellow water lily. The incisions made by the larvae of these two species are similar in several respects. They are always cut in the epidermis covering the anterior ends of puparia. Both types are of such form as to produce lids which open readily when gentle pressure is applied from within. Both types of lids are attached along the side nearest the posterior end of the puparium.

Provisions for emergence in the two species differ in the following respects: (1) The incision made by H. confluens is in the shape of an arc extending approximately two thirds the circumference of an circle (Welch, 1914a) and has convergent ends; the incision made by *H. bergi* produces a U-shaped lid which is elongated in the longitudinal axis of the puparium and has parallel or slightly divergent ends. (2) The epidermal incision made by *H. bergi* is continuous, leaving no strands of tissue to hold the lid closed until the time of emergence. (3) Since *H. bergi* pupates just beneath the epidermis, there is no passage communicating between puparium and epidermal incision like that provided by *H. confluens*, which pupates deeper within the plant tissue.

H. bergi is the only species of *Hydrellia* herein discussed which provides for emergence of the adult in the manner described above. This is probably correlated with the fact that all other species of the genus reared during this investigation pupate in leaves, the epidermis of which is relatively thin and delicate and easily ruptured by the escaping imago.

In a few instances, puparia of this species were found with only their respiratory spines and posterior ends embedded in the *Potamogeton* stem, the greater part of these puparia protruding nakedly into the water. Such uncovered puparia were invariably found in leaf axils, where they looked very much like axillary buds. Perez (1901) described a similar habit in what appears to be a species of *Hydrellia* living on *P. pectinatum* in Europe.

In seasonal aspects, *H. bergi* is similar to the other species of *Hydrellia* discussed here. Emergence is not in well defined broods, but seems to be continuous throughout the summer. Both larvae and pupae were found in all 8 collections of *P. natans* spread through 2 summer months in 1940 as follows: June 10, 20, 29, July 7, 20, 28, August 1, 9. Apparently this species passes the winter as a larva on the food plant. Larvae were taken in Washtenaw County, Michigan on May 3, 1941, several weeks before adults were collected in nature.

Braconidae of 3 species, *Ademon niger* (Ashmead), *Chorebidea* sp. 2, and *Dacnusa* sp. 1, and the diapriid *Trichopria columbiana* (Ashmead) were reared from puparia of this fly.

Hydrellia ascita Cresson

Hydrellia ascita was described (Cresson, 1942) from flies which I reared during this study. Apparently the only other published reference to this species is that of Cresson (1944), who wrote, "Bred from pondweed in Michigan. Rare." Although not so stated, it seems likely that this record of Cresson is based entirely upon the type series which was reared during the summer of 1941, and sent to him for identification on October 27, 1941.

Specimens were found in Nigger Creek, Cheboygan County, Michigan. Larvae mine in thin, submerged leaves of *Potamogeton alpinus*, the mines being equally visible from either side of the leaf. Puparia which I am unable to distinguish from those of *H. ascita* were found on *P. amplifolius*, *P.*

angustifolius, *P*. *epihydrus*, *P*. *foliosus*, *P*. *illinoensis*, *P*. *Oakesianus*, *P*. *Richardsonii*, and *P*. *zosteriformis*. Cresson included only the flies reared from *P*. *alpinus* in his type series, however, and indicated (unpublished correspondence) that the others probably represent either a variety of *H*. *ascita* or an undescribed species.

Egg and first instar larva unknown.

Second Instar Larva (living): Similar to third instar larva in shape and color; length 1.2-2.4 mm.; pharyngeal skeleton similar to that of third instar larva (Pl. IV, Fig. 2) in shape and color, 0.24-0.26 mm. long.

Third Instar Larva (living): Quite similar to *H*. *bergi* (Pl. III, Fig. 1) in shape, color, and setal patterns, but smaller; 2.4-5.0 x 0.6-0.8 mm.; pharyngeal skeleton and mouth hook as shown (Pl. IV, Fig. 2), 0.35-0.49 mm. long.

Puparium: (Pl. V, Fig. 2) Very similar to that of *H*. *bergi* in shape, color, and setal patterns, but smaller; 2.8-3.7 mm. long; enclosed pharyngeal skeleton and mouth hook as illustrated (Pl. IV, Fig. 2) and described for larva; pupa at first light, becoming dark gray before emergence.

Egg masses resembling those of other species of *Hydrellia* were found on *P*. *alpinus*. Since the source of these eggs is unknown, and since they failed to hatch, their identity remains in doubt.

Mines of *H*. *ascita* in thin, submerged leaves are equally visible from either side and most readily found by examination of leaves with transmitted light.

Little is known concerning the seasonal aspects of this species. Puparia were collected on August 21, 1941. Larvae and puparia were collected during the last half of July and first half of August, 1946.

_H_. _ascita_ is parasitised by two species of Braconidae: _Dacnusa_ sp. 3, and _Chorebidella_ sp.

Hydrellia _caliginosa_ Cresson

Hydrellia _caliginosa_ was described (Cresson 1936) from specimens collected on the yellow water lily in Maine. The only published reference to the biology of this species appears to be that of Cresson (1944), who wrote, "A rare species from Maine and Michigan. It is associated with spatter dock and pondweed." While not so stated, it seems probable that the latter record is based upon a single specimen reared in this study and sent to Cresson for identification on October 27, 1941.

The puparium of the specimen referred to above was extracted from a mine in a leaf of _P_. _praelongus_ taken at Ocqueoc Lake, Presque Isle County, Michigan, on July 13, 1941. Since this specimen is the only _H_. _caliginosa_ among the hundreds of _Hydrellia_ encountered during this study, it appears that the species either is rare in Michigan or that it normally infests some other plant.

No further information was obtained concerning the biology of this species. Neither egg nor larva was observed.

Puparium: Transparent brown; 3.45 x 0.95 mm.; elongate and tapering gradually to the posterior end like those of H. bergi and H. ascita; respiratory spines terminal; dorsal setae at least in intersegmental grooves of all abdominal segments; ventral setal pattern similar to that of H. ascita (Pl. V, Fig. 2); pharyngeal skeleton (Pl. IV, Fig. 6) 0.46 mm. long, shaped somewhat like that of H. ascita but more extensively pigmented, opaque black pigment continuous from cheliform spot back to dorsoventral fork.

Notiphila loewi Cresson (Diptera: Ephydridae)

Several European authors (Müller, 1922; Varley, 1937; Hennig, 1943; and others) have contributed to knowledge of the biology and metamorphosis of Notiphila. It seems that larvae and pupae of most species live in the soil in bottoms of lakes, ponds, and streams and have sharp, hollow posterior respiratory spines by means of which they obtain oxygen from the intercellular gas spaces of aquatic plants.

Apparently, very little is known about the immature stages of Notiphila in this country. Johannsen (1935) omitted the genus from his key to larvae and puparia of aquatic Ephydridae and wrote, "Though the larvae of at least some members of . . . Notiphila . . . are aquatic, they either have not been described at all or have not been described in sufficient detail to be included in the above key. The eggs of Notiphila are laid on water plants." Cresson (1944, 1946), who presented biological notes on many of the Ephydridae, discussed (1946) 21 species of Notiphila, but ventured no statement regarding their biology and immature stages. Concerning N. loewi, he wrote, "A relatively common species from Canada, Maine, New Hampshire, Michigan, Minnesota, Ohio, Illinois, Tennessee, Florida, Wyoming, Colorado, Utah, and Washington".

In the present study, a few larvae and many puparia of N. loewi were found attached to the roots of P. alpinus and P. Richardsonii in several localities in Cheboygan County, Michigan. Puparia were also found on roots of P. pectinatus in Cheboygan County.

Egg and immature larva unknown.

Mature Larva (living): (Pl. VI, Fig. 1) Elongate, cylindrical, tapered toward both ends; about 8.0 x 1.2 mm.; light gray; segments not distinct; no creeping welts apparent; metapneustic with posterior spiracles in the form of slits near the tips of 2 hollow terminal spines; anterior end with paired, 3-segmented antennae, inferior tubercles, and mouth hooks; pharyngeal skeleton (Pl. VI, Fig. 2) composed of pharyngeal and hypostomal sclerites, colored as shown and bearing 2 mouth hooks; pharyngeal sclerite about 0.64 mm. long, with lateral halves connected together by anterodorsal bridge and both dorsal rods forked posteriorly.

Puparium: (Pl. VI, Fig. 3) Cylindrical and tapered more gradually to posterior than to anterior end; transparent brown; 4.6-5.1 x 1.4-1.7 mm.; terminal respiratory spines conspicuous, about 0.18 mm. long; anal plate extending around approximately one-half the circumference of puparium, and bearing anus as midventral, longitudinal slit; enclosed pharyngeal skeleton as figured (Pl. VI, Fig. 2) and as described for larva; living pupa at first light colored, later dark brown, with red color of compound eyes conspicuous.

Little information was obtained concerning biological aspects of _N. loewi._ Nothing was observed to indicate that the larvae feed on _Potamogeton_ tissues. The form of the respiratory spines and the fact that larvae and puparia were found thus attached to _Potamogeton_ roots suggest that these flies may be dependent on plants for oxygen supply during their larval and pupal stages.

Hydromyza confluens Loew (Diptera: Cordyluridae)

Studies on _Hydromyza confluens_ (Scatophagidae) by Needham (1908) and Welch (1914a, 1917) have revealed that its normal food plant is the yellow water lily. They reported that the larva lives within lily petioles, feeds on petiole tissues, and produces gall-like swellings. Pupation occurs within the cavity excavated by the larva, the puparium being completely covered by plant tissue.

A puparium which I found attached by its posterior respiratory plates to the roots of _Potamogeton alpinus_ in Nigger Creek, Cheboygan County, Michigan, June 25, 1946, was detached from the root and placed on moist cotton in a rearing bottle.

The freshly emerged male imago was discovered 13 days later, at 7:37 A.M. After this specimen had stroked the wings and body, stamped around, and rubbed the tarsi together for 14 minutes, the wings expanded rather suddenly. This specimen, dry and in very good condition, was killed and pinned 2 days later, and has been identified as Hydromyza confluens Loew by Fred M. Snyder, of Orlando, Florida.

Except for the posterior respiratory plates, which were covered by plant tissue, the major portion of this puparium projected into the flocculent, black silt bottom in a manner similar to that of Notiphila loewi (Pl. VI, Fig. 3). It is evident that the respiratory plates were well embedded in plant tissue because the puparium remained attached to the root and was pulled up through the silt with the plant. Under these unusual circumstances, development apparently had proceeded normally.

Trichopria columbiana (Ashmead) (Hymenoptera: Diapriidae)

Although ants serve as hosts of some species (Kiefer, 1916), most Trichopria are internal parasites of Diptera which represent many families and inhabit widely separated geographic regions. African Trichopria have been reared from Trypetidae (Rev. Appl. Ent., 1914), Stratiomyidae (Cros, 1935), Drosophilidae (Priesner, 1940), and Glossinidae (Nixon, 1940). Other species parasitize Micropezidae puparia in South America (Ogloblin, 1934) and the Solomon Islands

(Berg, 1947), and Javanese Trichopria have been reared from Syrphidae (Kieffer, 1907), Stratiomyidae (Bischoff, 1932), and Tachinidae (Ferrière, 1933). Roberts (1935) and Scotland (1939) reported Trichopria from Sarcophagidae and Ephydridae puparia in this country.

Habits of the various Trichopria species differ greatly. According to Clausen (1940), most species of this genus oviposit in fly puparia, but T. stratiomyiae (Cros, 1935) infests and kills the larva of its host. Some Trichopria develop singly, only one parasite being produced in each host. Females of other species either lay several eggs in each victim or lay eggs each of which develops by polyembryony into several specimens. Roberts (1935) got an average of 23 Trichopria adults from each parasitized sarcophagid puparium, and Cros (1935) obtained 293 parasites from one host. Apparently most species of this genus and their hosts are terrestrial insects, but Bischoff (1932) and others have called attention to several which are aquatic.

Although Trichopria columbiana was described (as Diapria columbiana Ashmead, 1893) more than half a century ago, nothing has appeared in the literature concerning its biology and host relations.

Specimens of T. columbiana were encountered in Cheboygan, Presque Isle, and Washtenaw Counties, Michigan. Adults were reared from puparia of Hydrellia bergi, H. cruralis, H. luctuosa and H. pulla which were found in Potamogeton alpinus, *P. amplifolius*, *P. epihydrus*, *P. gramineus*, *P. natans*, *P. praelongus*, and *P. Richardsonii*. No host puparium was found to produce more than one specimen of *T. columbiana*.

The larva of *T. columbiana* differs from all other *Hydrellia* parasites encountered in its failure to consume all tissue within the puparium. An internal parasite, it leaves the host's body wall intact except at the site of its exit. Presence of this hollow shell of host tissue within the puparium readily distinguishes puparia vacated by *T. columbiana* from those which have yielded either *Hydrellia* or any other species of parasite.

Wing buds, legs, bristles, and other pupal structures prove that the remains in some puparia are excavated bodies of fly pupae. However, the majority of host remains lack these characteristic pupal structures, and it is evident that these represent either *Hydrellia* killed during the prepupa stage (Snodgrass, 1924) or larvae of Braconidae known to parasitize these flies. There seems to be a sharp decrease in the yield of braconid parasites as well as that of *Hydrellia* in late July or early August each year, as adults of *T. columbiana* begin to emerge. On the other hand, secondary parasitism can hardly account for all the host remains which lack pupal structures, since these remains are relatively much more numerous than puparia which yield braconid parasites during any season.

Adults of *T. columbiana* emerge by cutting a roughly circular hole with their mandibles through the Hydrellia puparium. Although these emergence holes were not in the same position in all puparia, they were located so that part of the dorsocephalic cap was removed in all 108 puparia examined.

Ovipositing females of T. columbiana freely enter the water in search of hosts. Their bodies seem to be covered with a hydrofuge, oily film which enables them to submerge without danger of permanent wetting.

Emergence and oviposition of T. columbiana were observed in the laboratory under a dissecting microscope. A female Trichopria was observed moving around within a Hydrellia puparium and cutting an emergence hole. When the hole was large enough she came out, experiencing some difficulty in freeing her abdomen from some waste material in the puparium. Then, standing on the vacated puparium at least an inch below the water surface, she brushed and preened her body and wings with the tarsi as other freshly emerged insects do in the air, dislodging some bubbles which adhered to her body.

Presently she left the empty puparium and swam about with her legs, holding the wings motionless over her abdomen. The envelope of air which enclosed the mid-region of her body and presumably supplied oxygen for respiration tended to buoy her up, and her body was constantly held at a downward angle so that the swimming motions would counteract this tendency. After swimming for 10 or 12 minutes, she encountered a puparium which contained a Hydrellia pupa. For at least 5 minutes, she walked around on this puparium, frequently touching it with her antennae. Then, standing with the tip of her abdomen over the center of the puparium, she suddenly lowered her abdomen, pierced the puparium with her ovipositor, and seemed to make at least 6 more vigorous thrusts.

Leaving this puparium, she swam around for several minutes, found another puparium, and repeated the performance. Then she came to the surface and crawled out into the air. No moisture was seen on her body, and she flew away after resting only 1 or 2 seconds. At least 30 minutes had elapsed between emergence and the time she left the water.

A few days later, at 11:08 A.M., another Trichopria female was observed standing on an empty puparium beneath the water surface, preening herself and straightening her wings with her hind tarsi. Since this rearing bottle had been checked a few minutes earlier, it is evident that she had just emerged. She swam about making no attempt to come to the surface. Although she spent much time walking around on some well matured Hydrellia puparia, feeling them with her antennae, she did not oviposit in them. Forty-six minutes later, she came to the surface and quickly flew away.

Considering the great scarcity of males during late summer, it seems probable that eggs laid by unmated females of T. columbiana are capable of developing parthenogenetically. Of the 137 adult specimens examined in this investigation, 136 are females. There is no previous record of any male specimen of T. columbiana, and this sex remains undescribed. Sanders (1911) found that eggs laid by virgin females of the closely related Diapria conica develop parthenogenetically into males.

This species was not reared from puparia produced by hibernating larvae of the host nor from puparia collected in the spring. Adults emerged during the last week of July, August, and September from Hydrellia which had been collected as larvae or pupae during the summer. This may indicate that T. columbiana hibernates as an adult and does not resume activity early enough to parasitize the first Hydrellia of the season.

Pteromalidae (Hymenoptera)

A single specimen representing the family Pteromalidae, but unidentified as to genus, was reared from material collected in Cheboygan County, Michigan, in August, 1940. The adult emerged from a puparium of Hydrellia cruralis which had been extracted from a mine in Potamogeton amplifolius.

Ademon niger (Ashmead) (Hymenoptera: Braconidae)

Information which has been presented (Rousseau, 1907; Schulz, 1907, 1910; Heymons und Kuhlgatz, 1909) on the biology of European species of Ademon stresses their aquatic habits and adaptations. Apparently A. decrescens is the only species whose host relations are known. It has been reared (Thienemann, 1916) from puparia of Hydrellia chrysostoma and H. nigripes, and (Vaysière, 1933) H. nasturtii.

Considerably less is known concerning the biology of Ademon species on this continent. It seems that very little has been published about the biology and nothing concerning host associations of A. niger. Gahan (1915) stated that adults were collected on duckweed (Lemna). Analostania tenuipes, which C. F. W. Muesebeck considers synonymous with A. niger (personal correspondence), was described (Viereck, 1916) from 3 females collected by sweeping over aquatic vegetation near Washington, D. C.

Immature specimens of A. niger were collected in Cheboygan and Washtenaw Counties, Michigan. Adults were reared from puparia of Hydrellia cruralis, H. bergi, and H. ascita, found in Potamogeton amplifolius, P. natans, P. alpinus, P. praelongus, and P. zosteriformis.

Observations made during this investigation tend to support most of the statements of Gahan (1915) regarding host relations of the Opiinae. He wrote, ". . . the egg of the parasite is apparently in all cases deposited in or upon the host larva in one of its immature stages. In all instances observed, the host larva completed its development and assumed the pupal stage before being killed by the parasite. The parasitic larva then underwent its transformation in the puparium and emerged at about the time when the adult fly would have emerged."

A. niger was reared repeatedly from Hydrellia which pupated in closed rearing bottles in the laboratory. Some of the infested Hydrellia were collected as immature larvae. In all cases, infestation in the laboratory was impossible.

Infested larvae complete their growth and form normal puparia. True pupation, however, does not occur. After formation of the host puparium, the parasitic larva feeds and develops so rapidly that the entire host is consumed before the transformation from prepupal (Snodgrass, 1924) to pupal stage. About four days after the puparium is formed the mature parasitic larva can be seen moving about slowly within it. These larvae are gray with conspicuous spots of chalky, opaque white. Less than 24 hours later, the lightly pigmented pupa is visible. Approximately 11 to 15 days elapse between formation of the host puparium and emergence of the adult parasite.

The imago of A. niger escapes from the host puparium by cutting a roughly circular emergence hole with its mandibles. This hole is larger than that made by Trichopria columbiana and it is usually cut through the posterior part of the dorsal cephalic cap and through the puparium immediately behind it. When, rarely, this parasite develops in a reversed position in the puparium, it may emerge by cutting a hole near the posterior end.

A puparium which has yielded A.niger can be readily identified by its contents and by the size and shape of the emergence hole. This species leaves only its transparent larval and pupal exuviae and relatively large, dark, compact, subcylindrical mass of excrement. This mass, the waste material which accumulates in the hind gut of the parasite during its larval and pupal stages, is egested just before emergence.

Apparently A. niger passes the winter within the host larva. Three specimens were reared from Hydrellia collected as larvae in Third Sister Lake, Washtenaw County, Michigan, on March 30, 1942. It seems extremely unlikely that adults of A. niger were available to infest these larvae during the two-week interval between melting of the ice cover and collection of this material. If adults of the parasite had spent the winter in hibernation it appears improbable that they would emerge in the snow and cold weather which persisted at that time. Adults were not observed in nature in Washtenaw County until the last week of May.

A. niger swims like A. decrescens (Rousseau, 1907), using only the legs and holding the wings motionless over the abdomen. One specimen was observed to stay under water continuously for 35 minutes, alternately swimming and walking on the substratum. A bubble of air enclosed the mid-region of its body beneath the bases of its wings.

The body of A. niger seems to be covered with a hydrofuge oily film. Specimens emerging from the water appear dry and are able to fly immediately.

Chorebidea (Hymenoptera: Braconidae)

Insects of the genus Chorebidea (Chorebus of authors, but not of Haliday) have not been recorded previously from North America. The 2 new species designated here as Chorebidea sp. 1 and Chorebidea sp. 2 will be described in G. T. Riegel's forthcoming revision of certain genera of Dacnusinae.

European papers concerning biology of Chorebidea (Rousseau, 1907; Schulz, 1907, 1910; Morley, 1924) all stress their aquatic habits and adaptations. The only recorded host relationships in the genus seem to be those of C. najadum and C. natator, both of which were reared (Thienemann, 1916) from Hydrellia chrysostoma which were mining in Potamogeton lucens.

Specimens of Chorebidea sp. 1 were collected in Cheboygan, Emmet, and Washtenaw Counties, Michigan. Adults were reared from puparia of Hydrellia cruralis found in Potamogeton amplifolius, P. epihydrus, P. gramineus, P. nodosus, P. praelongus, and P. Richardsonii.

Adult parasites apparently oviposit into young larvae of their hosts. Several specimens were reared from Hydrellia which were collected as immature larvae and kept in screened containers in the laboratory. The Hydrellia larva completes its growth and forms a normal puparium. Then the parasitic larva feeds and develops so rapidly that its host is consumed without attaining the pupal stage. Less than 3 days after the puparium is formed the mature *Chorebidea* larva is visible within it. This larva is light pearl gray, appearing brownish through the transparent brown puparium. No host tissue can be seen at this time, and the absence of its characteristic green color provides an easy means of macroscopically distinguishing parasitized puparia. About 24 hours later the *Chorebidea* pupa is visible. It appears light brown at first, but becomes much darker as it matures. In those instances in which both events were observed 10 to 15 days elapsed between formation of the host puparium and emergence of the adult *Chorebidea*.

Emergence of *Chorebidea* sp. 1 was observed through a dissecting microscope. A specimen which was ready to emerge was discovered exerting pressure with its head and thus beginning to loosen the dorsocephalic cap of the host puparium. All 6 legs obtained anchorage on the wall of the puparium and pushed simultaneously. The large mandibles opened and closed vigorously but without damaging nor even contacting the puparium wall. There were intervals of rest and of activity. As the *Chorebidea* pushed the dorsocephalic cap completely free it popped out of the puparium, broke through the surface film immediately, and flew away less than a second after it left the water.

A puparium which has yielded *Chorebidea* sp. 1 can be identified easily by its contents and by the emergence hole. Like *Ademon niger*, this species consumes the entire host, leaving only its own exuviae and a dark, compact, subcylindrical mass of fecal material in the puparium. However, the emergence apertures of 74 puparia vacated by Chorebidea sp. 1 were found without exception to be of the type made by pushing off the intact dorsocephalic cap. The fecal mass is not always present in vacated puparia. It may in some instances be voided after emergence, or it may drop out of some puparia following escape of the parasite.

Chorebidea sp. 1 passes the winter within the host larva. Adults were reared from puparia formed by Hydrellia larvae which were collected in plants living beneath the ice in Third Sister Lake, Washtenaw County, in January, February, and March. These larvae had evidently become infected before the lake surface froze the previous autumn.

Adults of Chorebidea sp. 2 were reared from puparia of Hydrellia bergi found in P. natans and P. Richardsonii in Cheboygan County, Michigan. This species is quite similar to sp. 1 in biology, host relationships, mode of emergence, and appearance of its vacated puparia. Both species seem highly specific in selection of hosts. Although 5 species of Hydrellia were often found closely associated and many Chorebidea were reared from them, all specimens of sp. 1 came from H. cruralis, and all sp. 2 came from H. bergi.

Chorebidella sp. (Hymenoptera: Braconidae)

G. T. Riegel (1947) erected the genus Chorebidella to receive the species under discussion here, and showed in his key how it differs from closely related genera of Dacnusinae.

Morphological characters of Chorebidea and Chaenusa are combined in Chorebidella, and it is of interest that species of all 3 genera have been reared from Hydrellia. European species of Chaenusa were reared from Hydrellia by Thienemann (1916) and Karny (1934).

Specimens of Chorebidella sp. were collected in Cheboygan and Washtenaw Counties, Michigan. Two adults were reared from puparia of Hydrellia ascita taken from mines in Potamogeton alpinus, and one from H. cruralis taken from P. amplifolius. The parasitized puparia were collected on August 21, 1941 and May 3, 1942.

Dacnusa (Hymenoptera: Braconidae)

Species of the genus Dacnusa (Dacnusinae) whose host relationships are known are parasitic in phytophagous Diptera. The majority of these dipterous hosts belong to the family Agromyzidae and are leaf miners in terrestrial plants. Included in the list of hosts are a few species of gall-forming Agromyzidae and some leaf-mining species belonging to the families Drosophilidae (Gahan, 1913; Frost, 1924), Anthomyiidae (Frost, 1924), Ephydridae (Ruschka und Thienemann, 1913), Chloropidae (Rev. Appl. Ent., 1927) and Psilidae (Nixon, 1937).

Two European species of Dacnusa, one of which parasitizes species of Hydrellia, are known to have aquatic habits and adaptations. Rousseau (1907) and Schulz (1907, 1910) discussed the swimming motions of *D. rousseaui*. *D. obscuripes* has been reared from *Hydrellia* sp. mining in *Potamogeton natans* (Ruschka und Thienemann, 1913; Thienemann, 1916).

Three species of *Dacnusa* were reared from *Hydrellia* puparia during this investigation. Since none of these are described, it is not possible to refer to them with specific names. Each seems to be restricted to a single host species. They will be identified here as *Dacnusa* sp. 1, the species reared from puparia of *H. bergi*; *Dacnusa* sp. 2, which is parasitic in *H. luctuosa*; and *Dacnusa* sp. 3, reared from puparia of *H. ascita*.

Dacnusa sp. 1 was collected in Cheboygan County, Michigan, during June, July, and August. More than 70 adults were reared from puparia of *Hydrellia bergi* extracted from mines in *Potamogeton natans* and *P. zosteriformis*. None was obtained from *Hydrellia* of the other 4 species often closely associated with *H. bergi*.

Dacnusa sp. 1 lays its eggs in the larvae of its host. It was reared repeatedly from *Hydrellia* which were collected as larvae and kept in closed rearing bottles. Infected larvae complete their growth and form normal puparia. Then the parasitic larva develops rapidly, killing and entirely consuming the host while it is in the prepupal stage. About 2 days after formation of the host puparium, the mature parasitic larva is visible moving about within it. The larva is light gray, appearing brownish through the transparent brown puparium. In another 24 hours, the Dacnusa pupa is visible. The pupa is light brown at first, but gradually turns darker as it matures. The adult parasite emerges 12 to 15 days after formation of the host puparium.

The imago of Dacnusa sp. 1 escapes by cutting a transverse slit around approximately half the circumference of the metathoracic segment of the puparium. This slit is not nearly wide enough to allow egress of the parasite, which must bend and temporarily deform the puparium in forcing its way out. In about half of the puparia examined the uncut arc of the metathoracic segment was broken during emergence, and the anterior end of the puparium was detached intact.

Puparia which have yielded Dacnusa sp. 1 are readily distinguished from those vacated by the host fly or by any other parasite. Whether or not the anterior end of the puparium breaks off, the emergence aperature of this species is quite characteristic. Together with the transparent larval and pupal exuviae of Dacnusa, a compact fecal mass similar to those left by Ademon niger and Chorebidea sp. is usually found within the puparium.

A female Dacnusa sp. 1 which was observed under a dissecting microscope remained submerged continuously for more than half an hour, apparently ovipositing in Hydrellia which were mining the stems of P. natans. She traversed the length of each stem, touching it with her antennae at short intervals throughout its length. The last few segments of the antennae were laid flat against the stem, moved ahead a few millimeters, and again pressed against it. When they touched a spot within which a host larva was mining, the parasite walked forward until the tip of her abdomen was opposite this point, then suddenly thrust her ovipositor through the plant epidermis and presumably into the host larva. She apparently oviposited in pupae as well as larvae, but these eggs probably failed to develop. No Dacnusa was reared from a puparium known to contain a host pupa.

As this female left one stem and attempted to walk along the smooth glass bottom of the rearing bottle to another stem, she lost her footing and was carried upward by a large bubble which adhered beneath her wings. She counteracted this buoyant effect by swimming vigorously downward with all six legs, her wings being held motionless over her abdomen. Then she encountered another piece of mined stem and repeated her earlier performance.

When she finally came to the surface, she broke through the surface film easily, appeared dry at once, and flew away within 1 or 2 seconds.

Dacnusa sp. 2 was collected in Cheboygan County, Michigan, during July and August. Adults were reared from puparia of Hydrellia luctuosa extracted from mines in Potamogeton alpinus and P. zosteriformis.

Like those of Dacnusa sp. 1, specimens of this species lay their eggs in larvae of the host, which complete their growth and form normal puparia before showing any effects of parasitism. The parasitic larvae then kill and consume the hosts while they are in the prepupal stage.

In speed of development and appearance of larva and pupa Dacnusa sp. 2 is similar to Dacnusa sp. 1 but somewhat smaller. Like sp. 1, it consumes all host tissues and leaves only its own exuviae and a compact fecal mass within the puparium. However, this species differs in its method of emergence. Instead of cutting the puparium with its mandibles, it escapes like the host fly, by pushing off the dorsocephalic cap.

Dacnusa sp. 3 was collected in Cheboygan County, Michigan, during August. Adults were reared from puparia of Hydrellia ascita extracted from mines in Potamogeton alpinus.

Although adults of this species are easily distinguished from those of sp. 2, these 2 species are quite similar in size, speed of development, appearance of larva and pupa, and method of escape from the host puparium.

It seems probable that metamorphoses of the 3 Dacnusa species discussed here are synchronized with metamorphoses of their hosts in a manner similar to that of D. areolaris (Haviland, 1922). Haviland stated that the larva of D. areolaris remains in its first instar within a trophic membrane until the mature host larva ceases feeding and prepares to pupate. Then its development to the adult stage takes place in a period equal to the puparium stage of the host. The mandibles of parasitic hymenopterous larvae in general are better adapted for prehension than for mastication, and some break down host tissue by a kind of external digestion before feeding upon it. As pointed out by Haviland, however, those which delay their development until the host organs disintegrate to reorganize into pupal structures acquire a semiliquid diet without predigesting the host tissue.

SUMMARY

1. Limnological relations of insects to plants representing 17 species of Potamogeton were studied in 5 counties in the Lower Peninsula of Michigan.

2. Insects of 42 species reared from Potamogeton are listed and the host plants of each recorded. Approximately 64 per cent of this fauna is phytophagous; the remainder includes parasites, insects protected by living within Potamogeton tissues, and insects which draw oxygen from these plants.

3. The identified insects directly related to Potamogeton belong to 32 species, including 17 species of Diptera (chiefly Chironomidae and Ephydridae), 6 species of Trichoptera, 4 of Lepidoptera, 3 of Coleoptera, and 2 species of Homoptera. Odonata (Zygoptera and Anisoptera) unidentified beyond suborder and representing an unknown number

of species hatched from eggs found within the plants. Parasitic Hymenoptera of 10 species, at least 6 of which remain undescribed, were reared from the insects directly related to Potamogeton.

4. The total number of species of insects found associated with each plant is as follows: P. alpinus, 13; P. amplifolius, 25; P. epihydrus, 6; P. filiformis, 0; P. foliosus, 2; P. Freisii, 1; P. gramineus, 10; P. illinoensis, 5; P. natans, 23; P. nodosus, 6; P. Oakesianus, 3; P. pectinatus, 1; P. praelongus, 10; P. pusillus, 0; P. Richardsonii, 18; P. Robbinsii, 6; P. zosteriformis, 7.

5. Plants of the genus Potamogeton suffer injuries of various types due to infestation by these insects. The phytophagous species mine, channel, skeletonize or entirely consume leaves; burrow in, or gnaw away superficial patches of stems, roots, or flowering peduncles; or suck plant juices. Injuries from insects seeking shelter within plant tissues include stem-burrows of Chironomidae larvae, punctures from ovipositors of Odonata, and defoliation by case-making larvae of Lepidoptera and Trichoptera. Larvae of Ephydridae (Diptera) and Donacinae (Coleoptera) pierce the epidermis when they insert their respiratory spines to obtain oxygen.

6. The biology of insects found associated with Potamogeton is treated in some detail. Various degrees of aquatic adaptation are illustrated by Potamogeton insects. Representatives of most of the species studied hibernate as

larvae, on or within host plants living beneath the ice. Striking differences in local population densities of the insect fauna are presented. The Chironomidae are classified here into 3 groups on the basis of their relations to the plants.

7. Immature stages of certain species are described and illustrated for the first time. Attention is given to early stages representing 7 species of Diptera recently described from specimens reared in connection with this investigation and to those of some other species the adults of which were described previously. A key is presented to larvae and puparia of Hydrellia (Ephydridae) found on Potamogeton.

8. Potamogeton species support a large and heterogeneous assemblage of insects which are directly, intimately, and in some instances probably obligatorily related to these plants.

LITERATURE CITED

Ashmead, W.H.
1893 Monograph of the North American Prototrypidae. Bul. U. S. Nat. Mus., 45:1-472.

Au, S.H.
1941 Megamelus davisi infesting water lily in Hawaii. Jour. Econ. Ent., 34:415.

Barnard, K.H.
1911 Chironomid larvae and watersnails. Ent. Mo. Mag., 47:76.

Becker, T.
1926 Ephydridae. In Lindner, Die Fliegen der palaearctischen Region. Bd. VI_1, 56a:1-104. Stuttgart.

Bellrose, F.C., Jr.
1941 Duck food plants of the Illinois River Valley. Bul. Ill. State Nat. Hist. Surv., 21:237-280.

Berg, C.O.
1947 Biology and metamorphosis of some Solomon Islands Diptera. Part I: Micropezidae and Neriidae. Occ. Pap. Mus. Zool. Univ. Mich., 503:1-14.

1948 A technique for projecting the images of living animals. Trans. Am. Micr. Soc., 67: *In press*.

Berg, K.
1941 Contribution to the biology of *Acentropus niveus* (Oliv.). Vidensk. Medd. fra Dansk naturh. Foren., Bd. 105:60-139.

Bill, J.P.
1932 Swarming Chironomidae. Psyche, 39:68.

Bischoff, H.
1932 Hymenoptera (excl. Formicidae und Cynipidae) der Deutschen Limnologischen Sunda-Expedition. Arch. f. Hydrobiol., Suppl. 9:738-746.

Branch, H.E.
1923 The life history of *Chironomus cristatus*, with description of the species. Jour. N. Y. Ent. Soc., 31:15-30.

1931 Identification of chironomid egg masses II. Trans. Kans. Acad. Sci., 34:151-57.

Brocher, F.
1910 Diptères et Hyménoptères dits "aquatiques." Ann. Biol. Lac., 4:170-186.

Buckler, W.M.
1876a On the larva and habits of *Paraponyx stratiotalis*. Ent. Mo. Mag., 12:160-63.

1876b On the larva of *Hydrocampa nymphaealis* and its habits. *Ibid*., 12:210-13.

1877 Natural history of *Hydrocampa stagnalis*. *Ibid*., 14:97-103.

1881 Further notes on the early stages of *Hydrocampa nymphaealis*. Ibid., 17:249-254.

Burtt, E.T.
1940 A filter-feeding mechanism in a larva of the Chironomidae (Diptera: Nematocera). Proc. Roy. Ent. Soc. Lond., (A) 15:113-121.

Claassen, P.W.

1921 *Typha* insects: their ecological relationships. Cornell Univ. Agr. Exp. Sta., Mem. 47:459-531.

1922 The larva of a chironomid (*Trissocladius equitans* n. sp.) which is parasitic upon a may-fly nymph (*Rithrogena* sp.). Kans. Univ. Sci. Bul., 14:395-405.

Clausen, C.P.

1940 Entomophagous insects. x + 688 pp. New York.

Collin, J.E.

1928 A new species of *Hydrellia* (Diptera, Ephydridae) mining the stems of water-cress. Ent. Mo. Mag., 64:128-29.

Cresson, E.T., Jr.

1932 Studies in the dipterous family Ephydridae. Paper IV. Trans. Am. Ent. Soc., 58:1-34.

1934 Two new species of the genus *Hydrellia* from Mount Desert, Maine. Ent. News, 45:234-36.

1936 Descriptions and notes on genera and species of the dipterous family Ephydridae. II. Trans. Am. Ent. Soc., 62:257-270.

1941 New genera and species of North American Ephydridae (Diptera). Ent. News, 52:35-38.

1942 Descriptions of two Nearctic species of the genus *Hydrellia* reared from Pond-weed (Diptera: Ephydridae). Ent. News, 53:78-79.

1944 Synopses of North American Ephydridae (Diptera). II. The tribes Hydrelliini, Hydrinini and Ilytheini of the subfamily Notiphilinae, with descriptions of new species. Trans. Am. Ent. Soc., 70:163-180.

1946 Synopses of North American Ephydridae (Diptera). III. The tribe Notiphilini of the subfamily Notiphilinae. *Ibid*., 72:227-240.

Cros, A.

1935 Biologie du *Trichopria stratiomyiae* Kieffer. Soc. d'Hist. Nat. de l'Afrique du Nord, Bul. 26:131-36.

Dyar, H.G.

1906 The North American Nymphulinae and Scopariinae. Jour. N. Y. Ent. Soc., 14:77-107.

Fellton, H.L.
1940 Control of aquatic midges with notes on the biology of certain species. Jour. Econ. Ent., 33:252-264.

Fernald, M.L.
1932 The linear-leaved North American species of Potamogeton, section Axillares. Mem. Am. Acad. Arts and Sci., 17 (1):1-183.

Ferrière, C.
1933 Chalcidoid and proctotrupoid parasites of pests of the coconut palm. Stylops, 2:86-108.

Forbes, W.T.M.
1910 The aquatic caterpillars of Lake Quinsigamond. Psyche, 17:219-227.

1923 The Lepidoptera of New York and neighboring States. Cornell Univ. Agr. Exp. Sta., Mem. 68:1-729.

Frohne, W.C.
1938 Contribution to knowledge of the limnological rôle of the higher aquatic plants. Trans. Am. Micr. Soc., 57:256-268.

1939a Semiaquatic Hymenoptera in North Michigan lakes. Ibid., 58:228-240.

1939b Biology of Chilo forbesellus Fernald, an hygrophilous crambine moth. Ibid., 58:304-326.

1939c Observations on the biology of three semiaquatic lacustrine moths. Ibid., 58:327-348.

1939d Biology of certain subaquatic flies reared from emergent water plants. Pap. Mich. Acad. Sci., Arts and Lett., 24:139-147.

Frost, S.W.
1924 A study of the leaf-mining Diptera of North America. Cornell Univ. Agr. Exp. Sta., Mem. 78:1-228.

Gahan, A.B.
1913 New Ichneumonoidea parasitic on leaf-mining Diptera. Canad. Ent., 45:145-154.

1915 A revision of the North American Ichneumon flies of the subfamily Opiinae. Proc. U. S. Nat. Mus., 49:63-95.

Goetghebuer, M.
1913 Études sur les chironomides de Belgique. Acad. Roy. Belg. (Cl. d. Sci.), Mém. III$_6$:1-26.

1914 Recherches sur les larves et les nymphes des chironomides de Belgique. Ibid., Mém. III$_7$: 1-48.

1919 Observations sur les larves et les nymphes de quelque chironomides de Belgique. Ann. Biol. Lac., 9:51-79.

Gripekoven, H.
1914 Minierende Tendipediden. Arch. f. Hydrobiol. u. Planktonkunde, Suppl. Bd. 2:129-230.

Hart, C.A.
1895 On the entomology of the Illinois River and adjacent waters. Bul. Ill. State Lab. Nat. Hist., 4:149-273.

Haviland, M.D.
1922 Larval development of Dacnusa areolaris, a parasite of Phytomyzinae, with a note on certain chalcid parasites of phytomyzids. Parasit., 14:167-173.

Hendel, F.
1926 Blattminenkunde Europas, I, Die Dipterenminen, Lf. 1. 64pp. Vienna. (Original not seen)

Hennig, W.
1943 Übersicht über die bisher bekannten Metamorphosestadien der Ephydriden, mit Neubeschreibungen nach dem Material der Deutschen Limnologischen Sundaexpedition. (Diptera: Ephydridae). Arb. morphol. taxon. Ent., 10:105-138.

Hering, M.
1930 Beiträge zur Kenntnis der Ökologie und Systematik blattminierender Insekten (Minenstudien X). Zeit. angew. Ent., 17:431-471.

1935-'37 Die Blatt-Minen Mittel- und Nord-Europas. iii + 631 pp. Neubrandenburg. (Original not seen)

Heymons, R. u. H., und Kuhlgatz, T.
1909 Collembola, Neuroptera, Hymenoptera, Rhynchota. In Brauer, Die Süsswasserfauna Deutschlands, 7:1-112. Jena.

Hoffman, C.E.

1940a Morphology of the immature stages of some Northern Michigan Donaciini (Chrysomelidae; Coleoptera). Pap. Mich. Acad. Sci., Arts and Lett., 25:243-290.

1940b The relation of *Donacia* larvae (Chrysomelidae; Coleoptera) to dissolved oxygen. Ecol., 21:176-183.

1940c Limnological relationships of some Northern Michigan Donaciini (Chrysomelidae; Coleoptera). Trans. Am. Micr. Soc., 59:259-274.

Jeffrey, R.W.

1877 *Hydrocampa stagnalis* bred. Ent. Mo. Mag., 14:116.

Johannsen, O.A.

1905 Aquatic nematocerous Diptera, II: Chironomidae. N. Y. State Mus. Bul., 68:76-331.

1935 Aquatic Diptera, Part II. Orthorrhapha-Brachycera and Cyclorrhapha. Cornell Univ. Agr. Exp. Sta., Mem. 177:1-62.

1937a Aquatic Diptera, Part III. Chironomidae: Subfamilies Tanypodinae, Diamesinae, and Orthocladiinae. *Ibid.*, 205:1-84.

1937b Aquatic Diptera, Part IV. Chironomidae: Subfamily Chironominae. *Ibid.*, 210:1-52.

1942 Immature and adult stages of new species of Chironomidae (Diptera). Ent. News, 53:70-75.

1943 Adult and immature stages of *Cricotopus elegans* n. sp. (Chironomidae, Diptera). *Ibid.*, 54:77-79.

Karny, H.H.

1934 Biologie der Wasserinsekten. xv + 311 pp. Vienna.

Kettisch, J.

1936-'37 Zur Kenntnis der Morphologie und Ökologie der Larve von *Cricotopus trifasciatus*. Konowia, 15:248-263, 16:153-163, 193-204.

Kieffer, J.J.

1907 Beschreibung neuer Proctotrypiden aus Java. Zeit. f. syst. Hymenop. u. Dipt., 7:310-313. (Original not seen).

Kieffer, J.J. (continued)
1916n Diapriidae. In Schulz, Das Tierreich. Lf. 44:xxx + 627 pp. Berlin.

Körtung, A.
1931 Ueber die Entwicklung der grauen Gerstenminierfliege (Hydrellia griseola Fall.) bei verschiedener Ernährung. Zeit. f. Pflanzenkrank. u. Pflanzenschutz, 41:321-333.

Krecker, F.H.
1939 A comparative study of the animal population of certain submerged aquatic plants. Ecol., 20:553-562.

Leathers, A.L.
1922 Ecological study of aquatic midges and some related insects with special reference to feeding habits. Bul. U. S. Bur. Fish., 38:1-61.

Lindeman, R.L.
1941 Seasonal food-cycle dynamics in a senescent lake. Am. Midl. Nat., 26:636-673.

1942 Seasonal distribution of midge larvae in a senescent lake. Ibid., 27:428-444.

Lloyd, J.T.
1921 The biology of the North American caddis fly larvae. Bul. Lloyd Libr. Bot., Pharm., and Mat. Med., 21:1-124.

McAtee, W.L.
1939 Wildfowl food plants. 141 pp. Ames, Iowa.

Malloch, J.R.
1915a The Chironomidae, or midges, of Illinois, with particular reference to the species occurring in the Illinois River. Bul. Ill. State Lab. Nat. Hist., 10:273-543.

1915b Some additional records of Chironomidae for Illinois and notes on other Illinois Diptera. Ibid., 11:305-364.

Marchal, P.
1903 Sur la biologie d'Hydrellia. Bul. Soc. Ent. Fr., 72:236-37.

Martin, A.C. and Uhler, F.M.
1939 Food of game ducks in United States and Canada. U. S. Dept. Agr., Tech. Bul. 634:1-156.

Miall, L.C.
1895 The natural history of aquatic insects. 395 pp. London.

Miller, E.R.
1912 Butterfly and moth book. 249 pp. New York.

Miller, R.B.
1941 A contribution to the ecology of the Chironomidae of Costello Lake, Algonquin Park, Ontario. Univ. Toronto Studies, Biol. Ser., 49:1-63.

Moore, E.
1915 The Potamogetons in relation to pond culture. Bul. U. S. Bur. Fish., 33:251-291.

Morley, C.
1924 Notes on Braconidae: xiii - Dacnusides. The Entomologist, 57:193-98, 250-55.

Müller, G.W.
1892 Beobachtungen an im Wasser lebenden Schmetterlingsraupen. Zool. Jahrb., Syst., Geog., Biol., 6:617-630.

1922 Insektenlarven an Wurzeln von Wasserpflanzen. Naturw. Ver. Neuvorpommern Rügen, Mitt., 48 u. 49 Jahrgang, 1920 u. 1921 :30-50.

Muttkowski, R.A.
1918 The fauna of Lake Mendota -- a qualitative and quantitative survey with special reference to the insects. Trans. Wis. Acad. Sci., Arts and Lett., 19:374-482.

Needham, J.G.
1908 Notes on the aquatic insects of Walnut Lake. In Hankinson, A biological survey of Walnut Lake, Michigan. Report of the Biological Survey of the State of Michigan, Publ. by the State Board of Geological Survey as part of the Report for 1907, pp. 252-271.

Nixon, G.E.J.
1937 The British species of Dacnusa (Hymenoptera, Braconidae). Trans. Soc. Brit. Ent., 4:1-88.

1940 A new African diapriid. Bul. Ent. Res., 31: 59-60.

Ogden, E.C.
1943 The broad-leaved species of Potamogeton of North America north of Mexico. Rhodora, 45:57-105, 119-163, 171-214.

Ogloblin, A.
1934 Una especie nueva del género Trichopria del Brasil (Hym., Diapriidae). Rev. de Ent. 4:60-65.

Ong, E.R. de
1922 A rice leaf-miner. Jour. Econ. Ent., 15:432.

Oosting, H.J.
1932 Distribution of the genus Potamogeton in Michigan. Pap. Mich. Acad. Sci., Arts and Lett., 40:141-171.

Packard, A.S.
1884 Habits of an aquatic pyralid caterpillar. Am. Nat., 18:824-26.

Perez, T.d.St.
1901 Osservazioni biologische sopra un Braconide aquatico, Giardinaia urinator, e descrizione di due altri imenotteri nuovi. Zool. Jahrb., Syst., Geog., Biol., 15:625.

Priesner, H.
1940 On some Egyptian Diapriidae (Hymenoptera: Proctotrupoidea). Soc. Fouad ler Ent., Bul. 24:71-81.

Reaumur, R.A.F.
1736 Mémoires pour servir a l'histoire des insectes. Tome 2. xlviii + 514 pp. Paris.

Rev. Appl. Ent.
1914 Viaggio in Africa per cercare parassiti di mosche dei frutti. (Original paper by F. Silvestri not seen) Rev. Appl. Ent., (A) 2:316-17.

1927 Observations on the gout-fly (Chlorops taeneopus Meig.) and its parasites. (Translation from Polish. Original paper by J.W. Ruszkowski not seen). Rev. Appl. Ent., (A) 15:556.

Richardson, R.E.
1921 Changes in the bottom and shore fauna of the middle Illinois River and its connecting lakes since 1913-1915 as a result of the increase, southward, of sewage pollution. Bul. Ill. State Lab. Nat. Hist., 14:33-75.

1925 Illinois River bottom fauna in 1923. Ibid., 15:387-422.

Riegel, G.T.
1947 The American species of Dacnusinae, excluding certain Dacnusini (Hymenoptera: Braconidae). 8 pp. Urbana, Illinois.

Roberts, R.A.
1935 Some North American parasites of blowflies. Jour. Agr. Res., 50:479-494.

Rousseau, E.
1907 Les Hymenopteres aquatiques. Ann. Biol. Lac., 2:388-401.

Ruschka, F. und Thienemann, A.
1913 Zur Kenntnis der Wasser-Hymenopteren. Zeit. f. Wiss. Insektenbiol., 9:82-87.

Sadler, W.O.
1935 Biology of the midge Chironomus tentans Fabr., and methods for its propagation. Cornell Univ. Agr. Exp. Sta., Mem. 173:1-25.

Sanders, G.E.
1911 Notes on the breeding of Tropidopria conica Fabr. Canad. Ent., 43:48-50.

Schulz, W.A.
1907 Schwimmende Braconiden. Ann. Soc. Ent. Belg., 51:164-173.

1910 Süsswasser-Hymenopteren aus dem See von Overmeire. Ann. Biol. Lac., 4:194-210.

Scotland, M.B.
1934 The animals of the Lemna association. Ecol., 15:290-94.

1939 The Lemna fly and some of its parasites. Ann. Ent. Soc. Am., 32:713-18.

Shelford, V.E.
1918 Conditions of existence. Pp. 21-60, in Ward and Whipple, Fresh-water Biology. New York.

Snodgrass, R.E.
1924 Anatomy and metamorphosis of the apple maggot, Rhagoletis pomonella Walsh. Jour. Agr. Research, 28:1-36.

Taylor, T.H.
1928 The watercress stem-miner. Ent. Mo. Mag., 64:126-28.

Thienemann, A.
1909 Die Bauten der Chironomidenlarven. Zeit. f. d. Ausbau d. Entwickelungslehre, 3:138-150.

1916 Ueber Wasserrhymenopteren. Zeit. f. Wiss. Insektenbiol., 12:49-54.

1933 Chironomiden-Metamorphosen. III Zur Metamorphose der Orthocladiariae. Deut. Ent. Zeit., 1933:1-38.

Townes, H.K.
1938 Studies on the food organisms of fish. N. Y. State Cons. Dept. Biol. Surv., 12:162-175.

1945 The Nearctic species of Tendipedini [Diptera, Tendipedidae (= Chironomidae)] . Am. Midl. Nat., 34:1-206.

Varley, G.C.
1937 Aquatic insect larvae which obtain oxygen from the roots of plants. Proc. Roy. Ent. Soc. Lond., (A) 12:55-60.

Vayssière, P.
1933 La Mouche du Cresson (Hydrellia nasturtii Collin [Dipt., Ephydridae]) et son parasite (Ademon decrescens Nees [Hym., Braconidae]). Bul. Soc. Ent. Fr., 38:86-87.

Viereck, H.L.
1916 One new genus and five new species of ichneumon-flies. Proc. Biol. Soc. Wash., 29:165-172.

Welch, P.S.
1914a Observations on the life history and habits of Hydromyza confluens Loew (Diptera). Ann. Ent. Soc. Am., 7:135-147.

Welch, P.S. (continued)

1914b Habits of the larva of *Bellura melanopyga* Grote (Lepidoptera). Biol. Bul., 27:97-114.

1915 The Lepidoptera of the Douglas Lake region, northern Michigan. Ent. News, 26:115-19.

1916 Contribution to the biology of certain aquatic Lepidoptera. Ann. Ent. Soc. Am., 9:159-190.

1917 Further studies on *Hydromyza confluens* Loew (Diptera). *Ibid.*, 10:35-46.

1922 The respiratory mechanism in certain aquatic Lepidoptera. Trans. Am. Micr. Soc., 41:29-50.

1924 Observations on the early larval activities of *Nymphula maculalis* Clemens (Lepidoptera). Ann. Ent. Soc. Am., 17:395-402.

1935 Limnology. xiv + 471 pp. New York.

Welch, P.S. and Sehon, G.L.

1928 The periodic vibratory movements of the larva of *Nymphula maculalis* Clemens (Lepidoptera) and their respiratory significance. Ann. Ent. Soc. Am., 21:243-258.

Wesenberg-Lund, C.

1915 Insektlivet i Ferske Vande. 524pp. Copenhagen.

1943 Biologie der Süsswasserinsekten. 682 pp. Copenhagen.

Wilke, S.

1924 Die graue gerstenminier Fliege, *Hydrellia griseola* Fall. (Dipt. Ephydr.). Deut. Ent. Zeit., 6 (1924): 172-179.

Willem, V.

1907 *Nymphula stratiotata*. Ann. Soc. Ent. Belg., 51:289-290.

1908 Larves de chironomides vivant dans des feuilles. Bul. L'Acad. Roy. Belg. (Cl. d. Sci.), 1908: 697-704.

1910 Une nouvelle larve, mineuse, de Chironomide. *Ibid.*, 1910:33-37.

Williams, F.X.
1938 Biological studies in Hawaiian water-loving insects. Part III Diptera or flies, A. Ephydridae & Anthomyiidae. Proc. Haw. Ent. Soc., 10:86-90.

Wilson, H.F. and Vickery, R.A.
1918 A species list of the aphididae of the world and their recorded food plants. Trans. Wis. Acad. Sci., Arts, and Lett., 19:22-355.

PLATE I

Distinguishing characters of _Cricotopus elegans_ and _Glyptotendipes dreisbachi_ larvae and pupae (Chironomidae)

Fig. 1. _Cricotopus elegans_: Right mandible of larva in dorsal view.

Fig. 2. _C. elegans_: Antenna of larva.

Fig. 3. _C. elegans_: Labial plate of larva in normal convex shape.

Fig. 4. _C. elegans_: Labial plate of larva, flattened.

Fig. 5. _C. elegans_: Ninth and part of eighth abdominal segments of pupa.

Fig. 6. _Glyptotendipes dreisbachi_: Antenna of larva.

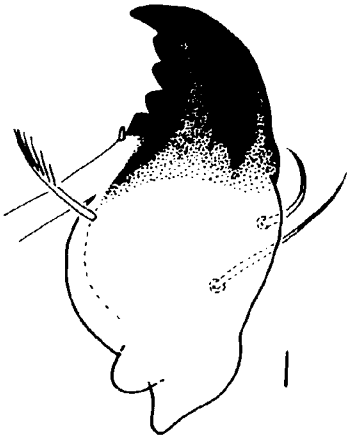
Fig. 7. _G. dreisbachi_: Labial plate of larva in right ventrolateral view.

Fig. 8. _G. dreisbachi_: Right mandible of larva in dorsal view.

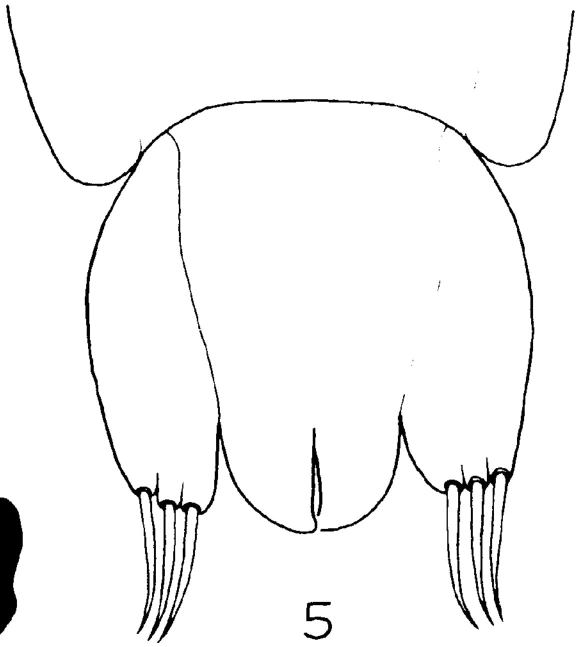
Fig. 9. _G. dreisbachi_: Labial plate and right paralabial plate of larva in ventral view.

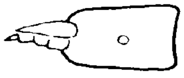
Fig. 10 - 13. _G. dreisbachi_: Mace-like processes on abdominal segments 3 - 6 of pupa, respectively.

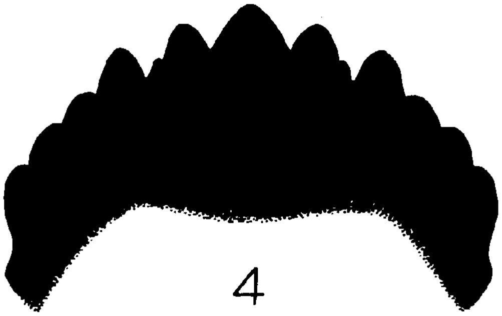
Fig. 14. _G. dreisbachi_: Comb at right posterolateral angle of eighth abdominal segment of pupa.

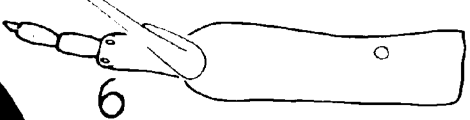

1


3

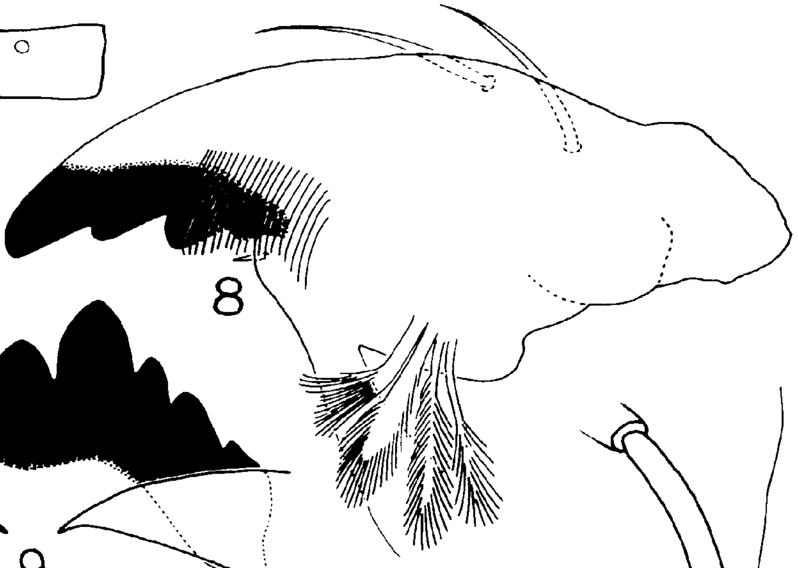

5

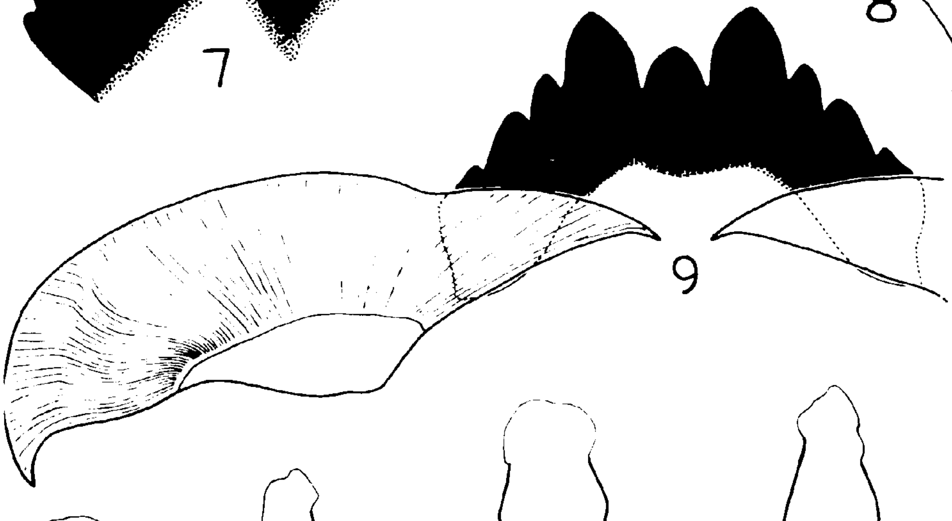

2


4


6

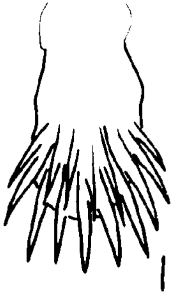

7


8


9


10


11


12


13

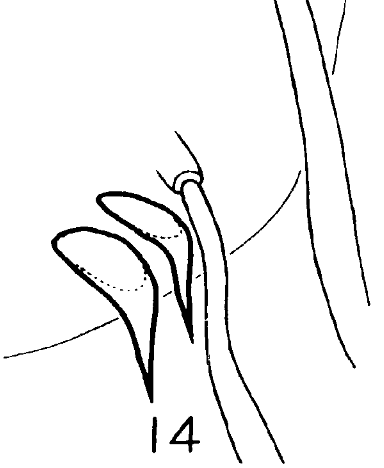

14

PLATE II

Distinguishing characters of Polypedilum larvae and pupae (Chironomidae)

Fig. 1. Polypedilum ophioides: Antenna of larva.

Fig. 2. P. ophioides: Labial plate and right paralabial plate of larva in ventral view.

Fig. 3. P. ophioides: Right mandible of larva in dorsal view.

Fig. 4. P. ophioides: Comb at right posterolateral angle of eighth abdominal segment of pupa.

Fig. 5. Polypedilum illinoense: Labial plate and right paralabial plate of larva in ventral view.

Fig. 6. P. illinoense: Antenna of larva.

Fig. 7. P. illinoense: Right mandible of larva in dorsal view.

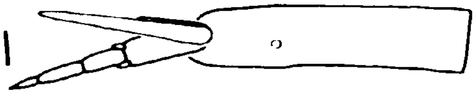
Fig. 8. P. illinoense: Comb at right posterolateral angle of eighth abdominal segment of pupa.

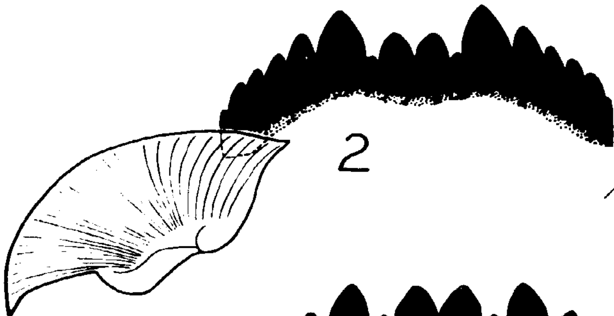
Fig. 9. Polypedilum sordens: Left mandible of larva in dorsal view.

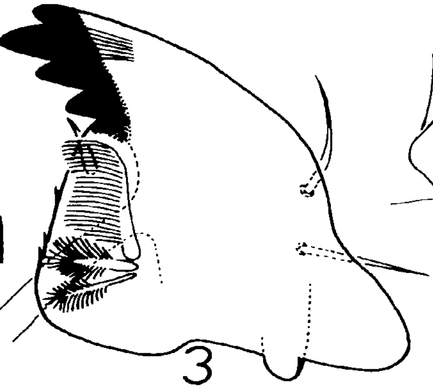
Fig. 10. P. sordens: Labial plate and right paralabial plate of larva in ventral view.

Fig. 11. P. sordens: Antenna of larva.

Fig. 12. P. sordens: Comb at right posterolateral angle of eighth abdominal segment of pupa.

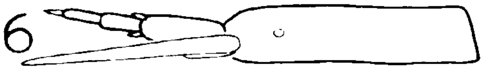

1

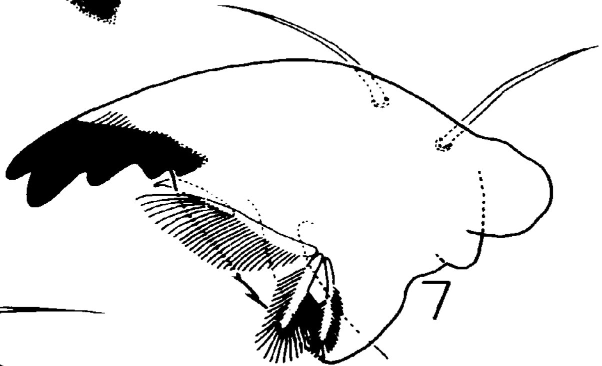

2

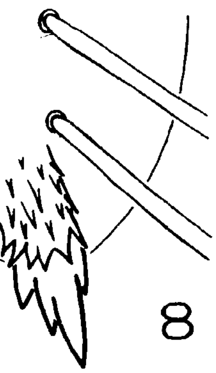

3

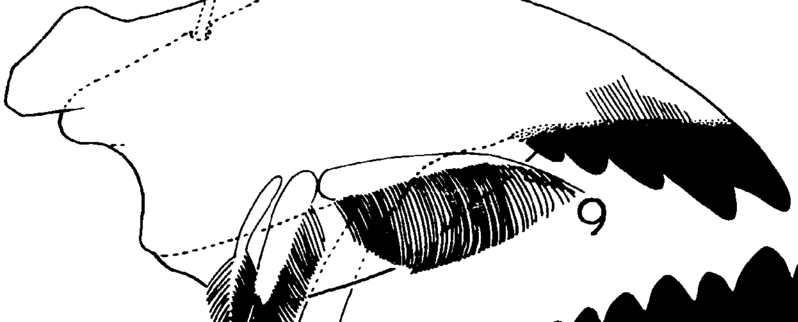

4

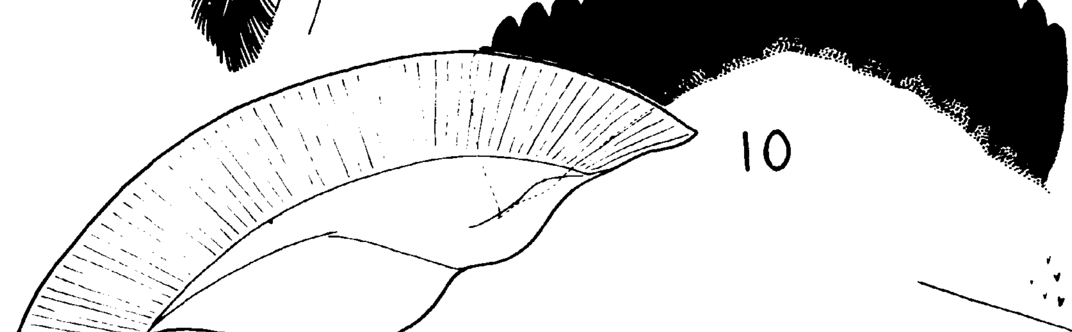

5


6


7


8


9


10


11

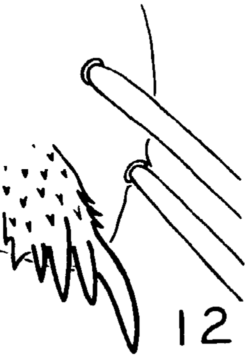

12

PLATE III

Eggs and larvae of *Hydrellia* (Ephydridae)

Fig. 1. *Hydrellia bergi*: Lateral view of whole larva.

a. pl.	Anal plate.
c. w.	Creeping welt.
p. s.	Pharyngeal skeleton.
r. sp.	Respiratory spine.

Fig. 2. *H. bergi*: Lateral view of anterior end.of larva.

a.	Antenna.
i. t.	Inferior tubercle.
m. h.	Mouth hook.

Fig. 3. *H. bergi*: Egg.

Fig. 4. *Hydrellia pulla*: Egg.

m.	Micropyle.

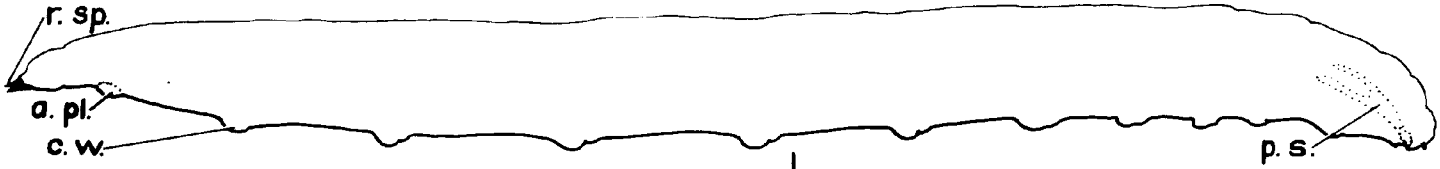
Fig. 5. *Hydrellia cruralis*: Egg.

Fig. 6. *H. cruralis*: Ventral view of posterior end of larva.

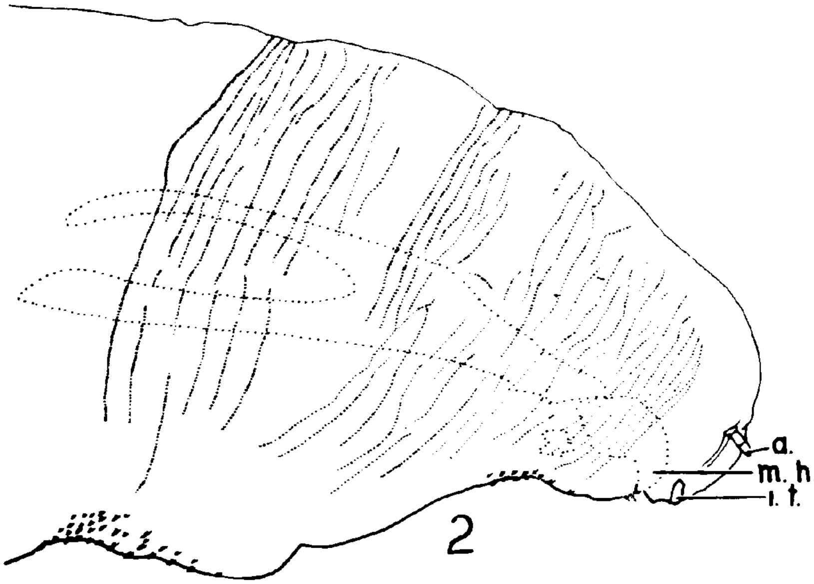
a. pl.	Anal plate.
a. s.	Anal slit.
c. w.	Creeping welt.
r. sp.	Respiratory spine.

Fig. 7. *H. cruralis*: Lateral view of anterior end of larva.

Fig. 8. *H. cruralis*: Lateral view of whole larva.

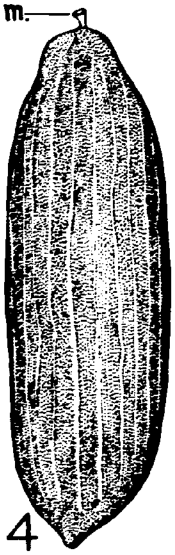


1

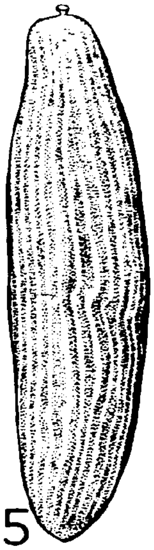


2

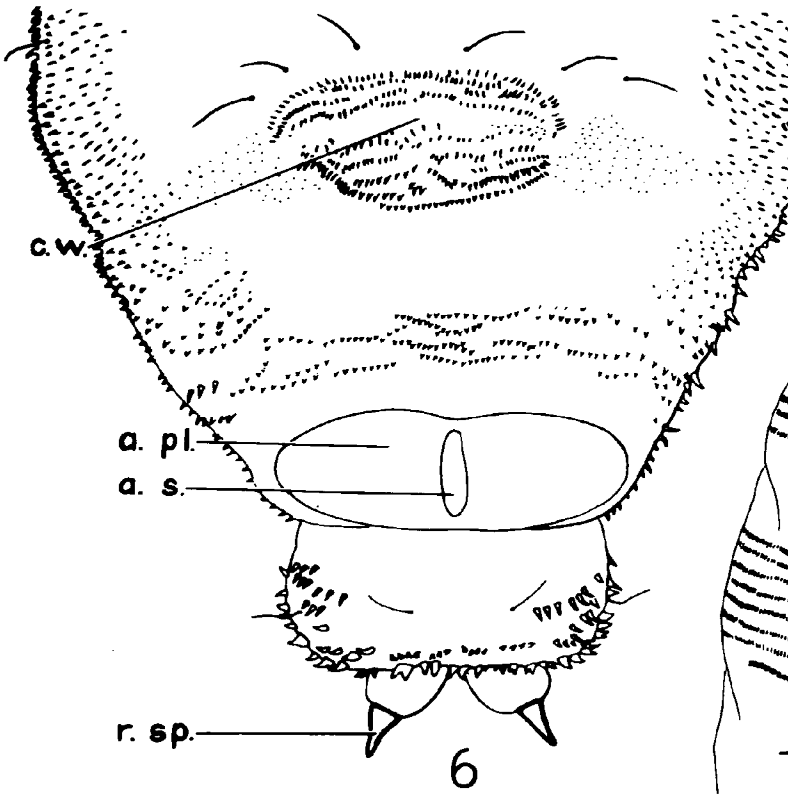
3



4

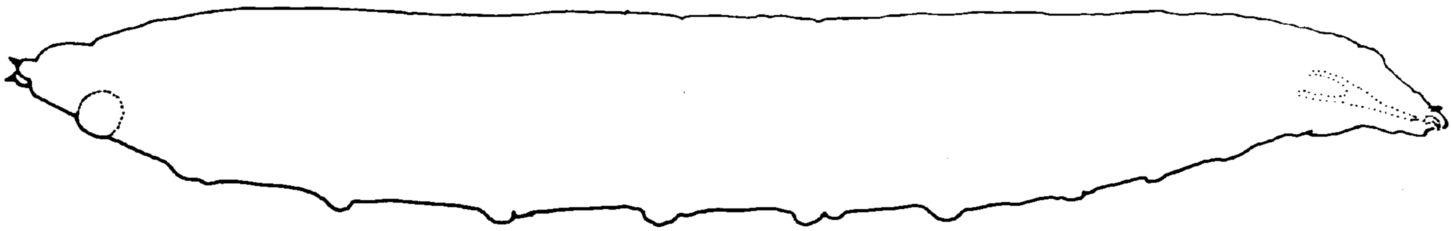


5



6

7



8

PLATE IV

Pharyngeal skeletons and mouth hooks of *Hydrellia* (Ephydridae)

Fig. 1. *Hydrellia luctuosa*.

c. s.	Cheliform spot.
d. r.	Dorsal rods.
m. h.	Mouth hook.
v. r.	Ventral rods.

Fig. 2. *Hydrellia ascita*.

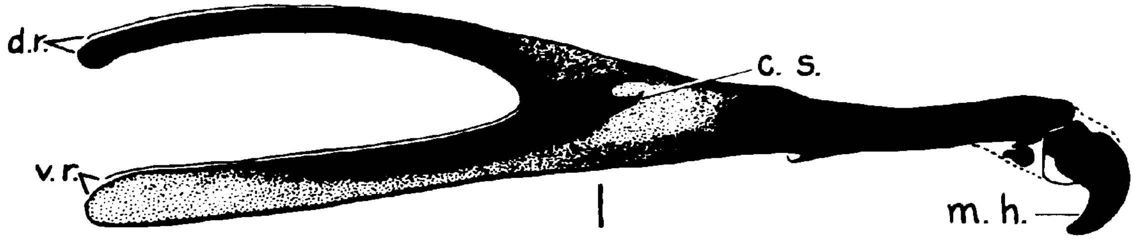
Fig. 3. *Hydrellia bergi*.

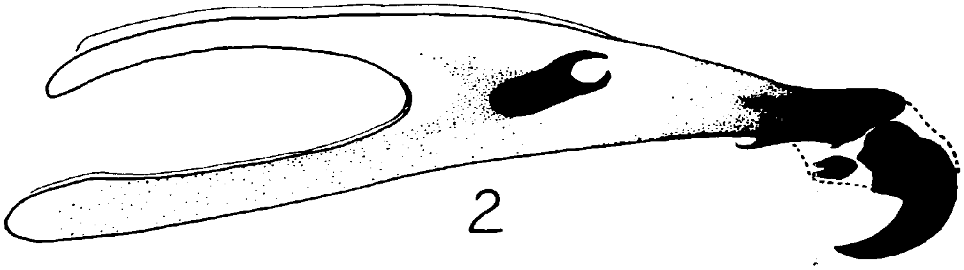
Fig. 4. *Hydrellia cruralis*.

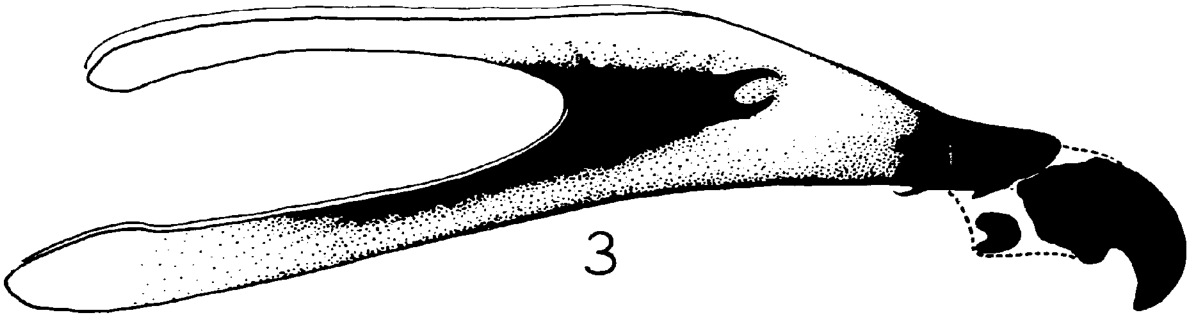
Fig. 5. *Hydrellia pulla*.

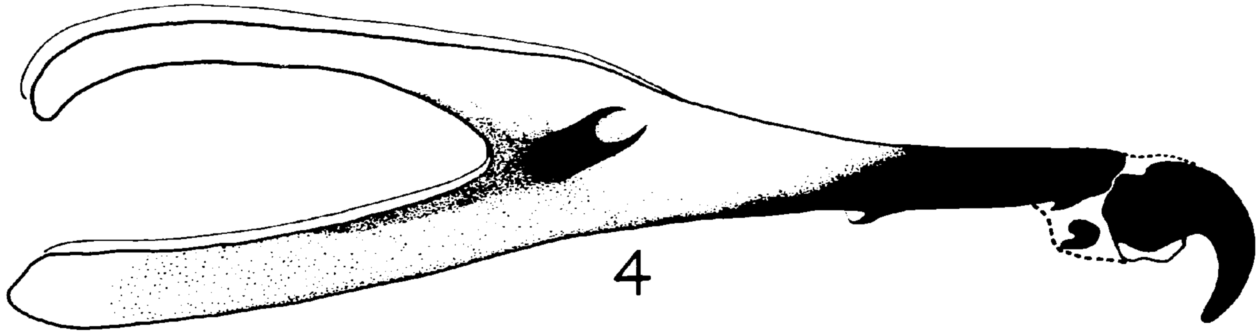
a. p.	Length of portion of pharyngeal skeleton anterior to dorso-ventral fork.
l.	Total length of pharyngeal skeleton.
s.	Breadth of shank.
v. p.	Dimension between ventral projections.
v. r.	Length of ventral rods.

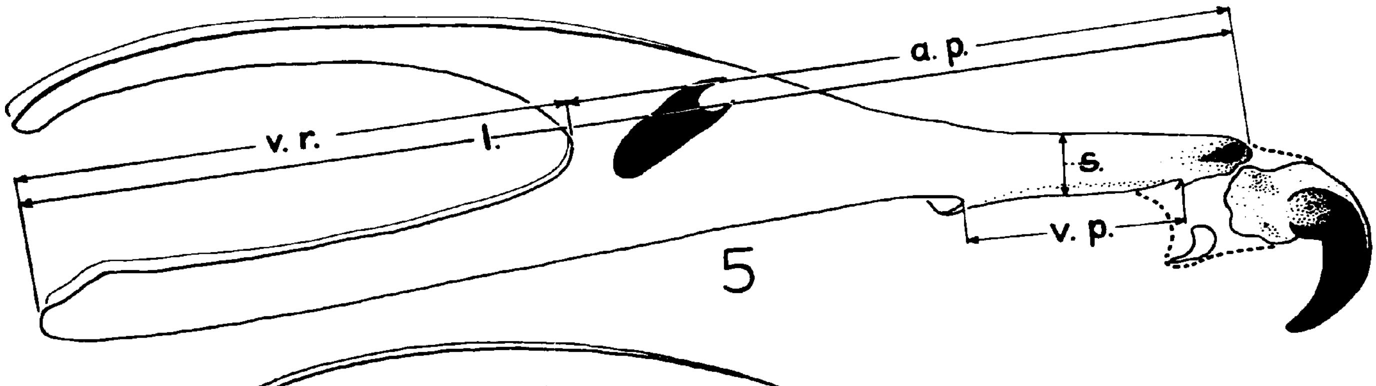
Fig. 6. *Hydrellia caliginosa*.


1


2


3


4


5

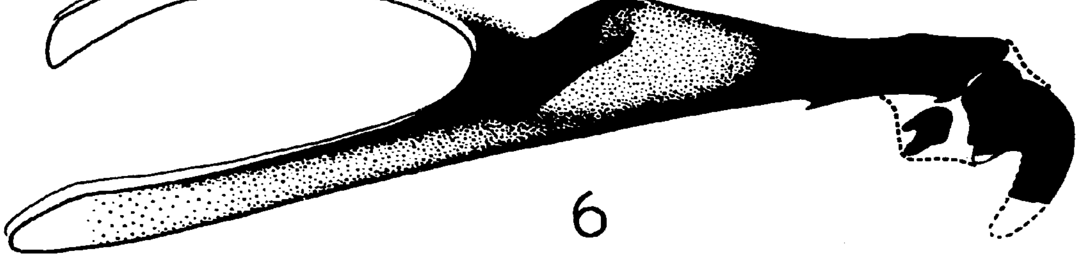

6

PLATE V

Puparia of *Hydrellia* (Ephydridae)

Fig. 1. *Hydrellia luctuosa*.

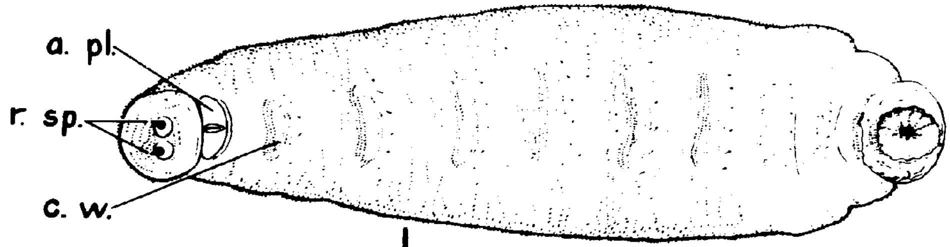
a. pl.	Anal plate.
c. w.	Vestige of larval creeping welt.
r. sp.	Respiratory spines.

Fig. 2. *Hydrellia ascita*.

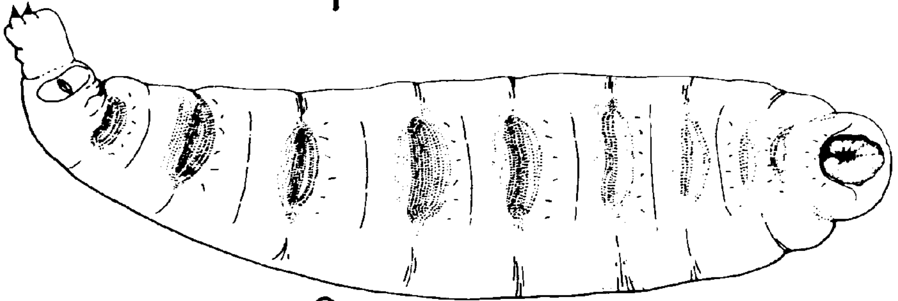
Fig. 3. *Hydrellia bergi*.

Fig. 4. *Hydrellia cruralis*.

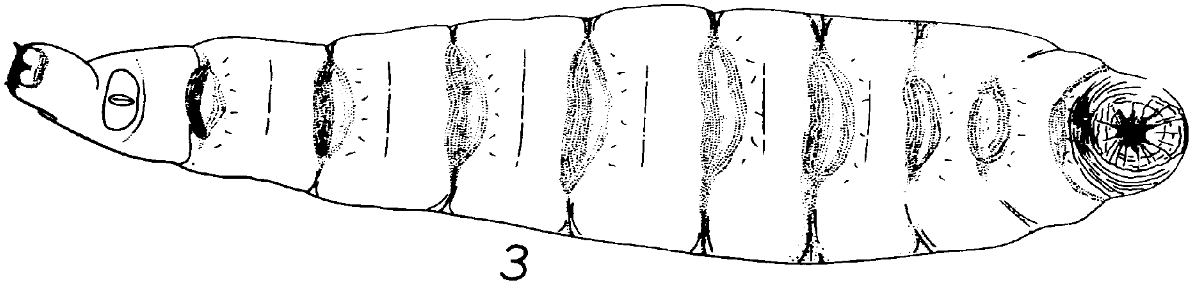
Fig. 5. *Hydrellia pulla*.



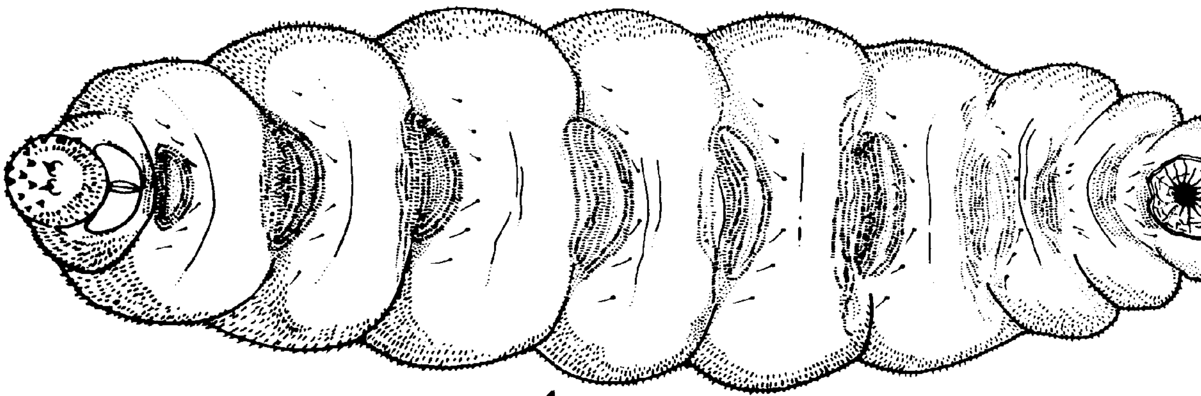
1



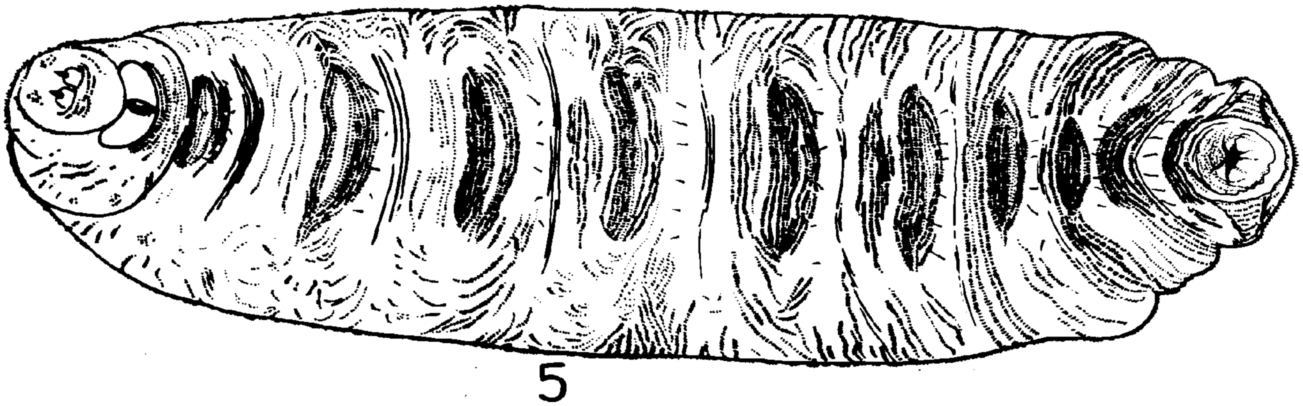
2



3



4



5

PLATE VI

Immature stages of *Notiphila loewi* (Ephydridae)

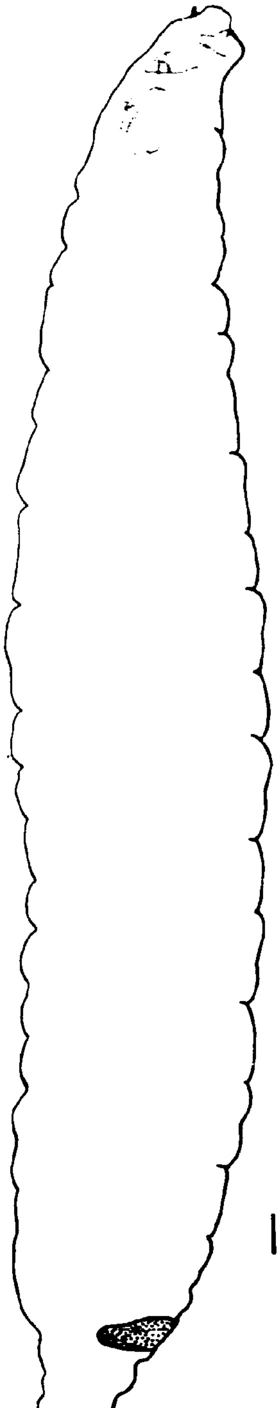
Fig. 1. Lateral view of larva.

Fig. 2. Pharyngeal skeleton and mouth hooks.

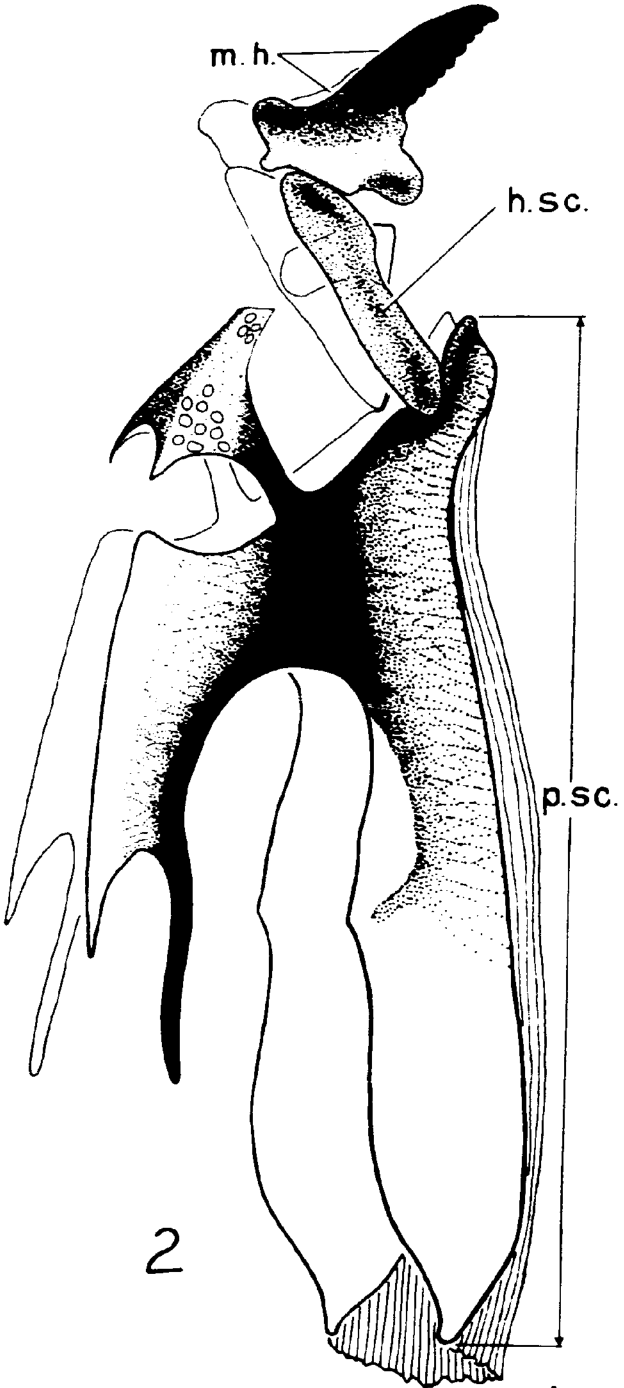
h. sc.	Hypostomal sclerite.
m. h.	Mouth hooks.
p. sc.	Pharyngeal sclerite, showing total length.

Fig. 3. Lateral view of puparium, attached to root.

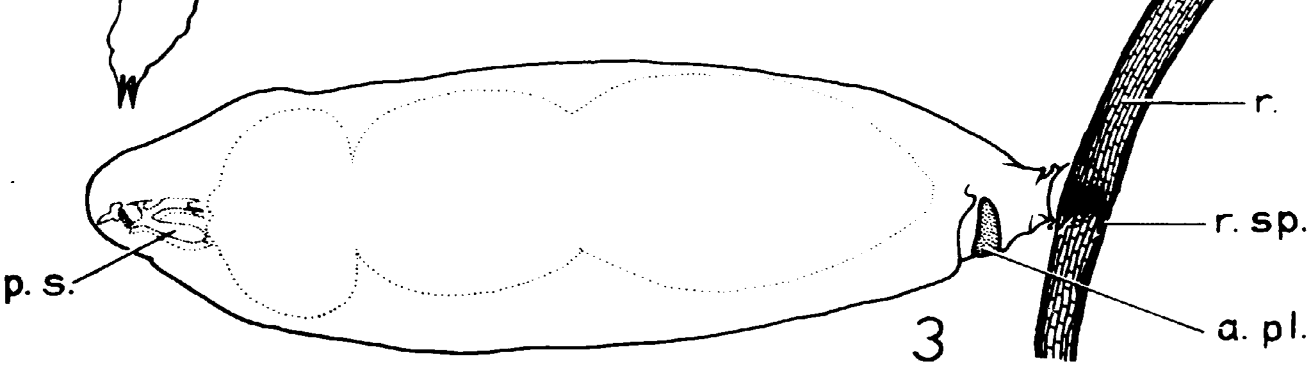
a. pl.	Anal plate.
p. s.	Pharyngeal skeleton.
r.	Root of *Potamogeton*.
r. sp.	Respiratory spines.



1



2



3

NAME AND ADDRESS	DATE