HILGARDIA

MIDGES ASSOCIATED WITH CALIFORNIA RICE FIELDS, WITH SPECIAL REFERENCE TO THEIR ECOLOGY (DIPTERA: CHIRONOMIDAE)

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INTRODUCTION

ACCORDING TO Jones *et al.* (1950)[3] rice was first grown commercially in California in 1912. Until recently this crop was apparently free of insect pests. As indicated by de Ong (1922) and Lange *et al.* (1953) there were occasional outbreaks of the rice leaf miner (*Hydrellia griseola* Fallen) in 1922 and 1953. In 1959 a potential rice pest, the rice water weevil (*Lissorhoptrus oryzophilus* Kuschel), was discovered in the northern part of the Sacramento Valley. Most of the work combining entomology and rice culture in California, however, has been concerned with the problem of mosquito breeding in rice fields.

Although chironomids have long been recognized as the predominant insects in and about rice fields, it was not until 1953 that plant injury by midge larvae was reported. At this time, severe damage to rice seeds and young seedlings by feeding of the larvae was observed in the Stockton area. Sporadic evidence of injury by the larvae was noted again in 1954, but losses were less than in 1953.[4]

The scarcity of information concerning the Chironomidae in California, as well as the indication that some species were of economic importance in rice culture, served as the stimulus for the present investigation which was begun in 1955. The objectives were to determine which species were actually inhabitants of rice fields, the ecological niche or role they occupied, and their effect on the rice plants. The field work, which extended through the summer

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of 1958, was concerned principally with the ecological relationships of the aquatic stages. Observations and tests were made to discover possible correlations between certain environmental factors and the observed variations in chironomid populations of different fields, particularly the differences noted between first- and second-year fields.

REVIEW OF LITERATURE

Although many publications are concerned with members of the Chironomidae, relatively little is known about them in light of the fact that they are of world-wide distribution and are among the most abundant insects. Most early publications were either taxonomic or morphological studies which usually omitted the ecological information.

Since almost all fresh-water habitats support chironomids, aquatic surveys necessarily include information on the relationships of the larvae and their environments. Among the earliest of these surveys in the United States was that of Walnut Lake, Michigan, by Needham (in Hankinson, 1908). An outstanding faunal study was that of Muttkowski (1918) in which he recorded 35 species of chironomids from Lake Mendota in Wisconsin. Despite the fact that he included the Ceratopogoninae which subsequently have been elevated to family rank as the Heleidae, midges still constituted the major part of the benthic fauna. Lundbeck (1926a) stressed the importance of chironomids in the bottom fauna of lakes of northern Germany and was among the first to demonstrate graphically the seasonal variation in the larval population of these lakes. Eggleton (1931) observed similar fluctuations among midge larvae in his survey of the bottom fauna of various lakes in Michigan and New York. Chironomids were found to be among the most abundant organisms reported by Crisp and Lloyd (1954) in their survey of woodland mud flats in England. Brues (1927, 1928) observed numerous larvae of *Chironomus* sp. in the mud of shallow thermal pools or hot springs at temperatures ranging to 120° F.

Studies dealing with the life history or biology of a single species which have contributed important ecological information are: Branch (1923) on *Chironomus cristatus* Fabr.; Sadler (1935) on *Chironomus tentans* Fabr.; and Rempel (1936) on *Chironomus hyperboreus* (Staeger). These studies, however, all were concerned with large mud-dwelling species, which had slight effect upon higher aquatic plants. Kettisch (1936–37) reported on a small plant-eating form in his treatment of the larvae of *Cricotopus trifasciatus* Panzer.

Finally a number of papers have been devoted primarily to the populations of chironomids in different ecological situations. Fellton (1940) discussed the biology of 13 species breeding in recently created lakes at the site of the New York World's Fair of 1939. Miller (1941) studied the distribution and ecology of 50 species of chironomids in Costello Lake of Ontario, Canada. Lindeman (1942a) contributed to the knowledge of seasonal distribution and biology of midges in a senescent eutrophic lake in Minnesota. The intimate relationship of nine species of chironomid larvae with *Potamogeton* was investigated by Berg (1950). Roback (1955) reported on the ecology of 12 species of midges inhabiting a cold spring in Massachusetts. A comparative

study of chironomids from many diverse bodies of water was also done by Roback (1957). In addition, this paper presents the most comprehensive treatment of the taxonomy of the larval stage since those of Johannsen (1937*a*, *b*). Mundie (1957) made a major contribution in his investigation of the ecology of Chironomidae in storage reservoirs in England. The work of Thienemann (1954) presented an essentially complete treatment of the wide variety of ecologic situations in which the Chironomidae have been studied. However, data from only one investigation of midges in rice fields of southern Europe are included. Thienemann (1954; pp. 540–543, 746) listed the species of chironomids from rice fields of southern Sumatra and mentioned a study in west Java in which the larvae were used as food for carp in rice fields. The economic importance of two species of chironomids in rice fields of France was compared and the harmful activities of larvae of *Cricotopus trifasciatus* Panzer were discussed by Risbec (1952).

Concerning information on the family in California, Townes (1945) indicated locality records for the state in his revision of one tribe within one subfamily. Wirth and Stone (in Usinger, 1956) also included those species reported from California and provided some general life history notes as well as keys to the genera. The tribe Chironomini of the subfamily Chironominae of California has been revised recently by Sublette (1960).

MATERIALS AND METHODS

Adult midges were obtained for this investigation by several methods. Many were captured when flushed from vegetation along margins of rice fields and from mating swarms over or near the fields by use of the conventional aerial net.

Emergence Traps

A total of 3,651 midges was taken in 12 emergence traps placed in rice fields. Four traps were low pyramidal modifications of the funnel trap used by Brundin (1949) (fig. 1). The framework was constructed of 2 inch × 2 inch redwood and was covered with no. 16 mesh copper screen. Each trap was 6 inches high and had basal dimensions of 2 feet × 2 feet. A mason-type quart jar, the bottom of which was replaced by nylon cloth, was fastened into an inverted jar ring at the opening in the top of the trap. By removing the jar and capping it under water, both adults and pupal exuviae were obtained without loss. One of these large traps was placed in each of the four fields studied. These pyramid traps were held at the proper water depth by two redwood stakes attached to opposite sides. The framework of the large traps served as the point of attachment for maximum-minimum thermometers. One disadvantage of these traps in rice fields was that they crushed the rice and other emergent vegetation down into the water, thus considerably modifying the immediate habitat.

The other eight emergence traps were smaller and were designed to sample habitats of limited size without greatly altering the environment (fig. 2). They had an inside diameter of 6 inches and covered only 28 square inches of substrate. These traps were made by removing the bottoms of large-mouthed, one-gallon jars and by fitting cones of 40-mesh-per-inch copper hardware
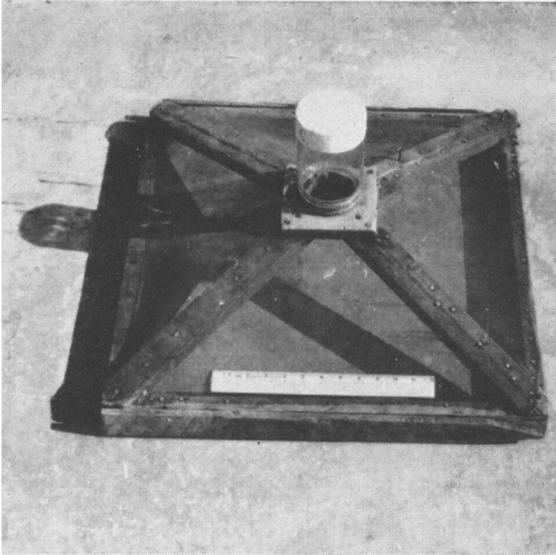
Fig. 1. Modified funnel-type emergence trap (base 2 ft. × 2 ft.) used to obtain newly-emerged adult midges and pupal exuviae.
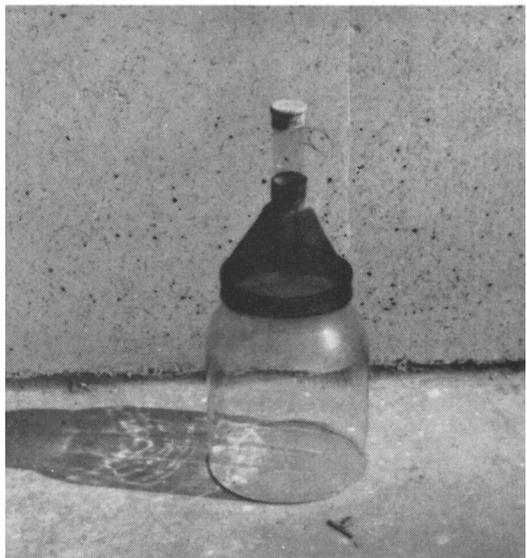

Fig. 2. Emergence trap made from 1-gallon jar (6-inch inside diameter), for obtaining newly-emerged adult midges and pupal exuviae.

cloth to the tops of the resulting cylinders. A stainless steel tube or collar 1 inch long and 1 inch inside diameter was soldered into the apex of each cone. The removable portion of this type of trap was made by replacing with nylon cloth the bottom of a plastic Lusteroid centrifuge tube 3½ inches long and slightly less than 1 inch diameter. With the plastic tube inserted in the collar, the jar was forced into the mud until the lower half of the plastic tube was under water. The tube could be removed and the lower end corked under water retaining the pupal exuviae in the water and the adults above it.

At the first of each season an attempt was made to maintain three small traps and one large one in each of the four fields studied, but the numbers taken were too great to count before the midges died and deteriorated. Thus, for most of the season one large and two smaller traps were used in each field. Initially, muskrats destroyed many of the nylon coverings of the tubes and jars making it necessary to cover them with cones of poultry wire.

In the laboratory, the plastic tubes containing the newly emerged adults were uncorked carefully over Petri dishes to remove the water and pupal exuviae and then quickly recorked with dry stoppers to prevent the escape of the adults. The loss by such transfer was negligible. The jars from the large traps were emptied into a white enamel pan. With an aspirator adapted from a small Japanese-built vacuum cleaner and powered by flashlight batteries, the adults were removed into a plastic aspirator tube. The aspirator tubes and the dry tubes from the smaller emergence traps were placed in a large cyanide jar to kill the adults. After removal of all dry adults, the emergence trap tubes and jars were washed out into their respective dishes or pans in order to recover pupal exuviae or floating adults which may have adhered to the sides of the tubes or jars. Both adults and pupal exuviae were counted with the aid of a dissecting microscope and most were saved as pinned specimens or preserved in 70 per cent alcohol for slide material.

Light Traps

Most of the adults were taken in a modified New Jersey mosquito trap as developed by Mulhern (1942) and adapted for direct current from a 6-volt automobile battery (fig. 3). This trap was suspended from a tripod which could be placed in the rice fields a considerable distance from the field margins. It soon became apparent that wind was a major deterrent to successful light trapping. In order to avoid wind difficulty when using the light trap, a sheet anchored by two stakes was used as a windbreak. In addition to those entering the trap, many midges settled on the sheet from which they were taken with the flashlight-vacuum aspirator.

Collecting Larvae

Larvae were easily obtained, but one problem, never resolved in this study, was that of a sampling method for obtaining accurate quantitative data. Samples of all types of aquatic vegetation from algae to higher plants were taken and in almost all instances, the larvae were so abundant that it was impossible to count them. Since the mud-dwelling forms were discovered to be limited principally to the upper 2 inches of relatively soft watery ooze, the shallow-water bottom sampler designed by Kellen (1954) proved ideal for

collecting them. Each mud sample was strained through a screen of 48 meshes per inch and the larvae were then washed into a collecting jar. In the laboratory, the larvae were either preserved in 70 per cent alcohol for slide mounts or used in attempts to rear adults.

Rearing Larvae

One necessary phase of the investigation was an accurate association of the larvae, pupae, and adults of the different species present in rice fields. Only 18 of the 30 different species taken in the emergence traps were successfully reared by the writer. Table 1 shows that rearing chironomids was not as easily accomplished as the literature often indicates. Of the 680 rearings attempted, only 183 (27 per cent) developed into adults. Roback (1957) obtained similar results in that only 266 (25 per cent) of 1,050 rearings attempted were successful. One complication involved the necessity of retrieving the larval and pupal exuviae. The rearing containers had to be small enough to permit recovery of these structures, yet large enough to supply sufficient oxygen and food for the larvae as well as to avoid rapid and extreme temperature changes. In 1955 and 1956 many different types of rearing containers were tried. Among these were glass test tubes, perforated plastic centrifuge tubes to permit water movement and aeration, finger bowls, small flat caster dishes, jelly cups, plastic cups, and Petri dishes. A few individuals were reared in each of these, but by far the most practical container was the Petri dish. This
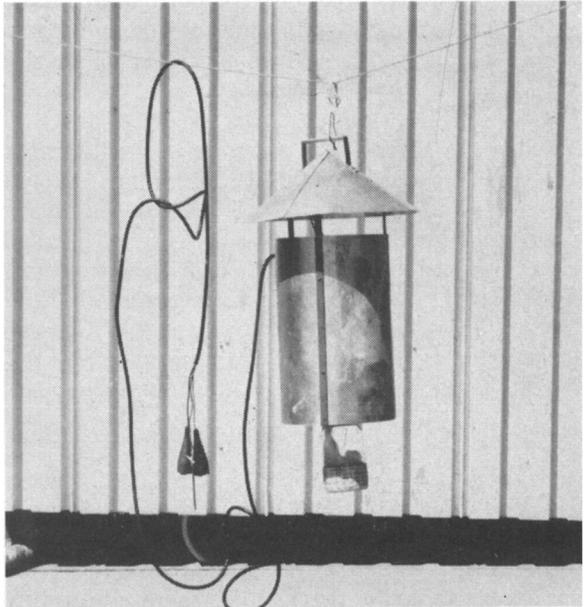

Fig. 3. Modified New Jersey mosquito light trap for obtaining adult midges in and near rice fields.

TABLE 1

DATA ON THE REARING OF CHIRONOMIDS IN THE LABORATORY

Year	Rearings attempted	Mortality of immature stages and successful rearings					
		Larvae losses		Pupae losses		Adults reared	
		Number	Per cent	Number	Per cent	Number	Per cent
1955.................	35	12	34	15	43	8	23
1956.................	97	47	48	22	23	28	29
1957.................	128	67	52	34	27	27	21
1958.................	333	135	41	120	36	78	23
1959.................	87	26	30	19	22	42	48
Total.............	680	287	42	210	31	183	27

was 20 mm deep and was covered with nylon organdy attached to rings of cardboard which fit snugly yet were easily removable for capturing newly emerged adults.

The use of algae from the fields for food created the problem of contamination by larvae other than the one selected for rearing. To avoid this, prepared food material was tried. Stage *et al.* (1952) reported success in rearing mosquitoes using ground dog food, and also yeast and powdered milk. Sadler (1935) observed that *Chironomus tentans* thrived on dried buttermilk. None of these items proved satisfactory in the present investigation, since in most instances the material fermented and the larvae died. Finally a stock culture of algae and debris from a pond and from the American River was used successfully as food for the larvae. This material was examined carefully for contaminants before use and was used over again after each successful emergence.

Although no accurate records of temperature were kept on the rearings, it was found that during the extremely warm part of the summer greater success was attained by placing the larvae in cool locations. At the University of California at Davis, this was a coldroom maintained at a temperature of 60° F, and on the Sacramento State College campus a recently constructed controlled temperature room in which temperatures ranged between 65° and 78° F. It was observed that in cooler environments the larvae retained their normal coloring better and more of them survived. However, development appeared to be slower than in those which completed development at temperatures ranging from 82° F to 104° F in the laboratory.

Undoubtedly larvae of different species vary in their ability to withstand oxygen deficiencies brought about by temperature increases. It had been hoped that experimental work concerning temperature and dissolved oxygen ranges of tolerance of the larvae could be done, but unfortunately determinations for these factors were not possible in this investigation. Walshe (1947b and 1950) suggested that hemoglobin present in some larvae enables them to feed and develop in an environment low in oxygen, and also to recover from oxygen lack. It was observed in rearing larvae for this study that those species lacking hemoglobin were much more likely to succumb under conditions of

excessively high temperatures or decomposed plant material included as food than those species possessing the pigment.

One explanation of the high larval mortality was the use of immature larvae. These were used frequently because they appeared to be species encountered for the first time. The larval food supply appeared responsible in part for high mortality of the pupae. Many pupae developed almost to the point of emergence, but then apparently lacked the vitality to emerge from the exuviae at the water surface. They struggled rather violently for a considerable period of time beneath the surface film and then settled feebly to the bottom of the rearing dish and died. In general, the most successful rearings were accomplished with larvae of the last instar in Petri dishes using stock algae and debris as food and for tube building and at a water temperature of 60° to 65° F.

Slide Preparation

During this investigation, 453 slides were prepared. Most of these were of larvae, pupae, and the exuviae of reared specimens. However, slides also were made of adult genitalia, a few egg masses, and adults which were water soaked and could not be pinned. Initially several types of mounting media were used, but that of Hoyer was finally adopted because it permitted rapid mounting of specimens directly from 70 per cent alcohol. A few crystals of iodine were added to this medium as a stain to give greater contrast in the transparent exuviae. Although Hoyer's is not a permanent medium, those mounts which had the cover slips sealed with nail polish have remained in satisfactory condition for several years.

Measurement of Physical and Chemical Properties of the Water

At different stages of this study the physical and chemical properties of the water of rice fields were measured and recorded. Both the water temperature and that of the mud at the water-mud interface were measured early in the study by two 24-hour thermographs manufactured by the Foxboro Company. The leads of these were placed well out in the borrow pit of the rice check and the recording devices were located on one end of an open lattice type bridge across the check. Later in the study Taylor maximum and minimum thermometers were employed. The pH of the water was determined by the electrometric method using two different models of Beckman pH meters. For the most part the dissolved oxygen determinations were made by the Winkler method. In one field, however, this method failed, so that the Rideal-Stewart modification of the Winkler method as outlined by Welch (1948) was used. In order to collect the water sample from near the bottom of the check, without getting air into it, a vacuum pump similar to that shown in figure 56 of Whipple *et al.* (1927) was used. Water hardness was tested by both the La Motte soap method and by the Schwarzenbach Compleximetric method as outlined in "Standard Methods 10th edition" (American Public Health Association 1955). Early in the study a plankton count was made using the Sedgewick-Rafter Cell method as given in Standard Methods 10th edition (*op. cit.*). Finally in 1958, chemical analyses of water samples from four different fields were made by the Affleck Laboratories of Sacramento, California. Tests were run for total solids, iron, nitrogen albumin, and nitrites.

In order to determine whether or not larvae exhibited a preference for water depth or position of substrate, four redwood stakes, hereafter referred to as varied level stakes, were constructed and placed so as to periodically sample different ecological conditions in the fields. Each stake was 2 feet long, 2 inches wide, and had seven 2-inch-square shelves placed 2 inches apart (fig. 4).

Seed Damage Determination

Seed sample plots were used in four fields in 1958 to investigate possible damage to rice seed by chironomid larvae. These consisted of rectangular wooden frames covered with 1-inch poultry fence wire and anchored by stakes in the mud. Each frame held six plastic dishes of soil taken from the same rice check in which the tray was placed. Each of the six plastic dishes was 4½ inches long, 4 inches wide and 1 inch deep, with several small holes drilled through the bottom to admit water and prevent floating during placement of the tray in the rice check. Rice seeds were soaked for 24 hours; then the viability of 50 per cent of them was destroyed by exposure to heat of 305° F for one-half hour. The 100 seeds then were put into each of the dishes. Three dishes of viable and three of nonviable seeds were placed in each tray. Small rectangular pieces of fine hardware cloth were fitted into each dish to keep the seeds from floating when the tray was being submerged in the water. At one-, two-, and three-week intervals, two dishes, one of viable seeds and one of nonviable seeds, were removed from each field and the contents strained through a 48-mesh-per-inch screen for examination in the laboratory.

Fig. 4. Varied-level stake used to investigate larval preference of water depth and substrate position in different microhabitats of rice fields.

Algae Samples

In order to determine whether or not there was a correlation between the number of larvae developing successfully and the species of algae in the different fields, algal samples from a variety of habitats were collected every two weeks throughout the growing season of 1958. Identification to the generic level was made from temporary slide mounts in the laboratory.

ENVIRONMENTAL FACTORS OF RICE FIELDS

The rice fields in which the present investigation was conducted were located near Davis, Yolo County, and north of Sacramento near the community of Rio Linda, California. The initial work was done in a first-year field on the Frank Chiles Ranch, approximately three miles northeast of Davis. This field had alkaline soil and previously had been used for pasture. In fact, Mr. Chiles had never known it to have been cultivated. A deep well located near the west edge of the field provided the necessary water. Rice was not grown again on this land after the 1955 season.

In 1957 when comparative emergence trapping was begun, three of the four fields in which traps were placed were located approximately four miles west of Rio Linda. Field A, a first-year field south of Del Paso Road, was owned and operated by Jacob Bolen. Field B, a second-year field located on the east side of El Centro Road, also was owned by Mr. Bolen. Field C was a first-year field on the west side of El Centro Road and was owned and operated by E. D. Willey and Sons. Field D was a second-year field located five miles northeast of Davis and was operated by Woodland Farms, Incorporated.

Since all of these fields were removed from rice cultivation in 1958, four other nearby fields were selected for study during the second season of emergence trapping. Field E was a first-year field located west of former Field A on Del Paso Road and was owned by Jacob Bolen. Field F, a second-year field, was directly across Del Paso Road from Field E and belonged to John Waraas. Field G, a first-year field, was due north of the former Field C on the west side of El Centro Road, and was owned by E. D. Willey and Sons. Field H, a second-year field operated by E. Justin Snyder, was located four miles northeast of Davis.

The water supplying all of the fields investigated in 1957 and 1958 originally was pumped from the Sacramento River. The principal variants in water characteristics between fields were introduced during the distribution of the water to the fields. These were the varying length of time that the water remained in the canals while flowing to the different fields, and the fact that some of them received water that already had passed through either an alfalfa field or another rice field.

Of the water characteristics investigated in the present work, turbidity was discontinued because determinations revealed a much greater variation within a single check and certainly within one field than existed between two fields. However, Field D near Davis was characteristically turbid. Suspended particles of mud were responsible for this condition which was observed over the entire field throughout the 1957 season. The cause of the muddiness was never determined. The large populations of carp and crayfish may have roiled

the water, but these were present in all other second-year fields and most of the first-year fields as well. The usual condition in other rice fields was clear water in the channels and borrow pits with fairly rapid flow above and below the weir boxes. Observed turbidity was confined to water trapped in check corners or in dense beds of aquatic weeds that had been sprayed with 2, 4-D. Although clear, the water in Field B turned brownish toward the end of August and the first of September. No chemical analysis was made, but according to Whipple *et al.* (1927), this water is colored by iron which increases in amount as the dissolved oxygen of the water decreases.

In 1955, measurement of the physical-chemical factors of the water was emphasized. Once each month from May through August, water samples were
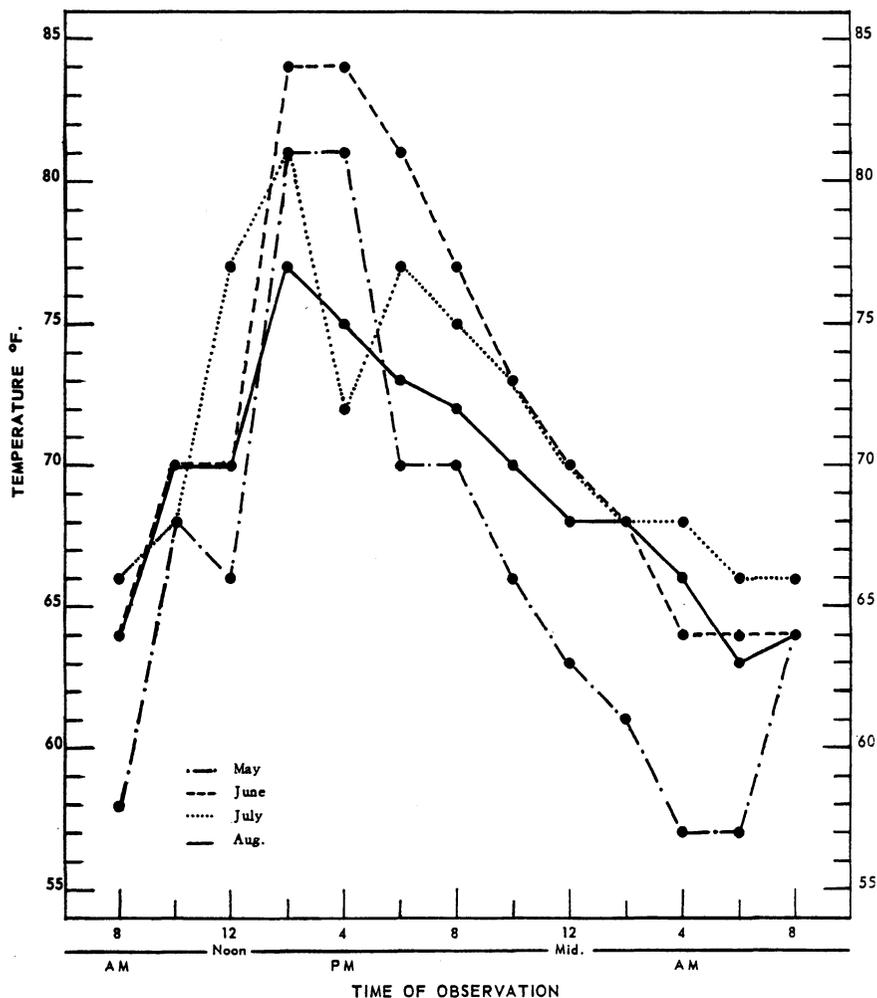
Fig. 5. Water temperatures in rice field near Davis, taken at 1-foot depth, once each month of 1955 season.
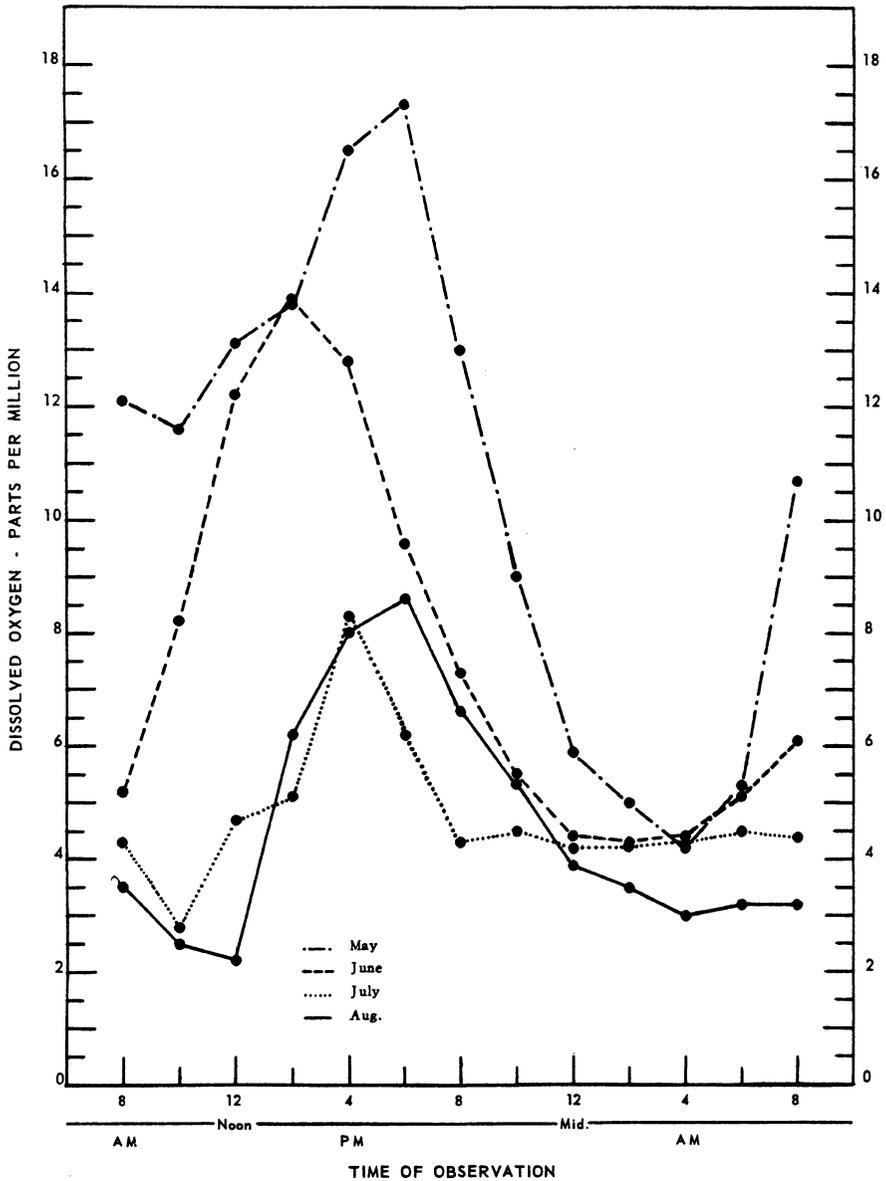
Fig. 6. Dissolved-oxygen readings of water in rice field near Davis.
Samples taken at 1-foot depth, once each month of 1955 season.

taken for tests every two hours during a 24-hour period. Tests were made for temperature, dissolved oxygen, pH, and total hardness (figs. 5 and 6). In addition, plankton counts were made during the sampling on May 25 and 26.

Some water conditions appeared comparatively stable for individual fields whereas others exhibited a general season trend or pattern in all of the rice

fields. The characteristic alkaline reaction (pH 8.1) of the well water remained relatively constant for the Chiles' field and was not observed in river water in the other fields. Also the well water maintained a total hardness of approximately 266 ppm, which was considerably higher than that of the moderately hard Sacramento River water (table 2). The values for pH and hardness of river water tested in the present study were in agreement with the pH of 7.2 and hardness of 124 ppm observed by Gerhardt and Sherman (1953) in old rice fields near Nelson, California. It appears that the pH and hardness of Sacramento River water are relatively stable. Table 2 shows that these two factors were essentially the same for all four rice fields tested in 1958, with only slight variations in their values from one week to the next. It

TABLE 2

PHYSICAL-CHEMICAL DATA FROM FOUR RICE FIELDS
INVESTIGATED IN 1958

Date	Temperature max.–min. °F	Dissolved oxygen, p.p.m.	Per cent saturation temperature °F	Water hardness, p.p.m.	pH
			Field E—first-year		
July 9–10	92–72	1.9	21% at 75°	102.6	7.2
July 17–18	81–64	3.5	36.5% at 67°	102.6	7.1
July 23–24	84–67	3.9	43% at 69°	119.7	7.1
Aug. 6–7	90–73	3.4	39% at 74°	102.6	7.2
Aug. 28–29	86–69	5.1	55% at 69°	102.6	7.0
Sept. 3–4	86–68	3.8	41% at 68°	102.6	7.2
			Field F—second-year		
July 9–10	.....*	...*	....	102.6	7.0
July 17–18	.....*	...*	..........*	102.6	7.2
July 23–24	.....*	...*	..........*	102.6	7.0
Aug. 6–7	84–72	0.6	12% at 74°	119.7	7.0
Aug. 28–29	78–69	0.5	5% at 69°	102.6	6.9
Sept. 3–4	78–68	0.5	4.5% at 68°	102.6	7.0
			Field G—first-year		
July 9–10	87–70	2.4	27% at 73°	102.6	7.2
July 17–18	76–65	3.4	35.5% at 66°	102.6	7.2
July 23–24	79–66	3.5	37% at 68°	119.7	7.1
Aug. 6–7	82–72	2.7	30% at 72°	102.6	7.2
Aug. 28–29	76–68	2.8	30% at 68°	119.7	7.0
Sept. 3–4	75–67	2.5	26% at 67°	119.7	7.2
			Field H—second-year		
July 9–10	84–72	7.6	90% at 78°	68.4	7.2
July 17–18	78–66	1.5	15% at 66°	102.6	7.1
July 23–24	82–68	0.4	3.5% at 68°	85.5	7.2
Aug. 6–7	89–70	2.2	24% at 70°	102.6	7.1
Aug. 28–29	78–66	2.3	24% at 66°	85.5	7.1
Sept. 3–4	77–62	4.2	42% at 62°	85.5	7.0

* No maximum-minimum thermometer available and the Winkler Method of obtaining dissolved oxygen values failed to give results.
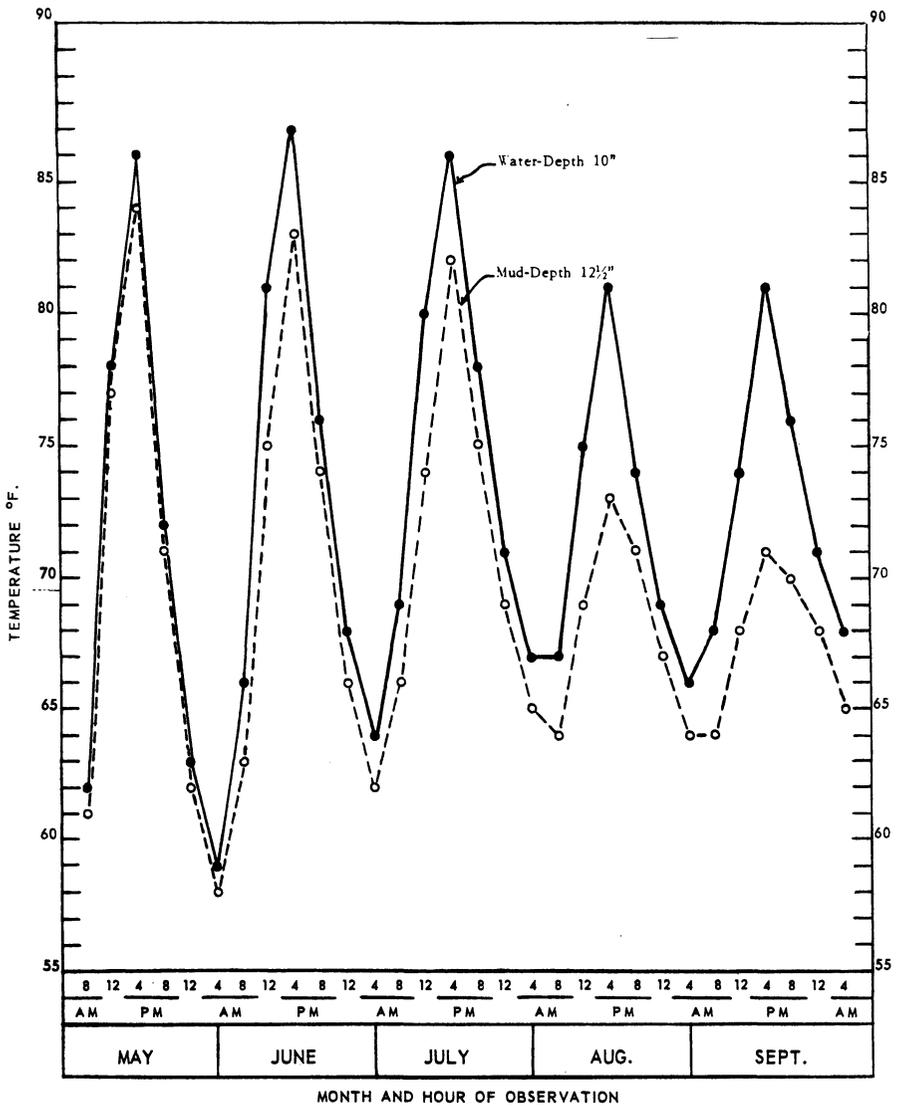
Fig. 7. Mean monthly temperatures of water and mud, for certain designated hours, in rice field near Davis, 1955 season.

cannot be concluded that pH and total hardness or alkalinity are invariably stable because as Ruttner (1953) clearly explains, photosynthetic activity may cause them to change. In bright sunlight when green plants utilize CO_2, its loss from the water results in a higher pH. This phenomenon was observed in the present investigation each month of 1955 in which tests were made. A maximum pH of 8.9 developed in the late afternoon and lasted well into the night. Changes in hardness by precipitation of calcium carbonate, which Ruttner (*ibid.*) observed to accompany photosynthesis, were not ob-

served in the present work. Minor fluctuations were observed, but the total hardness was always well above 201+ ppm which is given in the U. S. Geological Survey (1948; Paulsen 1953, p. 13), as very hard.

In contrast to the pH and total hardness, temperature and dissolved oxygen content of water in the rice fields fluctuated widely. The temperature extremes occurred in May before the emergence of the vegetation. The highest maximum temperature occurred in late June and early July and was followed by a gradual decline until the fields were drained in September (figs. 7 and 8). The diurnal temperature cycle in which the maximum temperature was reached at 4 p.m. and the minimum between 4 a.m. and 8 a.m. agreed with the findings of Schultz *et al.* (1956) for rice fields near Grimes, California, on August 6, 1954. Although the temperature range may vary from year to year, as observed for 1957 and 1958 (figs. 8 and 9), the sequence within this range was the same.

An aspect of water temperature impossible to measure in the present work, and which must be understood before definite relationships between larval populations and temperature can be established, was that of the temperature of the microenvironment. Smith (1954) aptly states that this is the microhabitat or the environment in which the organism actually exists and often is very different from one which we experience or investigate with conventional instruments. Figure 7 shows a lower temperature at the mud-water interface than in the water. The uniformly low mud temperatures toward the end of the rice season probably were due to shading by rice and other
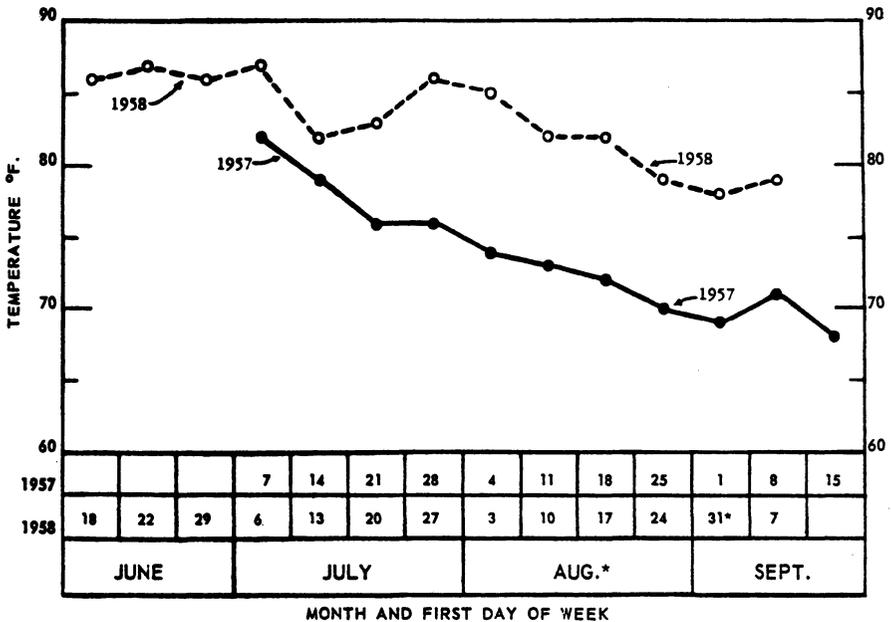

Fig. 8. Weekly average maximum temperatures of water in eight rice fields during 1957 and 1958 seasons.

vegetation. As yet little has been done in an intensive way to measure water temperatures in rice fields at different depths or under vegetation as compared with open water. An example of existing differences was noted on June 19, 1958, when the writer visited a rice field on the Miller Ranch near Liveoak, Sutter County, to investigate possible damage to rice by midge larvae. In the course of collecting samples at 10:40 a.m., two temperatures were recorded. One taken 2 inches below the water surface on top of an algal mat with the thermometer shaded was 86° F. The other taken 4 inches below the algae was 69° F. The 17-degree difference in a vertical distance of less than 6 inches indicates how widely temperatures may vary within a rice field and the inadvisability of basing conclusions on gross temperature readings.

Another physico-chemical factor in which a general pattern was demonstrated was dissolved oxygen content of the water. This value was highest in May. Then throughout the summer a decrease which was somewhat abrupt from June to July followed decay of vegetation and shading of the water by rice (fig. 6). In addition to the seasonal trend, a marked diurnal fluctuation in dissolved oxygen was observed. This showed a greater difference between maximum and minimum within the 24-hour sampling period than that observed when the different months were compared with one another. Such diurnal variations in dissolved oxygen have been reported frequently. Birge and Juday (1911; pp. 43, 55) and later Scott (1924) noted this phenomenon in several lakes in the United States. It was observed in a small pond by Iyengar (1930) and in rivers by Butcher *et al.* (1927). The last-named workers state that diatoms appeared to be responsible for the high oxygen levels since the oxygen produced by the higher green plants tended to escape as bubbles. If, as Whipple *et al.* (1927; pp. 262–64), contend, diatoms depend
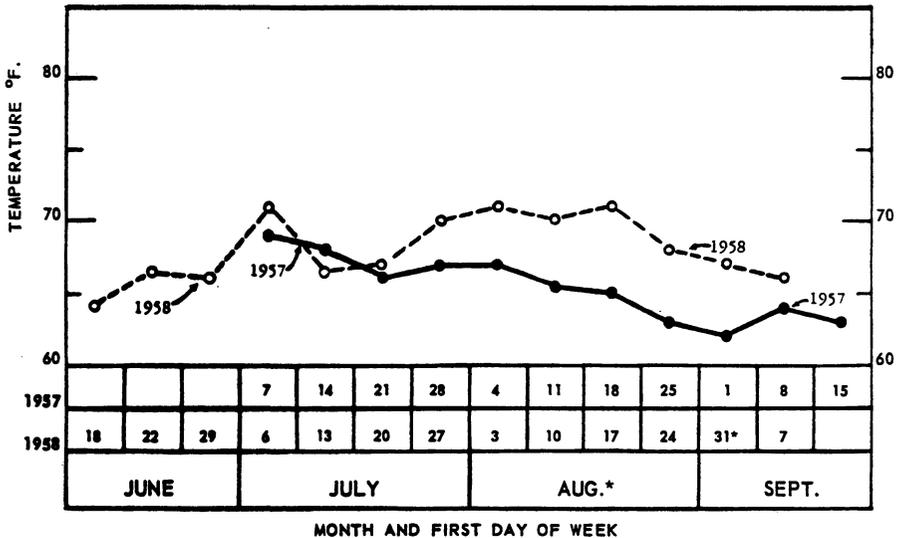

Fig. 9. Weekly average minimum temperatures of water in eight rice fields during 1957 and 1958 seasons.
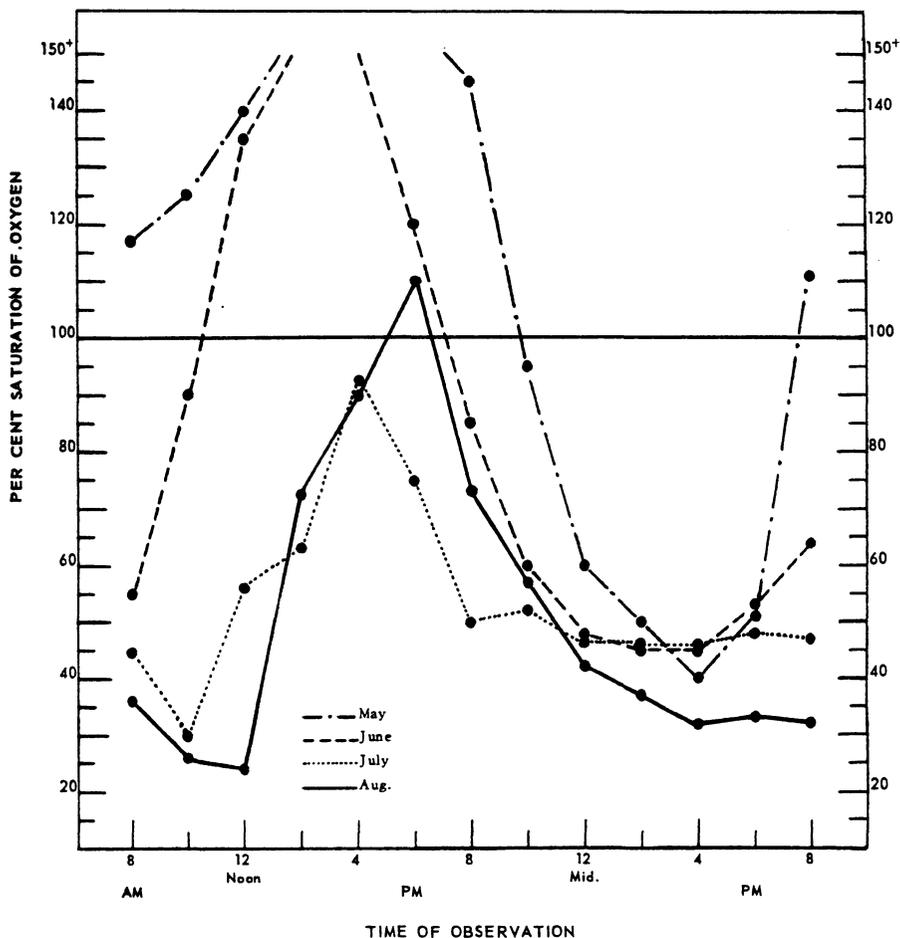
Fig. 10. Per cent saturation of oxygen in water of rice field near Davis, calculated once each month of 1955 season.

upon a bottom food supply which develops by decomposition during periods of stagnation, there is a delicate balance between these minute plants and the dissolved oxygen in the water of rice fields. As long as the water was flowing through the fields, no stagnation period was observed. Near the end of the season, however, as the water movement ceased, conditions were similar to those described by Whipple *et al.* (*loc. cit.*). The observations in this study concurred that photosynthetic activity of phytoplankton was largely responsible for the dissolved oxygen cycle in the water. Since the water samples were obtained from within an inch of the bottom in quiet water at a depth of 1 foot or more, oxygenation of the water from the air was negligible. In addition, it was noted that the dissolved oxygen readings were the lowest during the early morning hours when often the wind velocities were the greatest.

Perhaps a clearer picture of oxygen relationships is provided by figure 10 which shows the per cent saturation by month through the summer. The figures were obtained from Rawson's nomogram (Welch, 1948) which uses the dissolved oxygen content and the temperature of the water when the sample was taken, to derive the per cent saturation. Since the maximal limit of the chart is 150 per cent, some of the higher readings cannot be given. However, the minimal values for the latter part of August show the decline which normally occurs in rice fields. In general, similar conditions were observed in four other rice fields in 1958. Apparently the increased ammoniacal nitrogen from decomposition combined with increased respiration of larger green plants lowered the oxygen content of the water as was observed by Butcher *et al.* (1927) in rivers. This condition was most apparent in corners
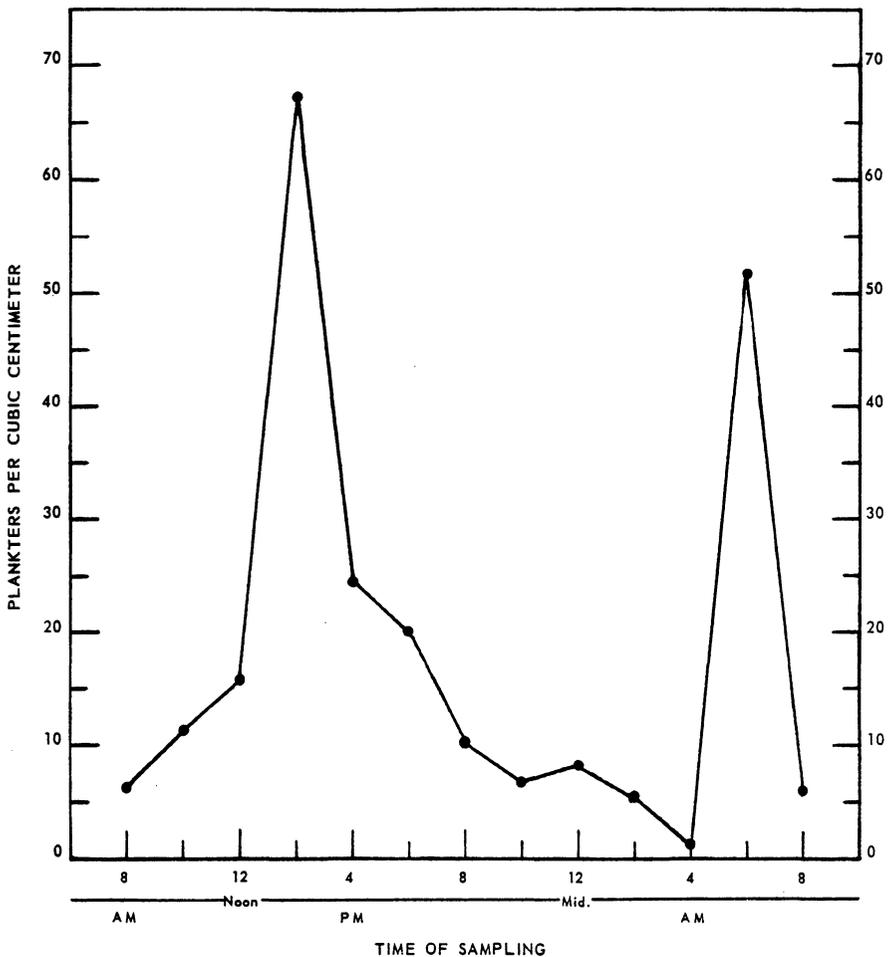

Fig. 11. Plankton count, taken at two-hour intervals May 25–26, 1955, in drainage water from one check in rice field near Davis.

and other locations in the checks where there was no water movement. It is probable the lowering of dissolved oxygen and the increase in the amount of deteriorated plant material affected the population density of midge larvae, but no direct relationship could be found.

On September 4, 1958, near the end of the rice growing season, a 1-quart sample of water was taken from each of the four fields for chemical analysis by a commercial laboratory. Tests were made for total solids, iron, albuminoid nitrogen, and nitrites. The results in table 3 show no correlation between any of the chemical factors and the age of the field. Gerhardt and Sherman (1953) found that of the dissolved solids, chlorides and sulfates were more concentrated in old rice fields whereas nitrates and iron concentrations were lower than in new fields. After extensive physico-chemical investigations, Senior-

TABLE 3

RESULTS OF CHEMICAL ANALYSES OF WATER FROM FOUR
RICE FIELDS INVESTIGATED IN 1958

Constituent	Field and constituents: (mgm) per liter			
	Field E First-year	Field F Second-year	Field G First-year	Field H Second-year
Total solids........................	240.0	270.0	260.0	260.0
Iron................................	0.1	0.2	0.2	0.35
Nitrogen (albuminoid)...............	0.08	0.04	0.04	0.08
Nitrite.............................	0.00	0.00	0.00	0.00

White (1928) concluded that no correlation existed between these factors and mosquito breeding.

According to Whipple *et al.* (1927; pp. 262–64), as the oxygen level drops and decomposition and stagnation begin to have an increased effect, more iron is liberated into the water, nitrates decrease, and nitrites increase. Table 3 indicates that Field H showed the greatest tendency toward characteristic decline since it had a greater increase in iron than the other fields. The complete absence of nitrite, however, implied that the critical level of oxygen depletion was never reached. These findings also failed to explain why the Winkler Method of dissolved oxygen determination was unsatisfactory in Field F and had to be replaced by the Rideal-Stewart modification.

From the plankton counts made early in the present study it was found that plankton movement in rice fields was essentially the same as that of streams. As can be seen from figure 11, there was a diurnal fluctuation of plankters with the greatest number in the early afternoon and a minimum at 4 a.m. Blum (1954) also observed the great increase during the day, but somewhat earlier, and a drop by midafternoon and a continued decrease to minimal values at night. This fluctuating pattern was due to the photosynthetic activity of the phytoplankton which was carried upward with the oxygen gas escaping from it. The zoöplankters probably also were carried upward at the same time. However, the abnormally high count recorded for the 6 a.m. sample cannot be explained by phytoplankton photosynthesis. Undoubtedly some disturbance of the rooted vegetation or bottom material

above the sampling site was responsible for it. Based on its plankton count early in the season a rice field more closely resembles a sluggish stream than any other natural body of water.

Jones *et al.* (1950) and Davis (1950) state that of the various types of soil used for rice growing in the Sacramento Valley, the heavy clays and adobe-clay soils are best adapted for this crop because they require less water than lighter soils to produce a crop. In addition, rice is frequently grown to leach the alkali from certain soils such as that on which this study began in 1955. All other fields investigated contained the typical heavy adobe-clay soil. However, there was a considerable difference in fertility in the different fields; the first-year fields showed greater fertility than the older ones. There also appeared to be a good correlation between soil fertility and the number of midges produced. Both Field C and Field G had heavy amounts of organic material plowed under in preceding years and it was reflected both in plant development and midge numbers. Field C had been in improved clover pasture supporting a large herd of cattle and Field G had been in pasture one year, followed by a heavy oat-vetch cover crop the next. In Field G some of this partly decayed plant material was present on the bottom of the checks most of the summer of 1958. In addition, commercial ammonium sulfate was applied to all fields at seeding time to enable the developing rice seedlings to emerge from the water earlier than the watergrass and other weeds.

Fig. 12. Cross-section of one rice check in Field E, viewed from outlet weir box. Note growth of aquatic weeds and absence of rice in cross-channel indicated by stake.

The three functions of water in rice culture (according to Davis, 1950) are to supply requisite moisture for the normal life processes of the rice plants, to control weeds, and to serve as a temperature regulator. By submergence of the land to attain these objectives, a unique aquatic environment is created. One important characteristic of a rice field is that it is a shallow temporary body of water in which many sedentary aquatic forms are unable to survive, whereas other more active species can establish themselves quickly and develop in enormous numbers. Conditions in a rice field, however, are not those presented by a shallow pond or lake because of the continual water movement during the growing season. Another important characteristic is that created by the rice plants themselves which usually form a much denser stand of emergent vegetation than that observed in natural shallow streams or ponds.

Although fields of rice appeared uniform, actually considerable variation existed within individual fields. Uneven land created the problem of weeds which, according to Davis (*op. cit.*), are best controlled by keeping the water at a depth of 3 to 5 inches on the high spots and sacrificing stands of rice in deeper water. Thus in the borrow pits from which much of the more fertile topsoil had been removed in forming the check banks, the water was deeper than in the rest of the check and supported little or no rice. That rice which succeeded in growing in the borrow pits was slower to emerge from the water and usually remained on the surface, thus providing a suitable microhabitat for many midge larvae. As the season progressed, watergrass and tall weeds shaded the borrow pits, keeping the water much cooler than in shallow areas of the fields. As the water moved through the fields, it formed definite channels across the checks from intake weir box to the outlet. Rice did not thrive in the channels, but many aquatic weeds grew in profusion and provided additional substrate for midge larvae (fig. 12).

Improper cultivation of some fields resulted in high spots where the water was only 2 or 3 inches deep. In these areas the water lost its temperature stability and was within a degree of the air temperature. This condition was unfavorable for the rice and usually watergrass became abundant. Occasionally, however, as Field F in 1958, the watergrass did not invade the shallows which remained in full sun (fig. 13). In May and early June common water nymph filled the spaces between thinly scattered rice plants. As the temperature increased in June and July, *Chara* began to replace the common water nymph. By August the latter had deteriorated and was almost completely replaced in the shallow water by *Chara*.

In the comparative study of first- and second-year rice fields, the following 16 species of aquatic plants except rice and algae were recorded from the eight fields under investigation:[5]

Marsiliaceae
   Clover fern *Marsilea mucronata* A. Br.

Salviniaceae
   Duckweed fern *Azolla filiculoides* Lam.

[5] Classification is that of Mason (1957).

Typhaceae
Common cat-tail *Typha latifolia* L.

Najadaceae
Common water nymph *Najas guadalupensis* Morong.

Zannichelliaceae
Grass wrack *Zannichellia palustris*

Alismaceae
Water plantain *Alisma plantago-aquatica* (Greene)
Burhead *Echinodorus cordifolius* (L.) Griseb.
Arrowhead *Sagittaria latifolia* Willd.
  Sagittaria calycina Engl.

Gramineae
Barnyard or watergrass *Echinochloa crusgalli* (L.) Beauv.

Cyperaceae
Common tule *Scirpus acutus* Muhl. ex Bigel.

Lemnaceae
Water lentil or duckweed *Lemna minor* L.

Onagraceae
Yellow water-weed *Jussiaea californica* (Wats.) Jepson
False loose-strife *Ludwigia palustris* (L.) Ell.

Scrophulariaceae
Bacopa or water hyssop *Bacopa nobsiana* Mason

Lentibulariaceae
Common bladderwort *Utricularia vulgaris* L.

Samples of most of these were examined in the laboratory for larvae. Seven additional weeds occur in rice fields farther north (Davis, 1950), but were not found in the present work.

Although some aquatic plants were common to all fields, there was considerable individual variation between fields of the same age as well as apparent differences between fields of different ages (table 4). Although this table indicates that water plantain (*Alisma plantago-aquatica*), burhead (*Echinodorus cordifolius*), and arrowhead (*Sagittaria* sp.) were present in all the fields, they were not equally abundant. Except in Fields A and E, aerial applications of the herbicide 2,4-D were made shortly after the vegetation had emerged from the water. Thus in the treated fields these three plants were in various stages of decay and rejuvenation. In the two untreated fields, the channels were filled with these emergent weeds of which burhead and water plantain were most numerous. This was in agreement with Davis (1950) who observed that the growth of these two plants is favored by cooler water; they are often present in large quantities in the first or intake checks where the water is cold and the stands of rice are relatively poor.

The growth of common water nymph (*Najas guadalupensis*) also was enhanced by the cooler water in the channels and borrow pits. The usual con-

dition in these places was a relatively dense growth of burhead and water plantain with the submergent common water nymph growing in dense tangles in the opening between the emergent plants. As the season progressed, the water nymph began to decline and became brown both from decay and a coating of algae.

Grass wrack (*Zannichellia palustris*) also occurred as part of the submerged vegetation of rice fields. In the more alkaline fields near Davis it was abundant, but in the other fields it was less common than the water nymph. Mason (1957) reports that it is a common species particularly in subsaline habitats.

One of the most troublesome weeds of rice fields is barnyard or watergrass (*Echinochloa crusgalli*). Its abundance depends largely upon irrigation practices. Davis (1950) states that the seed of this grass must be under water from 5 to 7 inches deep to prevent its emergence. He indicates also that it is extremely aggressive and often succeeds in growing even when good cultural

Fig. 13. Shallow part (6-inch depth) of second-year rice field (Field F). Note trap F₄ in sparse rice near stake (upper left).

practices are used. In Field D near Davis, the water level was dropped in early June and this field was soon overgrown with watergrass. In Field G there were a few shallow checks in which the watergrass was able to emerge and thrive at the expense of the rice. However, in most of the fields it flourished only on the check banks at the edge of the water and was not actually a part of the aquatic vegetation.

Bacopa or water hyssop (*Bacopa nobsiana*) occurred in small amounts in all of the fields where the rice was sparse. However, it was a relatively unimportant part of the aquatic flora, for as Davis (1950) indicates, it is present early in the season and soon disappears.

A few species of plants such as clover fern (*Marsilea mucronata*), yellow water-weed (*Jussiaea californica*), false loose-strife (*Ludwigia palustris*), and common bladderwort (*Utricularia vulgaris*) were present only in certain fields in which conditions were favorable for their growth. In those fields in which they grew, they formed a significant part of the flora.

Those plants which occurred most consistently in second-year or older rice fields were duckweed fern (*Azolla filiculoides*), water lentil or duckweed (*Lemna minor*), common cat-tail (*Typha latifolia*), and common tule (*Scirpus acutus*) (figs. 14 to 16). Both duckweed fern and water lentil appeared on the water surface early in August. They were confined to quiet water which was at least partially shaded. Cat-tails and tules first appeared as small plants toward the end of the season in first-year fields. Since they are perennial plants which develop heavy rootstocks, apparently they are able to

TABLE 4

THE RELATIVE ABUNDANCE OF AQUATIC PLANTS EXCLUSIVE OF ALGAE IN FIRST-YEAR AND SECOND-YEAR RICE FIELDS

Common names of plants	Rice fields grouped according to age							
	First-year fields				Second-year fields			
	A*	C	E*	G	B	D	F	H
Clover fern	−	++	−	−	−	−	−	−
Duckweed fern	−	−	−	−	+	−	++	++
Common cat-tail	+	+	+	+	+++	+++	+++	+++
Common water nymph	+++	++	+++	+++	+++	++	+++	+++
Grass wrack	?	?	?	?	?	+	?	+
Water plantain	+++	+	+++	+	+	+	+	+
Burhead	+++	+	+++	+	+	+	+	+
Arrowhead (two species)	+++	+	+++	+	+	+	+	+
Barnyard or watergrass	+	+	+	++	+	+++	+	++
Common tule	−	−	−	−	+	++	++	++
Water lentil or duckweed	−	−	−	−	+	?	+	+
Yellow water-weed	−	−	−	−	−	+	−	−
False loose-strife	−	−	−	++	−	−	−	−
Bacopa or water hyssop	+	++	+	+	+	+	+	+
Common bladderwort	−	−	−	+	++	−	−	−

Legend: ? Favorable habitat but none observed
          − Absent
          + Present
        ++ Moderately abundant
     +++ Abundant
* No application of herbicide.

withstand drainage and cultivation because early in June they became conspicuous in the borrow pits and channels of the second-year fields. Cat-tails were more common in the field proper whereas the tules were present in and along the margins of ditches near the fields.

The high percentage of negative emergence trap results from second-year fields in 1957 (figs. 17 and 18) indicated the possibility of a toxic agent in the water. Purdy (1924) interpreted the absence of mosquito larvae in certain rice fields near Nelson, California, as due to the presence of the blue-green alga *Tolypothrix*. Matheson and Hinman (1928) reported that *Chara fragilis* apparently was lethal to four species of mosquitoes. In a later publication (1930) the same authors explained that the harmful action of *Chara*

Fig. 14. Standing water in corner of check in second-year rice field (Field H). Note surface film of duckweed fern (*Azolla filiculoides*) and dense growth of common cat-tail (*Typha latifolia*) characteristic of older rice fields.

Fig. 15. Moving water near weir box in second-year rice field
(Field F). Note growth of common cat-tail (*Typha latifolia*).

was due to the physical effects of excess oxygen production rather than to
a toxic compound. Wheeler *et al.* (1942) observed that frozen and vacuum-
dried blue-green algae exhibited greater toxicity to mice than fresh material.
Ingram and Prescott (1954) reported cattle mortality in Minnesota due to
the toxicity of *Gloeotrichia echinulata* and *Anabaena* sp. Because of these
observations a survey of the algae in the fields and their seasonal status was
conducted throughout the 1958 season.

A seasonal succession of algae occurred in both old and new rice fields (figs.
19 and 20). The number of species in a first-year field was greater than in a
second-year field, but the dominant species in both exhibited much the same
succession pattern. Shortly after flooding, the water surface of most fields
was covered with bladder-like gelatinous masses of the blue-green alga
Gloeotrichia. This species appeared to thrive in the bright sunlight. At about
the time that the rice was 6 inches above the water the *Gloeotrichia* began to
deteriorate, and eventually most of it was reduced to a frothy scum of bubbles.
Frequently this material covered the stems and leaves of the partly emergent
higher plants.

Spirogyra first appeared in or near the weir boxes in cool, fast-moving
water. Soon it became a dominant species hanging in long strands from sup-
porting objects in the channels and borrow pits. No significant difference was
observed in its abundance in the fields of different ages.

Both *Oedogonium* and *Mougeotia* were well established early in the season in quiet, sunny locations of older fields. Here they formed characteristic algal mats. Although both species were represented in first-year fields, they were not so abundant as in older fields and did not form mats.

Cladophora was confined to cool moving water of the weir boxes or channels. It appeared later than *Spirogyra* and often grew in close association with it, but was never as abundant as the latter.

The more highly organized *Chara* appeared several weeks earlier in the older fields than in the new fields. The warm shallow water of Field F appeared particularly well suited for its growth.

Desmids and diatoms were considered as a unit because they appeared together in all samples. Figures 19 and 20 indicate a uniform population of these two groups, but undoubtedly, as Senior-White (1926) indicates, there is a fluctuation of these microscopic plants similar to that observed for larger species. The sampling method used in the present study was not sufficiently refined to distinguish any trend or variation in their abundance.

Fig. 16. Standing water (1-foot depth) in corner of check in second-year rice field (Field F). Note disintegrating algae mats on water surface and watergrass (*Echinochloa crusgalli*) and common tule (*Scirpus acutus*) on check bank.
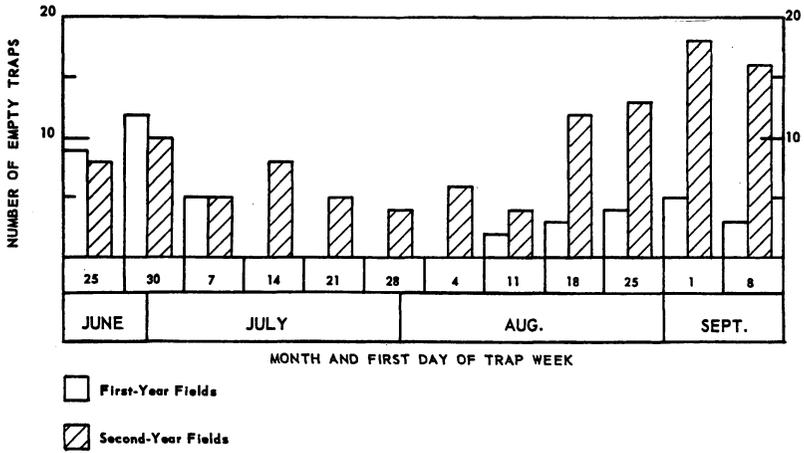
Fig. 17. Empty emergence traps (exclusive of accident) recorded from six traps in two first-year and six in two second-year rice fields, 1957 season.

Fig. 18. Empty emergence traps (exclusive of accident) recorded from six traps in two first-year and six in two second-year rice fields, 1958 season.

CYANOPHYTA (Blue-Green Algae)

Gloeotrichia sp.

Anabaena sp.
Cylindrospermum sp.

CHLOROPHYTA (Green Algae)

Spirogyra sp.

Mougeotia sp.

Oedogonium sp.
Cladophora sp.

Bulbochaete sp.
Pediastrum sp.
Hydrodictyon sp.
Scenedesmus sp.

CHAROPHYTA

Chara sp.

EUGLENOPHYTA

Euglena sp.
MISCELLANEOUS -
CHLOROPHYTA - (Desmids)
and CHRYSOPHYTA - (Diatoms)
(Considered Together)
RHODOPHYTA (Red Algae)
Compsopogon sp.

TAXONOMIC UNIT

18 22   29   6   13   20   27   3   10   17   24   31   7
JUNE   JULY   AUG.   SEPT.

MONTH AND FIRST DAY OF WEEK
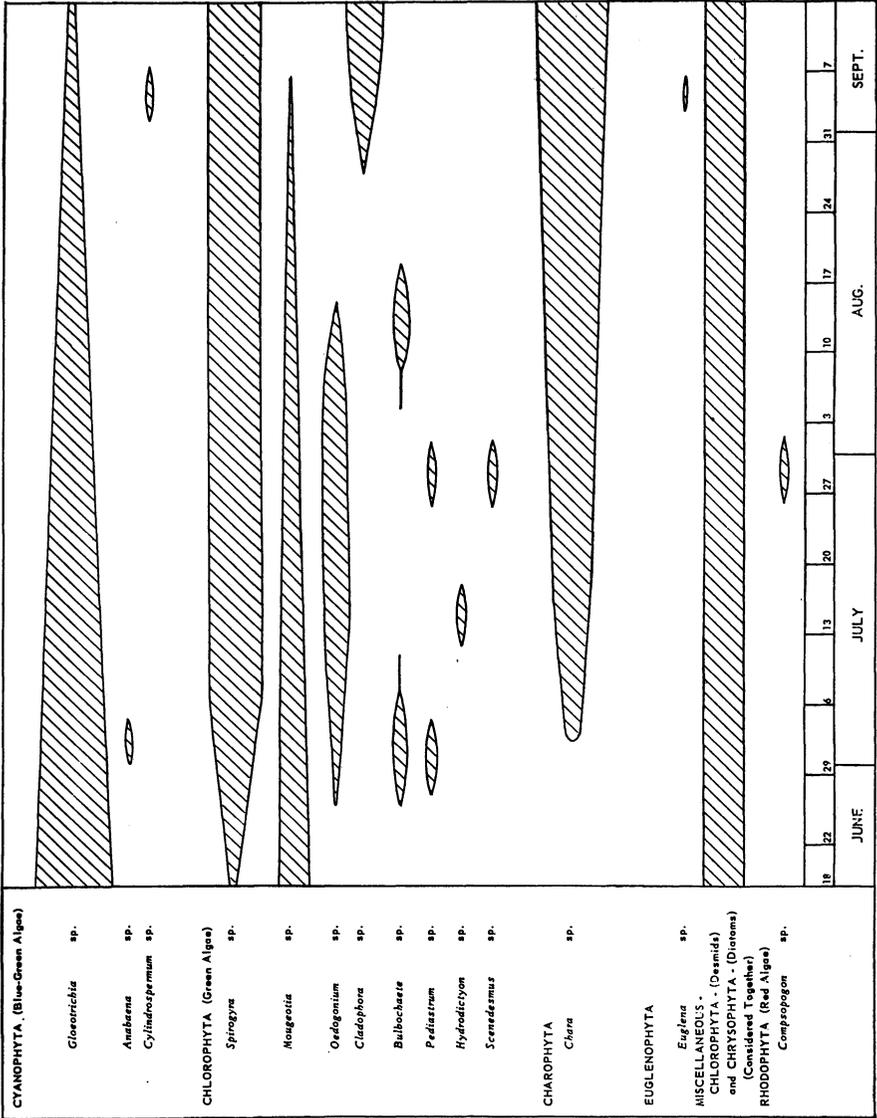
Fig. 19. Relative abundance of algae in two first-year rice fields, 1958 season.

TAXONOMIC UNIT

CYANOPHYTA (Blue-Green Algae)

Gloeotrichia   sp.

Anabaena   sp.

Oscillatoria   sp.

CHLOROPHYTA (Green Algae)

Spirogyra   sp.

Oedogonium   sp.

Mougeotia   sp.

Cladophora   sp.

Ulotrix   sp.

Zygnema   sp.

CHAROPHYTA

Chara   sp.

MISCELLANEOUS -
CHLOROPHYTA - (Desmids)
and CHRYSOPHYTA - (Diatoms)
(Considered Together)

| 18 | 22 | 29 | 6 | 13 | 20 | 27 | 3 | 10 | 17 | 24 | 31 | 7 |
| | JUNE | | JULY | | | | AUG. | | | | | SEPT. |

MONTH AND FIRST DAY OF WEEK
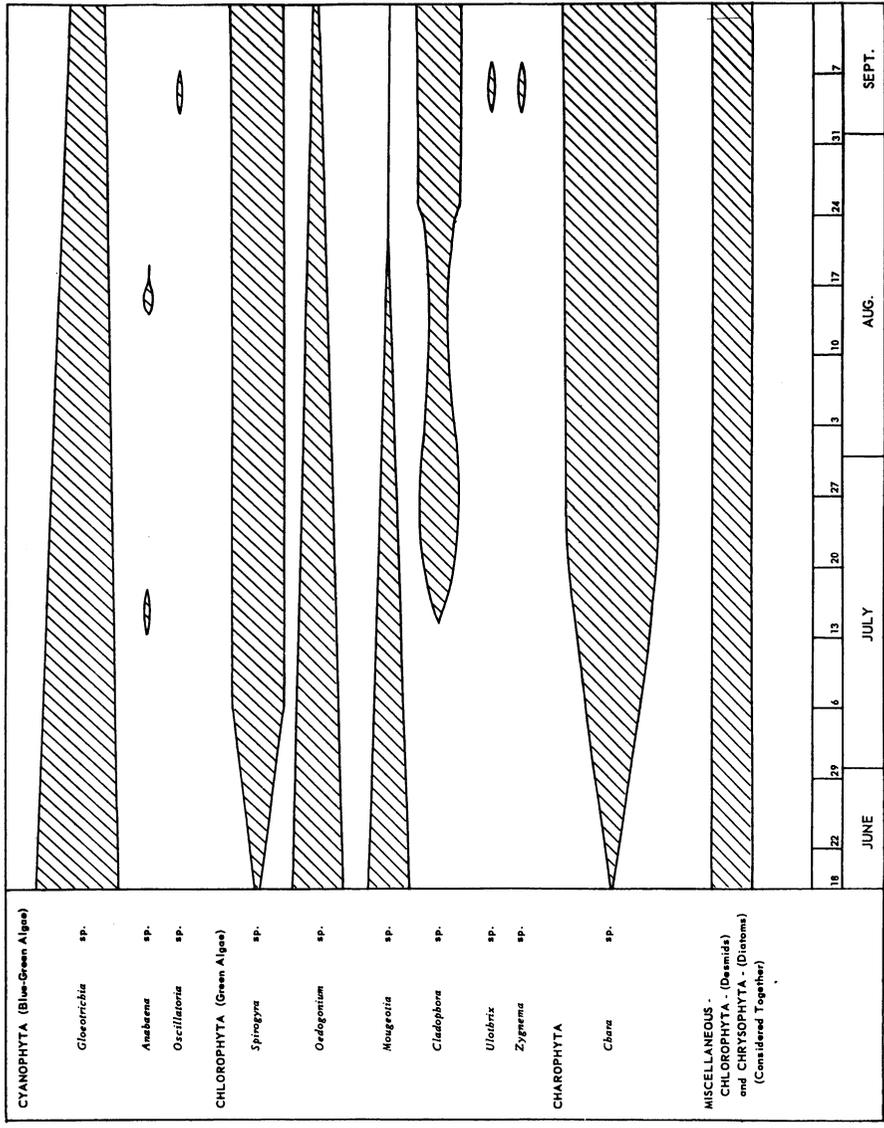
Fig. 20. Relative abundance of algae in two second-year rice fields, 1958 season.

TAXONOMY AND DESCRIPTION OF LIFE HISTORY STAGES

General Considerations of the Taxonomic Problems in Chironomidae

A number of circumstances have been responsible for the state of transition and uncertainty which exists in the taxonomy of the Chironomidae. Controversy over the use of the generic names proposed by Meigen has resulted in confusion. As Townes (1945) indicates, the name *Tendipes* Meigen, 1800, was adopted by many taxonomists as the type genus of the family in place of the better known name of *Chironomus* Meigen, 1803. Thus the family name Tendipedidae was applied to this group of nonbiting midges and appeared in many publications. A recent ruling of the International Committee on Zoological Nomenclature (Bradley, 1957, p. 97, Art. 13, sect. 4(a)) has conserved the name Chironomidae because of its long standing in the literature. This ruling, however, did not discontinue the use of Meigen's generic names of 1800.[6] For this reason the name *Tendipes* is used in the present discussion. To be consistent, the generic name *Chironomus* probably will be adopted also, but that must await future action by the International Committee.

The wide geographic distribution of some species of chironomids has resulted in renaming some previously described European species collected in the United States. In addition, certain workers have separated forms as new genera and species on the basis of differences considered as insignificant by other taxonomists. These actions have produced complex synonymies within the family.

Another factor contributing to the instability is that relatively few taxonomic studies of chironomids have been made in America. The subfamilies Tanypodinae and Orthocladiinae in particular have many undescribed representatives in America. The investigation of almost any phase of the biology of midges results in the description of new species. Of the 36 species taken in or near rice fields from 1955 through 1958, 13 appear to be either new or recently named species.

Morphology of Adults and Description of Stages

Adult midges are typical nematocerous Diptera which superficially resemble mosquitoes. However, living chironomids can be quickly and easily recognized because of their habit of raising the forelegs from the substrate when at rest. Structurally, the costal wing vein of chironomids ends at or near the wing tip and there are no scales on either the wing margins or veins such as usually characterize the Culicidae. Chironomids are distinguished from the closely related Heleidae (= Ceratopogonidae) by the presence of a longitudinal groove or keel on the metanotum or postnotum, by the lengthened front legs, and by their nonfunctional mouth parts.

Adults. The structures of the adults which are used in classification have been given detailed treatment by Edwards (1929), Townes (1945), and Freeman (1955).

On the head the presence or absence of pubescence of the eyes is often used as a generic character. As Edwards (1929) indicates, the pubescence is always

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[6] Personal correspondence from Dr. James E. Sublette.

short and may require a magnification of 150 to be seen. The number of segments in the antennae also is of taxonomic importance. Freeman (1955) states that the apparent first or basal segment is actually the second segment or pedicel since the true first segment is suppressed. This pedicel is greatly enlarged in the males. Including the pedicel, the maximum number of antennal segments is 15. The fourteenth segment is greatly elongated and may be only indistinctly separated from segment 15 or in some groups (Orthocladiinae and Chironominae) these last segments are fused, thus reducing the number to 14. Further reduction may occur from fusion of some of the basal segments. The antennal ratio (A.R.) is a figure derived by dividing the length of the last two segments or last segment by the combined length of the rest of the flagellar segments. The flagellum of the male antenna is plumose, whereas that of the female is not. In some groups (Orthocladiinae and Chironominae) the number of antennal segments of the females is reduced to five or six apparent segments. Edwards (1929) calls attention to the hyaline sensory organs of the antennae of the female. These are paired structures on the apical part of each segment beyond the second. These differ from ordinary hairs in being extensions of the cuticle.

Frontal tubercles are often present. These are paired protuberances on the frons just above the antennal bases.

In the thoracic region, the size and outline of the reduced prothorax are used as a generic character in the Chironominae.

The distribution and pattern of the three rows of bristles on the mesonotum are used in generic and species identification. The acrostichal bristles are those of the central double row and the dorso-centrals make up the two lateral rows according to Freeman (1955), whereas Edwards (1929; p. 283) identifies the dorso-central hairs as those "occupying spaces between scutal stripes."

The color of the thorax, particularly that of the scutal stripes or thoracic vittae, is often used in the separation of species. However, Edwards (*loc. cit.*) warns of the high degree of variation including sex, age, season, and individual variability. On specimens which have been carefully prepared, often the degree and pattern of pruinosity or the powdery dust on the thorax are of taxonomic significance.

On the legs, the form and number of tibial spurs and combs are of taxonomic importance. These may be present on all tibiae as in the Tanypodinae and Orthocladiinae or reduced or absent on the anterior tibiae as in the Chironominae.

The leg ratio or L.R. is the figure resulting when the length of the fore basitarsus is divided by the length of the fore tibia. This measurement is useful in separating the subfamily Chironominae from the Orthocladiinae and Tanypodinae.

The presence or absence of a fringe of long hairs on the front tarsi called a "beard" is used as a species characteristic. However, it is greatly reduced or absent in all females and is often variable in males.

The presence or absence of pulvilli and the empodium on the fifth tarsal segment and relative size of these structures, when present, also are used in distinguishing species.

The wing venation and the various wing structures are of considerable taxonomic value. The squama, a lobe on the extreme posterior basal part of the wing, may or may not have a fringe of long hairs. The presence on the wing membrane of macrotrichia and microtrichia is of generic importance. The latter are often difficult to see.

The system of designating wing veins in the present keys (figs. 21 and 22) is the same as that used by Freeman (1955). This is the Comstock and Needham system as modified by Tillyard (1919, 1926). Important in the generic and specific levels is the condition of the costa, i.e. whether or not it is "produced" or extends beyond the end of vein R4 + 5.

Taxonomically, the male genitalia are the most important structures of the adult midge (fig. 23). The parts have been given a number of different names but the least complex and confusing are those of Townes (1945) and Johannsen and Townes (1952). The claspers consist of two segments, a basal coxite or basistyle and the apical style or dististyle. The coxites have lobes and appendages developed to a varying degree throughout the family. Freeman
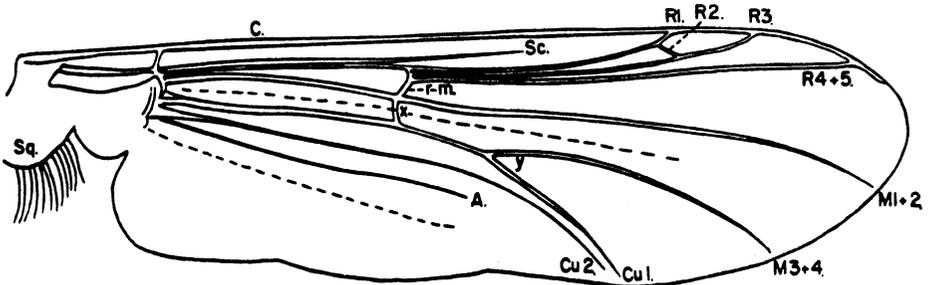
Fig. 21. Wing of *Procladius culiciformis* (L.) × 36.5. *A*, anal vein; *C*, costa; *Cu* 1, cubitus (first branch); *Cu* 2, cubitus (second branch); *M1 + 2*, medial (fused first and second branches); *R1*, radius (first branch); *R2*, radius (second branch); *R3*, radius (third branch); *R4 + 5*, radius (fused fourth and fifth branches); *Sc*, subcosta; *Sq*, squama; *r-m*, radio-medial crossvein; *x*, true base of *M3 + 4*; *y*, mediocubital fork or posterior fork.
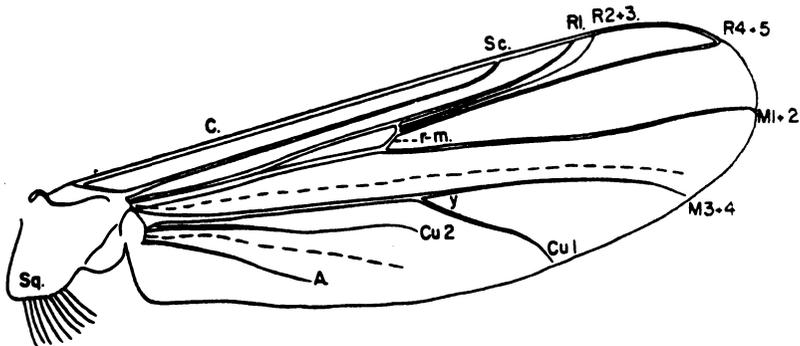
Fig. 22. Wing of *Tendipes (Cryptochironomus) tenuicaudatus* (Malloch) × 36.5. Vein designation as in fig. 21, except *R2 + 3*, radius (fused second and third branches)'.

(1955) assigns numbers to these, but the names "superior appendage," "inferior appendage," and "accessory appendage" of Johannsen and Townes (1952) have been used in the following keys. Freeman (1955) points out the importance of the struts associated with the ninth abdominal segment but probably the most important structure on the ninth segment is the anal point, a sharp projection from the middle of the ninth tergite. Its development when present or its absence is used extensively in separating genera and species.

The female midges are difficult to identify. Freeman (1955) observed differences in the spermathecae of females of several genera. The female genitalia were not studied in the present work, but other structural characteristics and the capture of pairs in copulation were used as criteria for assigning females to species.

Eggs. A considerable variation exists in the shape and size of the eggs of chironomids as shown by Thienemann (1954; Abb. 168). Most of them, however, are elongated or longer than wide. The eggs of all species are covered with a protective gelatinous material which absorbs water on contact and becomes greatly expanded. One of the earliest accounts of the eggs of midges is that of Miall (1895; pp. 146–48). He noted that the strings of eggs of *Chironomus* sp. were held in place near the surface by means of a mooring device that passed through each one and which was responsible both for holding the egg mass in place and for the elasticity of the gelatinous envelope.

Although many species produce linear egg ropes, there are a number of different shapes, some of which are illustrated in Miall (*op. cit.;* fig. 44). Branch (1928) published descriptions and figures of egg masses of several species and suggested a key to the eggs of chironomids. Subsequently, however,
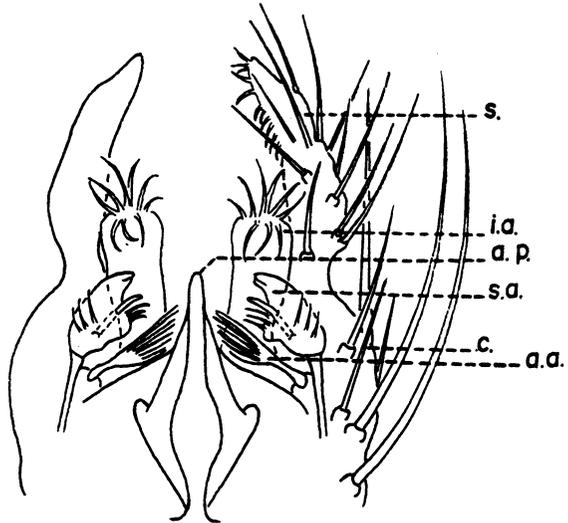
Fig. 23. Male genitalia of *Tanytarsus* n. sp. 6, × 150. *a.a.*, accessory appendage; *a.p.*, anal point; *c*, coxite or basistyle; *i.a.*, inferior appendage; *s*, style or dististyle; *s.a.*, superior appendage.
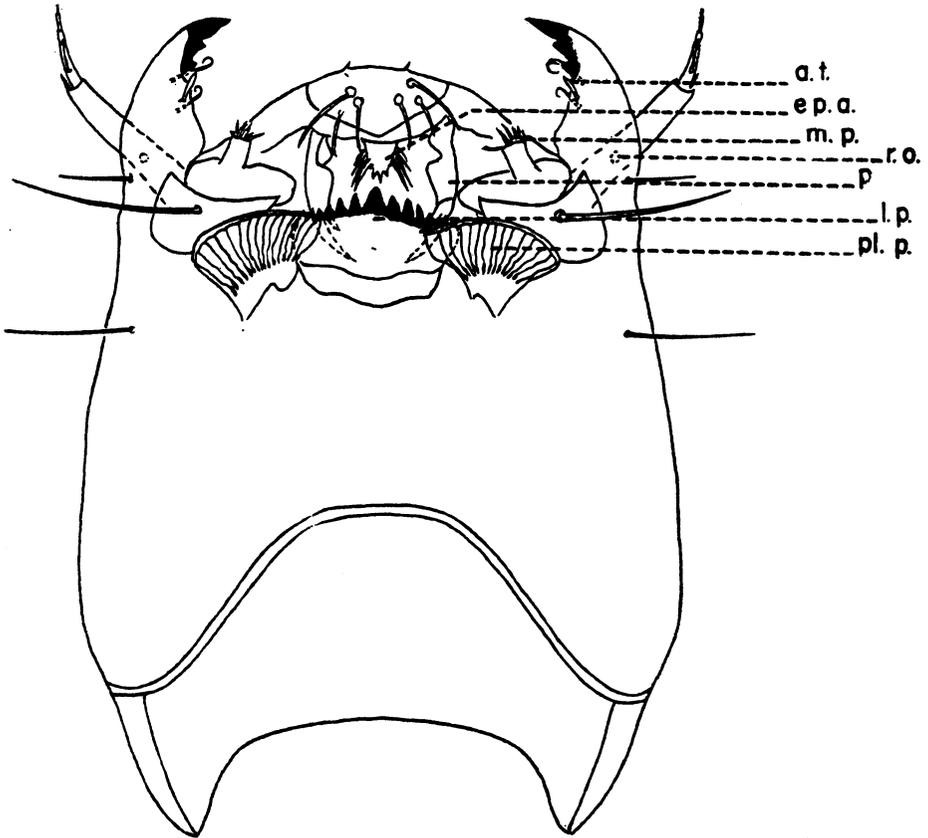
Fig. 24. Head of larva of *Tendipes (Cryptochironomus) chaetoala* Sublette, ventral view, ×150. *a.t.*, accessory tooth of mandible; *ep.a.*, epipharyngeal area of labrum; *l.p.*, labial plate; *m.p.*, maxillary palpus; *p*, premandible; *pl.p.*, paralabial plate; *r.o.*, ring organ of antenna.

Branch (1931) discovered that a wide degree of variability in egg masses existed within the single species *Chironomus decorus*. Kettisch (1936–37) also noted a variation in the egg masses of *Cricotopus trifasciatus* in that those produced in the autumn were larger and thicker than those observed at the other seasons of the year.

Larvae. Although the larvae of the various species in this family often may be distinctly different from one another, there are a few general characteristics which apply to the entire group. They all possess a complete non-retractable head capsule with opposable mandibles. Usually well-developed anterior or prothoracic and posterior prolegs are present. A few species lack posterior prolegs and have the prothoracic pair reduced to patches of spinules. Chironomid larvae do not have functional spiracles. Respiration is by means of anal gills on the twelfth or last body seg.nent, and in some species by additional ventral gills on the eleventh body segment.

In a combination morphological and ecological study, Leathers (1922) demonstrated the relationship between the food habits of larvae of several species of chironomids and their specialized mouth parts. Many of these structures are used in the identification and classification of midge larvae (fig. 24).

The various forms of antennae and antennal appendages are also of value in separating and classifying larvae (fig. 25).

Pupae. As in other nematocerous groups, chironomid pupae are exarate, or have the legs and wings free and not enclosed by the exuvia of the body. Also in common with other primitive forms, the pupae are relatively active. Some swim freely much as mosquito pupae, whereas others develop in cases constructed by the mature larva. The encased pupae are not inert, however, but by regular undulating movements of their abdomens keep the water circulating through their dwellings. In addition, they readily move backward or forward inside the tubes when touched.

Pupae usually possess functional prothoracic respiratory organs, the structure of which is taxonomically important. The abdomen terminates in a pair of pointed processes, or in the oval anal fins of the swimming paddle. Frequently the fins bear fringes of slender swimming hairs or filaments. The spinule and shagreen patterns of the abdominal tergites together with the presence or absence of spurs or combs on caudolateral angles of the eighth abdominal segments are useful in pupae classification (fig. 26).
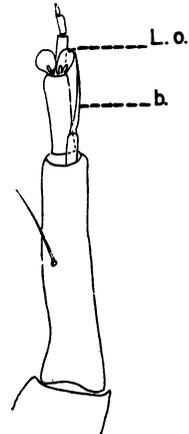
Fig. 25. Antenna of *Tanytarsus* (*Tanytarsus*) n. sp. 5, × 249. *L.o.*, Lauterborn organ; *b*, blade of antenna.
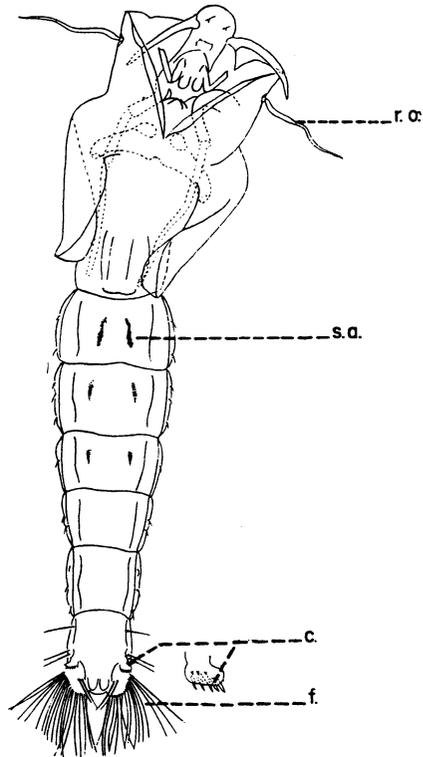
Fig. 26. Pupal exuvia of *Tanytarsus* (*Tanytarsus*) n. sp. 6, dorsal view, × 23. *c*, comb on caudo-lateral angle of eighth abdominal segment; *f*, swimming filaments of ninth abdominal segment or anal fin; *r.o.*, thoracic respiratory organ; *s.a.*, spinule area of third abdominal segment.

RECORD OF OCCURRENCE AND KEYS FOR IDENTIFICATION OF SPECIES IN RICE FIELDS

List of Species Encountered and Their Relative Numbers in Rice Fields

The classification system used in arranging the following list of species is that of Freeman (1955–1957, 1958) who combined several genera and designated some of them as subgenera. The species marked with an asterisk were taken in light traps in or near the rice fields; the species marked by a plus sign was reared from a larva taken in a mud sample from a first-year field; and the species designated by a minus sign was reared from a larva taken on the floating stem of cat-tail (*Typha latifolia*). All the remaining species were taken in emergence traps placed in the rice fields.

Subfamily Tanypodinae (Pelopiinae)
  Pentaneura (*Ablabesmyia*) *monilis* (L.)
  Pentaneura (*Ablabesmyia*) *aequifasciata* Dendy and Sublette
  Procladius culiciformis (L.)

Subfamily Orthocladiinae (Hydrobaeninae)
    Cricotopus bicinctus (Meigen)
    Cricotopus sylvestris (Fabr.)
    *Psectrocladius n. sp. 1
    Psectrocladius n. sp. 2
    Nanocladius n. sp.
    *Smittia n. sp.
Subfamily Corynoneurinae
    Corynoneura (*Corynoneura*) n. sp.
Subfamily Chironominae (Tendipedinae)
  Tribe Chironomini (Tendepedini)
    Pseudochironomus richardsoni Malloch
    Paralauterborniella species complex *elachista* (Townes₊ and
      subcincta (Townes)
    *Polypedilum (*Polypedilum*) *digitifer* Townes
    +*Phaenopsectra profusa* (Townes)
    Tendipes (*Tendipes*) *attenuatus* (Walker)
    Tendipes (*Tendipes*) *plumosus* (L.)
    Tendipes (*Endochironomus*) *nigricans* (Johannsen)
    Tendipes (*Dicrotendipes*) *californicus* (Johannsen)
    Tendipes (*Dicrotendipes*) *modestus* (Say)
    Tendipes (*Dicrotendipes*) *nervosus* (Staeger)
    Tendipes (*Cryptochironomus*) *chaetoala* Sublette
    Tendipes (*Cryptochironomus*) *darbyi* Sublette
    Tendipes (*Cryptochironomus*) *fulvus* (Johannsen)
    *Tendipes (*Cryptochironomus*) *frequens* (Johannsen)
    Tendipes (*Cryptochironomus*) *monochromus* van der Wulp
    Tendipes (*Cryptochironomus*) *tenuicaudatus* (Malloch)
    *Tendipes (*Cryptochironomus*) *curtilamellatus* (Malloch)
    Glyptotendipes (*Phytotendipes*) *lobiferus* (Say)
  Tribe Tanytarsini (Calopsectrini)
    −*Micropsectra nigripilus* (Johannsen)
    Tanytarsus (*Cladotanytarsus*) *viridiventris* (Malloch)
    Tanytarsus (*Rheotanytarsus*) n. sp. 2
    Tanytarsus (*Tanytarsus*) n. sp. 3
    Tanytarsus (*Tanytarsus*) n. sp. 4
    Tanytarsus (*Tanytarsus*) n. sp. 5
    Tanytarsus (*Tanytarsus*) n. sp. 6

Although 30 species of midges were recorded from the rice fields, most of these were taken in small numbers. Eighteen species were represented by less than 20 individuals taken during two seasons of trapping. The following species constituted most of the chironomid fauna encountered and are listed in order of the numbers trapped (see table 5 for number of each species).

1. *Tanytarsus* (*Tanytarsus*) n. sp. 5
2. *Paralauterborniella* species complex
3. *Tanytarsus* (*Cladotanytarsus*) *viridiventris*
4. *Tanytarsus* (*Tanytarsus*) n. sp. 6
5. *Cricotopus bicinctus*
6. *Procladius culiciformis*
7. *Tendipes* (*Tendipes*) *attenuatus*
8. *Tendipes* (*Cryptochironomus*) *tenuicaudatus*
9. *Cricotopus sylvestris*
10. *Pentaneura* species complex
11. *Corynoneura* n. sp.

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TABLE 5

NUMBERS OF MIDGES TRAPPED IN EIGHT RICE FIELDS
DURING THE 1957–1958 SEASONS

</div>

Taxonomic unit	Individuals trapped		
	1957	1958	Total number
Tanypodinae			
Pentaneura sp. complex	39	11	50
Procladius culiciformis	79	129	208
Orthocladiinae			
Cricotopus bicinctus	100	136	236
Cricotopus sylvestris	16	48	64
Psectrocladius n. sp. 2	14	2	16
Nanocladius n. sp.	3	0	3
Corynoneurinae			
Corynoneura n. sp.	31	11	42
Chironominae			
Chironomini			
Pseudochironomus richardsoni	1	0	1
Paralauterborniella sp. complex	166	269	435
Tendipes attenuatus	14	187	201
Tendipes plumosus	0	3	3
Tendipes nigricans	1	0	1
Tendipes californicus	8	3	11
Tendipes modestus	1	0	1
Tendipes nervosus	1	1	2
Tendipes chaetoala	7	6	13
Tendipes darbyi	5	1	6
Tendipes fulvus	3	9	12
Tendipes monochromus	0	2	2
Tendipes tenuicaudatus	41	68	109
Glyptotendipes lobiferus	0	2	2
Tanytarsini			
Tanytarsus viridiventris	180	173	353
Tanytarsus n. sp. 2	2	0	2
Tanytarsus n. sp. 3	2	1	3
Tanytarsus n. sp. 4	1	0	1
Tanytarsus n. sp. 5	806	823	1,629
Tanytarsus n. sp. 6	87	158	245
Total number	1,608	2,043	3,651

Key to Adults Taken in or near Rice Fields
Key to subfamilies of adult midges[7]

1. Base of M3 + 4 present .... Tanypodinae
   Base of M3 + 4 absent 2
2. Front basitarsus longer than front tibia, or rarely slightly shorter (L.R. nearly always
   greater than 1); styles of male genitalia always directed rigidly backward; middle
   and hind tibiae with spurs modified into combs .... Chironominae
   Front basitarsus shorter than front tibia (L.R. less than 1); styles of male genitalia
   folded inward; middle and hind tibiae with spurs not modified into combs 3
3. R4 + 5 completely fused with the thickened costa to form a "clavus" and with a false
   vein running close to the anterior margin on the outer half of the wing
                                                                      Corynoneurinae
   R4 + 5 not fused with the thickened costa .... Orthocladiinae

[7] Modified from Townes (1945) and Freeman (1955).

Key to genera and species of Tanypodinae[8]

1. Mediocubital fork proximal to the true base of M3 + 4; costa normally not produced
$$\textit{Pentaneura} \text{ Philippi}$$
　　Tibiae with three well-defined black rings – Subgenus (*Ablabesmyia*) Johannsen
　　　　Male genitalia: fig. 27. . . . . *Pentaneura (Ablabesmyia) monilis* (L.)
　　　　Male genitalia: fig. 28
$$\textit{Pentaneura (Ablabesmyia) aequifasciata} \text{ Dendy and Sublette}$$
　Mediocubital fork distal to the true base of M3 + 4; costa produced
$$\textit{Procladius} \text{ (Skuse)}$$
　　　　r-m cross vein and true base of M3 + 4 blackened, with clear areas before and
　　　beyond them; wings with apical half and posterior part of basal half faintly
　　　grayish; style characteristic.
　　　　Male genitalia: fig. 29. . . . . *Procladius culiciformis* (L.)

Key to genera and species of Orthocladiinae[9]

1. Vein R2 + 3 running close to or in contact with R4 + 5, obsolete apically and not ending
　　distinctly in costa. . . . . *Nanocladius* Kieffer
　　　　Male genitalia: fig. 30. . . . . *Nanocladius* n. sp.
　　Vein R2 + 3 separate from R4 + 5, ending distinctly in costa nearly midway or before the
　　middle of the distance between costal ends of R1 and R4 + 5. 2
2. Squama completely bare, Cu, ordinarily more or less curved; mediocubital fork distal
　　to r-m cross vein. . . . . *Smittia* Holmgren
　　　　Male genitalia: fig. 31. . . . . *Smittia* n. sp.
　　Squama with at least a partial fringe of 2 to 3 hairs, usually with a complete fringe;
　　Cu, ordinarily straight or scarcely bent; mediocubital fork about even with r-m
　　cross vein 3
3. Eyes pubescent; dorso-central hairs minute and decumbent; tibiae often with white
　　bands or completely white; terminalia often white; small pulvilli present or absent
$$\textit{Cricotopus} \text{ van der Wulp}$$

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[8] Modified from Edwards (1929) and Johannsen and Townes (1952).

[9] Modified from Edwards (1929), Goetghebuer (1932), Johannsen and Townes (1952), and Freeman (1956).
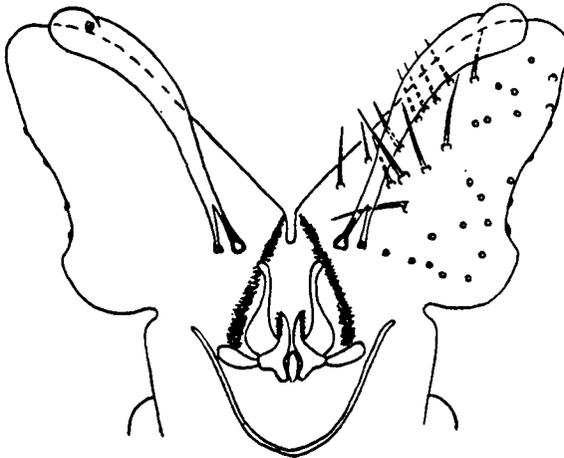
Fig. 27. Male genitalia of *Pentaneura (Ablabesmyia) monilis* (L.), × 120.

    a. Pulvilli absent; mid and hind femora with at least apical halves black; wings not distinctly milky; mesonotum shiny black with anterior angles yellow; first and fourth abdominal tergites yellow, the rest black...*Cricotopus bicinctus* (Meigen) Male genitalia: fig. 32

    b. Small pulvilli present; mid and hind femora for the most part yellow or white; wings distinctly milky; mesonotum yellow with dark bands well separated; first abdominal tergite yellow occasionally with dark or dusky markings, fourth and fifth tergites more or less blotched with yellow at base, seventh with yellow posterior margin ....*Cricotopus sylvestris* (Fabr.) Male genitalia: fig. 33

Eyes bare; dorso-central hairs distinct and erect; tibiae one color; pulvilli present broad and fairly long.....................................*Psectrocladius* Kieffer

    a. Male genitalia: fig. 34................................*Psectrocladius* n. sp. 1

    b. Male genitalia: fig. 35................................*Psectrocladius* n. sp. 2

Subfamily Corynoneurinae. Single genus, *Corynoneura* and single new species. Male genitalia: fig. 36

This subfamily, which contains two genera, is characterized by Freeman (1956; p. 360) as follows:

    R1 and R4 + 5 entirely fused with one another and almost entirely fused with the thickened costa to form a "clavus," which extends less than half the wing length in the male and not more than two-thirds of the wing length in the female; a false vein runs from r-m below the clavus and then close to the wing margin almost as far as the wing tip; wing membrane without macrotrichia or microtrichia, anal lobe of wing usually absent; squama bare; fourth tarsal segment shorter than the fifth and often more or less heart-shaped; male antenna with 10–13 segments; very small species, wing length less than 2 mm.

Attention is called by Freeman (*loc. cit.*) to the internal struts of the male genitalia which are useful in specific identification. Two important generic characteristics of *Corynoneura* are given by Freeman (*op. cit.; p. 361*), "Eyes bare; hind tibiae somewhat swollen at tip, obliquely truncate and with a conspicuous apical projection on inner side."
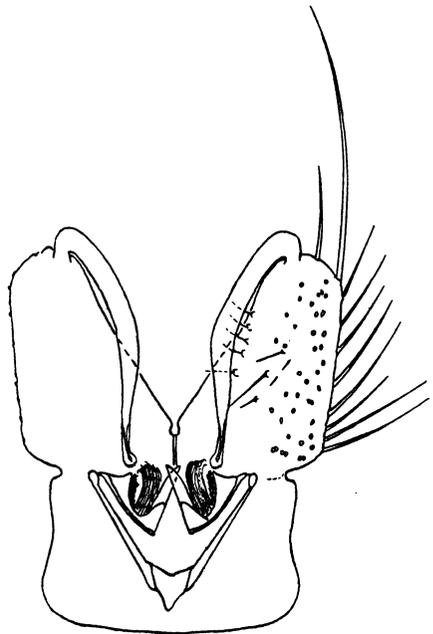
Fig. 28. Male genitalia of *Pentaneura* (*Ablabesmyia*) *aequifasciata* Dendy and Sublette, × 120.
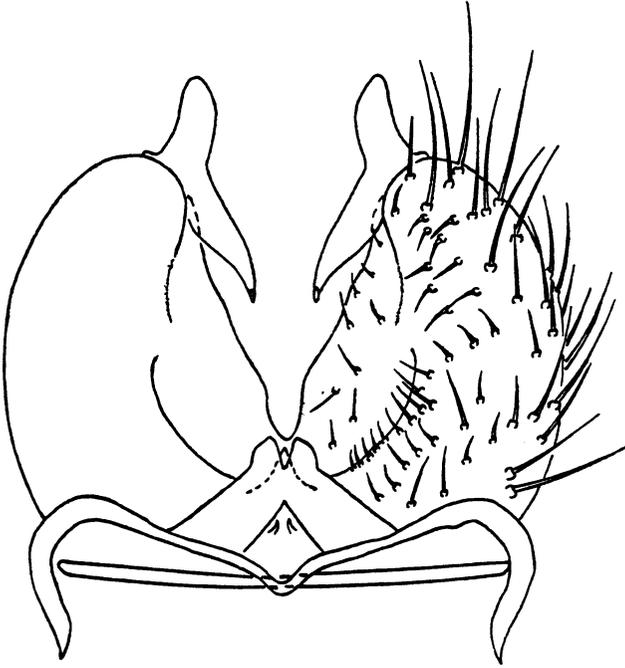
Fig. 29. Male genitalia of *Procladius culiciformis* (L.), × 135.

Fig. 30. Male genitalia of *Nanocladius*
n. sp., after Sublette. Magnification not
given.
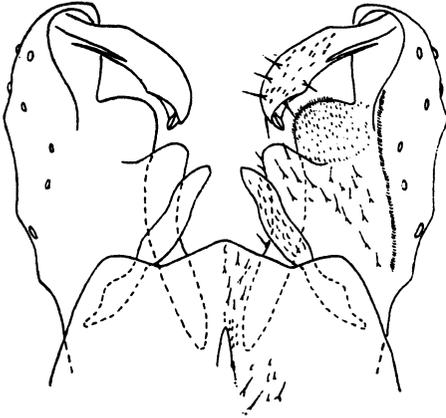
Fig. 31. Male genitalia of *Smittia* n. sp., after Sublette. Magnification not given.
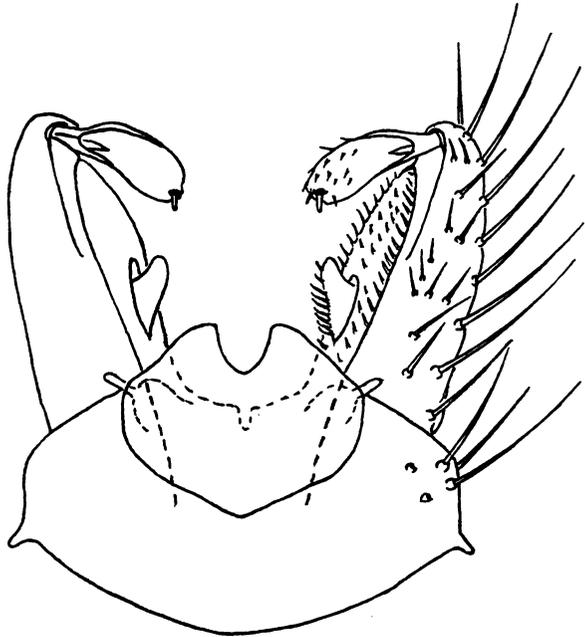
Fig. 32. Male genitalia of *Cricotopus bicinctus* (Meigen), × 150.

Fig. 33. Male genitalia of *Cricotopus sylvestris* (Fabr.), × 120.
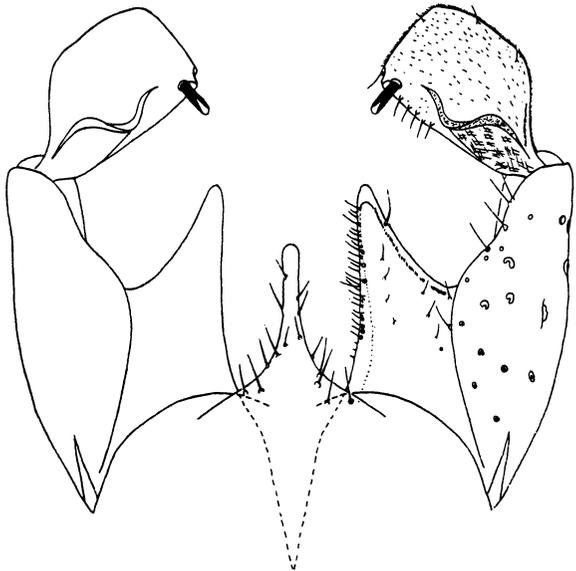
Fig. 34. Male genitalia of *Psectrocladius* n. sp. 1, after Sublette. Magnification not given.

Fig. 35. Male genitalia of *Psectrocladius* n. sp. 2, × 150.
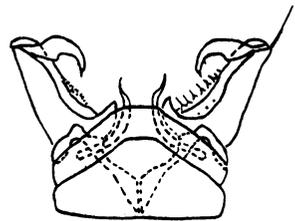
Fig. 36. Male genitalia of *Corynoneura* (*Corynoneura*) n. sp., × 150.

a.

b.

a.

b.

a.

b.
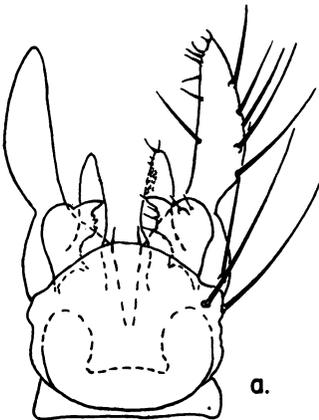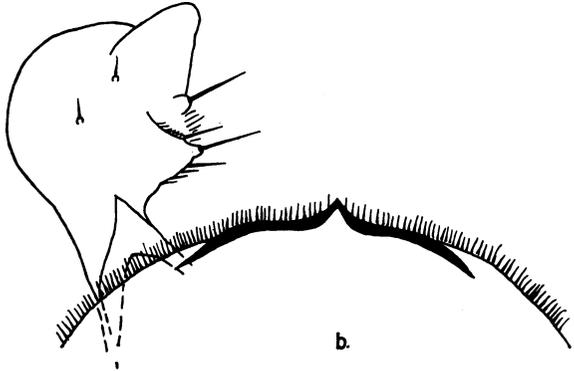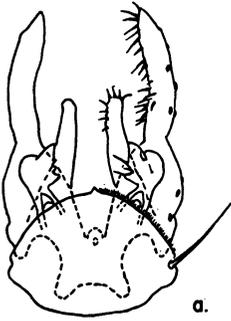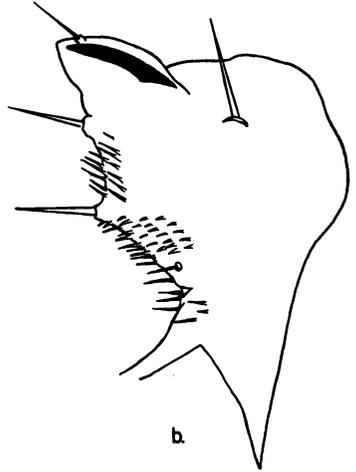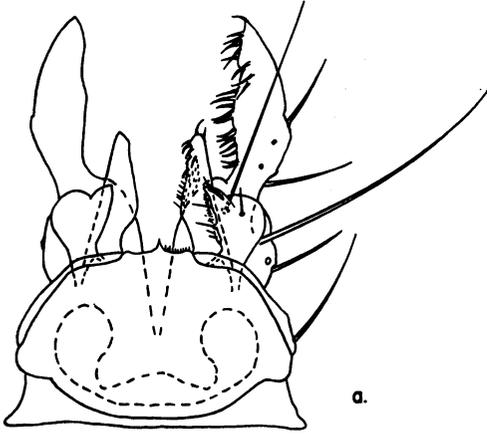
Key to tribes of Chironominae[10]

Wing membrane without macrotrichia, or if present, then squama with marginal fringe of long hairs; cross vein r-m definitely oblique to direction of vein $R4+5$; male genitalia without accessory appendages ....Chironomini

Wing membrane with macrotrichia, at least toward the apex, squama without fringe of hairs; cross vein r-m nearly parallel to and practically continous with $R4+5$; male genitalia with accessory appendages (fig. 23)..................Tanytarsini

Key to genera and species of Chironomini[11]

1. Squamal fringe absent; pulvilli vestigial...................*Paralauterborniella* Lenz
   Anal point present; wing with faint spots.....*Paralauterborniella subcincta* (Townes)
      Male genitalia: fig. 37
      Male genitalia: fig. 38 variant
   Anal point absent; wing uniformly pale without spots
                                          Paralauterborniella elachista (Townes)
      Male genitalia: fig. 39
   Squamal fringe present; pulvilli present, often conspicuous...................... 2

2. Male genitalia with pair of ventral appendages between bases of coxites; eyes widely separated above by more than twice the diameter of male pedicel; frontal tubercles absent; fore tibiae with conspicuous ventral black apical spur (fig. 40b)
                                          Pseudochironomus Malloch
      Male genitalia: fig. 40a..................*Pseudochironomus richardsoni* Malloch
   Male genitalia without ventral appendages; eyes not widely separated above; frontal tubercles present or absent; fore tibiae without conspicuous black apical spur.... 3

3. As viewed from above, all or part of prothorax hidden by anterior edge of mesonotum (fig. 41) 4
   As viewed from above, prothorax visible extending up to front of mesonotum, often collar-like, sometimes divided by suture but with two halves touching (fig. 42)
                                          Tendipes Meigen[12]

4. Antennal flagellum with 11 segments in male and 6 segments in female; frontal tubercles present; as viewed from above, pronotum completely interrupted by broad, crescent-shaped, median notch distinctly separating two lateral halves to give bilobed appearance (fig. 41) ....*Glyptotendipes* Kieffer
   Abdominal tergites 2 to 6 with median basal scar-like impressions
                                          Glyptotendipes lobiferous (Say)
      Male genitalia: fig. 43

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[10] After Townes (1945) and Freeman (1957).

[11] Modified from Goetghebuer (1928), Townes (1945), and Freeman (1957 and 1958).

[12] See later key to subgenera and species.

Opposite page, top to bottom: Fig. 37. Left, male genitalia of *Paralauterborniella subcincta* (Townes), × 125. Right, superior appendage enlarged, × 540.

Fig. 38. Left, male genitalia of *Paralauterborniella* sp. or atypical form of *P. subcincta* (Townes), × 125. Right, superior appendage and anal point enlarged, × 540.

Fig. 39. Left, male genitalia of *Paralauterborniella elachista* (Townes), × 150. Right, superior appendage enlarged, × 540.

Antennal flagellum with 13 segments in male and 5 segments in female; frontal
tubercles absent; as viewed from above, pronotum not interrupted by broad, crescent-
shaped, median notch... 5
5. Wing membrane with macrotrichia; combs of middle and hind tibiae fused or nar-
rowly separated, middle pair with one short spine, hind pair with 2 spines
Phaenopsectra Kieffer
Male genitalia: fig. 44 ....*Phaenopsectra profusa* (Townes)
Wing membrane without macrotrichia; combs of middle and hind tibiae adjacent or
fused; inner comb of middle tibiae and outer comb of hind tibiae with spines, other
combs unarmed ....*Polypedilum* Kieffer
Male genitalia: fig. 45........................*Polypedilum digitifer* (Townes)
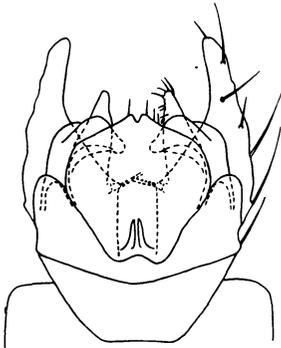
Fig. 40. Left, male genitalia of *Pseudochironomus richardsoni*
Malloch, × 75. Right, apical spur on fore tibia of *P. richardsoni*
Malloch, × 150.
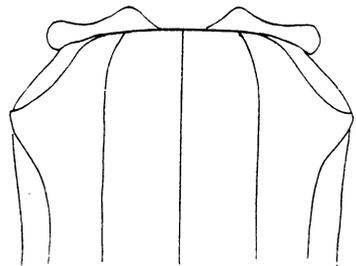
Fig. 41. Dorsal view of pronotum and ante-
rior part of mesonotum of *Glyptotendipes*
(Phytotendipes) lobiferus (Say), × 22.
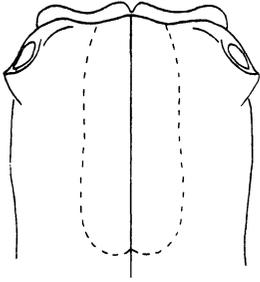
Fig. 42. Dorsal view of pronotum and anterior part of mesonotum of *Tendipes* (*Tendipes*) *attenuatus* (Walker), × 22.

Fig. 43. Male genitalia of *Glyptotendipes* (*Phytotendipes*) *lobiferus* (Say), × 75.
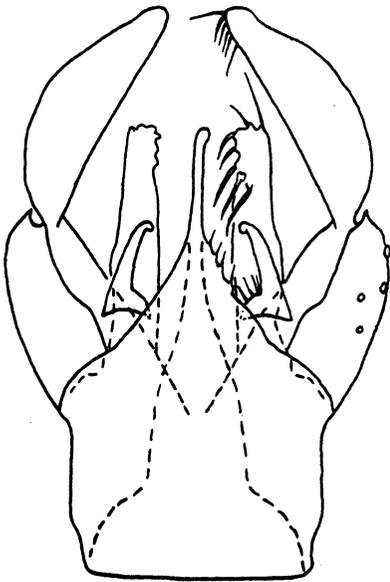
Fig. 44. Male genitalia of *Phaenopsectra profusa* (Townes), × 150.
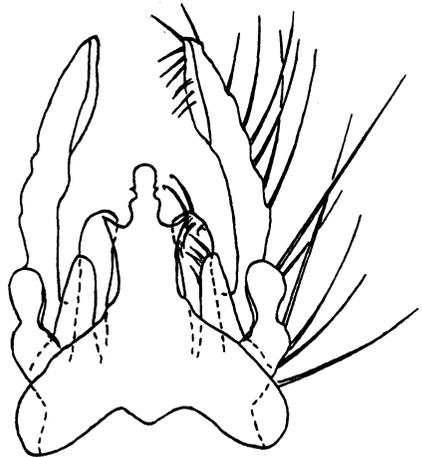
Fig. 45. Male genitalia of *Polypedilum* (*Polypedilum*) *digitifer* Townes, × 150.

Key to subgenera and species of Tendipes (= Chironomus)[13]

1. Prothorax collar-like with well-marked V-shaped median emargination; frontal tubercles present and elongate; male genitalia with both superior and inferior appendages present, inferior appendage broad and straight with long curved hairs at apex ....Subgenus *Tendipes* Meigen....................... 2
   Prothorax usually narrower (only occasionally collar-like), applied closely to front of mesonotum, without strong V-shaped median emargination but with small median suture; frontal tubercles absent or small, if present; inferior appendage of male genitalia often racket-shaped, narrowed basally or reduced..................... 3

2. Wing 3.0 to 6.4 mm long; style of male genitalia fairly broad
                                                    Tendipes attenuatus (Walker)
       Male genitalia: fig. 46
   Wing 4.8 to 7.5 mm long; style of male genitalia unusually narrow
                                                          Tendipes plumosus (L.)
       Male genitalia: fig. 47

3. Male genitalia with both superior and inferior appendages well developed; fifth segment of fore tarsi cylindrical...10
   Male genitalia with either superior or inferior appendages or both reduced and rudimentary; fifth segment of fore tarsi flattened.........................Subgenus *Cryptochironomus* Kieffer 4

4. Wing membrane with sparse macrotrichia
                               Tendipes (Cryptochironomus) chaetoala Sublette
       Male genitalia: fig. 48
   Wing membrane without macrotrichia...................................... 5

5. Male genitalia with inferior appendage reduced, with 1 or more apical bristles
                               Tendipes (Cryptochironomus) fulvus (Johannsen)
       Male genitalia: fig. 49
   Male genitalia with inferior appendage absent or small membranous lobe without microtrichia 6

6. Male genitalia with superior appendage a short, rounded structure............... 7
   Male genitalia with superior appendages linear or rod-shaped, usually with 2 apical setae 8

7. Wing length 2.5 mm or longer; leg ratio 1:27; vittae, mesosternum, posterior half of postnotum, and small spot on pleura anterior to wing bases blackish brown, contrasting sharply with pale green ground color
                               Tendipes (Cryptochironomus) darbyi Sublette
       Male genitalia: fig. 50
   Wing length less than 2.5 mm; leg ratio 2:2; thoracic coloration ochraceous
                         Tendipes (Cryptochironomus) curtilamellatus (Malloch)
       Male genitalia: fig. 51

8. Wing length 2.5 mm or longer; male genitalia with style long, relatively straight and not enlarged apically...........*Tendipes (Cryptochironomus) frequens* (Johannsen)
       Male genitalia: fig. 52
   Wing length less than 2.5 mm; male genitalia with style shorter, curved inward and apical portion enlarged 9

9. Male genitalia with superior appendage reaching apex of anal point
                         · *Tendipes (Cryptochironomus) tenuicaudatus* (Malloch)
       Male genitalia: fig. 53
   Male genitalia with superior appendage not reaching apex of anal point
                         Tendipes (Cryptochironomus) monochromus (van der Wulp)
       Male genitalia: fig. 54

10. Male genitalia with inferior appendage narrower basally and curved or bowed upward; antennal flagellum with 11 segments in male and 5 segments in female; front tibiae never spurred.............Subgenus *Dicrotendipes* Kieffer.....................11

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[13] Compiled from Townes (1945) and Freeman (1957).

Male genitalia with inferior appendage of more even width, not curved or bowed upward, antennal flagellum with 13 segments in male and 6 segments in female; scales at ends of front tibiae with spine at tip. . . . Subgenus *Endochironomus* Kieffer
Thorax blackish brown to light brown; abdomen pale green

Tendipes (*Endochironomus*) *nigricans* (Johannsen)

Male genitalia: fig. 55

11. Abdomen entirely brownish. . . . . . . *Tendipes* (*Dicrotendipes*) *californicus* (Johannsen)

Male genitalia: fig. 56

Abdomen entirely green or green with apical segments more or less brownish. 12

12. Male genitalia with superior appendage about 4.5 times as wide at end as at middle

Tendipes (*Dicrotendipes*) *modestus* (Say)

Male genitalia: fig. 57

Male genitalia with superior appendage not more than 2.5 times as wide at end as at middle . . . . *Tendipes* (*Dicrotendipes*) *nervosus* (Staeger)

Male genitalia: fig. 58
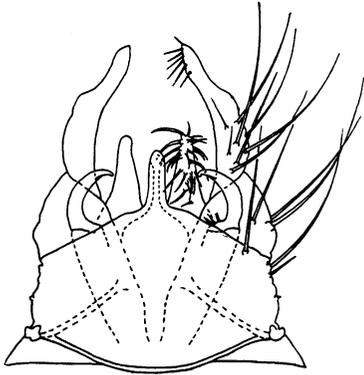
Fig. 46. Male genitalia of *Tendipes* (*Tendipes*) *attenuatus* (Walker), × 58.
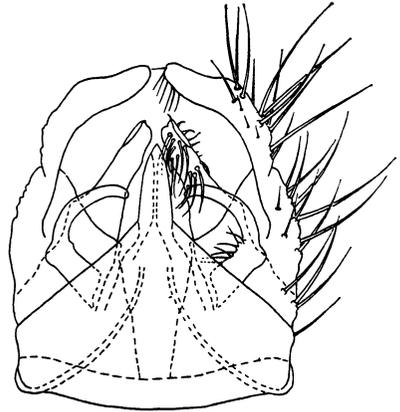
Fig. 47. Male genitalia of *Tendipes* (*Tendipes*) *plumosus* (L.), × 58.
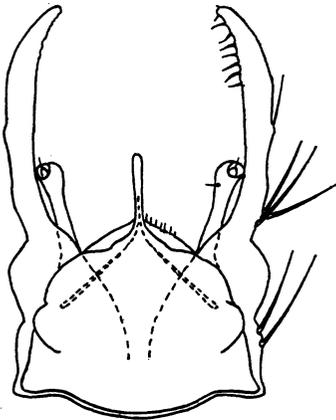
Fig. 48. Male genitalia of *Tendipes* (*Crypto-chironomus*) *chaetoala* Sublette, × 120.
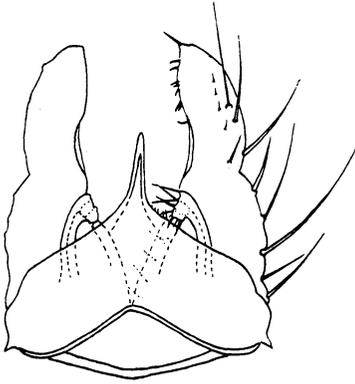
Fig. 49. Male genitalia of *Tendipes* (*Crypto-chironomus*) *fulvus* (Johannsen), × 75.

Fig. 50. Male genitalia of *Tendipes* (*Cryptochironomus*) *darbyi* Sublette, × 150.
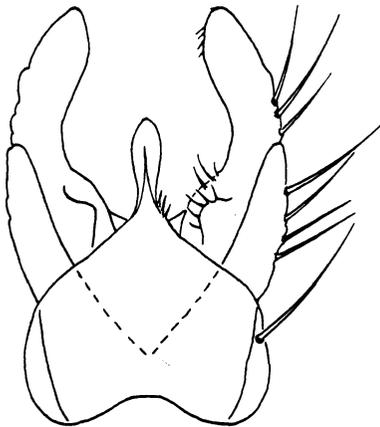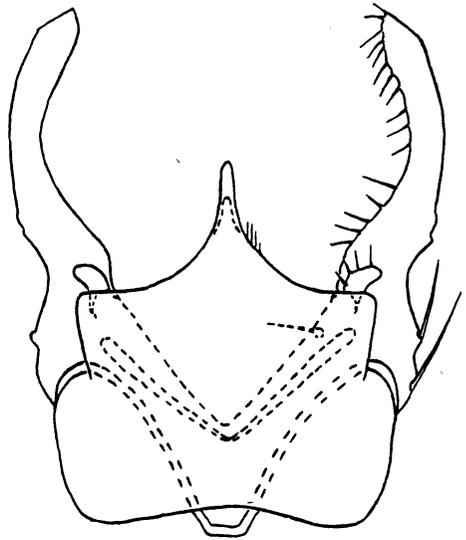
Fig. 51. Male genitalia of *Tendipes* (*Cryptochironomus*) *curtilamellatus* (Malloch), × 120.
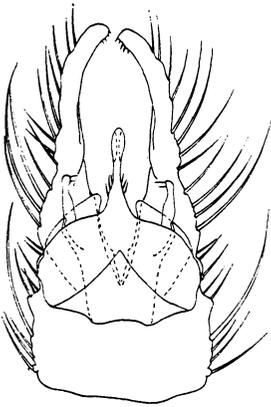
Fig. 52. Male genitalia of *Tendipes* (*Cryptochironomus*) *frequens* (Johannsen), × 58.
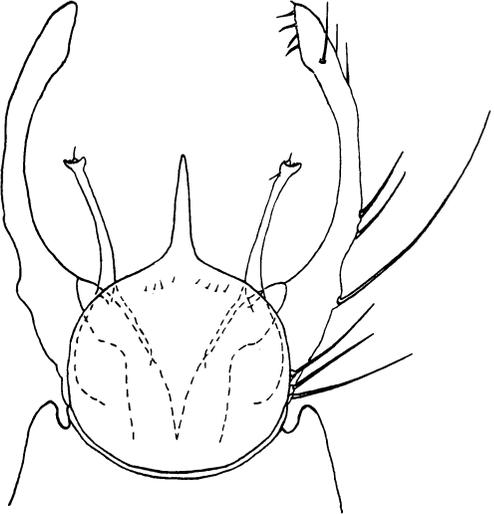
Fig. 53. Male genitalia of *Tendipes* (*Cryptochironomus*) *tenuicaudatus* (Malloch), × 111
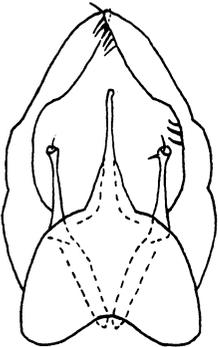
Fig. 54. Male genitalia of *Tendipes* (*Cryptochironomus*) *monochromus* van der Wulp, after Townes, 1945.
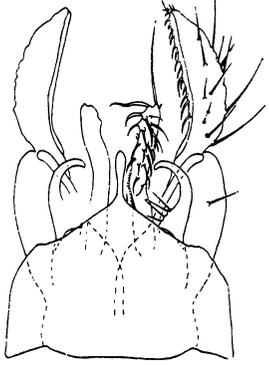
Fig. 55. Male genitalia of *Tendipes* (*Endochironomus*) *nigricans* (Johannsen), × 58.

Fig. 56. Male genitalia of *Tendipes (Dicrotendipes) californicus* (Johannsen), × 120.
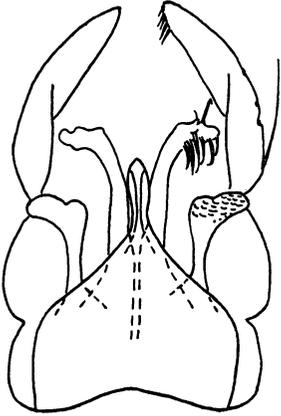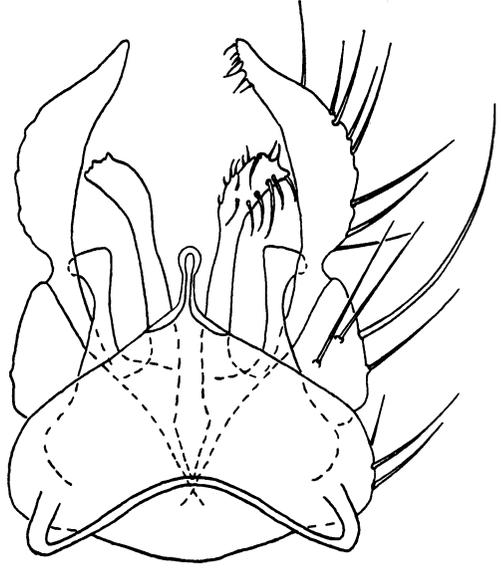
Fig. 57. Male genitalia of *Tendipes (Dicrotendipes) modestus* (Say), × 111.

Fig. 58. Male genitalia of *Tendipes (Dicrotendipes) nervosus* (Staeger), × 120.
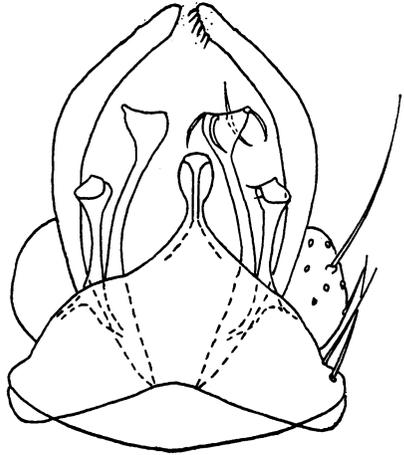
Key to genera and species of Tanytarsini[14]

1. Combs of middle and hind tibiae confluent ventrally, occupying more than half circumference of tibiae, without spurs; hairs of accessory appendage of male genitalia frequently expanded like droplets...........................*Micropsectra* Kieffer
    Fore basitarsus $\frac{1}{6}$ to $\frac{1}{10}$ longer than tibia; halteres of male fuscous or black, those of female paler; legs black; length 3.5 to 4.0 mm
    <div align="right">

Micropsectra nigripilus (Johannsen)
    </div>

    Male genitalia: fig. 59
    Combs of middle and hind tibiae at least narrowly separated ventrally, occupying at most half of the circumference of tibiae, usually both with spurs
    Tanytarsus van der Wulp.. 2
2. Accessory appendage of male genitalia with branched hairs; styles relatively short; macrotrichia only at extreme tip of wing........Subgenus *Cladotanytarsus* Kieffer
    Fused thoracic vittae, scutellum and postnotum black; fore basitarsus 1.5 times tibia in length; wing length 1.48 mm
    <div align="right">

Tanytarsus (Cladotanytarsus) viridiventris (Malloch)
    </div>

    Male genitalia: fig. 60
    Accessory appendage of male genitalia with hairs simple or flattened.............. 3
3. Veins R1 and R4 + 5 close together obliterating R2 + 3; styles of male genitalia abruptly contracted or attenuated at the apex or for apical half; frontal tubercles absent
    <div align="right">

Subgenus *Rheotanytarsus* Bause
    </div>

    Wing length approximately 1.59 mm; fore basitarsus approximately 1.66 times tibia in length; thoracic vittae yellowish brown, ground color of thorax yellowish white
    <div align="right">

Tanytarsus (Rheotanytarsus) n. sp. 2
    </div>

    Male genitalia: fig. 61
    Vein R2 + 3 present; styles of male genitalia evenly pointed or rounded at apex; frontal tubercles usually present..........Subgenus *Tanytarsus* van der Wulp.......... 4
4. Wing length 2.00 mm or longer; ground color of thorax including scutellum stramineous, thoracic markings light to dark brown; abdomen blackish brown with lateral areas dark olive green...............................*Tanytarsus (Tanytarsus)* n. sp. 6
    Male genitalia: fig. 23
    Wing length less than 2.00 mm; ground color of thorax including scutellum yellowish white to pea green; vittae yellowish brown to dark brown...................... 5
5. Leg ratio 1.5 or less (L.R. approximately 1.41; color bright green)
    <div align="right">

Tanytarsus (Tanytarsus) n. sp. 5
    </div>

    Male genitalia: fig. 62
    Leg ratio 1.6 or more.. 6
6. Wing length approximately 1.9 mm; fore basitarsus 2.3 times tibia in length
    <div align="right">

Tanytarsus (Tanytarsus) n. sp. 3
    </div>

    Male genitalia: fig. 63
    Wing length approximately 1.7 mm or less; fore basitarsus approximately 2.0 times tibia in length................................*Tanytarsus (Tanytarsus)* n. sp. 4
    Male genitalia: fig. 64

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[14] Compiled from Goetghebuer (1928), Edwards (1929), Johannsen and Townes (1952), Freeman (1958), and Sublette (MS.).
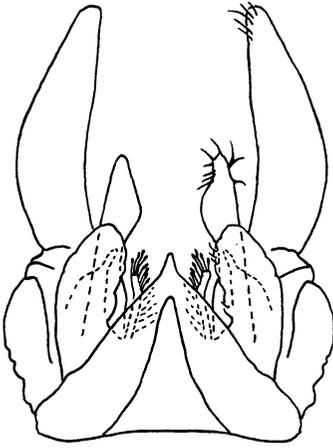
Fig. 59. Male genitalia of *Micropsectra
nigripilus* (Johannsen), × 120.
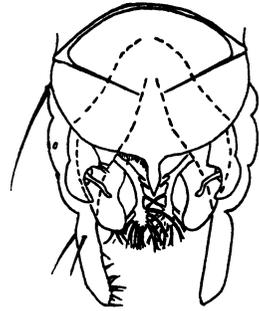
Fig. 60. Male genitalia of
Tanytarsus (*Cladotanytar-
sus*) *viridiventris* (Malloch),
× 120.
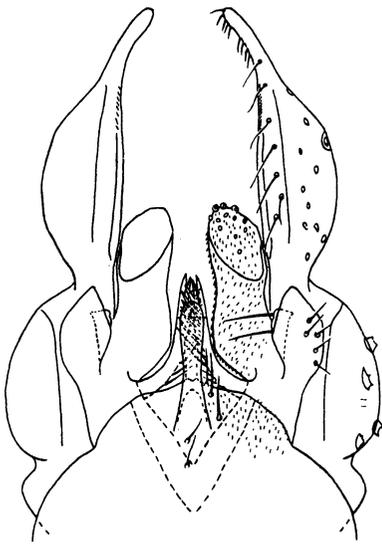
Fig. 61. Male genitalia of *Tanytarsus*
(*Rheotanytarsus*) n. sp. 2 after Sublette.
Magnification not given.
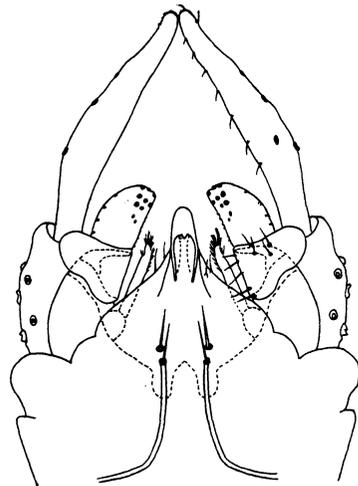
Fig. 62. Male genitalia of *Tanytarsus*
(*Tanytarsus*) n. sp. 5 after Sublette. Mag-
nification not given.
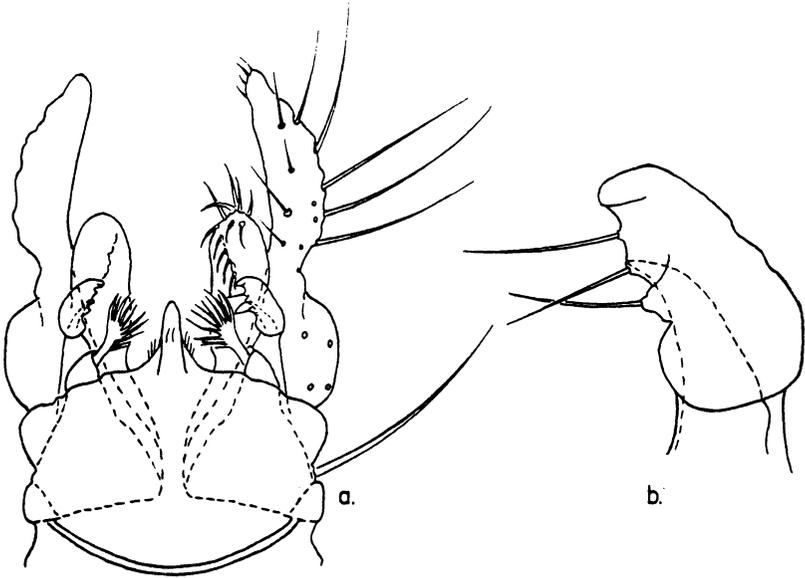
Fig. 63. Left, male genitalia of *Tanytarsus (Tanytarsus)* n. sp. 3, × 150.
Right, superior appendage, × 600.
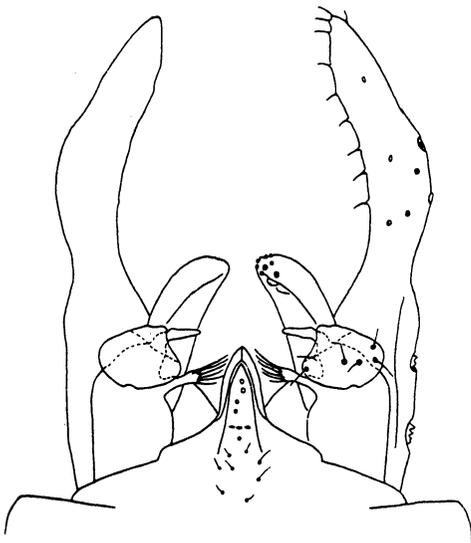
Fig. 64. Male genitalia of *Tanytarsus (Tany-tarsus)* n. sp. 4 after Sublette. Magnification not given.

Key to Larvae of Species Reared[15]

1. Antennae retractile into head (fig. 65) ; basal antennal segment three times as long as combined length of other antennal segments (fig. 66) ; prolegs long and stilt-like Tanypodinae 4

    Antennae not retractile; basal antennal segment less than three times as long as the combined length of other antennal segments; prolegs usually short.............. 2

2. Striated paralabial plates absent; mandibles without preapical mandibular comb (row of bristles overhanging mandibular teeth) 3

    Striated paralabial plates present; mandibles usually with preapical mandibular comb (row of bristles overhanging mandibular teeth) .... Chironominae 6

3. Antennae 5-segmented; short and thick set; posterior prolegs not elongated.......... Orthocladiinae 5

    Antennae 4-segmented, long and slender (fig. 67a) ; posterior prolegs elongated, stout brown spine near base of each posterior proleg (fig. 67b)........................ Corynoneurinae .... *Corynoneura* n. sp.

4. Segments of body with few scattered bristles; body slender; paralabial combs absent; both pairs of anal gills close to anal opening................ *Pentaneura* Philippi

        Posterior prolegs with three dark claws (fig. 68) ; body yellowish mottled with brown; mandible (fig. 69)

                Pentaneura (Ablabesmyia) aequifasciata Dendy and Sublette

        Posterior prolegs with 2 dark claws; lingua of hypopharynx with 5 black teeth; middle tooth shortest (fig. 70) ; mandible (fig. 71)

                  Pentaneura (Ablabesmyia) monilis (L.)

    Segments of body with lateral hair fringes; head and body broad; paralabial combs present (fig. 72) ; anal gills short, triangular ventral pair remote from anus on base of prolegs .... *Procladius* (Skuse)

        Body amber-colored; paralabial combs with 8 teeth; innermost teeth broad and light-colored; others brown; outermost teeth often extremely small

                  Procladius culiciformis (L.)

5. Labial plate with 13 teeth (fig. 73) ; mandibles without apparent corrugations on outer or convex edge, but with serrate inner margin (fig. 74) ; premandible simple; body without hair pencils............................. *Cricotopus bicinctus* (Meigen)

    Labial plate with 11 teeth; first lateral tooth notched (fig. 75) ; mandibles with corrugations on outer or convex edge; premandibles bifid; intermediate abdominal segments with hair pencils (fig. 76) .... *Cricotopus sylvestris* (Fabr.)

6. Antennae usually short, 4- to 6-segmented; rarely on tubercle; if so, tubercle is shorter than wide; lateral bristle usually absent; Lauterborn organs small, paired on second segment or alternate on second and third segment; not mounted on long petioles (fig. 77) ; accessory tooth of mandible not extending beyond apical tooth; abdominal segments without plumose bristles................ Chironomini 7

    Antennae long, 5-segmented; generally somewhat curved; mounted on prominent tubercle which is as long as or longer than wide; first segment with lateral bristle; Lauterborn organs paired on apex of second segment or slightly separated on second segment, may be mounted on long petioles; accessory tooth of mandible long bristle-like extending beyond apical tooth (fig. 78) ; abdominal segments 2 to 6 usually with caudo-lateral bifid plumose bristles................ Tanytarsini 15

7. Antennae with 6 segments (fig. 79) .... *Paralauterborniella* Lenz

        Median tooth of labial plate bifid and lighter colored than laterals (fig. 80) ; mandibles with prominent blade-like accessory tooth; premandibles bifid (fig. 80)

                Paralauterborniella elachista (Townes)

    Antennae with 5 segments... 8

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[15] Modified from keys of Goetghebuer (1927, 1928, and 1932), Johannsen (1937 *a* and *b*), Wirth and Stone in Usinger (1956), and Roback (1957).

8. Mature larvae blood-red in color (contain erythrocruorin)........................ 9
   Mature larvae not blood-red (lack erythrocruorin)..............................10

9. Without ventral gills on eleventh body (eighth abdominal) segment.................11
   With 2 pairs of ventral gills on eleventh body segment (fig. 81); labial plate with 13
   teeth; median tooth trifid and shorter than first laterals (fig. 82); basal tooth of
   mandibles pale; remaining teeth dark (fig. 83); caudo-lateral processes present on
   tenth body segment.....................*Tendipes (Tendipes) attenuatus* (Walker)

10. Paralabial plates in contact with 4 lateral labial teeth on each side (fig. 84); pre-
    mandibles with 2 blades or lobes (fig. 85a); blade of antenna attached laterally to
    second segment (fig. 86)..........*Tendipes (Cryptochironomus) chaetoala* Sublette
    Paralabial plates in contact with less than 4 lateral labial teeth on each side (fig. 87);
    premandibles with 5 blades or lobes (fig. 88); blade of antenna attached at distal end
    of first segment.............*Tendipes (Cryptochironomus) tenuicaudatus* (Malloch)

11. Labial plate with light-colored arched toothless median area flanked by oblique rows of
    dark teeth (fig. 89); antennal blade attached laterally to second segment (fig. 90);
    mandibles with broad accessory tooth (fig. 91a, 91b); premandibles 5-lobed (fig. 92)
                              Tendipes (Cryptochironomus) fulvus (Johannsen)
    Labial plate toothed entire width; antennal blade at distal end of first segment......12

12. Labial plate with 13 teeth, with large median tooth shorter than first laterals........13
    Labial plate with 16 teeth, with median pair shorter than first laterals..............14

13. Paralabial plates short (as wide as long), fan-shaped (fig. 93a); median tooth of labial
    plate as long as or longer than first lateral pair; epipharyngeal comb with 5 simple
    teeth (fig. 93c)................*Tendipes (Dicrotendipes) californicus* (Johannsen)
    Paralabial plates elongated (length three times the width), sausage-shaped (fig. 94);
    median tooth of labial plate much shorter than first lateral pair; epipharyngeal
    comb with 4 to 5 irregular trilobed teeth
                              Glyptotendipes (Phytotendipes) lobiferus (Say)

14. Mandibular teeth black; accessory tooth of mandible slender and curved near tip; first
    pair of lateral teeth of labial plate closely adjacent to medial pair (fig. 95); antennal
    blade reaches fourth segment; small blade at base of third segment between Lauter-
    born organs (fig. 96)..........*Tendipes (Endochironomus) nigricans* (Johannsen)
    Basal tooth of mandible part light and part black; accessory tooth of mandible slender
    but straight (fig. 97a); first pair of lateral teeth of labial plate well separated from
    medial pair (fig. 97b); antennal blade reaches beyond fourth segment; no additional
    small blade at base of third segment (fig. 77)......*Phaenopsectra profusa* (Townes)

15. Lauterborn organs attached to tip of first antennal segment (fig. 98); median tooth of
    labial plate with light central area and dark margins (fig. 99)
                              Tanytarsus (Cladotanytarsus) viridiventris (Malloch)
    Lauterborn organs attached to tip of second antennal segment; median tooth of labial
    plate either entirely light or dark..16

16. Lauterborn organs of antennae sessile or with petiole shorter than last 3 antennal
    segments (fig. 25); all teeth of labial plate dark (fig. 100); mandible with 4 teeth
    (all dark) (fig. 78); premandible bifid (fig. 101)...*Tanytarsus (Tanytarsus)* n. sp. 5
    Lauterborn organs of antennae petiolate, with petiole longer than last 3 antennal seg-
    ments (figs. 102 and 107); mandible with 5 teeth.............................17

17. Median tooth of labial plate lighter in color and more ventrally located than lateral
    teeth; is weakly trifid and has shoulder-like notches near base (fig. 103a); mandible
    with 4 black teeth and 1 light-colored tooth (fig. 103b); premandible with 4 blades
    (fig. 104) ....*Tanytarsus (Tanytarsus)* n. sp. 6
    Median tooth of labial plate as dark as lateral teeth; not trifid; without shoulder-like
    notches (fig. 105); mandible with 5 black teeth (fig. 106)
   *Micropsectra nigripilus* (Johannsen)
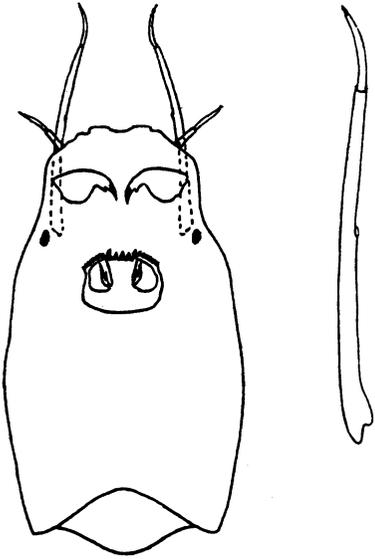
Fig. 65 (left). Head of larva of *Pentaneura* (*Ablabesmyia*) *monilis* (L.), ventral view showing retractile antennae, × 42.

Fig. 66 (right). Antenna of larva of *Pentaneura* (*Ablabesmyia*) *monilis* (L.), × 61.
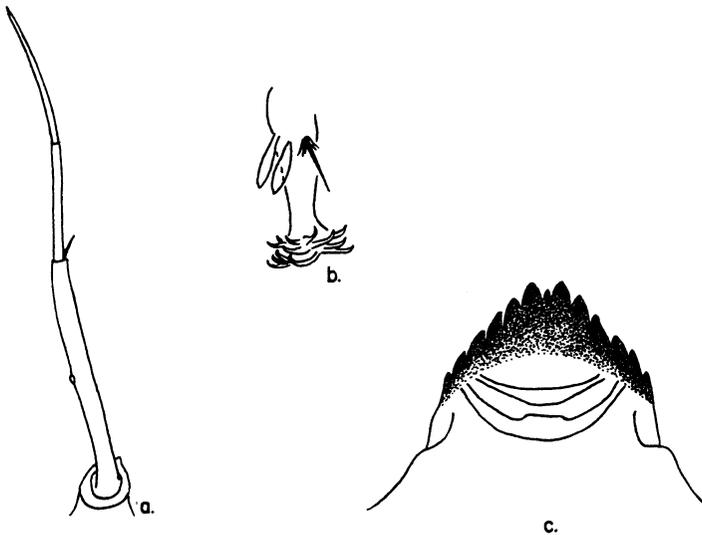

Fig. 67. *Corynoneura* (*Corynoneura*) n. sp. Left, antenna of larva, × 120; center, posterior proleg of larva, showing compound spine and two of the four anal gills, × 120; right, labial plate of larva, × 520.
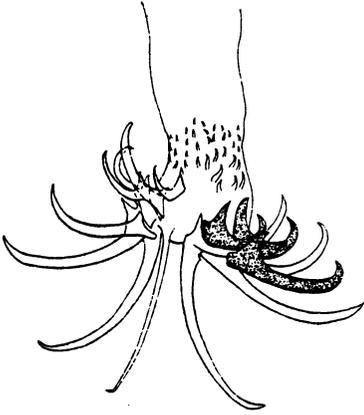
Fig. 68. Posterior proleg of larva of *Pentaneura (Ablabesmyia) aequifasciata* Dandy and Sublette, × 63.

Fig. 69. Mandible of larva of *Pentaneura (Ablabesmyia) aequifasciata* Dendy and Sublette, × 127.
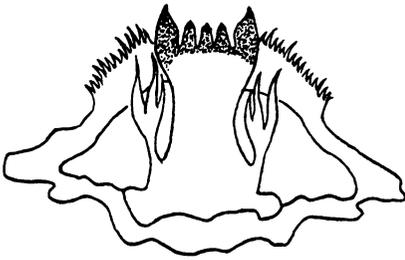
Fig. 70. Hypopharynx of larva of *Pentaneura (Ablabesmyia) monilis* (L.), × 127.

Fig. 71. Mandible of larva of *Pentaneura (Ablabesmyia) monilis* (L.), × 127.
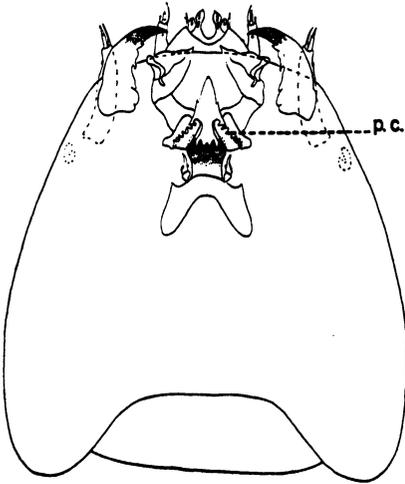
Fig. 72. Head of larva of *Procladius culiciformis* (L.), ventral view, × 60. *p.c.*, paralabial comb.
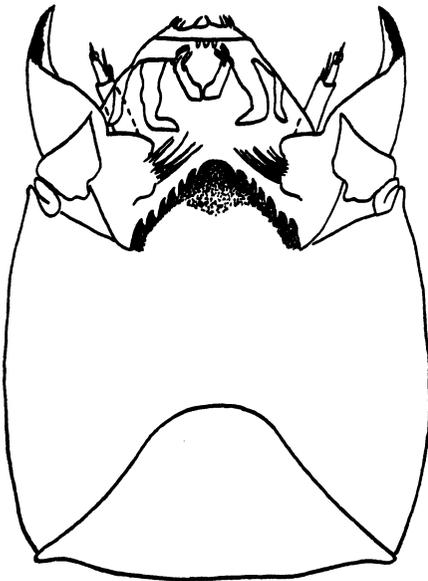
Fig. 73. Head of larva of *Cricotopus bicinctus* (Meigen), ventral view, × 120.

Fig. 74. Mandible of larva of *Cricotopus bicinctus* (Meigen), × 120.
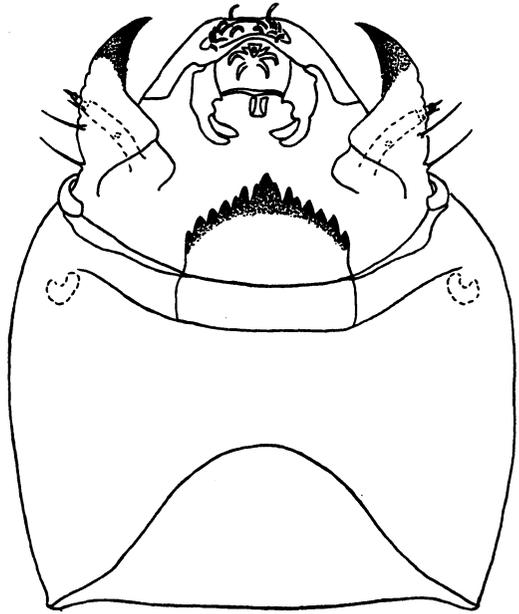
Fig. 75. Head of larva of *Cricotopus sylvestris* (Fabr.), ventral view, × 120.
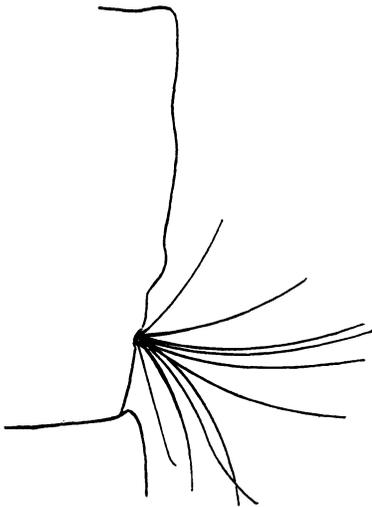
Fig. 76. Hair pencil on caudo-lateral margin of abdominal segments of larva of *Cricotopus sylvestris* (Fabr.), × 120.
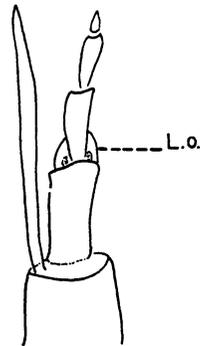
Fig. 77. Four terminal segments of antenna of larva of *Phaenopsectra profusa* (Townes), × 510. *L.o.*, Lauterborn organ.
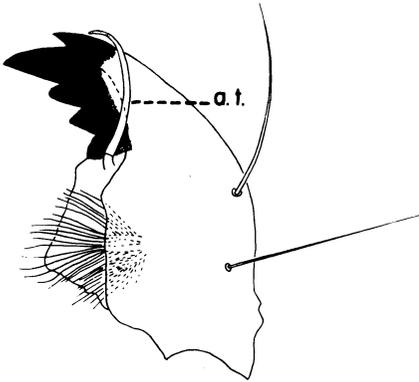
Fig. 78. Mandible of larva of *Tanytarsus* (*Tanytarsus*) n. sp. 5, × 290. *a.t.*, accessory tooth.

Fig. 79. Antenna of larva of *Paralauter-borniella elachista* (Townes), × 140.

Fig. 80. *Paralauterborniella elachista* (Townes). Left, mandible, labial plate, and paralabial plates of larva, × 140. Right, premandible of larva, × 590.
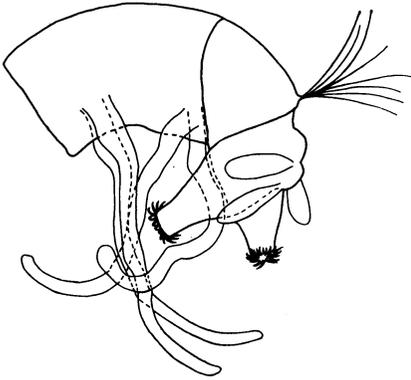
Fig. 81. Posterior end of larva of *Tendipes* (*Tendipes*) *attenuatus* (Walker), showing ventral gills on eleventh body segment, × 13.5.
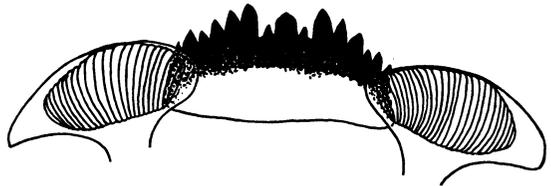

Fig. 82. Labial plate and paralabial plates of larva of *Tendipes* (*Tendipes*) *attenuatus* (Walker), × 120.

Fig. 83. Mandible of larva of *Tendipes* (*Tendipes*) *attenuatus* (Walker), × 120.
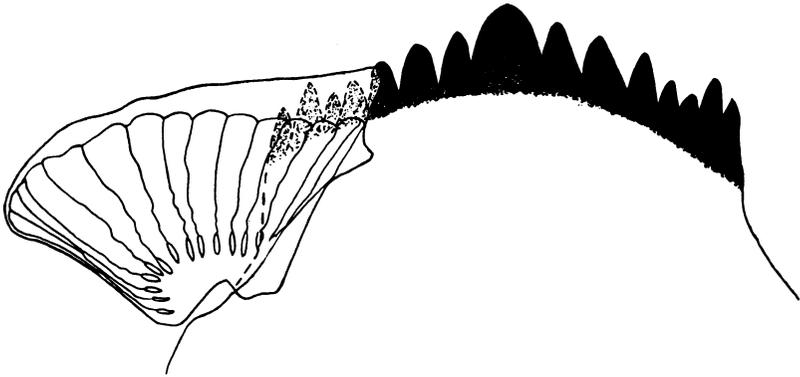
Fig. 84. Labial plate and one paralabial plate of larva of *Tendipes*
(*Cryptochironomus*) *chaetoala* Sublette, × 215.
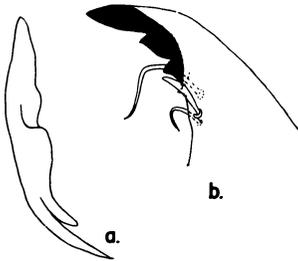
Fig. 85. *Tendipes* (*Cryptochironomus*) *chaetoala*
Sublette. Left, premandible of larva. Right, tip of
mandible of larva. Both × 255.
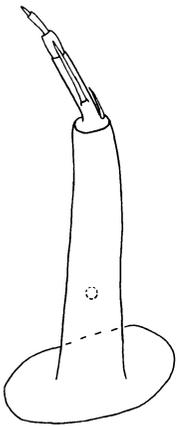

Fig. 86 (left). Antenna of larva of *Tendipes*
(*Cryptochironomus*) *chaetoala* Sublette, × 322.
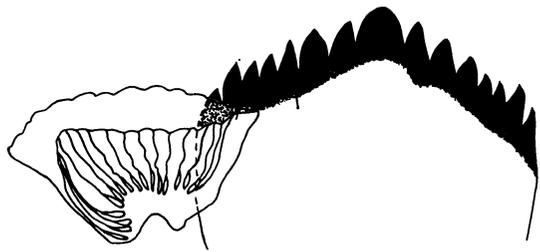
Fig. 87. Labial plate and one paralabial plate of larva
of *Tendipes* (*Cryptochironomus*) *tenuicaudatus* (Mall-
och), × 172.
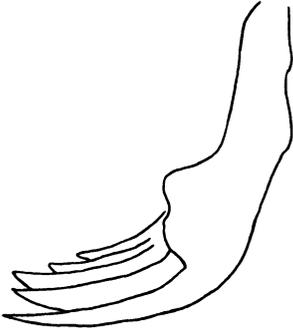
Fig. 88. Premandible of larva of *Tendipes (Cryptochironomus) tenuicaudatus* (Malloch), × 510.

Fig. 89. Labial plate and one paralabial plate of larva of *Tendipes (Cryptochironomus) fulvus* (Johannsen), × 120.
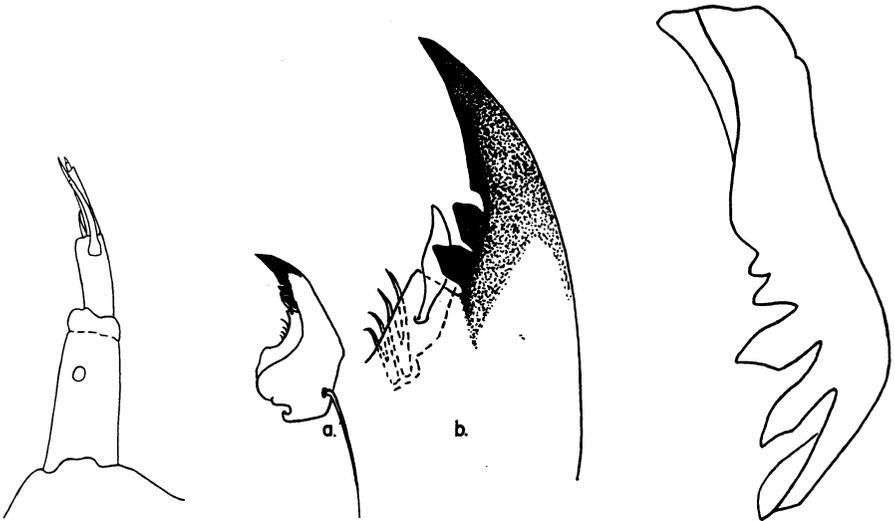
Fig. 90 (left). Antenna of larva of *Tendipes (Cryptochironomus) fulvus* (Johannsen), × 255.

Fig. 91 (center). *Tendipes (Cryptochironomus) fulvus* (Johannsen). *a,* mandible of larva; *b,* enlarged tip of mandible of larva, × 510.

Fig. 92 (right). Premandible of larva of *Tendipes (Cryptochironomus) fulvus* (Johannsen), × 510.
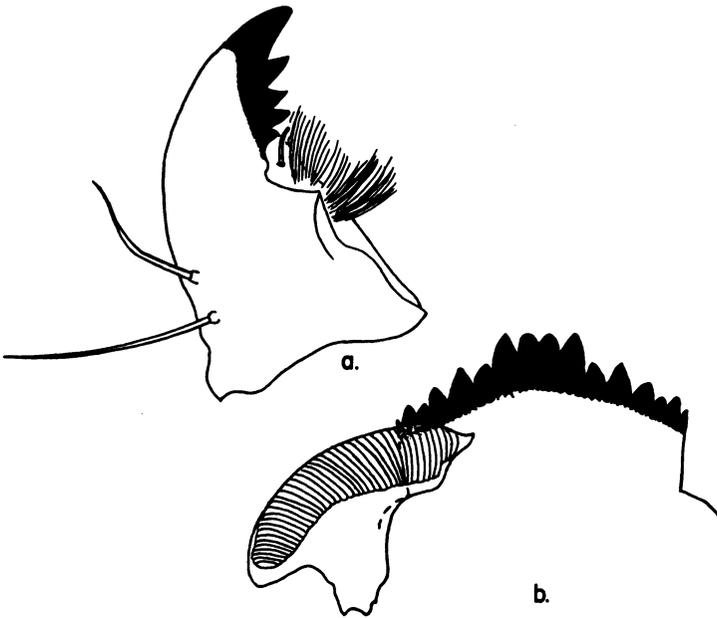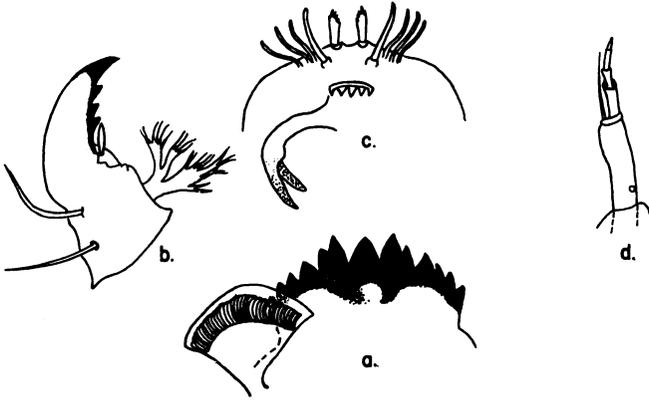
Fig. 96. Four terminal segments of antenna of larva of *Tendipes* (*Endochironomus*) *nigricans* (Johannsen), × 255.
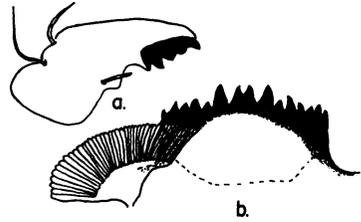
Fig. 97. *Phaenopsectra profusa* (Townes). *a*, mandible of larva; *b*, labial plate and one paralabial plate of larva. Both × 120.
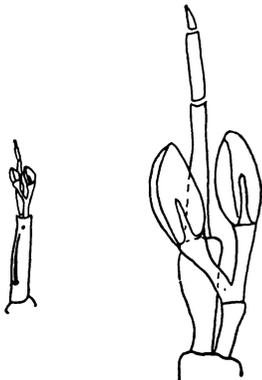
Fig. 98. Left, antenna of larva of *Tanytarsus* (*Cladotanytarsus*) *viridiventris* (Malloch), × 150. Right, enlargement of the four terminal segments and Lauterborn organs, × 510.

Opposite page, top to bottom: Fig. 93. *Tendipes* (*Dicrotendipes*) *californicus* (Johannsen). *a*, labial plate and one paralabial plate of larva; *b*, mandible of larva; *c*, epipharyngeal area of larva; *d*, antenna of larva. All × 120.

Fig. 94. Labial plate and one paralabial plate of larva of *Glyptotendipes* (*Phytotendipes*) *lobiferus* (Say), × 120.

Fig. 95. *Tendipes* (*Endochironomus*) *nigricans* (Johannsen). *a*, mandible of larva; *b*, labial plate and one paralabial plate of larva. Both × 140.
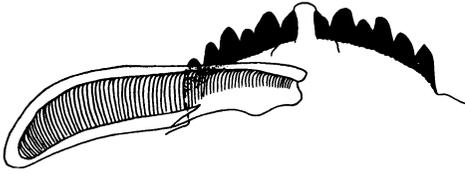
Fig. 99. Labial plate and one paralabial plate of larva of *Tany-tarsus (Cladotanytarsus) viridiventris* (Malloch), × 172.
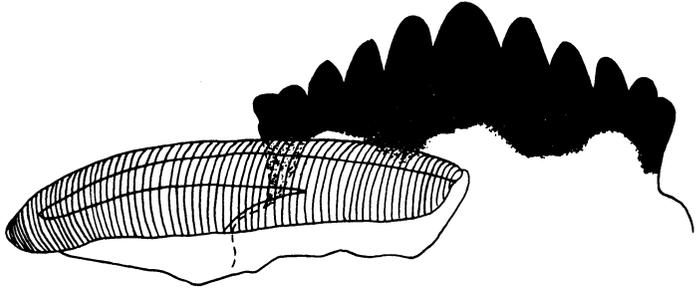
Fig. 100. Labial plate and one paralabial plate of larva of *Tanytarsus (Tanytarsus)* n. sp. 5, × 215.
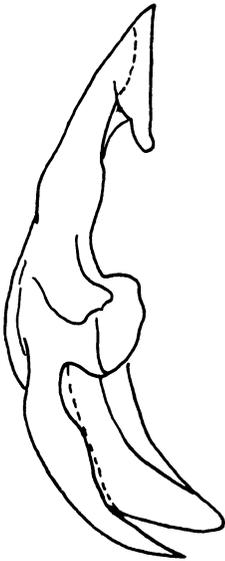
Fig. 101. Premandible of larva of *Tany-tarsus (Tanytarsus)* n. sp. 5, × 645.
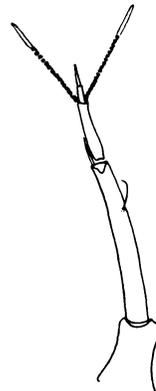
Fig. 102. Antenna of larva of *Tanytarsus (Tanytarsus)* n. sp. 6, × 75.
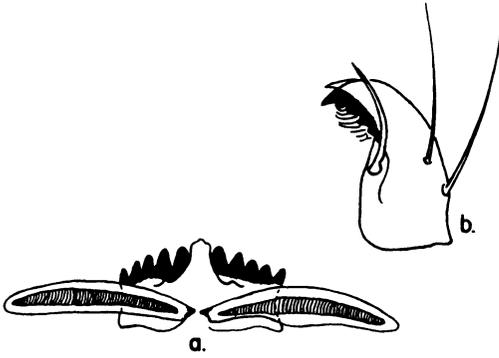
Fig. 103. *Tanytarsus* (*Tanytarsus*) n. sp. 6. *a*,
labial plate and paralabial plates of larva; *b*, man-
dible of larva. Both × 150.

Fig. 105. Labial plate and one paralabial
plate of larva of *Micropsectra nigripilus*
(Johannsen), × 150.
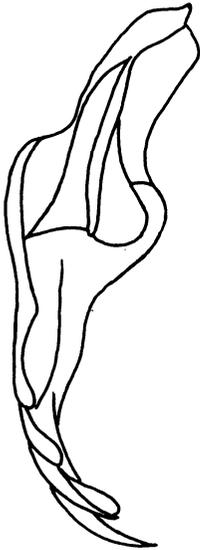
Fig. 104. Premandible of larva of *Tanytar-
sus* (*Tanytarsus*) n. sp. 6, × 610.

Fig. 106. Tip of mandible of larva of *Mi-
cropsectra nigripilus* (Johannsen), × 300.
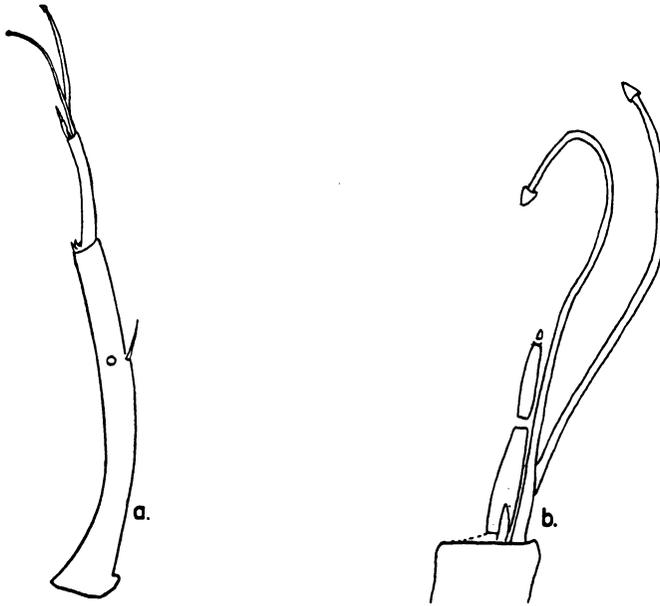
Fig. 107. *Micropsectra nigripilus* (Johannsen). Left, antenna of larva, × 150. Right, enlargement of terminal segments and Lauterborn organs, × 610.

Key to Pupae of Reared Species and Forms Associated with Adults by Exuviae[16]

1. Thoracic respiratory organs enlarged, dark-colored structures with open stigmata; abdominal segments without spine rows or caudo-lateral spines; anal segment generally with only 2 lateral bristles or filaments on each lobe or fin...................
   Tanypodinae 4
   Thoracic respiratory organs without open stigmata; some composed of numerous filaments; absent in some species.. 2

2. Thoracic respiratory organs absent...............................Corynoneurinae
   Three mm or less in length; enclosed in gelatinous case; abdominal segments each with 4 filaments on each side; tergites shagreened; anal lobes each margined with swim hairs with 3 larger filaments on each side among them (fig. 108)
                                                                    Corynoncura n. sp.
   Thoracic respiratory organs present....................................... 3

3. Thoracic respiratory organs somewhat rigid or erect tubular processes, which may bear spines; caudo-lateral corners of abdominal segment 8 unarmed (spurs absent); anal fins generally with 3 filaments, rarely with a fringe of swimming hairs.............
   Orthocladiinae 5
   Thoracic respiratory organs usually a tuft of filaments (2 to 100 in number), or may be simple long filiform process, when simple, the lobes of the anal segment with fringe of slender swimming hairs or filaments; abdominal segment 8 often armed with a spine or comb of spurs at the caudo-lateral corners........Chironominae........ 7

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[16] Modified from keys by Johannsen (1937a and b) and Roback (1957).

4. Outer margin of anal fins bare; the 2 filaments near middle of margin; thoracic respiratory organs oval-shaped, dark-brown with reticulate surface (fig. 109)

   Pentaneura Philippi

   Dorsal surface of abdominal segments with pattern of lateral markings (fig. 110); posterior points of anal fins with shoulder or ridge (fig. 111a)

   Pentaneura (Ablabesmyia) aequifasciata Dendy and Sublette

   Dorsal surface of abdominal segments without lateral markings; posterior points of anal fins more sloping without shoulder or ridge (fig. 111b)

   Pentaneura (Ablabesmyia) monilis (L.)

   Outer margin of anal fins with minute spinelets; inner or medial angle drawn out to a point, which may be bifid (fig. 112); thoracic respiratory organs linear or fusiform, brown in color with spines covering surface (fig. 113) ... *Procladius culiciformis* (L.)

5. Anal lobes margined with swim hairs and with 3 long bristles; eighth abdominal segment with 5 flattened filaments (fig. 114); second abdominal tergite with crescent-shaped ridge armed with recurved spines; socket-like protuberances on the pleura of second abdominal segment (fig. 115); thoracic respiratory organs spatulate with covering of moderately large spines (fig. 116) . . . .*Psectrocladius* n. sp. 2

   Anal lobes without swim hairs, but with 3 stiff bristles (fig. 117); eighth abdominal segment without flattened filaments; second abdominal pleura without protuberances; thoracic respiratory organs smaller, not spatulate. 6

6. Thoracic respiratory organs long, slender, and smooth (fig. 118); second abdominal tergite with shagreen anterior to recurved spines (fig. 119)

   Cricotopus sylvestris (Fabr.)

   Thoracic respiratory organs short, thick-set, covered with small spinules (fig. 120); second abdominal tergite without shagreen pattern anterior to recurved spines (fig. 121) . . . .*Cricotopus bicinctus* (Meigen)

7. Thoracic respiratory organs usually simple, may have hairs or spines; abdominal tergites with distinctive patterns of spinule patches or rows; caudo-lateral angles of abdominal segment eight armed with comb or spur. . . . . . . .Tanytarsini. 19

   Thoracic respiratory organs with at least 2 branches, often filamentous; abdominal tergites shagreened, but not in patterns as above; caudo-lateral angles of abdominal segment eight may or may not be armed with comb or spur. . . . .Chironomini. 8

8. Eighth abdominal segment without comb or spur. 9

   Eighth abdominal segment with comb or spur. 11

9. Cephalic tubercles double antler-like (fig. 122); anal lobes with swim hairs at margins (fig. 123) . . . .*Tendipes (Cryptochironomus) fulvus* (Johannsen)

   Cephalic tubercles simple (figs. 124 and 125); anal lobes each with a strap-like filament inset from marginal swim hairs (fig. 126) 10

10. Second abdominal segment with row of slender, colorless spines on posterior margin of sternite; bristle anterior to tubercle on pleuron a distance of twice its own length from tubercle (fig. 127) . . . .*Tendipes (Cryptochironomus) tenuicaudatus* (Malloch)

   Second abdominal segment without row of spines on posterior margin of sternite; bristle anterior to tubercle on pleuron a distance of less than its own length from tubercle (fig. 128) . . . .*Tendipes (Cryptochironomus) chaetoala* Sublette

11. Comb or spur at caudo-lateral angles of abdominal segment eight. 12

   Single slender spur located some distance anterior to caudo-lateral angles of abdominal segment 8 (fig. 129); thoracic respiratory organs branching, tree-like, three fourths as long as entire pupa (fig. 130); cephalic tubercles simple (fig. 131)

   Tendipes (Cryptochironomus) darbyi Sublette

12. Thoracic respiratory organs with 2 to 12 branches. 13

   Thoracic respiratory organs with a tuft of 20 or more thread-like filaments. 15

13. Thoracic respiratory organs with only 2 smooth branches (fig. 132); cephalic tubercles absent; spur on abdominal segment 8 of approximately 3 small teeth (fig. 133)

   Pseudochironomus richardsoni Malloch

   Thoracic respiratory organs with more than 2 branches may have spinules on surface (figs. 134a and 136a); cephalic tubercles present. 14

14. Cephalic tubercles wart-like; each with a depressed area of minute pointed papillae (fig. 134b); abdominal segment 8 with 4 long bristles (fig. 135)

Phaenopsectra profusa (Townes)

Cephalic tubercles not wart-like; each with long bristle (fig. 136b); abdominal segment 8 with 5 flat filaments................................*Paralauterborniella* Lenz

Differences observed in spurs on abdominal segment 8; pattern of spinules at posterior edge of abdominal tergite four; pattern of recurved hooks at posterior edge of abdominal tergite 2 (fig. 137)....*Paralauterborniella subcincta* (Townes)

Paralauterborniella sp.

Paralauterborniella elachista (Townes)

15. Mace-like process on abdominal segments 2 to 6 (fig. 138); abdominal segment 8 with 5 lateral filaments and comb of weak spines at caudo-lateral angle (fig. 139); cephalic tubercles acute with long preapical bristle (fig. 140)

Glyptotendipes (*Phytotendipes*) *lobiferus* (Say)

Abdominal segments without spiked or mace-like process........................16

16. Caudo-lateral angles of abdominal segment 8 with a comb of several independent teeth or spines (fig. 141); cephalic tubercles low and broad (fig. 142)

Tendipes (*Endochironomus*) *nigricans* (Johannsen)

Caudo-lateral angles of abdominal segment 8 with a compound spur with branches only partially separated 17

17. Spurs on caudo-lateral angles of abdominal segment 8 simple, slightly curved or sinuate tapering to a fine point; divided into 2 branches or spines (fig. 143)

Tendipes (*Dicrotendipes*) *californicus* (Johannsen)

Spurs on caudo-lateral angles of abdominal segment 8 flattened, not curved or sinuate; composed of 6 or more teeth (fig. 145)...................................18

18. Pupa 10 mm or less in length.............*Tendipes* (*Tendipes*) *attenuatus* (Walker)
Pupa 12 mm or more in length.................*Tendipes* (*Tendipes*) *plumosus* (L.)

19. Thoracic respiratory organs with inflated base supporting a number of fine filaments (fig. 146); third, fourth, and fifth abdominal tergites with small patches of spinules (fig. 147); comb at caudo-lateral angle of abdominal segment 8 with 6 or more large teeth and several smaller teeth (fig. 148); cephalic tubercles tall with bristle at least twice as long as height of tubercle (fig. 149)

Tanytarsus (*Cladotanytarsus*) *viridiventris* (Malloch)

Thoracic respiratory organs tubular, single, setaceous structures..................20

20. Apical half of thoracic respiratory organs with prominent spines (fig. 150); third, fourth, and fifth abdominal tergites with two contiguous or nearly contiguous patches of shagreen spinules (fig. 151); cephalic tubercles with bristles three times as long as height of tubercle (fig. 152)...............*Micropsectra nigripilus* (Johannsen)

Thoracic respiratory organs with minute spinules or smooth.....................21

21. Fourth abdominal tergite with central patch of dense black shagreen spines between 2 longitudinal patches of long shagreen spines (fig. 153); thoracic respiratory organs long, apparently smooth (fig. 154); discs of anal lobes with 1 filament each (fig. 155); cephalic tubercles extremely short compared with bristle (fig. 156)

Tanytarsus (*Tanytarsus*) n. sp. 5

Fourth abdominal tergite without central patch of dense black shagreen spines between longitudinal shagreen (fig. 26); outer ⅘ of thoracic respiratory organs with minute spinules (fig. 157); discs of anal lobes with 2 filaments each (fig. 26); cephalic tubercles acute ½ the length of the preapical bristle (fig. 158)

Tanytarsus (*Tanytarsus*) n. sp. 6
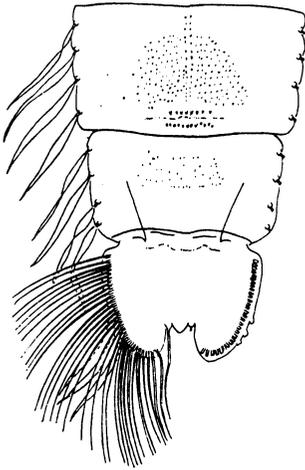
Fig. 108. Seventh, eighth, and ninth abdominal segments of pupa of *Corynoneura (Corynoneura)* n. sp., dorsal view, × 71.
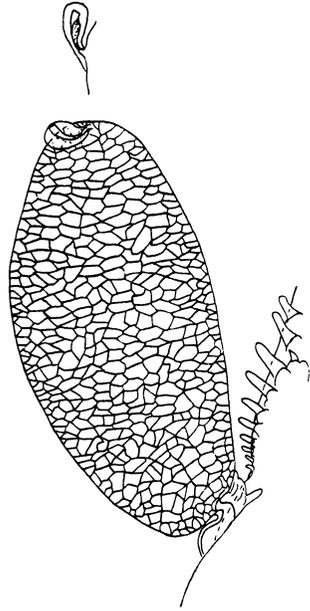
Fig. 109. Thoracic respiratory organ of pupa of *Pentaneura (Ablabesmyia) acquifasciata* Dendy and Sublette, × 71.
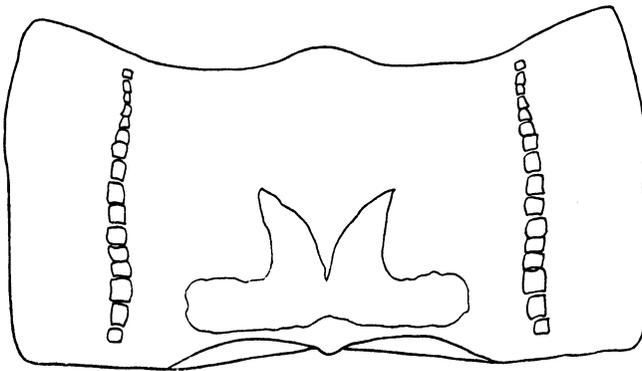
Fig. 110. Sixth abdominal tergite of pupa of *Pentaneura (Ablabesmyia) acquifasciata* Dendy and Sublette, × 40.
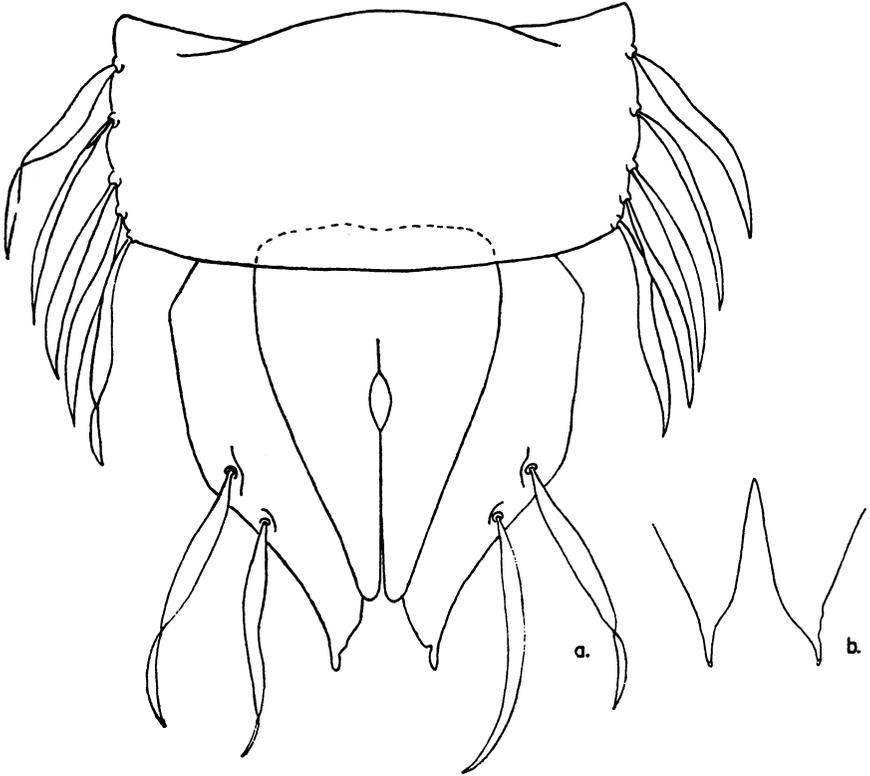
Fig. 111. Left, eighth and ninth abdominal segments of pupa of *Pentaneura* (*Abla-besmyia*) *aequifasciata* Dendy and Sublette, dorsal view, × 40; right, posterior tips of ninth abdominal segment or anal fin of pupa of *P.* (*Ablabesmyia*) *monilis* (L.), dorsal view, × 40.
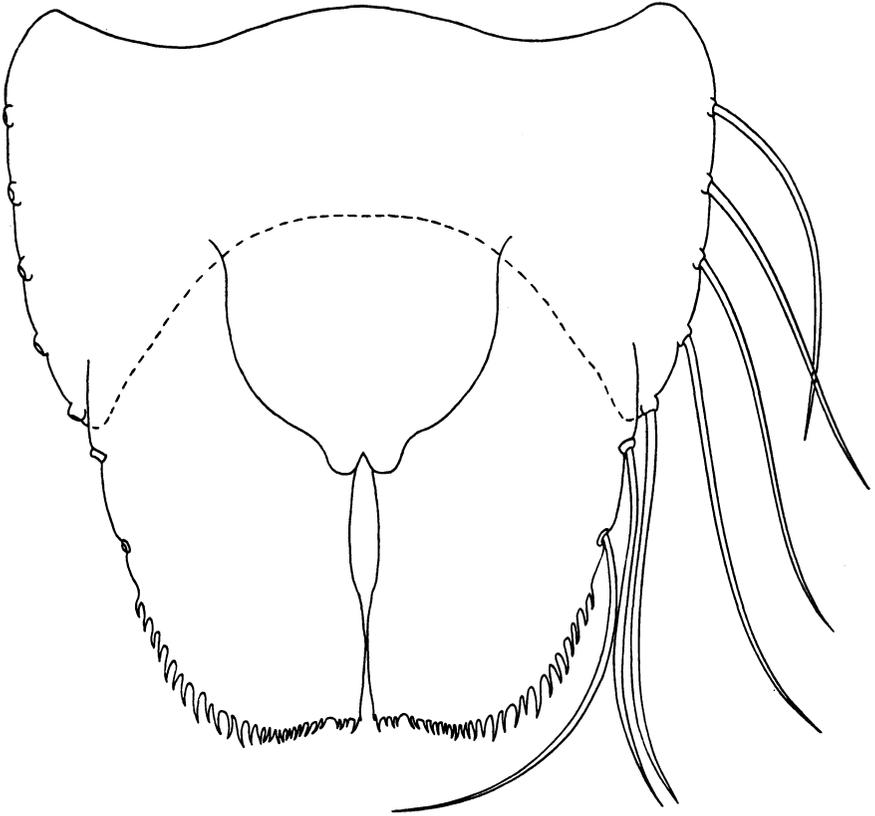
Fig. 112. Eighth and ninth abdominal segments of pupa of *Procladius culiciformis* (L), dorsal view, × 20.
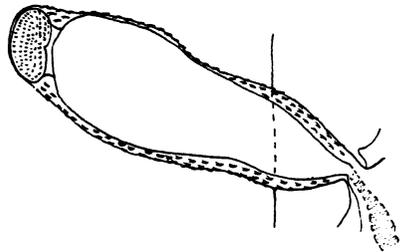
Fig. 113. Thoracic respiratory organ of pupa of *Procladius culiciformis* (L.), × 75.

Fig. 114. Eighth and ninth abdominal segments of pupa of *Psectrocladius* n. sp. 2, dorsal view, × 40.
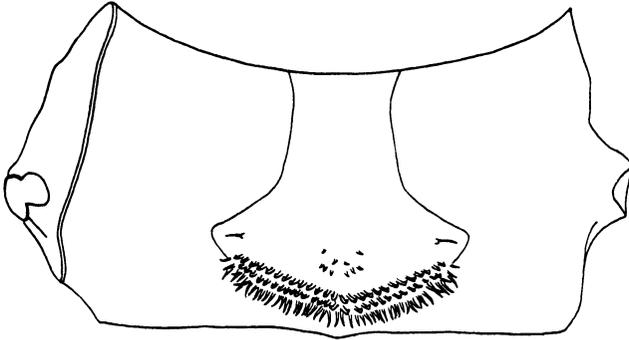
Fig. 115. Second abdominal segment of pupa of *Psectrocladius* n. sp. 2, dorsal view, × 40.
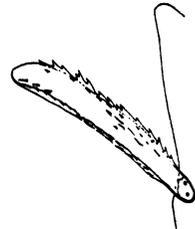
Fig. 116. Thoracic respiratory organ of pupa of *Psectrocladius* n. sp. 2, × 60.

Fig. 117. Ninth abdominal segment of pupa of *Cricotopus sylvestris* (Fabr.), dorsal view, × 75.
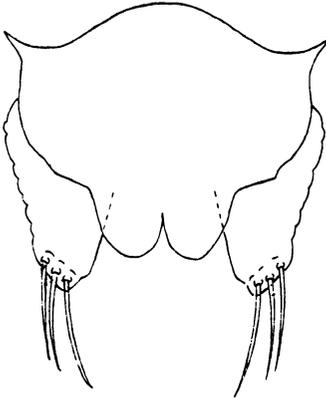
Fig. 118. Thoracic respiratory organ of pupa of *Cricotopus sylvestris* (Fabr.), × 75.
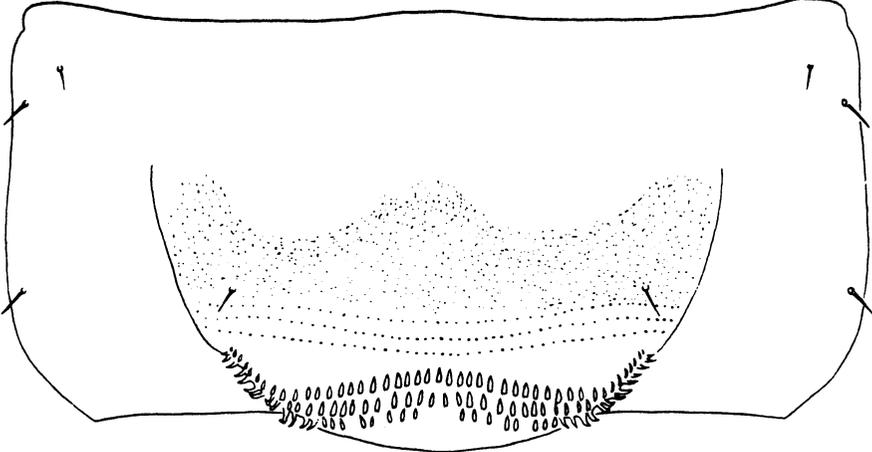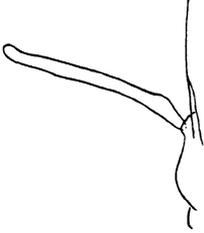
Fig. 119. Second abdominal segment of pupa of *Cricotopus sylvestris* (Fabr.), dorsal view, × 46.
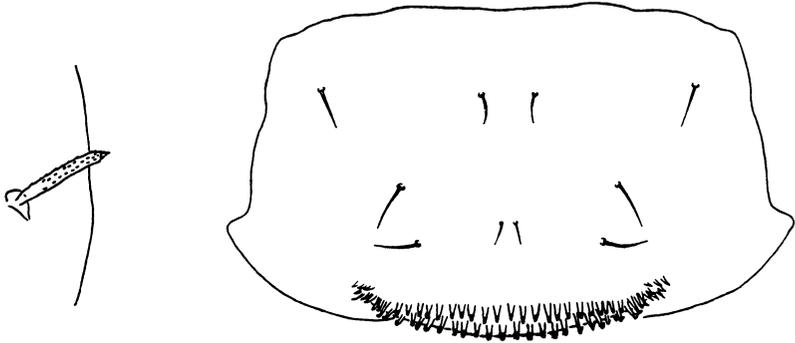
Fig. 120 (left). Thoracic respiratory organ of pupa of *Cricotopus bicinctus* (Meigen), × 70.

Fig. 121 (right). Second abdominal segment of pupa of *Cricotopus bicinctus* (Meigen), dorsal view, × 75.
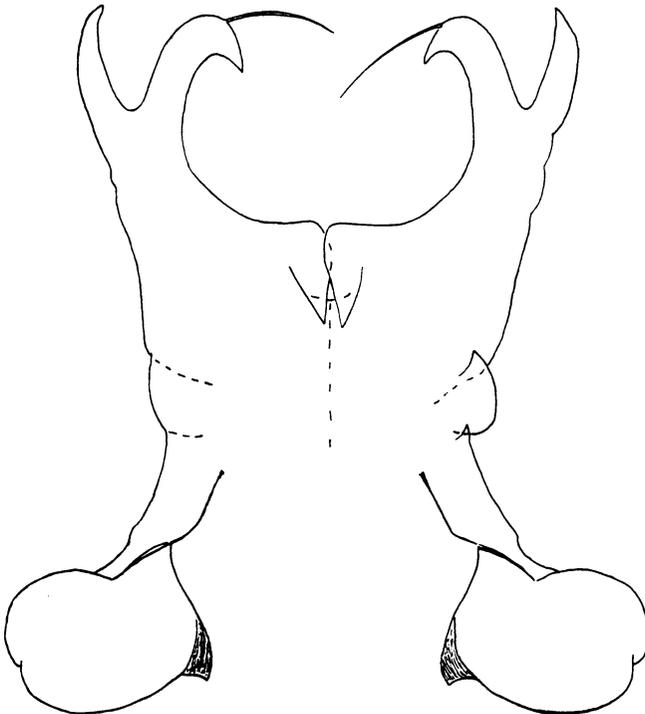
Fig. 122. Cephalic tubercles of pupa of *Tendipes (Cryptochironomus) fulvus* (Johannsen), × 46.
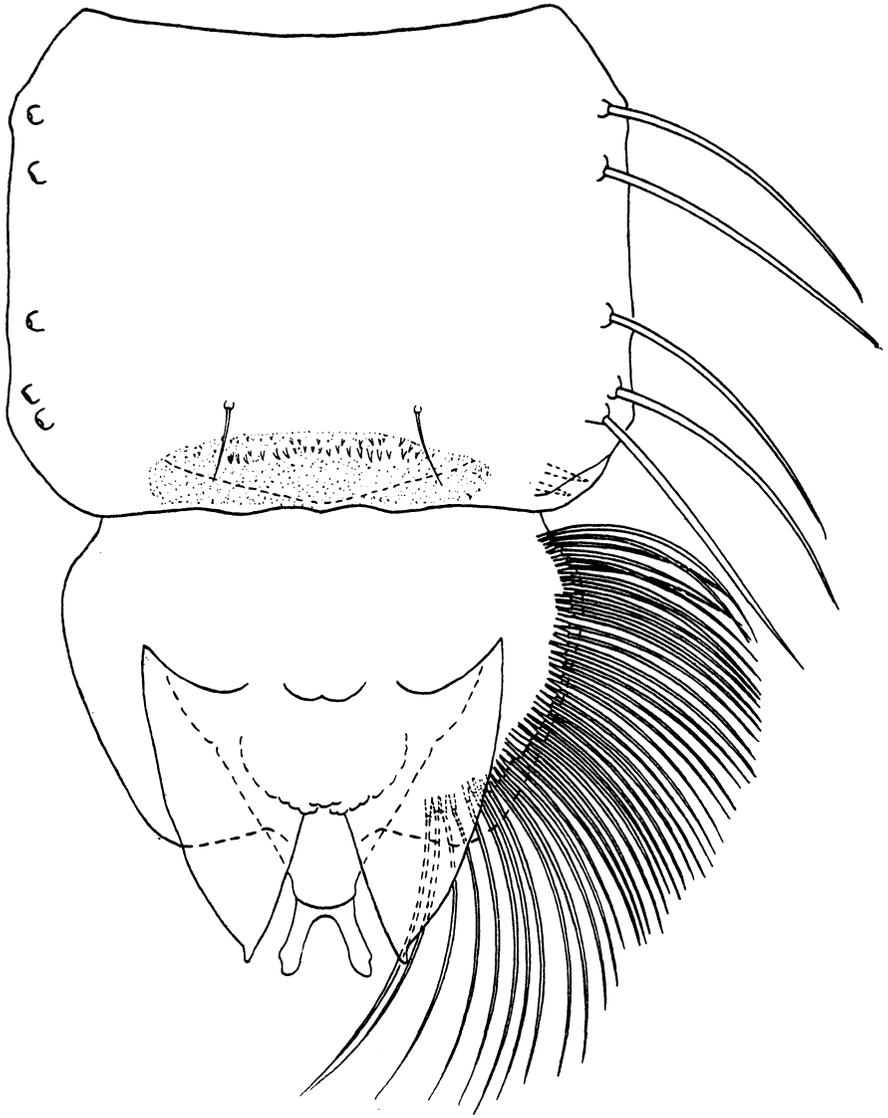
Fig. 123. Eighth and ninth abdominal segments of pupa of *Tendipes (Cryptochironomus) fulvus* (Johannsen), dorsal view, × 50.
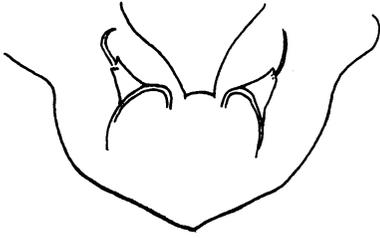
Fig. 124. Cephalic tubercles of pupa of *Tendipes* (*Cryptochironomus*) *tenuicaudatus* (Malloch), × 120.

Fig. 125. Cephalic tubercles of pupa of *Tendipes* (*Cryptochironomus*) *chaetoala* Sublette, × 120.
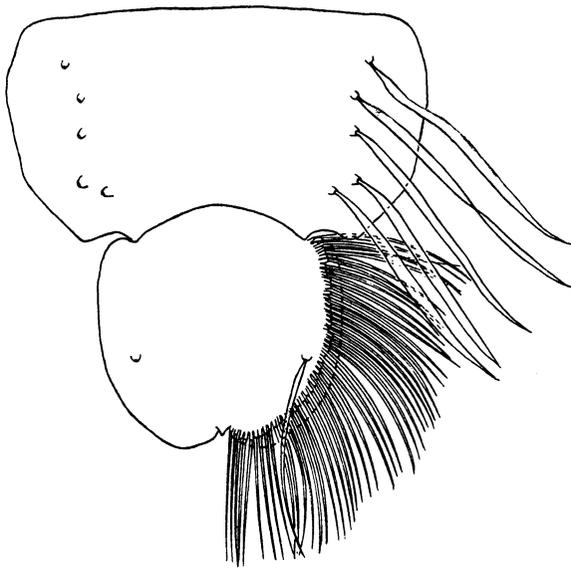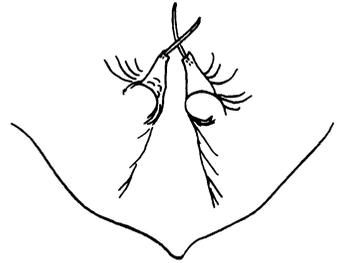
Fig. 126. Eighth and ninth abdominal segments of pupa of *Tendipes* (*Cryptochironomus*) *chaetoala* Sublette, dorsal view, × 75.
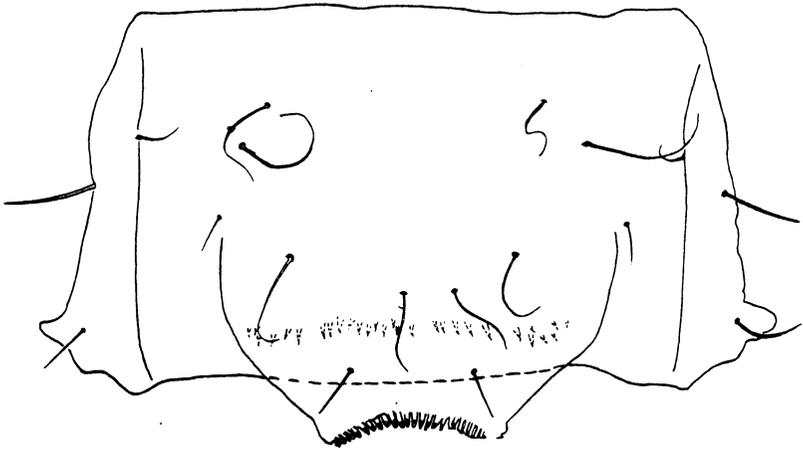
Fig. 127. Second abdominal segment of pupa of *Tendipes (Cryptochironomus) tenuicaudatus* (Malloch), dorsal view, × 50.
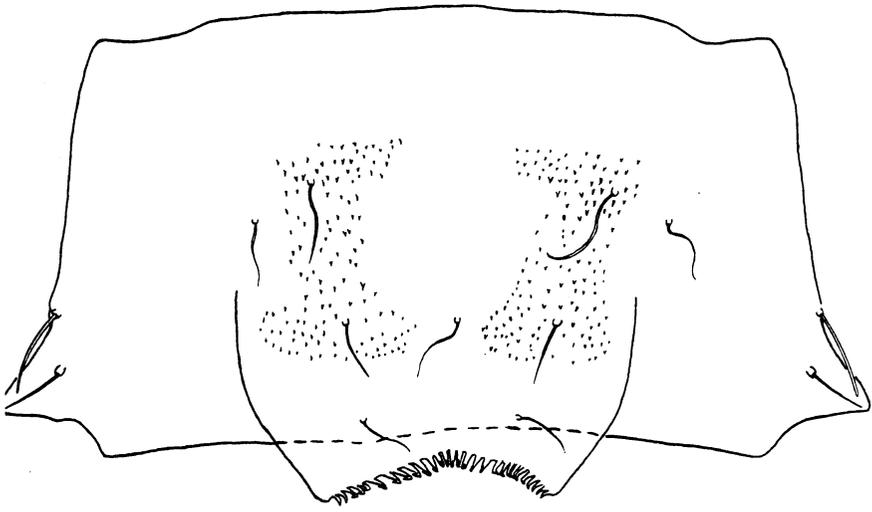
Fig. 128. Second abdominal segment of pupa of *Tendipes (Cryptochironomus) chaetoala* Sublette, dorsal view, × 50.
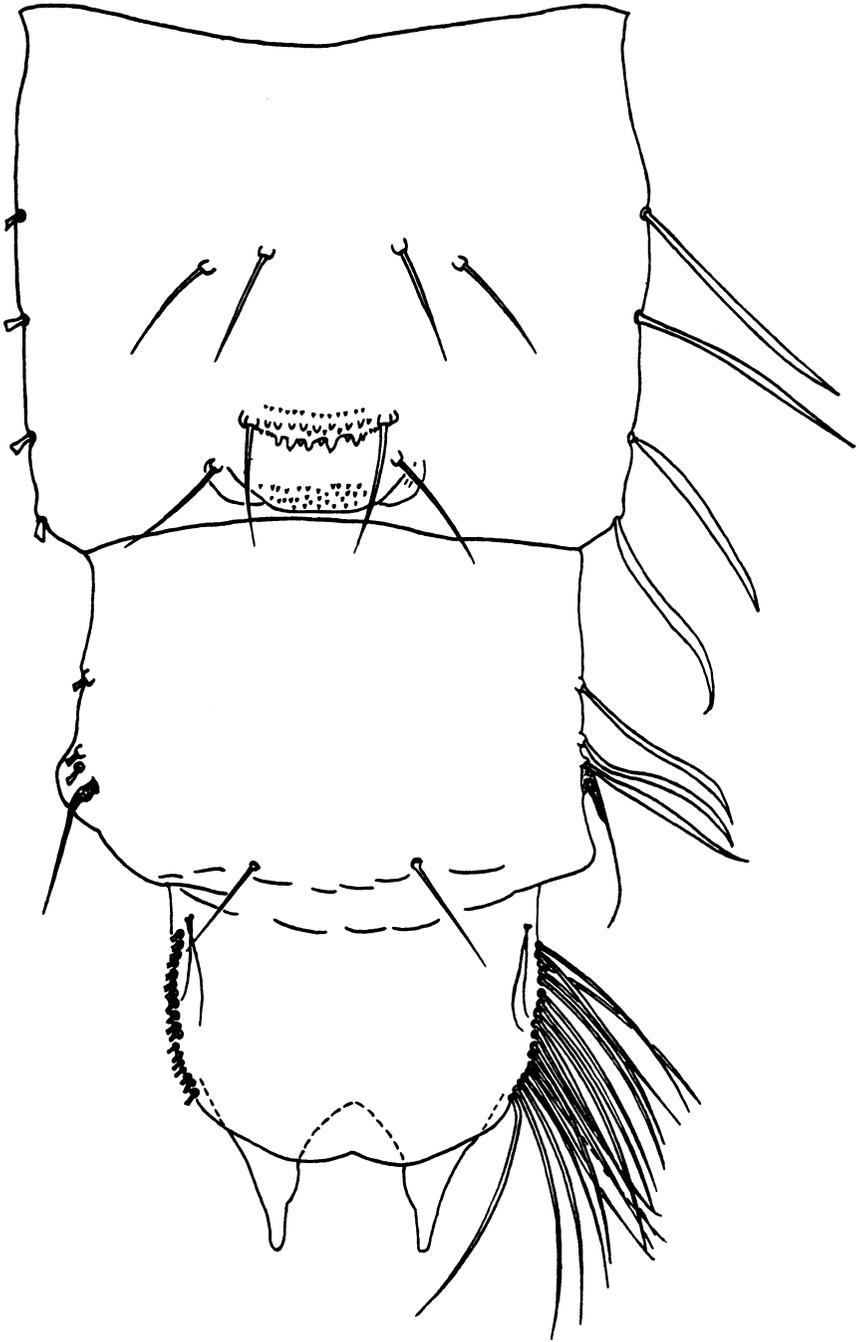
Fig. 129. Seventh, eighth, and ninth abdominal segments of pupa of *Tendipes* (*Cryptochironomus*) *darbyi* Sublette, dorsal view, × 28.
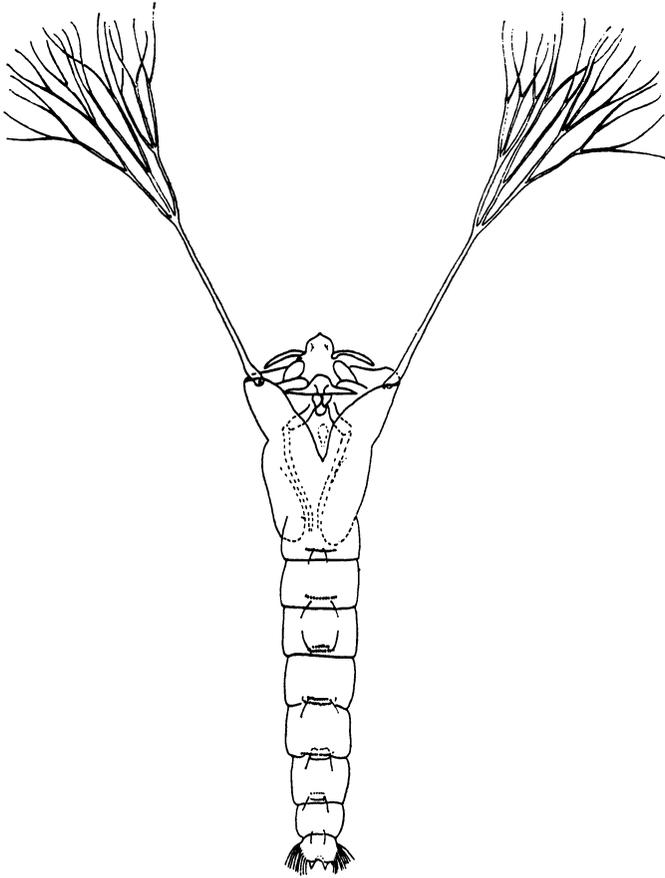
Fig. 130. Pupal exuvia of *Tendipes (Cryptochironomus) darbyi* Sublette, dorsal view, × 15.
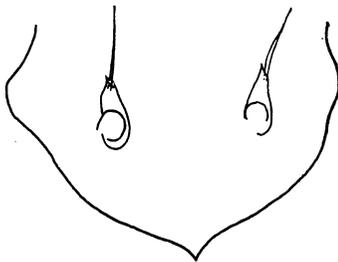
Fig. 131. Cephalic tubercles of pupa of *Tendipes (Cryptochironomus) darbyi* Sublette, × 120.
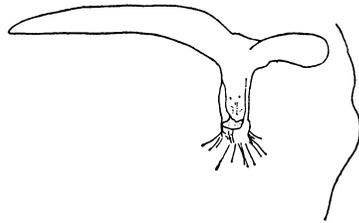
Fig. 132. Thoracic respiratory organ of pupa of *Pseudochironomus richardsoni* Malloch, × 60.
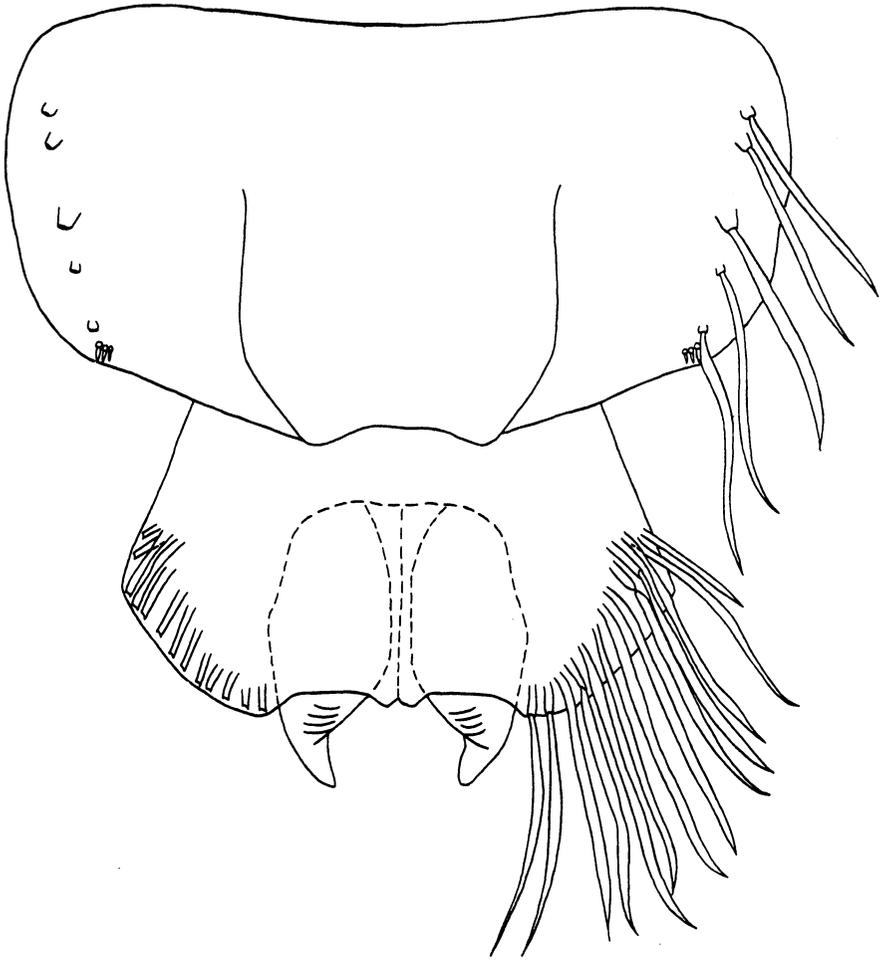
Fig. 133. Eighth and ninth abdominal segments of pupa of *Pseudochironomus richardsoni* Malloch, dorsal view, × 24.
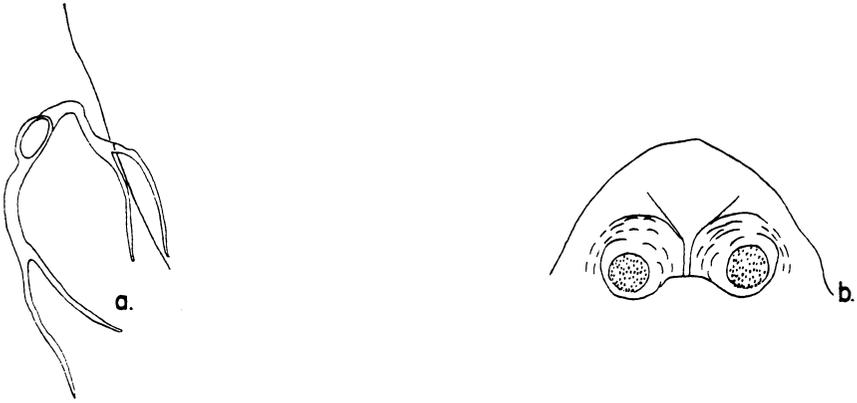
Fig. 134. *Phaenopsectra profusa* (Townes). Left, thoracic respiratory organ of pupa.
Right, cephalic tubercles of pupa. Both × 75.
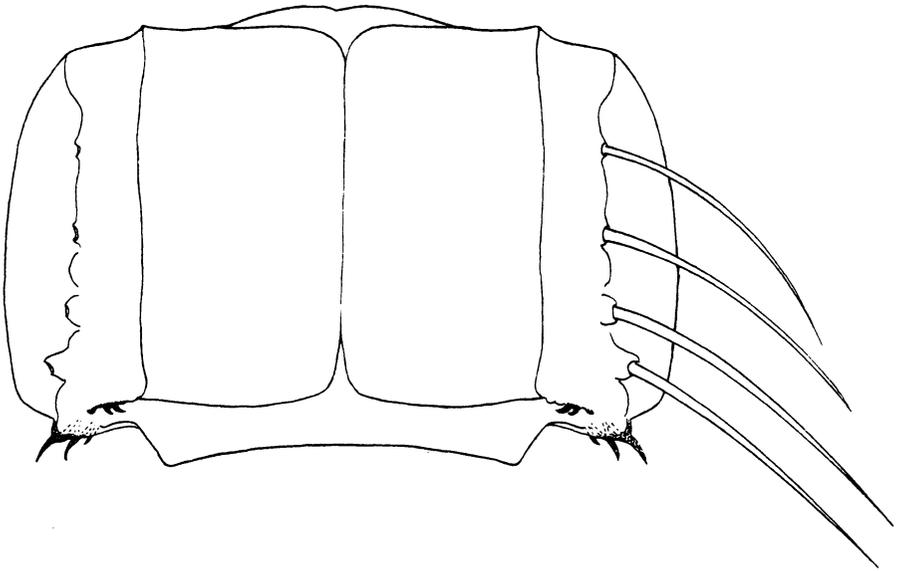
Fig. 135. Eighth abdominal segment of pupa of *Phaenopsectra profusa* (Townes),
dorsal view, × 50.
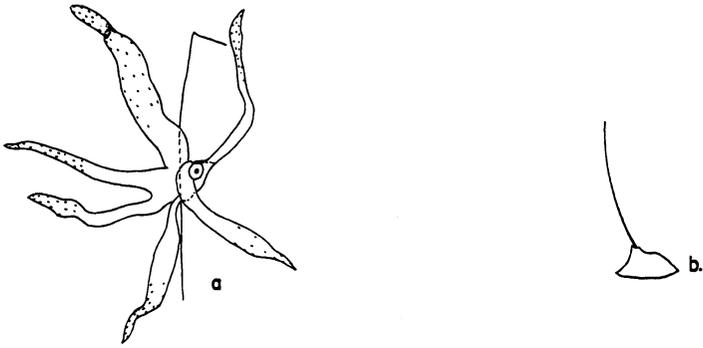
Fig. 136. *Paralauterborniella subcincta* (Townes). Left, thoracic respiratory organ
of pupa, × 60. Right, cephalic tubercle of pupa, × 120.
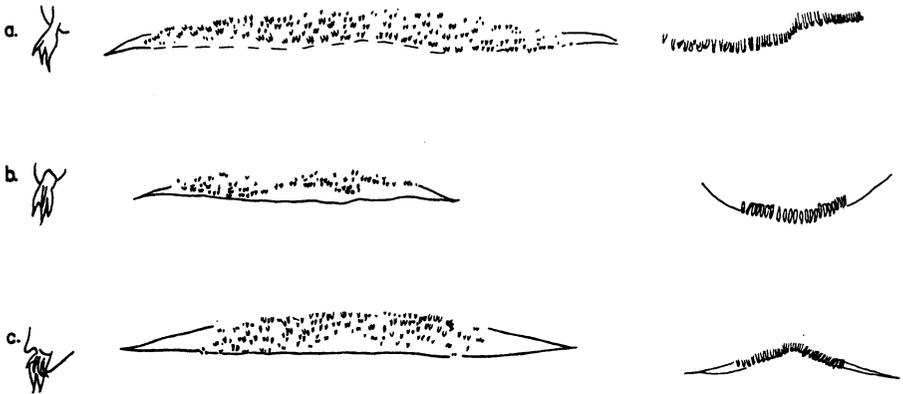
Fig. 137. Differences in spurs of eighth abdominal segments, pattern of spinules on pos-
terior edge of fourth abdominal tergite, and pattern of recurved hooks at posterior edge
of second abdominal tergite among pupae of: *a, Paralauterborniella subcincta* (Townes);
b, Paralauterborniella sp.; *c, P. elachista* (Townes). All × 120.
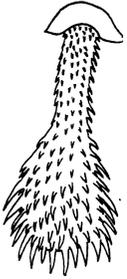
Fig. 138. Mace-like process on dorsal surface of sixth abdominal segment of pupa of *Glyptotendipes* (*Phytotendipes*) *lobiferus* (Say), × 60.
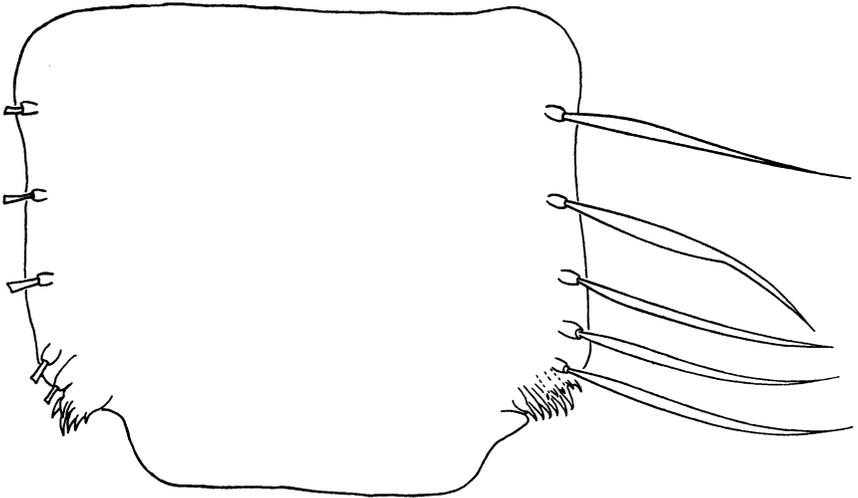
Fig. 139. Eighth abdominal segment of pupa of *Glyptotendipes* (*Phytotendipes*) *lobiferus* (Say), dorsal view, × 40.

Fig. 140. Cephalic tubercle of pupa of *Glyptotendipes* (*Phytotendipes*) *lobiferus* (Say), × 120.
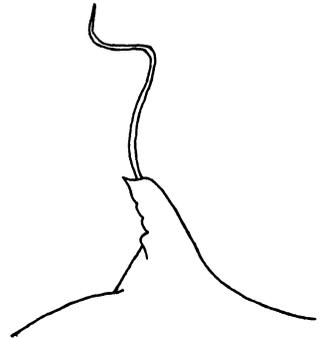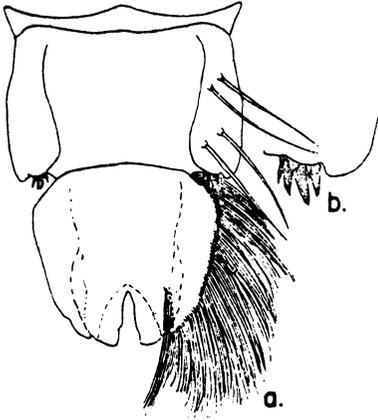
Fig. 141. *Tendipes* (*Endochironomus*) *nigricans* (Johannsen). *a*, eighth and ninth abdominal segments of pupa, dorsal view, × 26; *b*, caudo-lateral spur, × 150.
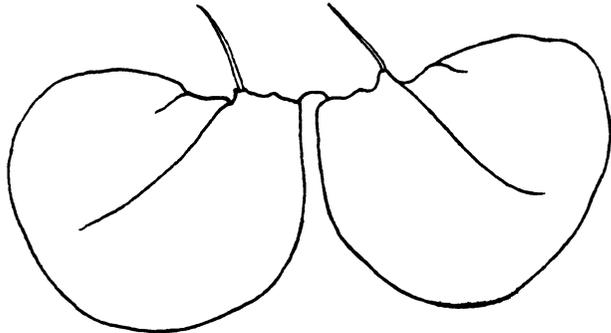

Fig. 142. Cephalic tubercles of pupa of *Tendipes* (*Endochironomus*) *nigricans* (Johannsen), × 150.
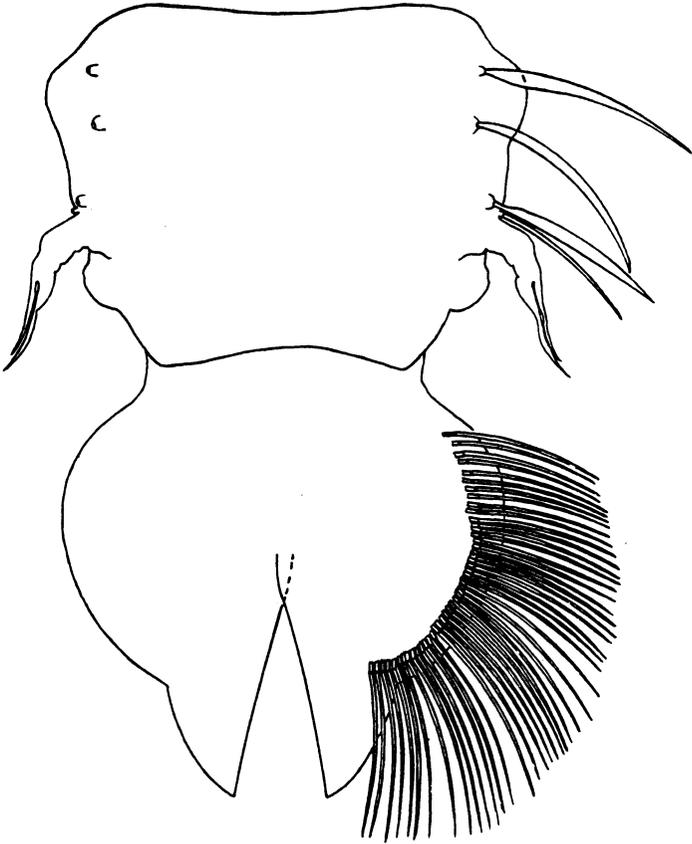
Fig. 143. Eighth and ninth abdominal segments of pupa of *Tendipes* (*Dicrotendipes*) *californicus* (Johannsen), dorsal view, × 46.
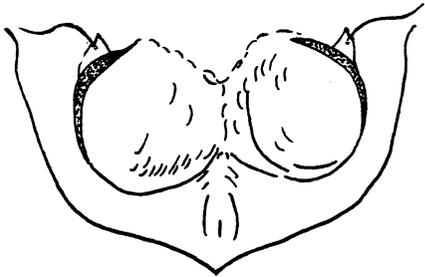
Fig. 144. Cephalic tubercles of pupa of *Tendipes* (*Dicrotendipes*) *californicus* (Johannsen), × 140.
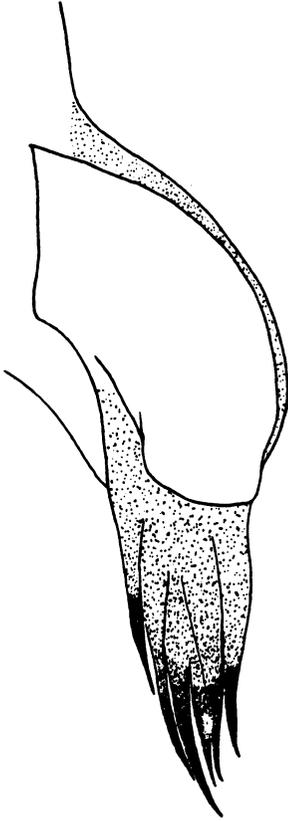
Fig. 145. Caudo-lateral spur of eighth ab-
dominal segment of pupa of *Tendipes (Ten-
dipes) attenuatus* (Walker), × 200.
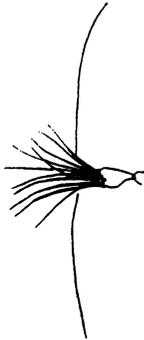
Fig. 146. Thoracic respiratory organ of
pupa of *Tanytarsus (Cladotanytarsus) viri-
diventris* (Malloch), × 75.
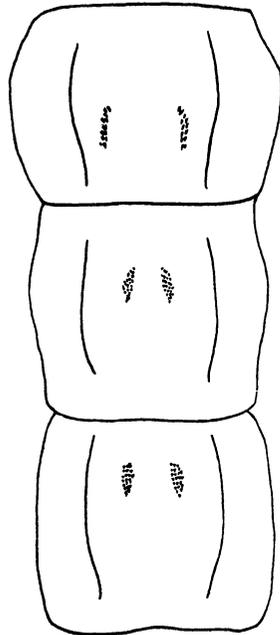
Fig. 147. Third, fourth, and fifth abdomi-
nal segments of pupa of *Tanytarsus (Clado-
tanytarsus) viridiventris* (Malloch), dorsal
view, × 49.
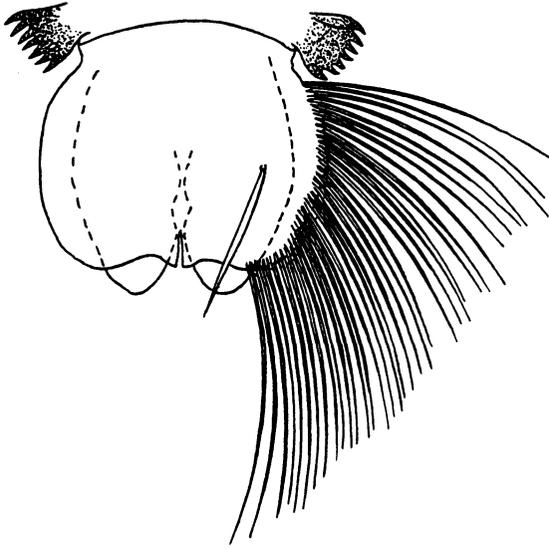
Fig. 148. Caudo-lateral spurs of eighth and entire ninth abdominal segment of pupa of *Tanytarsus (Cladotanytarsus) viridiventris* (Malloch), dorsal view, × 140.
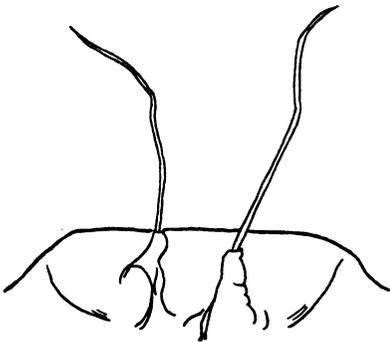
Fig. 149. Cephalic tubercles of pupa of *Tanytarsus (Cladotanytarsus) viridiventris* (Malloch), × 140.
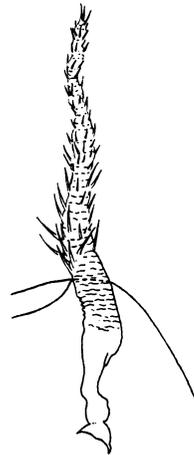
Fig. 150. Thoracic respiratory organ of pupa of *Micropsectra nigripilus* (Johannsen), × 70.
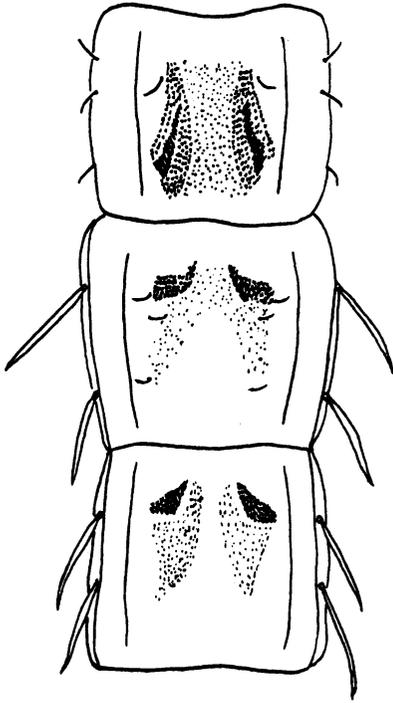
Fig. 151. Third, fourth, and fifth abdominal segments of pupa of *Micropsectra nigripilus* (Johannsen), dorsal view, × 49.
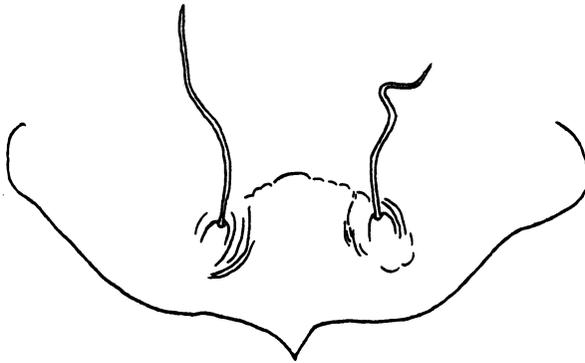
Fig. 152. Cephalic tubercles of pupa of *Micropsectra nigripilus* (Johannsen), × 140.

Fig. 153. Third, fourth, and fifth abdominal segments of pupa of *Tanytarsus* (*Tanytarsus*) n. sp. 5, dorsal view, × 49.
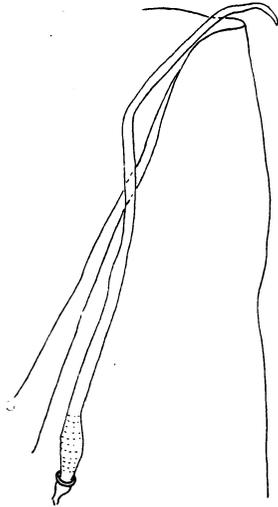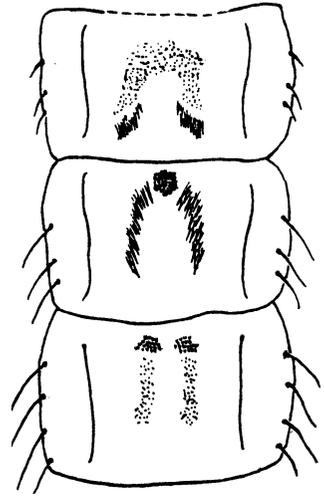
Fig. 154. Thoracic respiratory organ of pupa of *Tanytarsus* (*Tanytarsus*) n. sp. 5, × 295.

Fig. 155. Eighth and ninth abdominal segments of pupa of *Tanytarsus* (*Tanytarsus*) n. sp. 5, dorsal view, × 69.
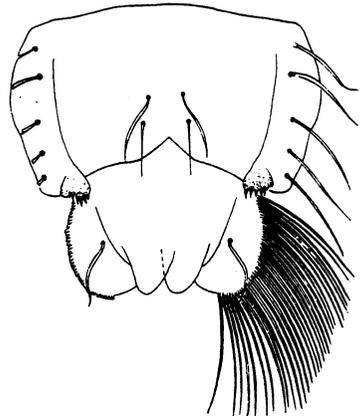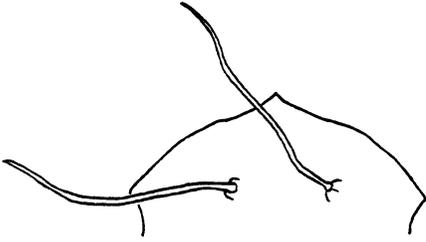
Fig. 156. Cephalic tubercles of pupa of *Tanytarsus* (*Tanytarsus*) n. sp. 5, ×140.
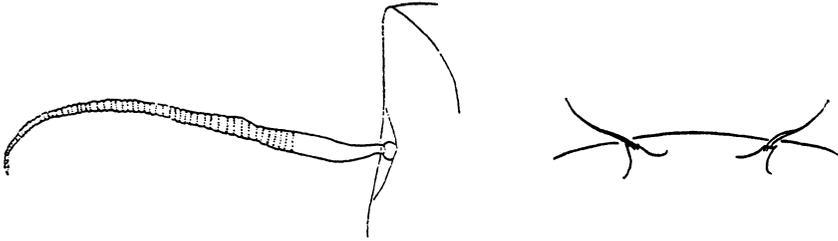
Fig. 157 (left). Thoracic respiratory organ of *Tanytarsus* (*Tanytarsus*) n. sp. 6, × 69.

Fig. 158 (right). Cephalic tubercles of pupa of *Tanytarsus* (*Tanytarsus*) n. sp. 6, × 140.

GENERAL CONSIDERATIONS OF THE BIOLOGY AND ECOLOGY OF CHIRONOMID POPULATIONS

Relative Importance of Subfamilies in Rice Fields

It will be noted in table 6 that the subfamily Chironominae, and particularly the tribe Tanytarsini within it, maintained a dominant position in the rice fields throughout the summer. Apparently the water temperature, food supply, and other environmental factors were near optimal for this group. The presence of one parthenogenetic species which also may have been paedogenetic undoubtedly contributed to the large numbers of this tribe.

In a study of the chironomid fauna of the Grosser Plöner See in Germany, Humphries (1938) also observed that the *Tanytarsus* group was the most important of the chironomid population from June through August. He noted that the critical factor which caused a decline in their numbers in autumn was a drop in the temperature of the surface water to 15° C (or 59° F). Although no such direct correlation was observed between water tem-

TABLE 6

RELATIVE NUMBERS AND PERCENTAGES OF ADULT CHIRONOMIDS TAKEN IN 24 EMERGENCE TRAPS IN EIGHT RICE FIELDS DURING 1957–58 ARRANGED BY SUBFAMILIES

Dates of trap weeks			Total number trapped	Number of midges and per cent of weekly and total catch arranged by subfamilies									
				Tanypodinae		Orthocladinae		Corynoneurinae		Chironominae			
										Chironomini		Tanytarsini	
Month	1957	1958		No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
June.........	.....	18–21	210	11	5.3	17	8.1	...	...	108	51.4	74	35.2
	25–29	22–28	376	30	8.0	3	0.8	...	...	130	34.6	213	56.7
	30– 6*	29– 5*	222	20	9.0	4	1.8	...	...	74	33.3	124	55.9
July.........	7–13	6–12	292	15	5.1	17	5.8	...	...	77	26.4	183	62.7
	14–20	13–19	445	21	4.7	22	4.9	...	...	71	16.0	331	74.4
	21–27	20–26	402	45	11.2	12	3.0	2	0.5	85	21.1	258	64.2
	28– 3†	27– 2†	453	40	8.8	56	12.4	3	0.6	76	16.8	278	61.4
Aug.........	4–10	3– 9	370	10	2.7	47	12.7	6	1.6	28	7.6	279	75.4
	11–17	10–16	236	14	6.0	35	14.8	10	4.2	38	16.1	139	58.9
	18–24	17–23	176	21	11.9	29	16.5	3	1.7	17	9.7	106	60.2
	25–31	24–30	129	6	4.7	18	14.0	5	3.9	29	22.5	71	54.9
Sept.........	1– 7	31†– 6	226	12	5.3	48	21.3	10	4.0	46	20.4	110	49.0
	8–14	7–12	109	13	11.9	11	10.1	3	2.8	19	17.4	63	57.8
	15–16	.....	5	...	...	...	...	...	...	1	20.0	4	80.0
Totals.........			3,651	258	7.1	319	8.7	42	1.1	799	21.9	2,233	61.2

* July.
† August.

perature and the Tanytarsini population in the present investigation, there was a general decrease in the number of emerging adults in the rice fields in September as the water temperature dropped. The lowest water temperature recorded was on September 1, 1957, when a minimum of 56° F was observed in Field B. The minimum temperatures for the remainder of the two seasons were above 59° F; thus apparently the critical minimum for this group was never attained. As can be seen in figure 9, the 1957 minimum water temperatures, with one exception, were lower than those of the corresponding dates in 1958, yet table 5 shows no great difference in the number of most species of this tribe taken in the emergence traps during the two seasons.

The tribe Chironomini was dominant only early in the 1958 season. This was due almost entirely to the emergence of adults of the genus *Paralauterborniella*. Throughout the rest of the season the percentage of the many species of this tribe was well below that of Tanytarsini.

The Orthocladiinae never dominated the fauna at any time, but they reached their greatest relative importance in September. This may have been in response to lower water temperatures which slowed the development of the other chironomids. Humphries (*op. cit.*) indicates that members of this subfamily were spring forms that emerged when the water temperature was relatively low. In addition, he states that some species had two generations per season, with the second emergence occurring in autumn after a drop in the temperature of the surface water.

The percentage figures for the Tanypodinae, although uniform throughout the rice season, were relatively small. Lundbeck (1926*b*) reports that the genus *Tanypus* exhibited a similar emergence pattern in lakes of northern Germany. This subfamily also was found to be of relatively slight importance in the chironomid fauna of the Grosser Plöner See by Humphries (1938).

The Corynoneurinae were the least abundant of any of the subfamilies encountered in the rice fields. The single species which represented this group was relatively late in emerging. No adults were captured until approximately the middle of the rice season.

Seasonal Variation in Numbers of Species and Individuals Emerging from Rice Fields

There were distinct differences between the 1957 and the 1958 seasons in the patterns of emergence of chironomids from the rice fields. Both the number of species and total number of individuals showed considerable variation (figs. 159 and 160). A greater number of species, but fewer individuals, emerged in 1957 than in 1958. During the former season both the greatest number of species and the maximum number of individuals were recorded in the latter part of July, whereas in 1958 there was no agreement as to the dates of these maximum figures.

In an attempt to ascertain whether either the number of species or the number of individuals emerging was correlated with the seasonal water temperatures, scatter diagrams were constructed using both the maximum temperatures of figure 8 and the average minima of figure 9. The diagrams failed to show any trend, but simply a vertical line. These results in the rice fields did not coincide with those of Miller (1941), who found that although the
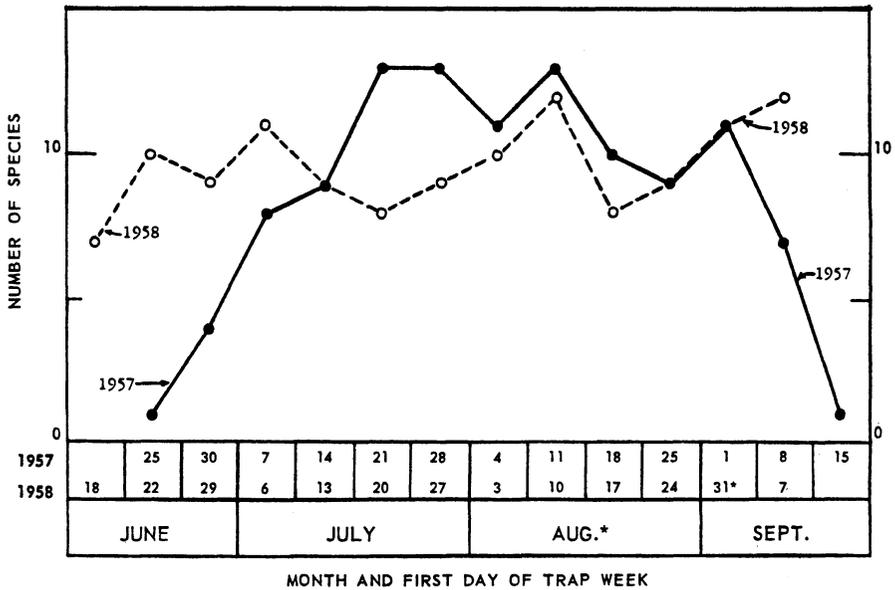
Fig. 159. Number of species of midges taken weekly in 24 traps in eight rice fields during two seasons.

water temperature had little effect on the number of individuals emerging from Costello Lake in the summer, the greatest number of species emerged during the week of highest average temperature.

In the present study it was believed that the generally higher water temperature of 1958 undoubtedly contributed indirectly to the greater number of individuals which emerged as compared with the previous season. Work in the field disclosed that both the air and water temperatures remained relatively high and constant during the nights of the last week of August and the first week of September of 1958. It appears that the warm nights were largely responsible for the emergence of a greater number of midges near the end of the 1958 season than was observed in 1957.

Relative Abundance in Rice Fields of Different Ages

Throughout the last two years of this study emphasis was placed on the comparison of chironomid populations in first-year fields with those of second-year fields. Both a greater number of species and more individuals were taken in the emergence traps in first-year fields than in those of older fields (table 7). Similar evidence was provided by a different approach. Figures 17 and 18 show that in both seasons there were many more instances in which emergence traps in second-year fields were empty than there were in first-year fields.

In attempting to ascertain the reason for this difference, several environmental factors were investigated. A difference in water temperature was
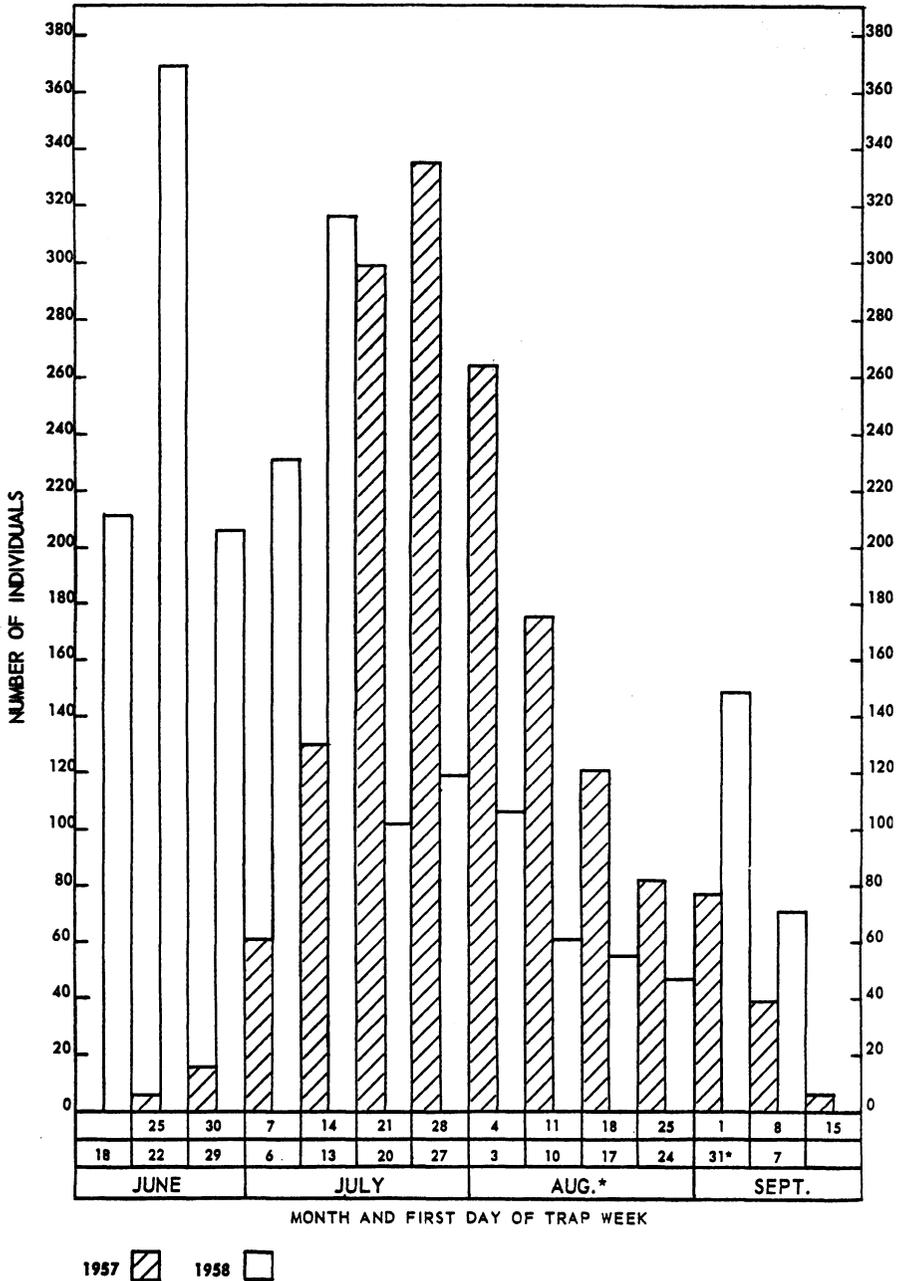
Fig. 160. Total number of midges taken weekly in 24 emergence traps in eight rice fields during two seasons.

TABLE 7
NUMBERS OF MIDGES CAPTURED IN 24 EMERGENCE TRAPS IN EIGHT
RICE FIELDS, IN RELATION TO FIELD AGE

Taxonomic unit	Numbers taken		
	First-year fields	Second-year fields	Total number
Tanypodinae			
Pentaneura two species *monilis* and *aequifasciata*............	39	11	50
Procladius culiciformis.......................................	115	93	208
Orthocladiinae			
Cricotopus bicinctus...	213	23	236
Cricdtopus sylvestris..	43	21	64
Psectrocladius n. sp. 2......................................	14	2	16
Nanocladius n. sp...	3	0	3
Corynoneurinae			
Corynoneura n. sp...	34	8	42
Chironominae			
Chironomini			
Pseudochironomus richardsoni................................	1	0	1
Paralauterborniella complex including *subcincta* and			
elachista...	303	132	435
Tendipes attenuatus...	187	14	201
Tendipes plumosus...	3	0	3
Tendipes nigricans..	1	0	1
Tendipes californicus.......................................	8	3	11
Tendipes modestus...	1	0	1
Tendipes nervosus...	2	0	2
Tendipes chaetoala..	4	9	13
Tendipes darbyi...	3	3	6
Tendipes fulvus...	7	5	12
Tendipes monochromus..	2	0	2
Tendipes tenuicaudatus......................................	46	63	109
Glyptotendipes lobiferus....................................	2	0	2
Tanytarsini			
Tanytarsus viridiventris....................................	285	68	353
Tanytarsus n. sp. 2...	2	0	2
Tanytarsus n. sp. 3...	2	1	3
Tanytarsus n. sp. 4...	1	0	1
Tanytarsus n. sp. 5...	1,165	464	1,629
Tanytarsus n. sp. 6...	122	123	245
Totals..	2,608	1,043	3,651

considered a possible cause, but as can be seen from figures 161, 162, 163, and
164 this difference during both seasons was slight. Therefore, it appears
doubtful that the variation in water temperature could account for the ob-
served difference in chironomid numbers in rice fields of different ages.

As previously indicated, it was thought that algal toxicity might have been
responsible for the smaller populations of midges in older fields. Gerhardt
(1953) indicates that blue-green algae produced a deterrent effect upon mos-
quito larvae in rice fields. Figures 19 and 20, however, do not show sufficient
differences between the algae of the older and newer fields to warrant a similar
conclusion concerning midge larvae. There was no evidence in any of the
fields of larval mortality due to algal toxicity.

Table 4 shows some differences in the species of higher plants which oc-
curred in the first- and second-year fields. It was believed, however, that the
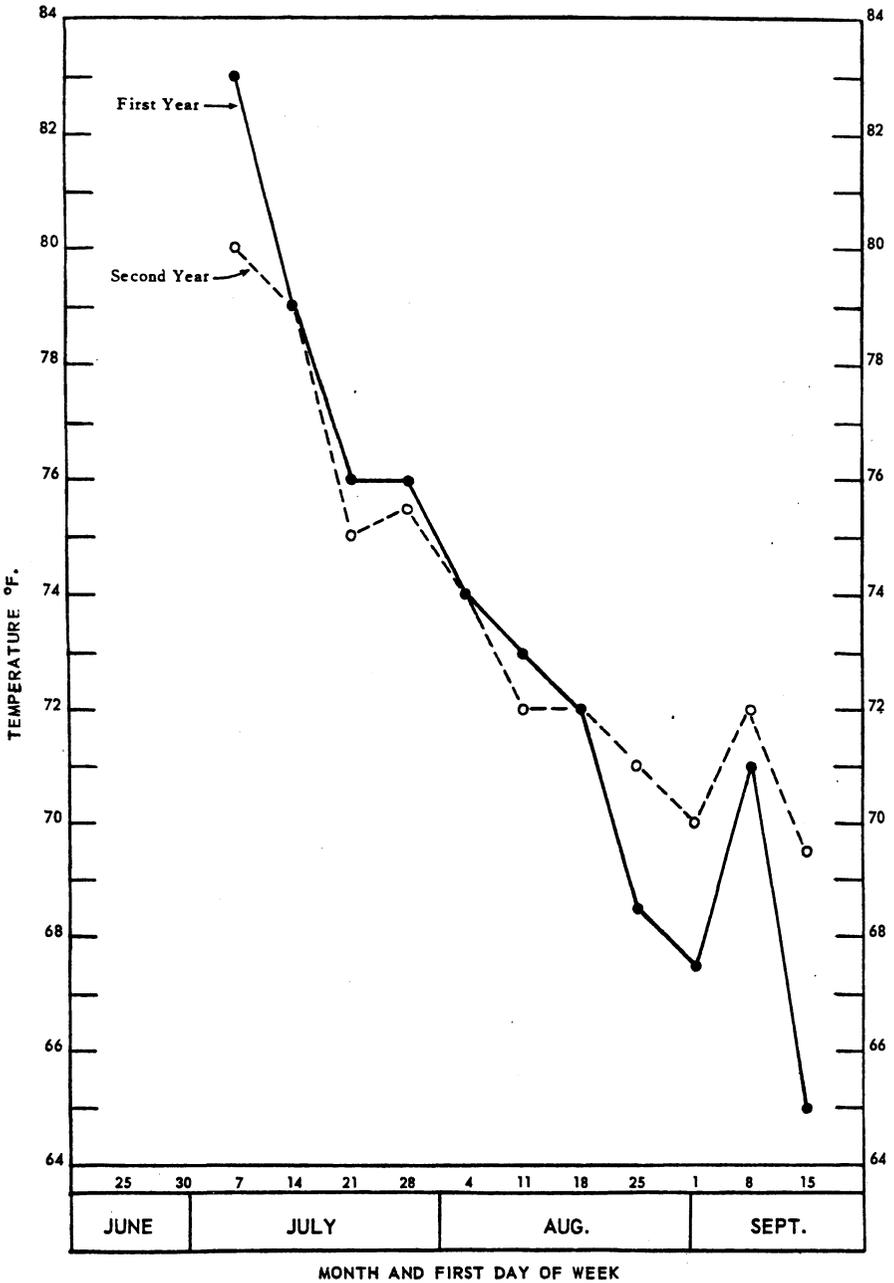
Fig. 161. Weekly average maximum water temperatures in two first-year and two second-year rice fields in 1957.
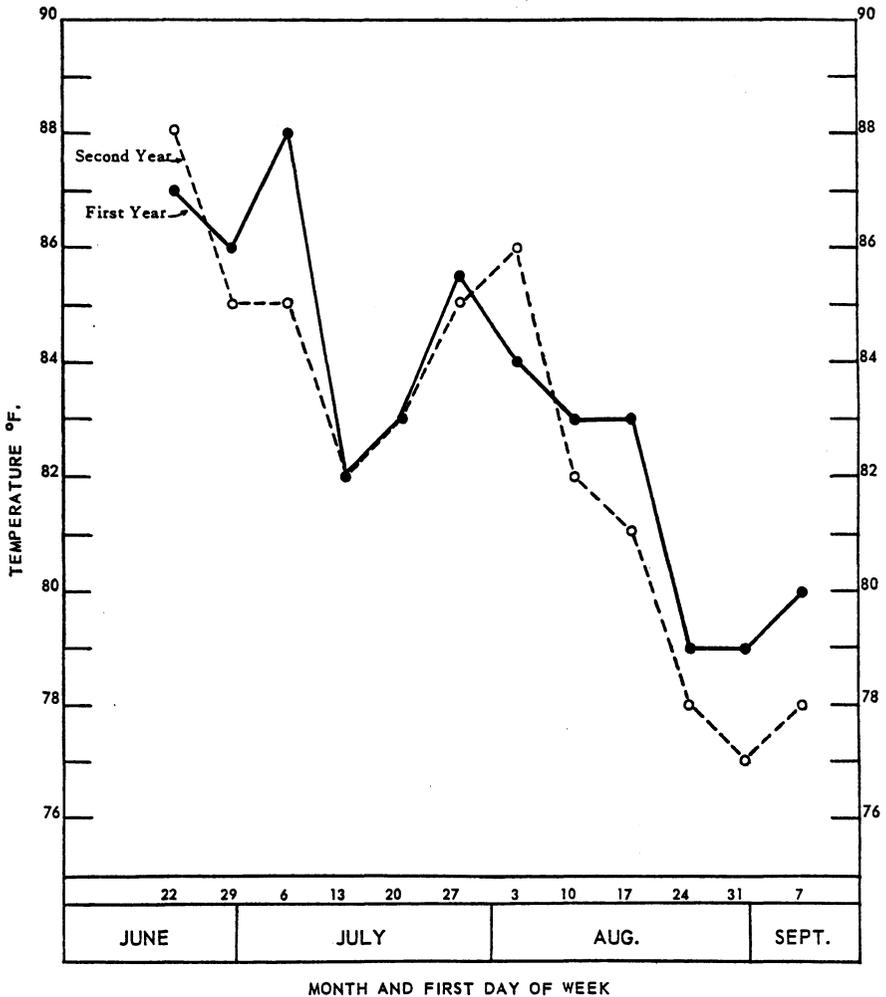
Fig. 162. Weekly average maximum water temperatures in two first-year and two second-year rice fields in 1958.

presence or the greater abundance of such species as duckweed fern, cat-tail, and water-lentil or duckweed in second-year fields was the result of a more basic dissimilarity rather than a cause for the difference in chironomid numbers.

Because of the difficulties encountered in obtaining dissolved oxygen values in Field F by the Winkler method, and the small amount obtained later using the modified procedure, it was believed that ferrous and nitrite ions may have been present in sufficient quantities to upset the oxygen balance. This would have been in agreement with the findings of Rossolimo (1939) who observed that the activities of *Chironomus plumosus* in Beloie Lake liberated enough of the readily self-oxidizing ferrous and ammonium ions from the mud to
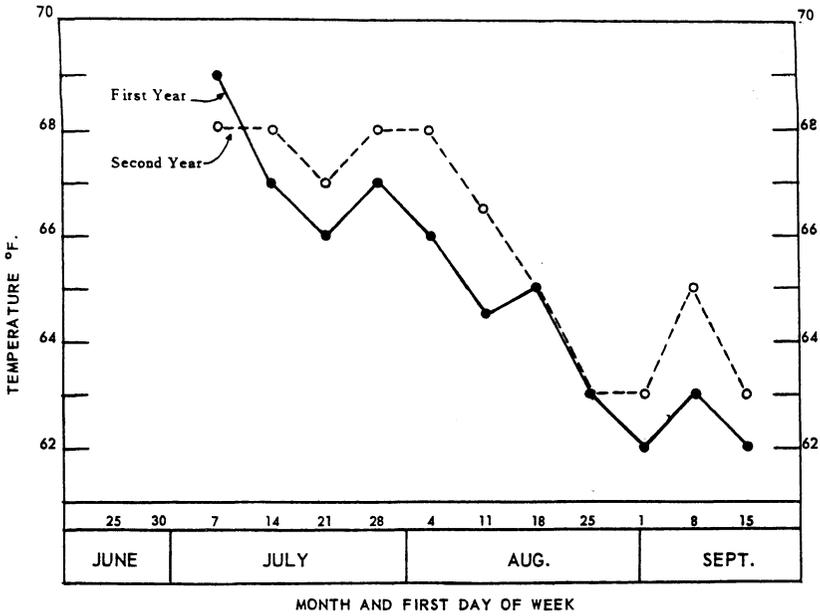
Fig. 163. Weekly average minimum water temperatures in two first-year and
two second-year rice fields in 1957.
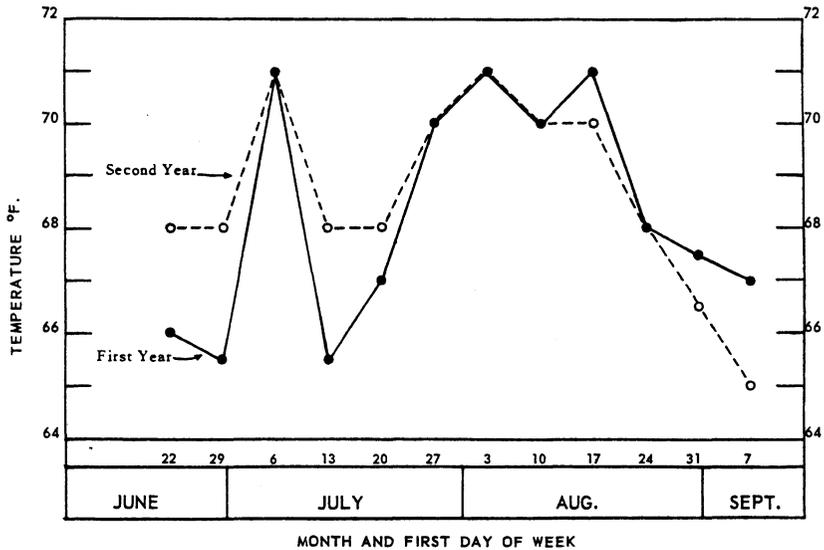
Fig. 164. Weekly average minimum water temperatures in two first-year and
two second-year rice fields in 1958.

cause a decrease in the oxygen of the water layer directly above the bottom. Table 2, however, indicates little or no agreement in the dissolved oxygen values of the two second-year fields. In addition, table 3 shows no correlation between field age and the amount of ferrous ion and a total absence of nitrite.

Although probably the result of some underlying physical differences, two biotic variations between these fields were observed, which may have had a direct effect upon chironomid numbers. One difference was in the amount of periphyton (the miscellaneous assemblage of organisms which grows or settles upon the free surfaces of submerged objects) present. This material serves as food for many species of midge larvae. Emergence traps which had been partly submerged in first-year fields for six days (June 18 to 24, 1958) were thickly coated with periphyton which supported many tube-dwelling chironomid larvae. In contrast, emergence traps removed after four days (June 21 to 25, 1958) in the second-year Field H were completely clean. A marked difference in the amount of this brownish-green scum also was observed on the varied level stakes used during August, 1958. Those placed in first-year fields for one week were heavily coated, but those from Field F contained scarcely any.

The second difference was the relative abundance of fresh-water snails. In second-year fields snails of the families Planorbidae (*Helisoma* sp.) and Physidae (*Physa* sp.) were extremely numerous, but were seldom seen in first-year fields. According to Pennak (1953; p. 621), the chief food of these mollusks is algae, algal debris, and diatoms. Perhaps the snails offer competition in the removal of material which otherwise would have been available to the chironomid larvae for food and tube construction.

Relationships of Populations and Aquatic Plants

A direct relationship was observed between the abundance of aquatic plants and the midges produced. Many more adult chironomids were captured in traps placed over submerged vegetation than in those placed in comparable sites without hydrophytes. Frohne (1938) states that aquatic insects are far less restricted to food plants than terrestrial forms but that there is a direct food relationship between aquatic plants and insects. McGaha (1952) observed that some aquatic insects were closely associated with a single species of plant, but that as a group they varied greatly in their degree of dependence upon plants.

In the present study neither obligatory food relationship nor host specificity was encountered. Most species of chironomids appeared to be associated with plants more for substrate or living space than for a direct food supply from the plants. Plant species that offered the largest surface area supported the greatest number of midge larvae. In a study of animal populations on submerged aquatic plants of the western part of Lake Erie, Krecker (1939) found that multibranched plants such as *Myriophyllum* and *Potamogeton* supported much greater numbers of midge larvae than *Vallisneria,* the form of which is similar to rice or young watergrass.

The three species in the family Alismaceae were the dominant vascular aquatic plants of the rice fields. Of these, burhead (*Echinodorus cordifolius*) was by far the most important in providing suitable microhabitats for chiro-

nomid larvae. When young and submergent, the water plantain (*Alisma plantago-aquatica*) and arrowhead (*Sagittaria* sp.) because of their ribbed stems and large leaves furnished a considerable surface area for the tube-dwelling larvae, although not nearly as much as did *Echinodorus* plants which sent up a large rosette of linear leaves. These were wrinkled and ribbon-like in form. Phytoplankton and debris settled in the wrinkles to provide optimum conditions for the development of the larvae of several species of chironomids. In addition, when water plantain and arrowhead had emerged from the water, only the stems and the underside of a few leaves were suitable for the larvae, whereas in the deeper water of the borrow pits, the burhead leaves remained submerged and ribbon-like. Mason (1957; p. 109) indicates that these plants rarely produce normal adult leaves when growing in deep water.

Because of their dense growth, water nymph (*Najas guadalupensis*) and grass wrack (*Zannichellia palustris*) were extremely important in the development of large numbers of chironomids. Although the water nymph was much more abundant than grass wrack, they were considered together because of the striking similarity in growth pattern. As is indicated by Mason (*op. cit.*; pp. 83, 89), the leaf arrangement of these plants, although opposite, often appears whorled because of the number of leaves crowded in the axils. This characteristic had a significant bearing upon the number of larvae supported. Early in June when these plants were thriving, literally thousands of chironomid larvae were present on a handful of this vegetation. Each apparent whorl of leaves harbored from 10 to 15 larvae.

Although most of the chironomids living on such submerged vegetation built tubes of silk and algae, some free-living forms, as *Corynoneura* sp. and *Procladius culiciformis*, also were taken on it. As these plants declined, the number of larvae on them became noticeably less. For example, a sample of water nymph taken August 25, 1958, from Field H, which earlier would have been swarming with larvae, had only 28 individuals on it.

Although watergrass (*Echinochloa crusgalli*) was often plentiful in certain fields, it was relatively unimportant to midge larvae. As with the rice plants, the principal contribution of the watergrass was to shade shallow parts of the field, enabling the mud-dwelling chironomids to survive. A few tube-dwellers utilized the underwater stems, but principally those of plants near the margins between the open water and the dense vegetation.

Water hyssop (*Bacopa nobsiana*), although not abundant, was an important species in the chironomid larvae production. It appeared early in the year when there was still much open water and its trailing habit of growth together with the opposite, sessile leaves provided considerable surface area upon which newly hatched larvae found living space. As periphyton developed on the stems and lower surfaces of the leaves, the midge larvae were provided with an abundance of food and material for tube construction.

Clover fern (*Marsilea mucronata*) occurred only in Field C in areas where the rice was sparse and the water warm throughout most of the summer of 1957. As with water hyssop, it was also an important habitat for midge larvae. Its creeping growth habit of slender rhizomes with the relatively large four-part leaf blades (fig. 165) provided optimum conditions for larval development.

Yellow water-weed (*Jussiaea californica*) was present in only one location of Field D, a second-year field. Since it is a perennial, this plant probably became established late in the previous season, because by mid-July it had covered a considerable area. Because such a small amount was present, it could not be considered of great importance. In the nearby ditches and other more permanent bodies of water, however, *Jussiaea* formed the principal habitat for many chironomids, notably two species of *Cricotopus*.

Common bladderwort (*Utricularia vulgaris*) was scarce in the rice fields. It appeared late in the season in Field B in 1957 and Field G in 1958. Samples were obtained the first week of September and in both fields many chironomid larvae were observed among its finely dissected leaves. McGaha (1952) reports only one species of insect in the order Trichoptera as inhabiting *Utricularia*. Needham and Lloyd (1937; p. 285) mention that many small aquatic animals are captured in the bladders of this plant. Undoubtedly some young midge larvae may have been killed in this way, but probably many more were able to develop due to the presence of the plant in the fields.

Although Claassen (1921) recorded a number of species of insects inhabiting the various parts of *Typha* plants, neither the cat-tail (*Typha latifolia*) nor the common tule (*Scirpus acutus*) contributed much to the habitat of chironomid larvae. A few were found on the underwater portions of these plants, but no more than on any other submerged material. The two surface film plants, duckweed fern (*Azolla filiculoides*) and water lentil (*Lemna minor*) also were unimportant in supporting larvae. The principal contribution made by all of these plants was that of shading the water, thus helping to maintain somewhat stable temperatures.

Fig. 165. Standing water in a first-year rice field (Field C).
Note floating leaves of clover fern (*Marsiles mucronata*).

Several of the algae became sufficiently abundant in the rice fields to have a direct effect upon the numbers of chironomid larvae.

The blue-green alga (*Gloeotrichia*) which was the dominant form early in the season furnished microhabitats for many larvae as long as the gelatinous bladder-like structures were firm. When the alga began to deteriorate and break up, no larvae were found. Their absence could have been due to the extremely high water temperature at the surface where the alga was floating. The provision of living space appeared to be the only benefit derived from this plant because larvae were not observed feeding on it either in the field or in the rearing dishes in the laboratory. There was no indication of the production of toxic substances by *Gloeotrichia* in the rice fields, but when larvae were left overnight in pans with this alga, a high mortality resulted. This was interpreted as caused by the production of excessive amounts of carbon dioxide by plant respiration in darkness, rather than a toxic secretion, because the same thing happened with pans of the green alga *Spirogyra* and the vascular plant, common water nymph. When a light was left burning the mortality was less, but still many larvae died. Possibly there was an accumulation of nitrogenous products of decay which could be diluted to the point of toleration in the field but not in the laboratory. Gerhardt (1957) found no lethal effects on mosquito larvae produced by dissolved nitrogenous compounds in rice fields.

The green alga (*Spirogyra*) was utilized extensively by several species of midge larvae which inhabited cool, moving water (fig. 166). This plant furnished both a substrate and food for *Cricotopus* larvae.

The *Oedogonium* and *Mougeotia* mats present in the older fields supported numerous chironomids as well as many insect predators. It was not determined whether the midges fed upon these two species of algae or whether they ate the debris which collected on the mats.

Since *Cladophora* was growing in cool, moving water, many *Cricotopus* larvae were expected to be in it. However, surprisingly few were found in the samples taken. In contrast, Mundie (1957) reported great numbers of *Cricotopus sylvestris* larvae from *Cladophora* in the eutrophic lakes of England.

The stonewart (*Chara*), which Needham and Lloyd (1937; p. 137) characterize as one of the most specialized of the fresh-water algae, proved to be an enigma. Its whorls of branchlets similar to those of the common water nymph provided support for large populations of larvae early in the season. However, by August their numbers had greatly decreased and few adults emerged from the *Chara* in the warm, shallow areas. It was not discovered whether it was generally unsuitable water conditions or a toxic substance produced by the *Chara* that was responsible for the drop in midge production. Morgan (1930; p. 55) states that because of its calcareous covering, few herbivorous species eat *Chara,* but that large numbers of desmids and diatoms settle on it, providing food for many vegetarians. Needham and Lloyd (*op. cit.*; p. 138) indicate that the strong odor which characterizes this plant is from sulfurous compounds, but state nothing concerning toxicity. In the laboratory, larvae lived only a short time if left in the pan or dish with *Chara*. Shortly after being placed in the pan most of the larvae clustered near the water surface

and undulated vigorously, then they usually swam a short distance before stiffening out and settling to the bottom. In view of the findings of Matheson and Hinman (1928 and 1930) previously cited, this complex relationship between *Chara* and larval insects warrants a thorough investigation from a biochemical approach both in the field and the laboratory.

Activity of the Adults

Although the attraction to light of most species of chironomids is well known, the activity of the different species during the night is not completely understood. Palmén (1955) noted in his study of the periodicity of emergence of chironomids, that in a number of species, emergence occurred exclusively around midnight. An indication of variation in species' activity was observed on July 5, 1957. A light trap had been started in Field C at 9:00 p.m. when the air temperature was 80° F and there was a wind of 8 to 10 miles per hour from the south. Many different species were alighting on the sheet windbreak and entering the trap, but no adults of the common species, *Procladius culiciformis,* appeared until 9:45 p.m. During the next 15 minutes until the trap was shut down, at least 30 individuals were taken from the sheet and in the trap.

In an attempt to discover if there was a temporal difference in the activity of *Procladius culiciformis* and some of the other species of chironomids, the light trap was run for several hours in Field A on the night of August 2–3, 1957. As shown in table 8, the trap was in operation for an hour and then

Fig. 166. Rapidly moving water below a weir box in a first-year rice field (Field C). Note trap C_1 which was placed over large masses of *Spirogyra.*

shut off for an hour in order to empty the killing jar and to recharge the auto-
mobile battery which was used to supply the power. The trap was first started
at 8:30 p.m., 14 minutes after sunset. At this time the air temperature was
84° F and a south wind of 4 to 6 miles per hour was blowing. The air tempera-
ture dropped to 71° F at 10:30 p.m., 68° F at 12:30 a.m., and to 66° F at
1:30 a.m. when the trapping was concluded. By 1:00 a.m. the wind had in-
creased to between 6 to 8 miles per hour and the chironomid catch declined
to only 35 individuals during this hour.

The results presented in table 8 cannot be considered conclusive based on a
single trap night, but they indicate that most species were active at twilight.
Some of the more common forms such as *Tanytarsus viridiventris* were rela-
tively numerous throughout the night. At least one species, *Tendipes tenui-
caudatus,* was taken in greater abundance during the second hour's trapping.
The numbers of other species such as *Paralauterborniella* sp. and *Tanytarsus*
n. sp. 5 decreased sharply after the first hour. As noted previously, *Procladius
culiciformis* tended to become more active during the later hours. This may
not have been entirely a time difference, but also could represent a greater
tolerance by this species for lower air temperature or increased wind velocity.

The swarming characteristics of midges observed in and near rice fields
agreed with those reported by several European workers. Mundie (1956) and
Nielsen and Greve (1950) have called attention to the variation exhibited by
the different species in time of flight and in the altitude aboveground. The
relationship between the abundance of midges in flight and the orientation

TABLE 8

ADULT MIDGES ATTRACTED TO LIGHT FROM 8:30 P.M. AUG. 2, 1957, TO
1:30 A.M. AUG. 3, 1957, IN FIRST-YEAR RICE FIELD

Taxonomic unit	Hours of trapping and number and sex of adults taken						Total
	P.M. 8:30–9:30		P.M. 10:30–11:30		A.M. 12:30–1:30		
	Male	Female	Male	Female	Male	Female	
Procladius culiciformis	—	1	—	13	—	9	23
Cricotopus bicinctus	3	4	—	1	—	—	8
Cricotopus sylvestris	3	4	1	3	2	—	13
Unidentified Orthocladiinae	—	2	—	2	—	—	4
Corynoneura n. sp	—	—	1	—	—	—	1
Paralauterborniella sp.?	12	5	3	1	2	—	23
Polypedilum digitifer	1	—	—	—	—	—	1
Tendipes attenuatus	3	4	—	—	—	1	8
Tendipes californicus	1	1	—	—	—	—	2
Tendipes fulvus	1	—	1	—	—	2	4
Tendipes tenuicaudatus	9	21	15	37	3	5	90
Tendipes sp. ?	—	8	—	12	—	—	20
Glyptotendipes lobiferus	2	—	—	—	—	—	2
Tanytarsus viridiventris	20	7	18	6	4	1	56
Tanytarsus n. sp. 5	—	32	—	12	—	3	47
Tanytarsus n. sp. 6	5	5	1	—	1	—	12
Tanytarsus sp.?	—	2	—	2	—	2	6
Totals	60	96	40	89	12	23	320

of the swarms over some favored location as well as the reaction of the indi-
viduals within the swarm to wind have been clearly indicated by Gibson
(1945).

In the present investigation it was noted that the relative size of the midge
appeared to be the determining factor in time of swarming and the height
at which the swarms were formed. Many mixed swarms containing several
species were encountered in the rice fields. In agreement with Gibson (*op.
cit.*) the smaller forms such as *Corynoneura* sp., *Tanytarsus viridiventris*, and
Paralauterborniella sp. swarmed close to the ground or water. These small
midges also were often seen swarming during the daytime as mentioned by
Nielsen and Greve (1950). The larger midges such as *Tendipes attenuatus*
appeared more tolerant of the wind and consequently swarmed at a greater
height than the smaller species. Warm nights with temperatures of 80° F or
above were optimum for the formation of huge swarms of these larger males.
However, on June 28, 1958, at 8:40 p.m. when a south wind of 8 to 10 miles
per hour was blowing and the air temperature was only 71° F, a large swarm
of *Tendipes attenuatus* was in flight near Field G. The manner in which they
rose and fell with the gusts of wind, keeping their bodies oriented to face it,
agreed with the detailed description of the mating swarm of this species as
given by Ping (1917). The high-pitched hum produced by this swarm could
be heard for a considerable distance. The lower edge of the swarm was main-
tained about 10 feet aboveground at the lowest undulation in the flight
pattern.

There were more swarms and the groups were larger in the evening than at
other times during a 24-hour period. This agreed with the findings of Mundie
(1956; fig. 3) who noted slight activity by midges at Staines South Reservoir
between 11:00 p.m. and 5:00 a.m. Many smaller swarms, however, were seen
in the rice fields during the morning hours. Most of these were mixed swarms
of small species, but occasionally a larger species such as *Tendipes fulvus*
was seen. These morning swarms were usually observed in protected areas
and low over the water or on the leeward side of a building. In contrast to
evening swarms, even the larger midges seldom rose high in the air.

The principal factor governing swarming of midges appeared to be wind
velocity. Mundie (1956) lists several factors such as wind, temperature, and
light intensity. In his laboratory experiments, however, Gibson (1945) found
that midges tolerate a fairly wide range of light intensity, but that a slight
change in wind velocity causes a marked decrease in activity. Lewis *et al.*
(1954) concluded that the presence of larger numbers of adults of *Tanytarsus
lewisi* Freeman in their light traps at Khartoum on certain nights was be-
cause a wind with a velocity of more than 11 miles per hour blew the midges
toward the city. In the present investigation, strong wind prevented com-
pletely the activity of most species even though the air temperature was
favorable. The effects of light intensity were not studied.

Oviposition by the females of most of the species of midges inhabiting the
rice fields was not observed. However, the observation of females of various
species in flight close to the water during the cool morning hours and also
in the evening was believed to indicate that oviposition occurred at these
times. This view was strengthened by the fact that the only instances of

oviposition which were witnessed occurred in the morning. This is in agreement with the detailed observations made by Ping (1917) of early morning oviposition by a female *Tendipes attenuatus*. Leathers (1922) noted this species ovipositing during the evening near Ithaca, New York.

Further study, similar to that of Gibson (1945) involving both field and experimental work, is needed to understand the activity patterns of the adult midges emerging from the rice fields.

Biology of the Larvae

Most of the rice fields studied became populated with chironomid larvae both from eggs deposited by females and by individuals which were carried into them with the water. The field near Davis in which the 1955 work was done was supplied by well water which was pumped through a newly constructed ditch so there was no possibility of larvae being carried into the field at the time of flooding. The water was turned into this field on April 27, and by May 2, five days later, brownish patches of algae were forming on the bottom. During the day the oxygen evolved by photosynthesis caused many of the masses to rise to the surface. On May 10 many first instar *Tanytarsus* larvae were observed in these surface algal mats as well as in the algae on the bottom of the check. Since the eggs hatch in approximately two days, the females had oviposited in this check 11 days after it was flooded.

Evidence of introduction of the larvae with the river water was noted on several occasions. A typical instance was recorded in Field G on May 16, 1958, 13 days after the water was first pumped into this new field. Many third and fourth instar larvae of *Tendipes attenuatus* were taken from mud and algal scum on the underside of a piece of wood which was floating in the field. These would not have had time to develop to this extent from eggs deposited after the introduction of the water. In addition, the brownish algae which coated all the partly decayed cover crop on the bottom of Field G supported great numbers of *Tanytarsus* larvae. They were at least two weeks old because the green coloration of the thorax and the pink abdomen already had been acquired. It was observed in the laboratory that these colors became established in approximately 16 days after hatching. Thus the larvae must have been carried into the field with the algae or on the layer of periphyton coating other floating vegetation.

Most of the existing microhabitats of the rice field were occupied by one or more species of chironomid larvae. Although they were often seen wriggling through the open water, these larvae could hardly be considered as typical nekton animals. The younger instars were easily disturbed or dislodged from plants and other forms of substrate. However, they invariably settled quickly at some different location and began feeding or spinning silken tubes. Early in the season many *Tanytarsus, Paralauterborniella,* and *Cricotopus* larvae were noted within the bladder-like masses of the alga *Gloeotrichia* which covered the water surface of most of the fields. Also before the rice emerged, the larvae of the several species of *Tanytarsus* inhabited most of the bottom surface. Several species of the genus *Tendipes*, particularly *Tendipes attenuatus,* were widespread in and under the ooze layer or top 2

inches of the bottom. Although not so abundant in any single location as the various tube-dwelling forms, *Procladius culiciformis* larvae were encountered in all the microhabitats that supported the numerous plant feeders.

After the rice had emerged from the water in the shallower parts of the checks, the number of chironomids taken from this location decreased noticeably. The bulk of the population throughout the rest of the season was from the weedy areas supporting little or no rice, such as the borrow pits, check corners, and channels through the checks (figs. 12 and 167).

Although Berg (1950) observed several species of midge larvae living within or protected by the tissues of *Potamogeton,* a higher aquatic plant, few larvae were found utilizing this microhabitat in the rice fields. Of those forms considered as leaf-channeling species by Berg (*op. cit.*), only *Cricotopus sylvestris* was recorded in this ecologic niche. As previously indicated, by far the greatest number of larvae in the rice fields was associated with the submerged vegetation, but almost all of them occurred there because of the surface area and periphyton provided.

Lack of time prevented experimental work in the laboratory to determine the temperature and dissolved oxygen levels which were critical for the various species. Since no sudden or extreme changes in these factors were noted in the field, few generalizations can be made concerning their effects as limiting factors. Certain species such as *Cricotopus bicinctus* and *Tendipes tenuicaudatus* were taken in greater numbers in the well-oxygenated moving water than elsewhere in the field, but even these two species exhibited a relatively wide range of tolerance. It was observed also that more individual midges were taken during the 1958 season when the water temperature was uniformly higher than during 1957 when the water became colder as the season progressed.

The principal food of most of the larvae consisted of diatoms and other phytoplankton which had settled on the aquatic vegetation and on the mud substrate of the field. *Cricotopus* larvae also fed extensively on filamentous green algae, most of which was *Spirogyra.* As mentioned previously, *Cricotopus sylvestris* also was observed in a few instances to have eaten the tissues of higher plants.

Larvae of four species, the three members of the Tanypodinae and *Tendipes fulvus,* were known predators. There were indications that three members of the subgenus *Cryptochironomus* were probably partly predaceous in their food habits.

The larvae of nearly all the species inhabiting the rice fields constructed silken tubes to which varying amounts of algae were added or adhered due to the sticky surface of the silk. Only five species were known to be free-living. The three species of Tanypodinae which ranged actively throughout most of the field in search of food did not spin tubes. Although not a predator, the single representative of the Corynoneurinae was also free-living and extremely active. According to Walshe (1951*b*), all the known members of the Chironominae inhabit some sort of silken case. The findings in the present investigation were different. *Tendipes fulvus* was noted to be a free-living predaceous species which did not construct tubes.

At the end of each rice season, samples were taken from all of the different fields to learn the effect of post-season drainage on the chironomid larvae. The following lists indicate the fate of the larvae in a typical sample taken from Field C two days after drainage:

Living larvae	Dead larvae
Cricotopus bicinctus...8 (nearly dead)	*Pentancura* sp......................1
Tendipes attenuatus 1	*Procladius culiciformis* 1
Tanytarsus sp..........great number	*Cricotopus bicinctus* 5
(nearly dead; most with drying	(pupae and great number of
tubes adhered to them)	larvae)

In contrast to the observations of Ping (1917) that larvae of *Tendipes attenuatus* survived for almost a month in moist cases out of the water, all larvae found in the rice fields 10 days after they were drained were dead.

The stage in which the different species of chironomids overwinter has received considerable attention in the literature with different conclusions drawn by the various authors. Branch (1923) indicates that the larvae of *Chironomus cristatus* are extremely resistant to freezing, hence spend the winter in this stage. *Cricotopus trifasciatus* was assumed by Kettisch (1936–37) to overwinter in the egg stage since the larvae ceased to undergo further development below 11° C. *Chironomus nigricans* also was believed to over-winter in the egg stage in Cedar Bog Lake by Lindeman (1942a). Andersen (1946; p. 46) clearly demonstrated the cold hardiness of chironomid larvae in Greenland lakes by chopping a block of frozen mud from a lake bottom and thawing it to liberate several species of larvae. According to this author, "All the larvae were swimming briskly about and did not differ in behaviour from those taken in ordinary bottom samples." Although not in this particular sample, Andersen (*loc. cit.*) indicates that both *Cricotopus* and *Corynoneura* larvae can withstand freezing. McGaha (1952) notes, in contrast to the report of Kettisch, that the first instar larvae of *Cricotopus trifasciatus* spend the winter beneath the ice near their food plants.

From the foregoing it appears most likely that chironomids spend the winter in the larval stage. All the species which were inhabitants of rice fields in the summer overwintered as larvae in nearby canals and ditches. Certain genera, e.g. *Micropsectra,* apparently continued to produce small generations of adults throughout the winter. Other tube-dwelling species such as the *Cricotopus* and *Tanytarsus* larvae were taken on floating and submerged stems of common tule and cat-tail. Most of these were second and third instars from the deeper water in the canals where there was less fluctuation of water temperature. In particularly mild, wet winters, as that preceding the 1958 rice season, many of the smaller species showed accelerated development early in the spring. By the time the rice fields were flooded in May, both adults and young larvae already were abundant.

Larvae of some of the larger forms such as *Tendipes attenuatus* and *Tendipes plumosus* inhabited the mud of the deeper canals during the winter. Both *Tendipes nigricans* and *Glyptotendipes lobiferus* larvae passed the winter in silken galleries inside the partially decayed common tule stems which floated in the larger canals. Berg (1950) also noted that *Glyptotendipes lobiferus* larvae overwintered in burrows in the stems of aquatic plants.
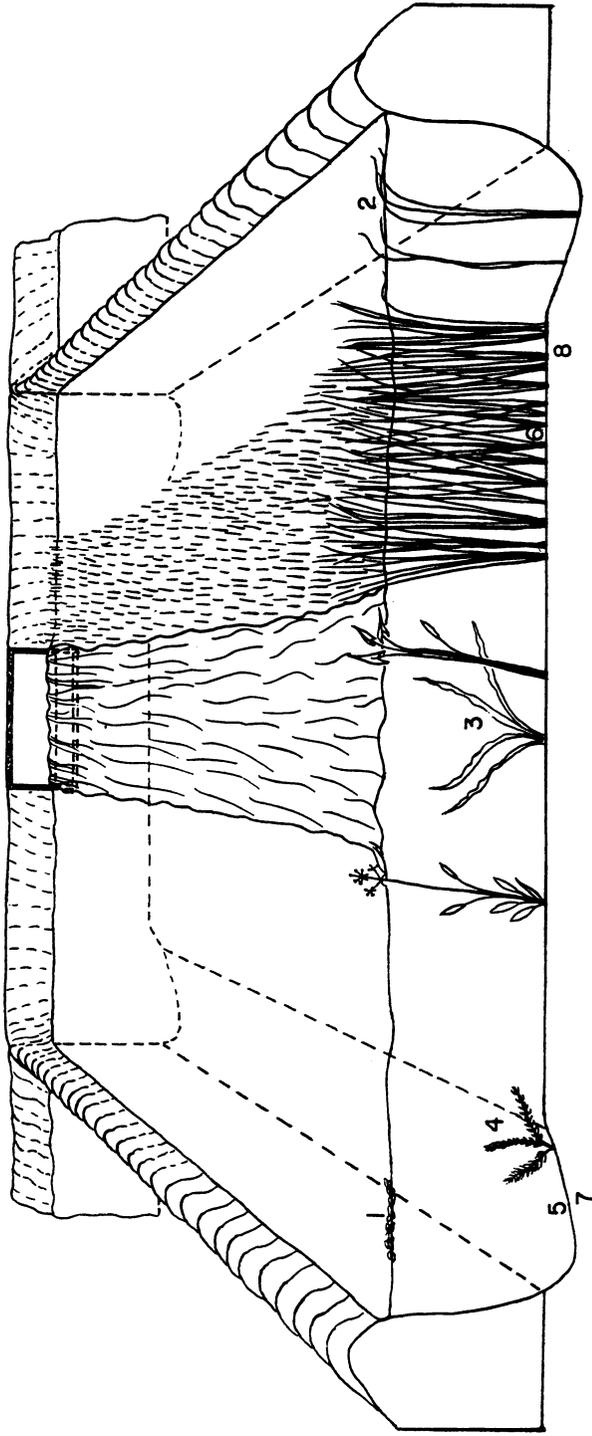
Fig. 167. Diagrammatic cross-section of rice check with intake weir box in background. Microhabitats illustrated: *1*, floating *Gloeotrichia*; *2*, tissues of higher plants (floating rice leaves in borrow pit); *3*, surface of submerged plants in moving water; *4*, surface of submerged plants in standing water; *5*, surface of mud in open water or under weeds; *6*, surface of mud under dense rice; *7*, beneath mud under dense rice; *8*, beneath mud in open water or under weeds; *8*, beneath mud under dense rice.

Additional work should be concentrated on the study of overwintering chironomid larvae to determine what controls their rate of development and whether or not adults of species other than *Micropsectra* emerge during the winter. This was not done in the present investigation.

DISCUSSION OF EACH SPECIES TAKEN IN OR NEAR THE RICE FIELDS (AUTECOLOGY)

The Tanypodinae

Three species of the subfamily Tanypodinae were represented in the adult midges taken by emergence traps in the rice fields. Two of these, however, were confused and considered as the single species, *Pentaneura monilis,* until the writer was informed by Dr. J. E. Sublette[17] that a new species, *Pentaneura aequifasciata,* described by Dendy and Sublette (1959), was present among the specimens sent to him for identification.

Pentaneura monilis (L.) and Pentaneura aequifasciata Dendy and Sublette. The genus *Pentaneura* constituted a relatively small part of the chironomid population in rice fields. Since it is now impossible to be certain of the correct species of all of the adults of this group which emerged during the two seasons, the data in figure 168 necessarily must be treated as representing only the genus. A review of the trapping data does, however, give indications of different emergence patterns which may be associated with the two different species. Of the members of this genus saved as specimens, the earliest record is that of a female identified as *Pentaneura aequifasciata,* which was taken by light trap in a rice field near Davis, July 19, 1956. Of the specimens of *Pentaneura* saved from the 1957 season, all of the *Pentaneura aequifasciata* were taken from Field C. Thirty-seven of the total of 39 individuals trapped in 1957 were from this field. One male *Pentaneura monilis* was taken in Field A, and a female, at the time thought to be the same species, was recorded from Field B. Only 11 adults of this genus were caught in the emergence traps during 1958. Five of these were retained as specimens and all were *Pentaneura monilis.* In 1958 the one adult and one pupa reared from larvae, taken in Fields F and G respectively, also were *Pentaneura monilis.* Since one specimen identified as *Pentaneura monilis* was obtained in 1957, the possibility exists that not all of the 37 adults from Field C were *Pentaneura aequifasciata,* but probably most of them were. It appears that this species became established in this one field and was able to maintain a stable, though small, local population during the 1957 season. In contrast, *Pentaneura monilis,* which was recorded from one second-year and three first-year fields, appeared sporadically and never became an important part of the rice field fauna.

Although there have been many published records of the different habitats in which *Pentaneura monilis* has been found, the questionable accuracy of identity of species creates some doubt as to which reports are reliable. Hauber (1945) in ecological notes on *Pentaneura monilis* mentions possible mistaken identity of this species which was reported from rain barrel water by

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[17] Personal correspondence.
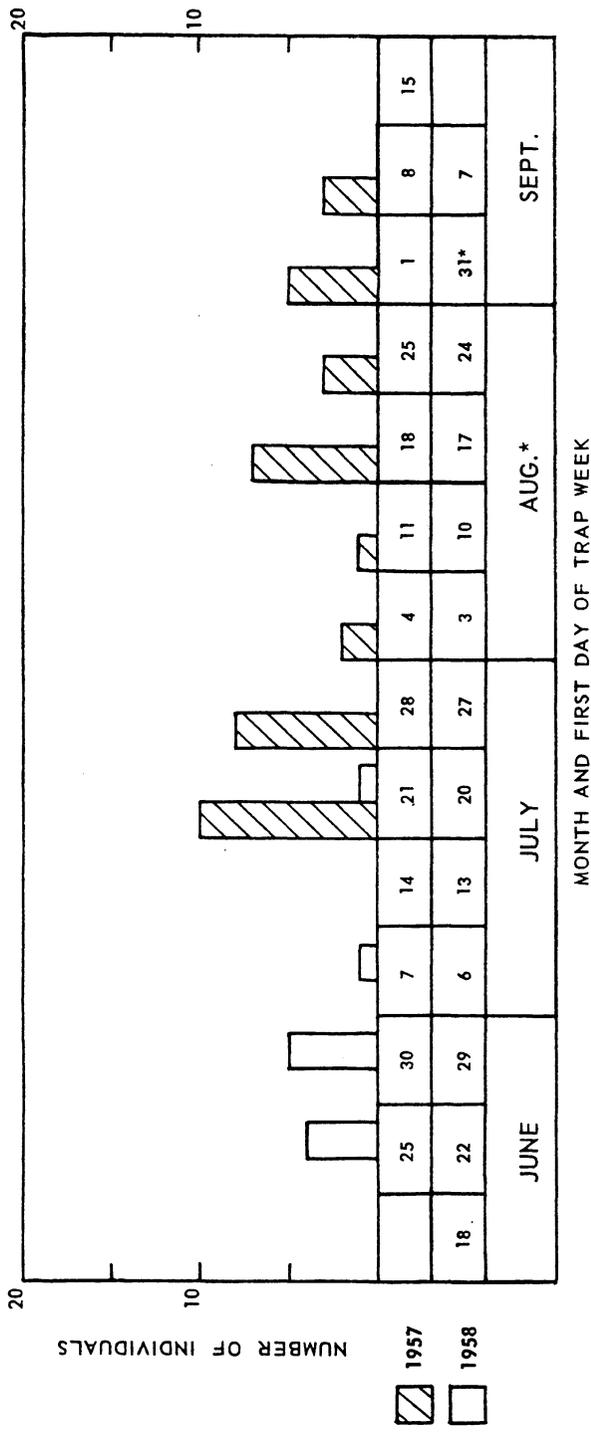
Fig. 168. Number of adult *Pentaneura* sp. taken weekly in 24 emergence traps in eight rice fields during two seasons.

Malloch (1915) and from the littoral zone of Lake Mendota by Muttkowski (1918). Yet Morrissey (1950) points out that what were thought to be *Pentaneura monilis* in Iowa studied by Hauber (1945) were actually *Pentaneura annulata* which had been confused with *Pentaneura monilis* earlier by Malloch (1915). This species has been reported by Brues (1928) from hot springs near Goldfield, Nevada, in water with a temperature of 35.4° C and near Convict Lake, California, in 35° C water. The larvae, however, were described as red whereas those of *Pentaneura monilis* are yellowish mottled with brown; thus it is likely that a species other than *Pentaneura monilis* was observed. Alexander (1925) in a faunal study of the Salt Fork of the Vermilion River indicates *Pentaneura monilis* as a species well able to withstand pollution. In England, Morgan (1949) noted the larvae of *Pentaneura monilis* moderately abundant in still water containing water weeds. Mundie (1957) found the optimum water depths for this species to be 1 and 2 meters in the Kempton Park East Reservoir and 3 meters at Staines South Reservoir. A few were taken as deep as 9 meters in the latter reservoir indicating possible profundal populations of this species. In a comparative study of chironomids of a chalk stream and a system of acid streams, Hall (1951) recorded *Pentaneura monilis* only from acid streams. In these, most of the larvae were taken from silt and mud of the slowly moving portions of the streams.

In the rice fields, adults of *Pentaneura* taken in 1957 emerged from moving water ranging in depth from 1 to 2 feet. Most of them were captured in relatively fast flowing water (fig. 166), but several individuals emerged from the slowly moving water of the borrow pits. With two exceptions all trap locations in which *Pentaneura* was obtained were above submerged vegetation such as water nymph, burhead, arrowhead, and *Spirogyra*. The two exceptions mentioned were trap records from the large pyramid trap placed in the deeper part of a borrow pit in sparse rice. There may, however, have been some unnoticed plant material present. Only one individual was taken from a second-year field in 1957 as compared with 38 from first-year fields. All were taken in traps placed in relatively open water and none from those in dense rice.

In 1958, of the 11 adults of *Pentaneura* trapped, 10 were from Field F, a second-year field. The one male taken in Field E was from a trap placed in quiet water 1 foot deep in sparse rice over submerged arrowhead. This location was not far from a drainage canal which contained water most of the year and which may have been a normal habitat of the larvae of this genus. Nine of the midges taken in the second-year field were from traps placed over *Chara*, water nymph, and water hysop, in moving water approximately 18 inches deep. The one unusual habitat represented was that of the last member of this genus taken on July 21. This trap was in quiet water only 7 inches deep which received full sunlight because of the sparse stand of rice. It was placed over dense *Chara* and water nymph. The single male died when partially emerged and became water-soaked and covered with a water fungus, thus could not be saved for positive identification.

As Johannsen (1937a) indicates, the larvae are free-living and do not construct silken cases or tubes. They are predaceous and as mentioned by Hauber (1945) are frequently cannibalistic. Both Muttkowski (1918) and

Leathers (1922) call attention to the peculiar rapid backward movements of the larvae which resemble those of the crayfish. The functional importance of the retractile antennae of the larvae in measuring the distance from their prey is discussed by Leathers (*op. cit.*). The larval feeding was also observed by Morgan (1949) who noted that the prey is either swallowed whole or the body contents sucked out. The function of the hypopharynx called "labial plate" by Morgan was clearly demonstrated, and mention was made of the antennae moving in and out during feeding.

The present study yielded little that was new regarding the larval food habits, as it is generally known that the members of this genus feed on other chironomids. Empty head capsules of blood-worms were found in the alimentary tract of these larvae by Miall and Hammond (1900; p. 7) and by Roback (1953). Similar evidence of *Pentaneura aequifasciata* utilizing larvae of *Tanytarsus* and of the subfamily Orthocladiinae from Field C can be seen in figure 169. Only the head capsule of the *Tanytarsus* larva is visible in figure 173 and this is somewhat difficult to discern.

The pupae are free-living and active much like those of mosquitoes. Based on a single observation, the pupal stage appears to be short. A larva, taken for rearing on July 21, pupated 14 days later on the morning of August 4, and the adult female *Pentaneura monilis* emerged that same evening.

As Morgan (1949) states, this group is remarkably free of parasites in all stages. She mentioned that ectozoic vorticellids were sometimes encountered on the heads of larvae from polluted streams, but no parasitic worms were found. No evidence of disease or parasitism was found in the *Pentaneura* in the present study.

Both males and females appeared at approximately the same time in 1958 in about the same numbers, six males and five females. In 1957 males outnumbered the females taken by 23 to 16.

Only two instances of males swarming were recorded. One male was taken on August 21, 1957, at 8 a.m. over the open water of the last check in Field C. This individual was in a small swarm consisting of males of *Tendipes* (*Cryptochironomus*) *tenuicaudatus* and *Tendipes* (*Cryptochironomus*) *frequens*. The presence of several species swarming together was often observed, but this was the only time that a male of the genus *Pentaneura* was noted in a mixed swarm. On August 31, 1958, at 7:35 p.m. just at sunset, a small swarm was seen in flight over the open water near the north edge of Field E. Twelve of these were captured and were identified as *Pentaneura monilis*.

The seasonal emergence of *Pentaneura monilis* from Dundas Marsh in Ontario was reported by Judd (1949 and 1953). The bimodal curve shown by Judd (1953; fig. 5) indicates the spring emergence of a small overwintering population and a major emergence of the offspring of the spring adults in July and August. Mundie (1957) has interpreted the pattern of emergence of *Pentaneura monilis* from Kempton Park East Reservoir as showing two generations per year.

As has been stated, two species were present in the rice fields; thus no accurate conclusions on the number of generations can be drawn. The emer-
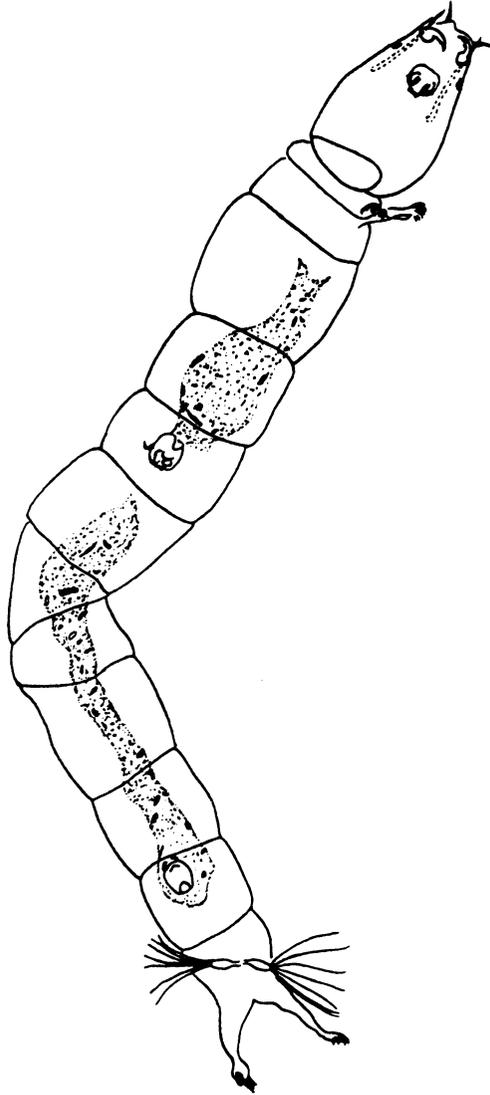
Fig. 169. Larva of *Pentaneura aequifasciata* Dendy and Sublette, showing
alimentary canal with prey species in it, × 18.7.

gence data of figure 168 are believed to show the establishment of a local population of larvae in one field early in 1957 and subsequent emergences throughout most of the season after mid-July. Larvae of this genus were taken from Field C as late as August 22. The presence of the other two adults of this genus in the other fields represented isolated records of occurrence. The few individuals which emerged in June and July of 1958 probably were the result of sporadic oviposition by females which emerged from the nearby canals in early May when the rice fields were first flooded.

Apparently the adults of *Pentaneura* are not as greatly attracted by light as are some other species of chironomids. Only a few were taken in three years of light trapping. Even on favorable nights, as that of August 31, 1958, when there was no wind and the air temperature ranged from 76° F at 7:50 p.m. when the trap was started to 69° F an hour later, no *Pentaneura* were taken at the light. This was the same night that the swarm of *Pentaneura monilis* had been observed at sunset approximately 50 yards south of where the trap was started.

Procladius culiciformis (L.). This was by far the most abundant of the three species of Tanypodinae which occurred in rice fields. These findings do not agree with the observations of Judd (1953) on the insects of Dundas Marsh, Ontario, in which *Pentaneura monilis* were more numerous than *Procladius culiciformis*. According to Johannsen (1937a) *Procladius culiciformis* ranges over most of the United States, and Edwards (1929) indicates that it is widely distributed and common in England. Edwards states that perhaps it is a variety of *Procladius choreus*. Mundie (1957) calls attention to the taxonomic difficulties within this genus in which three closely related species may account for the apparent extensive geographic distribution of *Procladius culiciformis*.

Oviposition of this species was not observed but apparently aquatic vegetation or other floating material is not as essential as it is for some other chironomids. Fellton (1940) observed the female of *Procladius* sp. ovipositing while resting on the surface of the water and the egg masses were generally found on the bottom of the lake.

On July 29, 1958, a long string of eggs believed to be those of *Procladius culiciformis* was taken together with a female of this species in a trap in Field G. The eggs were linear with straighter, more parallel sides than any others observed. Although not so pointed, they resembled fairly closely the egg of *Procladius culiciformis* as illustrated by Thienemann (1954; Abb. 168) which also shows the sides relatively straight. As can be seen in figures 170 and 171, the eggs were located almost exactly on the central axis of the gelatinous envelope which had wide margins of clear material free of eggs. Similar wide borders containing no eggs were reported by Branch (1928) for the spherical egg mass of *Procladius umbrata*.

A number of studies have shown that *Procladius culiciformis* larvae possess a wide range of tolerance of the various environmental factors. Eggleton (1931) records the larvae at depths of 10 to 28 meters in Douglas Lake and from 3 to 18 meters in Third Sister Lake of Michigan. Figures from an unpublished thesis, Wood (1938), are given by Lindeman (1942a) which show
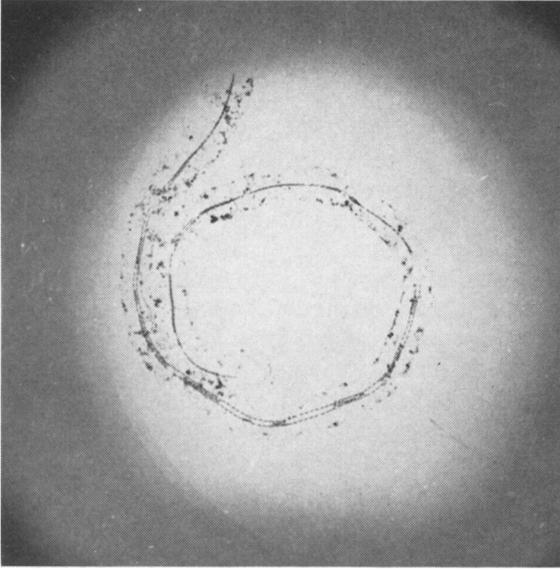
Fig. 170. Egg string believed to be that of *Procladius culiciformis* (L.), × 4.
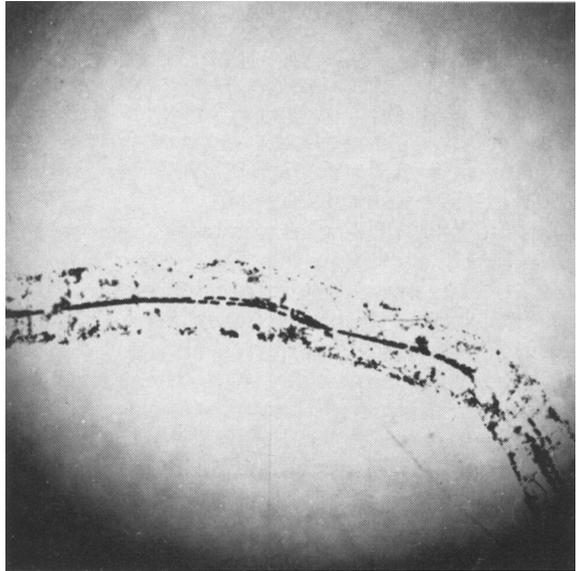
Fig. 171. Enlarged portion of figure 170, showing centrally-located eggs within the gelatinous envelope, × 9.

the larvae of *Procladius culiciformis* somewhat evenly distributed in Lake Minnetonka from depths of 4 meters to 15 meters but seldom present in deepest areas at 24 meters. Humphries (1938) considered *Procladius culiciformis* a synonym of *Procladius choreus* and noted that it was a common species in Grosser Plöner See. The larvae were taken at a depth of 2 meters in sand covered with algae. In two artificial lakes in New York ranging in depth from 1½ to 18 feet, Fellton (1940) reports larvae of *Procladius* sp. uniformly distributed between depths of 3½ and 5 feet. They were found in several types of substrate, some of which contained sewage sludge and decomposing vegetation, but were seldom encountered in the cleaner shallow areas. Miller (1941) attributed the wide distribution of larvae of *Procladius culiciformis* in Costello Lake, Ontario, to their habit of roaming and not building tubes as well as to their ability to withstand a wide range of temperature. In his study of the Tanypodinae of Iowa, Morrissey (1950) obtained many larvae from plant material in shallow ponds. Thienemann (1954; p. 396) has tabulated the occurrence of chironomid larvae in three of the oligotrophic crater lakes in the Eifel. In this table he has listed *Procladius culiciformis* under the deep fauna, whereas *Pentaneura monilis* is classified under shore fauna.

Considering the diversity of environmental conditions that the larvae of *Procladius culiciformis* can tolerate, it is not surprising that they should occupy almost all of the different aquatic habitats of a rice field. Since the larvae are free-living, active predators, they were not found inside the leaves or stems of aquatic plants, but this was the only possible chironomid habitat from which they were absent. Because these larvae were plentiful when other larvae were scarce, Fellton (1940) expresses doubt that the *Procladius culiciformis* larvae are predators. Roback (1953) reports finding plant material in the digestive tracts of larvae of this species taken from the mud and sand bottom of the Savannah River. Perhaps this species is capable of subsisting on plant material as well as animal matter, but findings of the present investigation indicate that most of its diet consists of other chironomid larvae and various worms. Figures 172 and 174 illustrate the use of a larval *Tanytarsus* n. sp. 5 as food by *Procladius culiciformis*.

Variation in water depth and movement had little bearing on the numbers of these larvae. Adults emerged in traps placed in warm shallow standing water as well as traps in deeper moving water. Larvae were taken on aquatic plant material as well as in mud samples, but it appeared that the most favorable habitat was the thin layer of ooze on the mud surface directly under submerged vegetation. More larvae were taken in this location than in any other. The only *Procladius culiciformis* larvae obtained on the varied level stakes were two which were in the thin film of mud which settled on the bottom shelf of a stake placed in moving water 14 inches deep in a borrow pit of Field G.

In the rice fields, the presence of an abundant food supply appeared to have greater direct effect upon the numbers of *Procladius culiciformis* larvae than any of the physical factors. Beneath masses of plant material such as *Echinodorus, Chara,* and *Spirogyra* there were many newly hatched chironomid larvae which had recently moved from the egg masses and were beginning
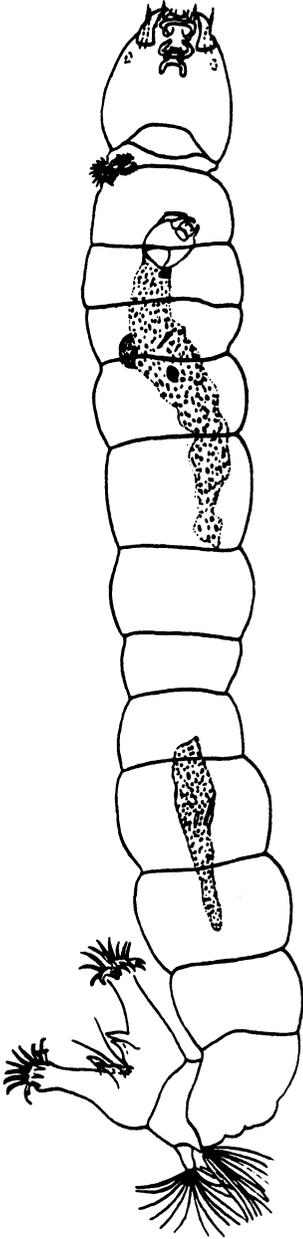
Fig. 172. Larva of *Procladius culiciformis* (L.), showing alimentary canal with prey species in it, × 18.7.

Fig. 173. Portion of a larva of *Pentaneura aequifasci-
ata* Dendy and Sublette, showing head capsule of a
Tanytarsus sp. larva in the alimentary canal, × 28.
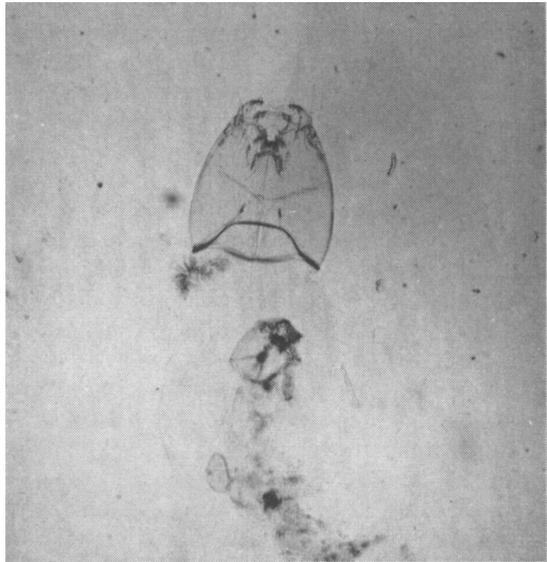
Fig. 174. Portion of a larva of *Procladius culici-
formis* (L.), showing head capsule of a *Tanytarsus*
n. sp. 5 larva in the alimentary canal, × 28.

to use the diatoms and other microscopic phytoplankton as food and for tube-building. In addition, this ooze layer supported many oligochaetes, nematodes, and flatworms which served as food for the *Procladius* larvae.

Many more individuals of this species were taken in the first-year fields than in the older fields (table 7). The work in a first-year field near Davis in 1955 presented an opportunity to observe the rate of development of *Procladius culiciformis* under field conditions. As previously stated, the water supply for this field precluded the introduction of any larvae at the time of flooding on April 27. The first adult of this species was taken in an emergence trap on June 21, 54 days after flooding or the earliest possible date of oviposition. This single female was followed by the emergence of two more females, one on July 5 and a third individual on July 19.

In general form and habits the pupae are similar to those of *Pentaneura*. As Fellton (1940) states, they actively move about throughout the pupal stage. Malloch (1915) gives the duration of this stage as about three days for *Procladius culiciformis*. Most of those reared in the present study emerged in from 2 to 2½ days after initial pupation.

No diseased or parasitized individuals were observed in any of the stages of *Procladius culiciformis* taken from rice fields. Larger predators such as fish, dragonfly naiads, and hydrophilid beetle larvae probably accounted for most of the larval and pupal mortality.

There appeared to be little or no interspecific competition between the two predatory species, *Pentaneura* and *Procladius,* despite the fact that, as figures 168 and 177 indicate, they must have been in approximately the same developmental stages at the same time. This assumes the same rate of development, which may not be correct. Field C was the only plot in which sufficient numbers of both species were present to make a comparison. In this field, 37 adult *Pentaneura* and 36 adults plus one active pupa or 37 *Procladius* were taken in 1957. A check was made of the other fields investigated during that season to determine whether the presence of *Pentaneura* in Field C had resulted in the development of fewer *Procladius* than elsewhere. This showed that almost as many adult *Procladius* had emerged from Field C as those of the other fields combined. Of these, the highest number was 27 from Field D, a second-year field, followed by eight from Field A, a first-year field, and seven from Field B, the other second-year field. A more intensive, critical study should be made to discover what slight difference in the ecologic niches of these two species allowed such an apparently orderly development of both.

During the two seasons of emergence trapping in the rice fields, almost twice as many female *Procladius culiciformis* adults were taken as males. In 1957 the numbers were 52 females to 26 males and for 1958, 80 females to 49 males. Miller (1941) recorded the peak emergence of the males of this species from Costello Lake about July 17, one week earlier than that of the females. The emergence pattern of the two sexes (figures 175 and 176), was not in agreement with that of this species in Ontario. The 1957 emergence peaks agree fairly well in that the largest number of males emerged on July 21, and the peak emergence of the females was on July 31. The figures for 1958, however, differ considerably. The peak emergence of the females was
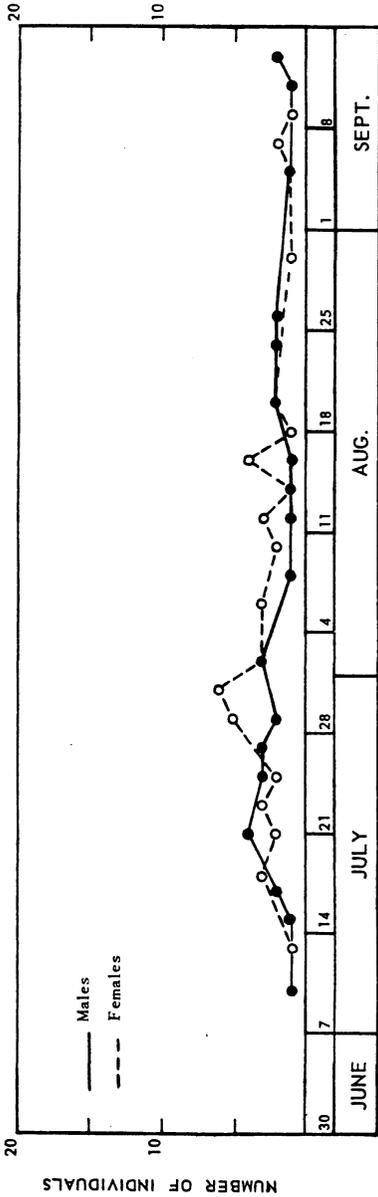
Fig. 175. Male and female *Procladius culiciformis* taken weekly in 12 traps in four rice fields during the 1957 season.
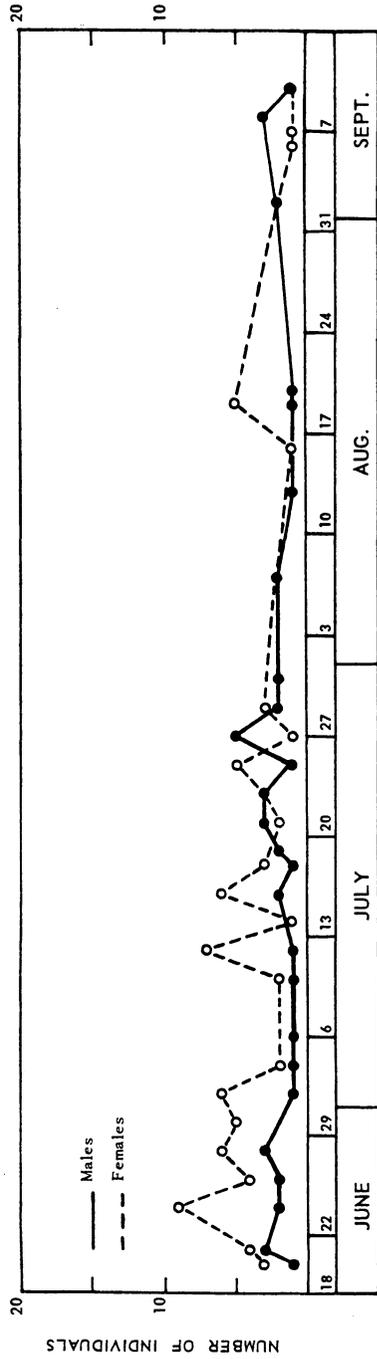
Fig. 176. Male and female *Procladius culiciformis* taken weekly in 12 traps in four rice fields during the 1958 season.

on June 24, whereas that of the males was on July 27. The appearance of this species so much earlier in the 1958 season than in 1957 suggests the possibility that the peak emergence of the males had occurred prior to the placement of the traps in the fields. The winter of 1957–58 was unusually warm and wet, and heavy late spring rains kept the ditches full of water until the last of May. Thus it is possible that this species became successfully established in the rice fields much earlier than usual. Several third- and fourth-instar larvae were taken from two of the fields on May 26, 22 days after the water had been introduced into them, which indicated that the species already had become well established.

No swarms of males definitely identified as *Procladius culiciformis* were observed. Fellton (1940) states that mating occurs in the swarms over the water.

The adults, mostly females, were readily attracted to lights, but they were never taken in the light trap in as great numbers as some of the other chironomids. Possibly this was due to the fact they did not become active until later in the evening after the light trap was shut off.

Most studies have shown that *Procladius culiciformis* has two generations per year in shallow lakes. This was the conclusion of Lindeman (1942*a*) from his review of the literature on seasonal distribution of this species and his work in Cedar Bog Lake. Mundie (1957) concurred that in the Kempton Park East Reservoir this species was bivoltine. The data of figure 177, especially those of 1958, indicate that two generations probably would be completed in rice fields if the season were prolonged two weeks or if this species became established soon enough at the beginning of the season.

The Orthocladiinae

Cricotopus bicinctus (Meigen). This species was unquestionably the most abundant of the subfamily Orthocladiinae encountered in the rice fields (table 5). Roback (1957) states that this is the commonest species of *Cricotopus* in the Philadelphia area. He recorded *Cricotopus bicinctus* from hard water streams, ponds, and in waters with pH readings greater than 8 and lower than 6.

Adult females of this species were observed ovipositing both late in the evening and in the morning before the water was exposed to direct sunlight. The situation most frequently chosen for oviposition was a small semi-open area of water among bits of emergent vegetation or mats of algae. Protection from strong wind appeared to be a primary requirement. A typical example of oviposition by *Cricotopus bicinctus* was seen on July 18, 1958, at 7:30 a.m. in Field F. The air temperature at that time was 61° F and there was a south wind of from 4 to 7 miles per hour. The section of open, rapidly moving water above a weir box was protected from the direct force of the wind and was shaded from the sun by tall watergrass and cat-tails on the check bank. Directly beneath the surface of the water there was a dense growth of water nymph, of which a few scattered stems extended above the water. Particles of disintegrating algae had adhered to these emergent fragments and had formed small mats or islands. When first noticed, the female midge was on one of these. She flew from this spot, slowly skimming the water surface. At points 6 to 8 inches apart, she quickly dipped the tip of her abdomen into the water.
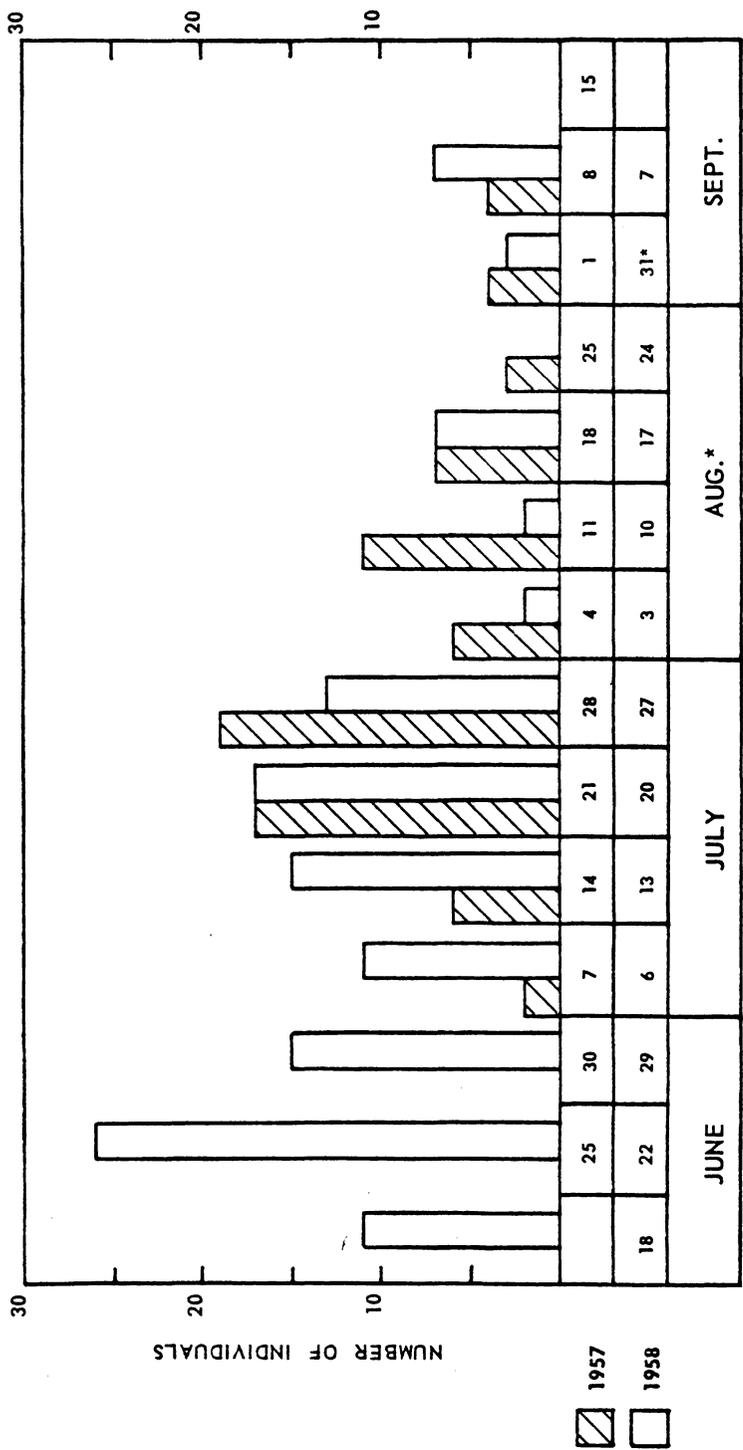
Fig. 177. Number of adult *Procladius culiciformis* taken weekly in 24 emergence traps in eight rice fields during two seasons.

She did not rest on the surface film, but remained in slow flight while touching the water. Almost as soon as she had moved from the algal mat, a water strider (*Gerris remigis* Say) darted in pursuit and nearly succeeded in catching her. After having apparently oviposited four or five times, this female settled on a piece of emergent vegetation and was caught by the writer and taken into the laboratory. When placed in a rearing cage over a finger bowl of water, she deposited a last small string of eggs. The eggs were long and slender and were arranged irregularly in the linear gelatinous envelope. Unfortunately all of the eggs hatched before drawings or photographs could be made. Similar slender, elongated eggs are shown in the illustration of part of the egg mass of *Cricotopus trifasciatus* by Malloch (1915; pl. XXXVIII, fig. 7).

The larvae of this species appeared to require water with a relatively high oxygen content. Since cold water holds more oxygen than an equal volume of warm water, most of these larvae were found in the cooler parts of the rice fields. In Costello Lake, Miller (1941) found *Cricotopus bicinctus* most successful at a station where the water temperature remained near 12° C (53.6° F) most of the summer. Judd (1957), however, took most of the adults of this species from stagnant water over a bottom of organic ooze and fine silt in a tributary of the Thames River of Ontario. This was the only published report seen which indicated that *Cricotopus bicinctus* larvae thrived in waters low in oxygen.

In the rice fields the optimum conditions were provided in the borrow pits and channels where the water was moving rapidly. In these portions of the field, although the water temperature seldom dropped below 60° F, it was lower than elsewhere because of the greater depth.

No adults were taken in traps located in quiet shallow water where the temperatures were often much higher than those given in figure 8. More study should be devoted to these temperature variations and to the species associated with the given conditions of the different microhabitats of a rice field.

Many more adults of *Cricotopus bicinctus* were taken by emergence traps in first-year fields than in older fields, as is shown by table 7. Larval counts made from the varied level stakes placed in different parts of the same field as well as those from plant and mud samples showed the greatest number present in moving water near the weir boxes, a few in the sluggishly moving water of the shallower borrow pits, fewer yet in quiet water near the edge of the rice, and none from beneath the dense rice.

Although taken in mud samples, these larvae more frequently were found on plants or other submerged or floating objects. It is believed that those taken in the bottom sampler were on the surface of the mud rather than in it. They were taken on all forms of submerged vegetation provided that the proper water conditions existed. In addition to inhabiting most of the aquatic plants growing in the rice fields, tremendous numbers of *Cricotopus bicinctus* larvae were taken on Sego pondweed (*Potamogeton pectinatus* L.) and American pondweed (*Potamogeton nodosus* Poir. apud Lam.) in the ditches adjoining the fields. Apparently the plane in which the plant or plant part grows is of little consequence to the larvae since they were found in all pos-

sible positions on the submerged vegetation. A similar distribution was noted on the varied level stakes. Larvae were just as plentiful on the vertical surfaces as on the shelves and were found on the underside of the shelves as often as on the upper surface. The angle formed between the shelves and the vertical stake proved to be a favored location, probably because of the protection afforded. No gradient in numbers of larvae with the depth of water was apparent. Their arrival at a given spot seemed to be fortuitous. If for some reason one place became unsatisfactory, or if the larvae were disturbed, they wriggled away to settle in another location.

The larvae of all species in this genus spin silken tubes in which development occurs. They incorporate less algal material into their cases than do most other tube-dwelling chironomids. These transparent tubes permit the larvae to be seen clearly as shown in Miall and Hammond (1900; fig. 8). The pupation case is not greatly different from that of the larva. In some of the rearings the larvae pupated in the larval tubes. In others, however, a more triangular-shaped case was spun by the last instar larva. This had slightly thicker walls than the larval tube and the larger end permitted a quick exit by the pupa at the time of emergence.

The undulating respiratory movements of both larvae and pupae within their tubes are similar to those of other tube-dwelling larvae in this family. These have been described often in the literature on chironomids. Walshe (1947a) thoroughly discusses the feeding and respiratory activities of larvae of *Chironomus*. Young *Cricotopus* larvae were extremely active and moved about much of the time. The mature larvae became sluggish and were reluctant to leave their tubes. If disturbed at one end, they often turned about in the tube and went to the other end or simply retreated, but would not leave until the tube was torn or the larva stuck with a dissecting needle.

Although not restricted to or entirely dependent upon *Spirogyra*, the presence of this alga in weir boxes and in the swift water below them was directly responsible for the successful development of large numbers of larvae. Literally hundreds of larvae were found in the masses of *Spirogyra* and the largest catches of adults were from traps placed over this plant material.

Spirogyra served the larvae of this species both as food and as substrate or support for their tubes. When feeding on *Spirogyra*, they oriented the filament lengthwise and beginning at one free end moved the strand backward into the mouth and over the labial plate. This was accomplished by hooking movements of the mandibles and the various elements of the epipharynx. Because of the difficulty of seeing all of the details of the feeding process, a positive statement cannot be made, but it appeared that the labial plate functioned as a rasping or grating organ. Larger pieces of vegetation such as algal filaments were forced over the labial teeth primarily by the action of the mandibles much as a carrot is pressed against a carrot grater. In this way the cell walls of the plant were broken or pierced and the cell contents released as food. Evidence which tended to support the contention that the labial plate functions by abrasive action was found in those individuals reared using larger or coarser fragments of plant material as food. The labial teeth of the larval head capsule of those individuals which were examined always showed much greater wear than did the mandibular teeth.

In addition to *Spirogyra* and other green algae, *Cricotopus bicinctus* larvae consumed many desmids and diatoms which had accumulated on the substrate supporting their tubes. More intensive study of the different species and relative abundance of these microscopic plants is necessary if the complete ecology of the chironomids is to be understood. There was no evidence of *Cricotopus bicinctus* larvae feeding on the tissues of higher plants in the rice fields. Many individuals were green in color due to the large amount of plant material in their alimentary tracts, but in all of those examined, this green material proved to be algae.

The larvae were eaten by a large number of different predators. Undoubtedly all the species of the Tanypodinae fed upon the young larvae. Certainly the larvae of hydrophilid and dytiscid beetles consumed many of them. Also the naiads of damselflies and dragonflies were prominent predators in all of the rice fields. In addition, several predatory species of the family Heleidae were represented in the insect fauna. One serious predator which killed larvae in the rearing dishes and probably also in the field was a relatively large nematode worm. Though no investigation was made, possibly the carp, which were especially numerous in the fields near Davis, ate fewer of these smaller larvae than those of the larger chironomids. Needham in Hankinson (1908) observed that the fish of Walnut Lake ate the larger larvae in preference to the more abundant smaller species. On at least one occasion a newly emerged adult *Cricotopus bicinctus* was found to be infested with small reddish aquatic mites. It is probable that initially they had attacked the pupa in its case, but had moved to the adult in the short time interval of emergence.

During the field work of this study interspecific competition was considered a possibility because the larvae of *Cricotopus bicinctus* were often taken in the same locations as those of other species, particularly *Cricotopus sylvestris*. More intensive work is necessary to prove or disprove the existence of competition and to discover the subtle differences in ecologic niches of the various species. One difference, however, was apparent. By comparing the emergence data of figure 180 with those of figure 181, a difference in the time of emergence between the two species of this genus can be seen. *Cricotopus bicinctus* became established later with the first adults emerging in the first week of July, whereas the adult emergence of *Cricotopus sylvestris* had already begun to decline by the third week of July. A comparison of the numbers of adults captured in light traps also indicated that *Cricotopus bicinctus* was later in emerging from the ditches and canals than *Cricotopus sylvestris*. Perhaps this temporal difference was sufficient to prevent most of the larvae from requiring exactly the same environmental factors at the same time.

Many more males than females of *Cricotopus bicinctus* were taken in the emergence traps. The totals for the two seasons were 145 males and 89 females. In 1957 (fig. 178), one peak emergence of males on July 29 preceded that of the females on August 2, but on August 12 both were on the same day. In 1958 (fig. 179), the peak emergence for both sexes occurred on the same day, August 2.

Cricotopus bicinctus males were often taken in mixed swarms with other species. Usually these were small groups of males of *Tanytarsus viridiventris*,
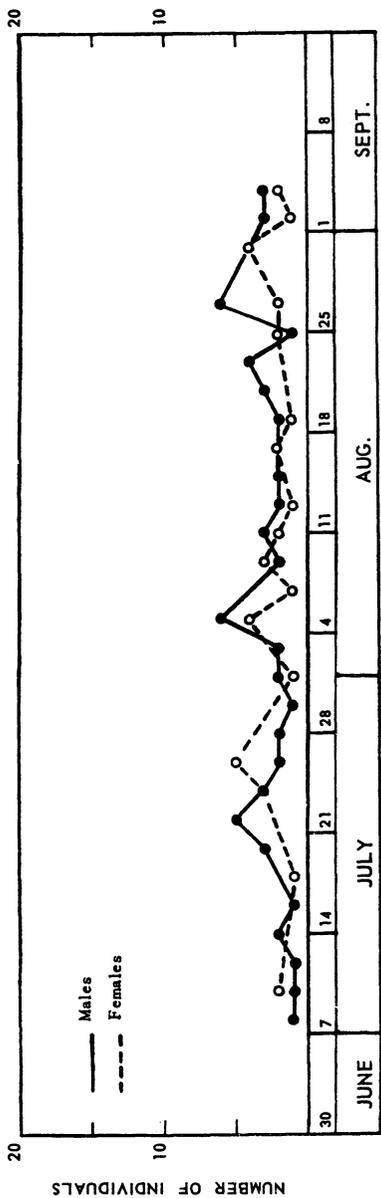
Fig. 178. Male and female *Cricotopus bicinctus* taken weekly in 12 traps in four rice fields during the 1957 season.
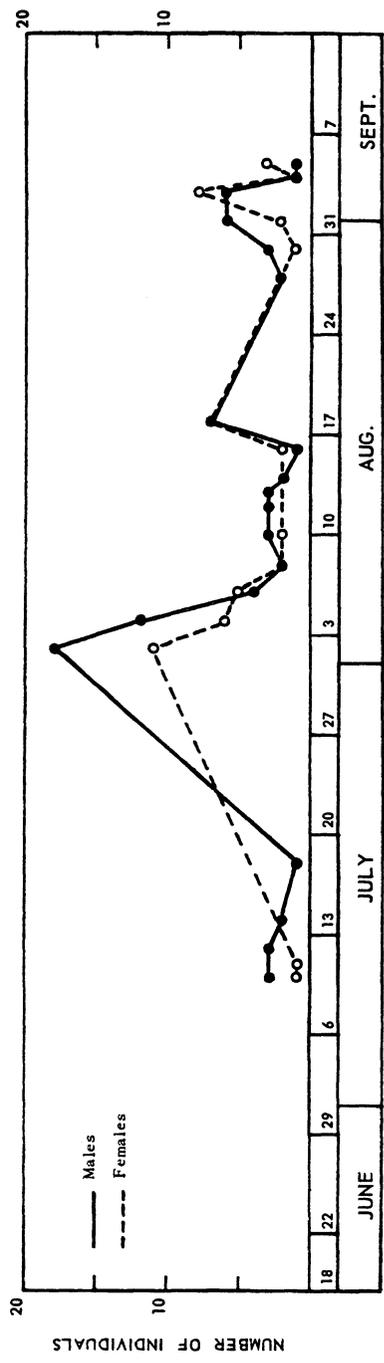
Fig. 179. Male and female *Cricotopus bicinctus* taken weekly in 12 traps in four rice fields during the 1958 season.

Cricotopus sylvestris, Tendipes tenuicaudatus, and other small midges. These small swarms never mounted high into the air as those of some of the larger species, but remained 2 or 3 feet above the open water of borrow pits or check corners protected from the wind by the vegetation on the check bank. The swarms formed quickly. One or two males would fly out from the vegetation and begin the characteristic weaving, dancing flight pattern. Soon other males would join them until within a few minutes there were 15 to 20 males in flight. Mundie (1957) observed small swarms of *Cricotopus bicinctus* late in May and throughout June at Kempton Park East Reservoir in England, but made no mention of mixed swarms.

In Costello Lake, Miller (1941) noted that the emergence of *Cricotopus bicinctus* from the shallowest station began on June 22, but most of the adults emerged from early July until late August. The peaks or greatest numbers did not occur at the beginning of the period of emergence as did the shallow-water species, but half way through the emergence period. Judd (1957) records the emergence period of this species from the Thames River, Ontario, as being from April 23 to October 8, with the maximum emergence on May 27 and June 5.

Cricotopus bicinctus emerged from the rice fields from early in July until September with an early peak emergence the last of July and the first part of August (fig. 180). There was also a later smaller peak emergence near the first of September. Only one generation was able to develop in rice fields, for as soon as the water was shut off, and even before all of it had drained out of the field, the larvae began to die. Many weakened and dead larvae were found in September before the weir boxes had been removed from the fields. Miller (1941) considered *Cricotopus bicinctus* a typical deep-water species which had only one generation per year in Costello Lake. In contrast, Humphries (1938) recognized *Cricotopus* (= *Trichocladius*) *bicinctus* from the littoral zone of the Grosser Plöner See as a common spring and autumn species with two generations each year.

Cricotopus sylvestris (Fabr.). The second species of the subfamily Orthocladiinae from the standpoint of numbers taken in rice fields was *Cricotopus sylvestris.* It was less abundant than *Cricotopus bicinctus,* as shown by the fact that only 64 individuals were taken in two seasons of emergence trapping (table 5).

It was unfortunate that no eggs definitely known to be those of *Cricotopus sylvestris* were seen. Thienemann (1954; Abb. 168) illustrates the ova of this species as being oval and thicker at one end than the other, whereas the eggs of the closely related *Cricotopus trifasciatus* are pictured by Malloch (1915; Plate XXXVIII) as long and slender.

Over twice as many individuals of *Cricotopus sylvestris* were taken from first-year fields as second-year fields (table 7). Although most of the individuals were from rapidly moving, deep, cool water, a number were caught in Field H from slow-moving shallow water, and one male was obtained August 18, 1958, in Field F from shallow, standing water exposed to the direct sunlight (fig. 13). Mundie (1957) states that in England this species occurs both in flowing and standing waters where it builds its tubes in the mud as well as on submerged aquatic vegetation. In the rice fields, larvae of
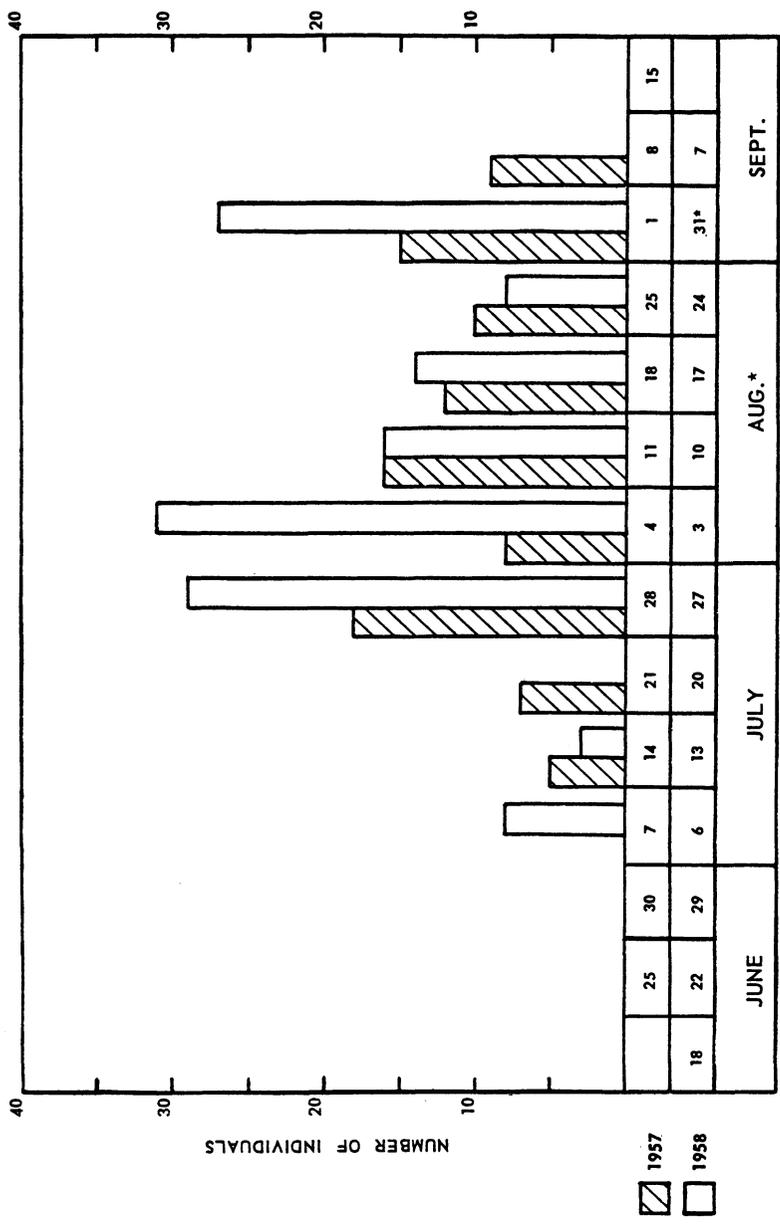
Fig. 180. Number of adult *Cricotopus bicinctus* take weekly in 24 emergence traps in eight rice fields during two seasons.

Cricotopus sylvestris were found in all of the different habitats sampled except dense rice. In view of the varied situations in which this species was able to survive, it is difficult to explain why more individuals were not captured.

According to Wirth (1957), *Cricotopus sylvestris* larvae inhabit channels which they make in the tissues of higher aquatic plants. In the present study, however, the transparent silken larval tubes were observed on the surface of mud and debris of bottom samples, but more frequently they were found on submerged aquatic vegetation. No particular species of higher plant appeared to be favored over any other. The number of larvae present was dependent primarily upon the surface area provided. Thus many more larvae were found on the wrinkled, ribbon-like leaves of burhead or in the dense growth of water nymph than on the stems of rice or young cat-tails. Green algae, particularly *Spirogyra,* usually harbored many larvae because of the food supplied in addition to the large amount of surface area provided. Mundie (1957) points out that large numbers of *Cricotopus sylvestris* adults emerged from the mats of *Cladophora* in the reservoirs in England during the summer months. *Cladophora* was noted in and near the weir boxes of several of the rice fields in July and August, 1958, but surprisingly few larvae were found in it. As shown in figures 19 and 20, this alga appeared much later in the first-year fields than in the second-year fields. Since the first-year fields supported the bulk of the *Cricotopus sylvestris* population, perhaps the *Cladophora* was too late in coming into the fields to be utilized extensively.

Any discussion of larval food habits of *Cricotopus sylvestris* is complicated by the possible misidentification of the species involved. Johannsen (1937a) states that the larvae of *Cricotopus sylvestris, trifasciatus,* and *tricinctus* are indistinguishable. It is possible that both *Cricotopus sylvestris* and *trifasciatus* occurred in the rice fields under investigation. A study such as that of Acton (1955) on the chromosomal characteristics of these larvae is necessary to determine which species are actually present and what their respective food habits are.

Early in the present study adult specimens were sent to Dr. W. W. Wirth of the United States National Museum and to Dr. S. S. Roback of the Academy of Natural Sciences of Philadelphia and all were identified as *Cricotopus sylvestris.* On the basis of adult characteristics (male genitalia and coloration) only *Cricotopus sylvestris* was presumed present in the rice fields.

Most reports of larvae of the genus *Cricotopus* feeding on higher plants concern the species *Cricotopus trifasciatus.* Kettisch (1936–37) describes the irregular galleries produced by this species feeding on the upper surface of floating leaves of *Potamogeton natans* in Austria. The relationship of the larvae to several species of *Potamogeton* in Michigan was clearly demonstrated by Berg (1949 and 1950). The manner in which these larvae attacked the leaves of rice in France was outlined by Risbec (1952). He found that they built their colorless silken galleries near the surface of the water and in the surface film which rises up the leaves.

For the most part the diet of the larvae of *Cricotopus sylvestris* consists of diatoms, algal debris, and green algae. However, there have been instances of their feeding on the tissues of higher plants. Johnson (1901) in a brief note

indicated that an adult *Cricotopus sylvestris* had been reared from a larva mining the leaves of *Victoria regia*.

Occasionally in California rice fields there was evidence of larval feeding on the rice plants. Both the germinating seeds and the leaves were attacked. The damage to seed rice by chironomid larvae will be discussed later. In feeding on the older rice plants, the *Cricotopus sylvestris* larvae attacked the underside of those leaves which were floating on the water surface.

On June 19, 1958, an example of this type of damage was seen on the Miller Ranch near Liveoak, Sutter County. The damaged plants were confined to the margins of the field in and near the borrow pits since the rice in the shallower areas had already emerged from the water and was standing erect. The floating leaves of the partly emerged plants were heavily coated on the undersides with algae and harbored many chironomid larvae representing at least three species. All were tube-dwelling forms and most of them were feeding on algae. Some *Cricotopus sylvestris* larvae, however, had rice leaf tissue in their intestinal tracts. Presumably these larvae had partly mined the lower epidermis and mesophyll to form grooves on the undersides of the leaves. The larval tubes were located in these excavations. At the anterior end of the tubes pieces of the upper epidermis had been eaten, producing a slit clear through the leaf. It was not determined whether the larvae were primary invaders and had caused all of the leaf damage or whether they had secondarily moved into the mines or grooves following initial damage by the rice leaf miner (*Hydrellia griseola* Fallen) or possibly that of the recently discovered rice water weevil (*Lissorhoptrus oryzophilus* Kuschel). In any event, their consumption of rice leaf tissue had enlarged the damaged areas of the leaves.

Another instance of *Cricotopus sylvestris* larvae attacking higher plants was observed on August 11, 1958, in Field E where there were indications that they had been feeding on the leaves of the aquatic weed, burhead. Most of the larvae on these leaves had only diatoms and brown detritus in their alimentary canals, but three *Cricotopus sylvestris* larvae appeared bright green due to the chlorophyll of recently consumed leaf tissue. Several of the ribbon-like submerged leaves and one of the surface leaves showed evidence of insect feeding, but the larvae had been dislodged before they could be associated definitely with the leaf damage.

Although no actual observations were made of either predation or parasitism of *Cricotopus sylvestris* larvae, doubtless they were attacked by the same natural enemies as were the larvae of *Cricotopus bicinctus*.

The possible interspecific competition between this species and *Cricotopus bicinctus* already has been discussed, but it would appear that because its larvae inhabited a larger number of the different habitats in the rice fields, *Cricotopus sylvestris* should have been the more abundant species. It was believed that the earlier emergence of most of the *Cricotopus sylvestris* adults before the emergence traps were placed in the fields was responsible for the great difference in the numbers of these two species taken. This was confirmed by the results from early-season light trapping. Only *Cricotopus sylvestris* was taken in June and early July. The earliest record of *Cricotopus bicinctus* taken by light trap was July 24, 1957.

The numbers of males and females of *Cricotopus sylvestris* which were captured in emergence traps were almost the same. In 1957, when only 16 individuals were taken, there were eight males and eight females. Of the 1958 total of 47 adults, 23 were males and 24 were females. The sex of the single pupa taken this second season was not determined. In both years the peak emergence of the two sexes occurred simultaneously. In 1957, this was on July 19; in 1958, it was on June 20.

Most swarming flights of this species were observed in the morning or evening. *Cricotopus sylvestris* was one of the few species which also swarmed in bright sunlight. Nielsen and Greve (1950) believed this irregular swarming was in response to a fall in light intensity associated with an approaching storm. However, one of the largest swarms of *Cricotopus sylvestris* seen by the writer in the four years of work in rice fields was in flight at 10:40 a.m., June 19, 1958, on a bright sunny day. The air temperature was 74° F and there was a south wind of from 3 to 4 miles per hour. A large cloud of males was weaving back and forth over a ditch and check bank and out over the open water of a rice check on the Miller Ranch near Liveoak, Sutter County. The swarm did not rise high in the air and there appeared less orientation into the wind by the individual insects than was true for the larger midges.

Frequently *Cricotopus sylvestris* males were taken in mixed swarms with those of *Tanytarsus viridiventris* and *Paralauterborniella* sp. Usually these small mixed swarms were morning flights, but on June 27, 1957, a fairly large mixed swarm consisting of all three species was seen shortly after sunset near Field D at Davis.

Most of the swarms containing males of this species were seen in June and early July. Bill (1932) reports the swarming of the closely related species, *Cricotopus trifasciatus*, in May, 1931, in the eastern United States.

Because of its appearance early in the summer (fig. 181), *Cricotopus sylvestris* could, and probably did, develop two generations per season in the permanent water of the ditches near the rice fields. In the fields, however, when the water was shut off, the developing larvae and pupae soon died. Humphries (1938) classed this species as "very rare" in the fauna of the Grosser Plöner See. It appeared May 14, 1936, until August 11 and reached peak emergence toward the end of May. A second generation occurred about October 10 in that area. Two generations were also recorded for *Cricotopus trifasciatus* emerging from the Dundas Marsh of Ontario (Judd, 1949; 1953).

Psectrocladius n. sp. 1. Since this species was taken only by means of a light, it was not definitely known to have emerged from the rice fields. All of the individuals were captured on September 3, 1957, in Field C. Of the seven males attracted to the light, five were taken in an aspirator from the sheet windbreak at 8:35 p.m., and two entered the light trap. The trap was in operation from 8:20 p.m. until 9:20 p.m. The air temperature when the trap was started one-half hour after sunset was 71° F and had dropped to 66° F one hour later. A south wind of 4 to 7 miles per hour was blowing all the time that the trap was running. The only nearby water other than that of Field C was in the drainage ditch along the north edge of this field.

Psectrocladius n. sp. 2. This species occurred in the rice fields in small numbers. A total of 18 individuals was taken in the seasons of 1957 and 1958.
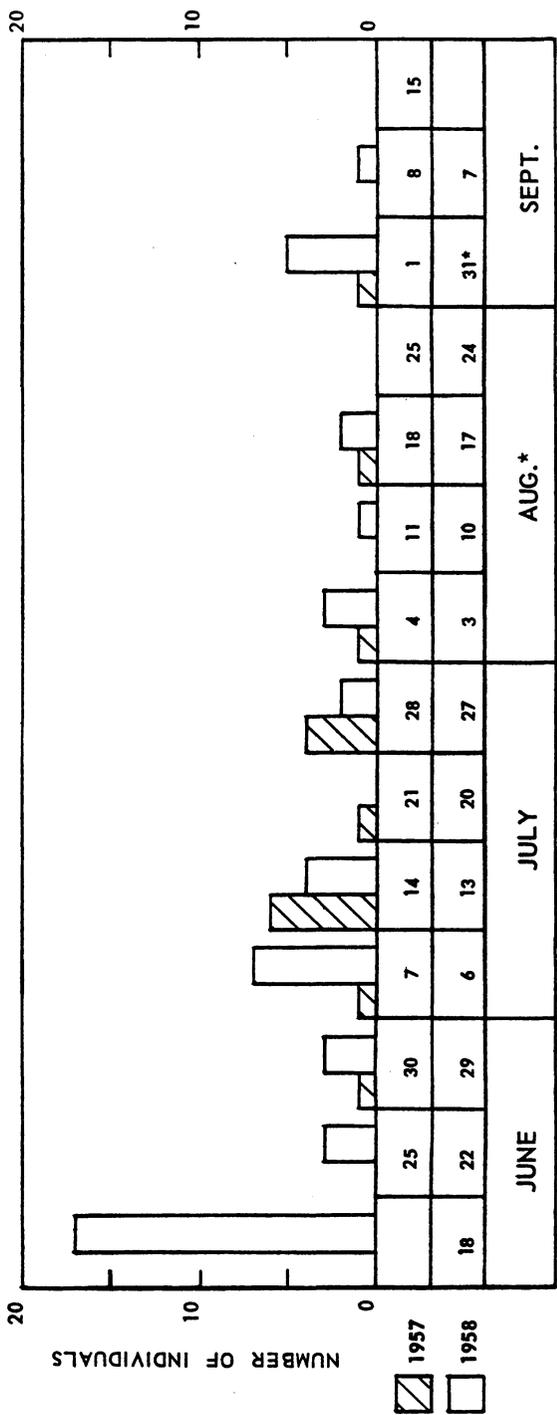
Fig. 181. Number of adult *Cricotopus sylvestris* taken weekly in 24 emergence traps in eight rice fields during two seasons.

Figure 182 shows that 14 were recorded from emergence traps in 1957 and two in 1958. The two remaining individuals were taken as pupae on September 23, 1957, in Field A. This first-year field was being drained at the time, and the water level had dropped considerably, leaving small pools containing weeds and algae which previously had been submerged. The two pupae, which were resting on the moist green algae in one of the puddles, were yellowish-brown with darker thoracic markings. To the unaided eye their most noticeable characteristic was the pair of short, erect, pencil-like thoracic respiratory organs. These individuals both emerged in the rearing dishes. The male was unable to get off of the water, consequently it was mounted on a slide together with the pupal exuvia. The female emerged easily and was saved as a pinned specimen.

All of the adults actually recorded from the rice fields were taken in traps placed over some form of submerged vegetation. *Spirogyra* and water nymph were the plants with which this species was most closely associated, but it also was taken over *Chara,* arrowhead, and burhead. Most of these midges were trapped over moving water, but there were two instances in which single individuals were taken from vegetation in standing water.

As can be seen in figure 182, most of the adults emerged during the last three weeks of July and the first two weeks of August. Of the 15 individuals taken during these weeks, nine were from Field C, three from Field B, two from Field A, and one from Field E. The single male taken on September 8, 1958, was from Field H near Davis. Twelve were from first-year fields and four were taken in second-year fields. Females outnumbered males 11 to five in the emergence trap material.

Nothing can be stated concerning the larvae of this species in the rice fields because none was successfully reared. Goetghebuer (1932) indicates that *Psectrocladius* larvae live in stagnant water among the algae where they construct silken galleries. Roback (1953) reports finding heads of other chironomid larvae in the digestive tract of *Psectrocladius* sp. *a* from the Savannah River. Mundie (1957) states that little is known concerning the feeding habits of *Psectrocladius,* but that the larvae probably feed on *Cladophora* and the organisms associated with it.

Nanocladius n. sp. Of the adult midges taken during this study, the genus *Nanocladius* was represented by only three males, all taken in Field C in July of 1957. According to Dr. James E. Sublette they represented a new species near *Nanocladius bicolor* Zett. No known females were captured either in the emergence traps or by light trap. The three individuals superficially resembled *Cricotopus sylvestris* but were much lighter in coloration. All were from emergence traps over submerged vegetation in moving water. No larvae known to be this species were obtained. Apparently populations of the genus *Nanocladius* are seldom large, for at Kempton Park East Reservoir, Mundie (1957) trapped only one female on June 28, and one male on July 12, 1951.

Smittia n. sp. Although four male *Smittia* n. sp. were captured, none was ever taken in any of the emergence traps. Three of these individuals were obtained by use of an aerial net early in 1955 and 1956 when survey work was being done to determine the species of chironomids inhabiting rice fields. The
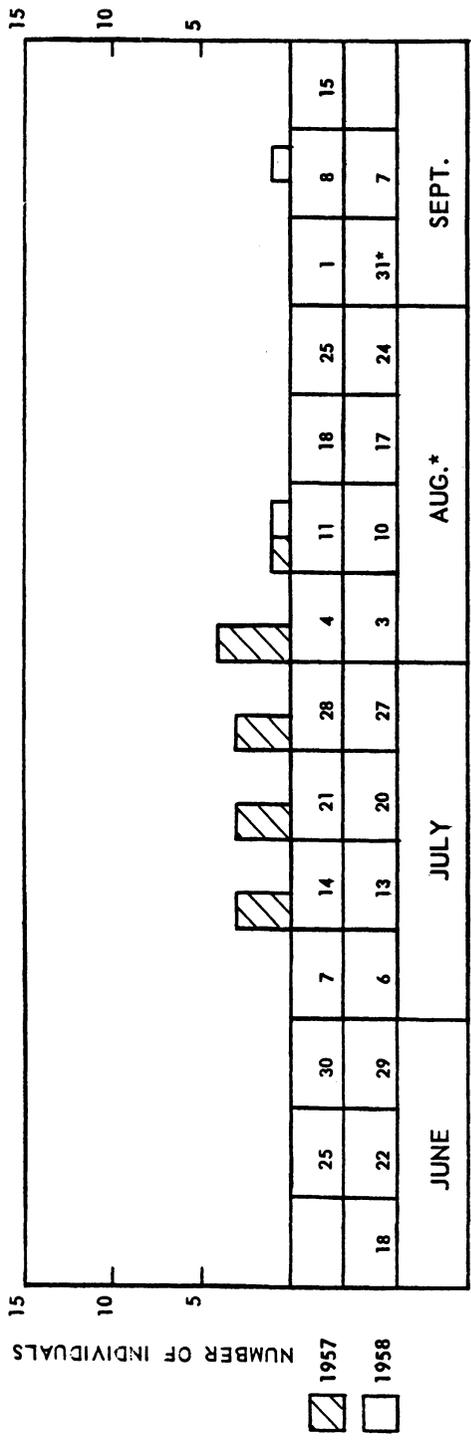
Fig. 182. Number of adult *Psectrocladius* n. sp. 2 taken weekly in 24 emergence traps in eight rice fields during two seasons.

fourth was taken on September 15, 1957, from a cobweb near the outlet of the last check in Field A. It was never learned whether or not the larvae of this species developed in the rice fields.

The Corynoneurinae

Corynoneura n. sp. Only one species in the subfamily Corynoneurinae occurred in the rice fields. This was an undescribed form in the genus *Corynoneura* and was by far the smallest chironomid encountered.

Oviposition by females of this species was not observed. Goetghebuer (1932) states that the eggs of *Corynoneura* are deposited on the surface of leaves of aquatic plants. Johannsen (1937a) describes the gelatinous egg masses as cylindrical in shape and both authors indicate that the eggs are irregularly arranged within the hyaline egg mass.

Most of the 42 adults were taken in emergence traps placed in weedy first-year fields. Only eight were from second-year fields.

Invariably the larvae were found on submerged aquatic vegetation in channels and borrow pits. Goetghebuer (1932) lists the undersides of leaves of *Nuphar* and *Potamogeton* as the microhabitat in which these larvae are frequently found and calls attention to the fact that they are often in groups in favorable locations. In the present study the free-living, extremely active larvae were readily recognized by their characteristic manner of swimming. This was a quick, jerky, shrimp-like motion in which the thoracic region was flexed, bringing the anterior and posterior ends of the larva toward each other and following which the body was straightened or extended.

Consistent with the apparent larval preference for submerged vegetation, all of the emergence traps in which this species was caught were over some form of aquatic plant material. Most of the adults emerged from masses of burhead and water nymph, but they were also taken over arrowhead, *Chara*, and *Spirogyra*. The trap sites at which *Corynoneura* occurred most frequently were in moving water, but six were in shallow, standing water. Andersen (1946) recorded *Corynoneura scutellata* in greatest numbers from the shallow waters of several east Greenland lakes.

As indicated by both Goetghebuer (1932) and Johannsen (1937a) the pupae were ensheathed in gelatinous coverings or cases which were attached to the aquatic vegetation.

Corynoneura larvae studied by Roback (1953) in the Savannah River fed almost exclusively on diatoms. In the rice fields diatoms constituted the major portion of the diet also. In addition, the larvae ate particles of disintegrated algae and other debris which characteristically accumulated on the wrinkled, submergent leaves of burhead and in the dense growth of water nymph and *Chara*.

No instances of predation or disease were noted among the larvae of *Corynoneura*. Possibly their small size and quick movements enabled them to escape from predators more easily than could the more lethargic tube-dwellers.

No other chironomid larvae were found occupying the same ecologic niche as *Corynoneura*, thus interspecific competition was not considered. Roback (1953) found several species in the same microenvironment in the Savannah

River, and this also was true in the rice fields. However, all of the other species were sedentary tube-dwelling forms which made their role in the community different from that of the active, free-living *Corynoneura* larvae.

The proportion of males to females in the number of adults which emerged during two seasons was 23 to 19. As shown in figure 183, the greater number of these was taken in 1957 for which the figures were 18 males and 13 females. In 1958 only five males and six females were taken. In both years the two sexes emerged either on the same day or within a day of each other.

The swarming habits of the males of *Corynoneura* differed from those of most other chironomids in that several swarms were seen in the daytime in bright sunlight. On July 28, 1957, at 10:15 a.m. a number of males of this species was netted from a small swarm close to the open water in Field A. In the same field on September 3, at 12:00 noon, a swarm of males was in flight in the direct sunlight over a weir box. Several of these also were taken in an aerial net.

As can be seen in figure 183, this species emerged too late in the season for the existence of two generations in the rice fields. The only first instar larva of this species ever found, however, was taken on September 4, 1958, at Trap H_1, which indicated the possibility of a second generation in the more permanent water outside the fields. Miller (1941; table 13) states that two generations of *Corynoneura celeripes* were produced in the shallower parts of Costello Lake.

The Chironominae

Tribe Chironomini. Although many different species of the subfamily Chironominae were recorded from the emergence traps in rice fields, most of them were present in small numbers.

Pseudochironomus richardsoni Malloch. The single adult female *Pseudochironomus richardsoni* which was found floating in Trap A_1 on August 16, 1957, was considered atypical for the rice field ecosystem. Johannsen (1937b) reports this species from fish ponds in Iowa. Hauber (1947), who collected the larvae in Crystal Lake, Iowa, indicates that the species is widespread in distribution but is not abundant as the other species of this genus. The trap in which the one individual was taken in Field A was in a borrow pit in which the standing water was approximately 2 feet deep. The vegetation beneath the trap consisted primarily of submerged water nymph, partly emergent water plantain, and a few rather weak rice plants.

Paralauterborniella sp. complex. Members of the genus of *Paralauterborniella* were abundant in the rice fields. This group was second highest in the number of adults taken in the emergence traps. In 1957, when the first adults trapped were identified as *Paralauterborniella subcincta*, it was believed that they all were the same species. Subsequent examination, however, has shown that at least two and possibly three forms or variants had been taken in the traps. Townes (1945) separates *Paralauterborniella* (= *Apedilum*) *subcincta* from *Paralauterborniella elachista* on the presence or absence of anal points on the male genitalia and on clear white wings as contrasted with weakly spotted wings. Figures 37, 38, and 39 show the variation in male genitalia encountered in the present study of this genus. The writer was not able to see definite spotting on the wings of *Paralauterborniella elachista*.
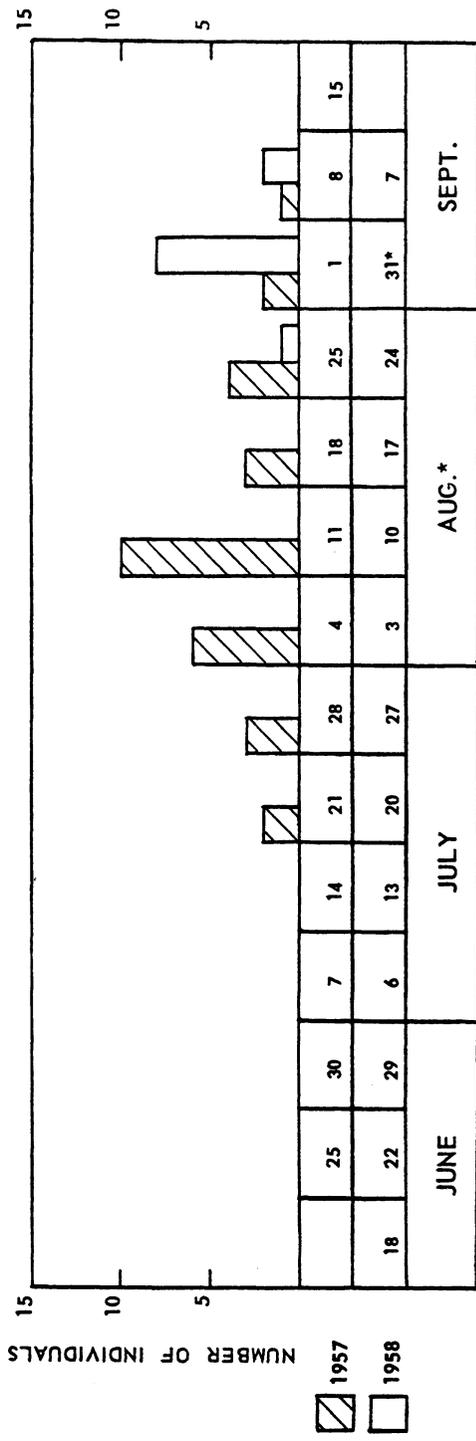
Fig. 183. Number of adult *Corynoneura* n. sp. taken weekly in 24 emergence traps in eight rice fields during two seasons.

Sublette (1960) believes this complex to be one abundant, exceedingly variable species and that the presence or absence of the anal point is due largely to differences in mounting techniques. The number of individuals reared was insufficient to indicate any clear-cut differences in the larvae and pupae, within this complex. Figures 137a, 137b, and 137c show the variations noted in the pupae of this group. Because of the uncertainty of species identity, all of the larval and emergence data have been considered at the generic level with the understanding that possibly two or more species may be involved.

Water depth and movement did not appear to be critical for the larval development. Adults were taken in traps in shady locations in the deep, cool, moving water of the borrow pits and also in shallow standing water, some of which received direct sunlight most of the day.

Over two thirds of the individuals captured were taken in emergence traps placed in first-year fields. Within a given field *Paralauterborniella* occupied all of the different habitats except that of dense rice. Most members of this group were taken in the borrow pits and in open corners of the fields probably because of the greater amount of submerged vegetation in those areas. Larvae were present on bottom debris and on the surface of the mud, but were most abundant on underwater plants. As with other chironomid larvae which inhabited this microhabitat, the surface area provided by the plants appeared to be of prime importance in determining the number of larvae present.

Paralauterborniella larvae constructed relatively short tubes of silk and bits of algal debris. Although less extensive, these cases were similar to those of the several species of *Tanytarsus* inhabiting rice fields (fig. 207). The living larvae were recognized by their relatively short, stout bodies lacking a pronounced hump or tubercle on the next to last body segment and their greenish-golden color. Usually the six segments of the antennae were difficult to see clearly because of the rapid movements of these exceedingly active larvae.

The pupation tube which was constructed by the last instar larva was a short, loosely woven pear-shaped structure open at both ends. Because of its shortness and the slight amount of algae and debris incorporated into it, the pupal chamber left the undulating *Paralauterborniella* pupa somewhat exposed at each end.

The food of *Paralauterborniella* larvae was principally diatoms, although bits of algal debris were also eaten. No instances of feeding on the leaves or stems of the higher plants were observed. In rearing dishes, and presumably in their natural habitat, the larvae did a considerable amount of feeding while actively crawling about rather than by constructing a tube and then passively feeding upon particles transported into it by water movement or by browsing around the mouth of the tube.

Although not actually observed, it is probable that the same predators and diseases acted upon the *Paralauterborniella* larvae as were observed for the genera *Cricotopus* and *Tanytarsus* which were present in the same microhabitat.

It is difficult to make any statement concerning interspecific competition with members of three genera occurring in much the same habitats, particularly since more than one species of each was present. An intensive study of the interrelationships of the larvae of those chironomids occurring on the

submergent vegetation in rice fields is necessary before drawing any conclusions as to interspecific competition.

The proportions of the sexes of the adults emerging during the two seasons were not consistent. In 1957 there were 102 females to 64 males, but in 1958 there were 145 males to 123 females. Figure 184 shows the peak emergences of the two sexes during 1957 to be at approximately the same time. At least early in 1958 the peak emergence of the males preceded that of the females (fig. 185) which agreed with the findings of Miller (1941) for chironomids emerging from the shallow waters of Costello Lake.

Since the males often swarmed during daylight hours, they were heavily preyed upon by several species of damselflies and by both cliff and barn swallows. In the evening hours the swarms were attacked by dragonflies and bats.

Most of the mating swarms in which *Paralauterborniella* was taken were mixed swarms. Frequently they were in company with *Tanytarsus viridiventris* which they resembled closely. *Tendipes tenuicaudatus, Tendipes chaetoala,* and occasionally *Cricotopus sylvestris* males were also taken together with those of *Paralauterborniella.* Swarming usually occurred close to the surface of open water, seldom higher than 5 feet above it.

Consistent with their tendency toward diurnal activity, members of this group also appeared at lights early in the evening. Table 8 shows a typical instance in which most of the *Paralauterborniella* were captured at the light shortly after sunset. It is possible that a greater sensitivity to the drop in air temperature was more responsible for decreasing the activity of this group than the changes in light intensity.

Trapping records indicated a considerable difference in emergence between the 1957 and 1958 seasons (fig. 186). The pattern of emergence for 1957 appeared to be that of a univoltine species, with the peak emergence of the one generation in the rice fields occurring approximately in the middle of the season. In 1958 the high peak early in the season together with a second peak in September suggested that two generations of this group had developed. The possibility of two species being lumped together prevents a conclusive statement as to the number of generations developed. Miller (1941; table 13) lists two species of *Chironomus* (*Lauterborniella*) which lived above the thermocline of Costello Lake and which had two generations. It is believed that probably two generations of *Paralauterborniella* do develop in permanent waters in the vicinity of the rice fields. As mentioned earlier, the winter of 1957–58 was unusually mild and wet. These climatic conditions could well have permitted rapid development and early emergence of overwintering larvae which had entered the rice fields when they were flooded early in May of 1958. This could account for the appearance of the second generation in September of 1958, but not in 1957, when lower water temperatures delayed development and prevented a second generation from emerging before the fields were drained.

Polypedilum digitifer Townes. This species was rare in the vicinity of rice fields. Apparently it seldom becomes abundant. Townes (1945) indicates a wide distributional range in his list of paratypes, but the largest series of individuals from any single locality is 6 males from Brownsville, Texas.
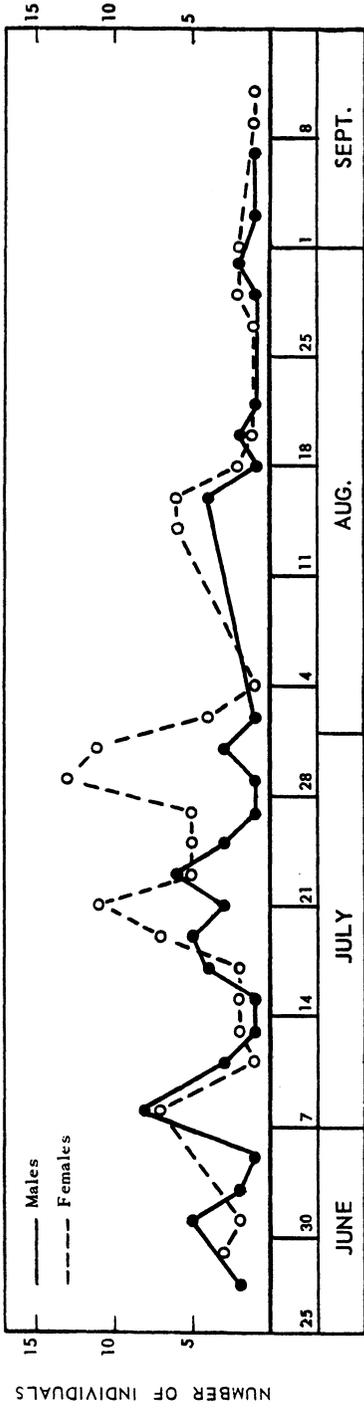
Fig. 184. Male and female *Paralauterborniella* sp. taken weekly in 12 traps in four rice fields during the 1957 season.

NUMBER OF INDIVIDUALS

35 30 25 20 15 10 5

Males
Females

18 22 | 29 6 | 13 20 27 | 3 10 17 24 | 31 7
JUNE | JULY | AUG. | SEPT.
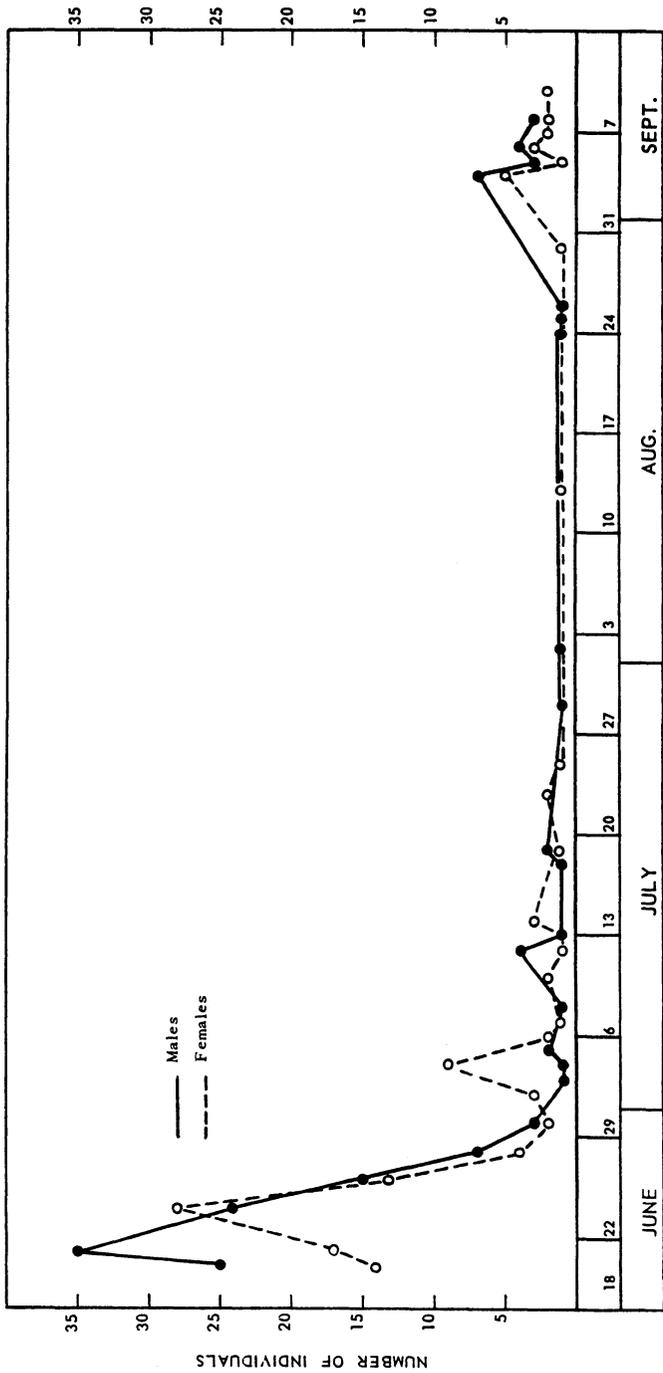
MONTH AND FIRST DAY OF TRAP WEEK

Fig. 185. Male and female *Paralauterborniella* sp. taken weekly in 12 traps in four rice fields during the 1958 season.
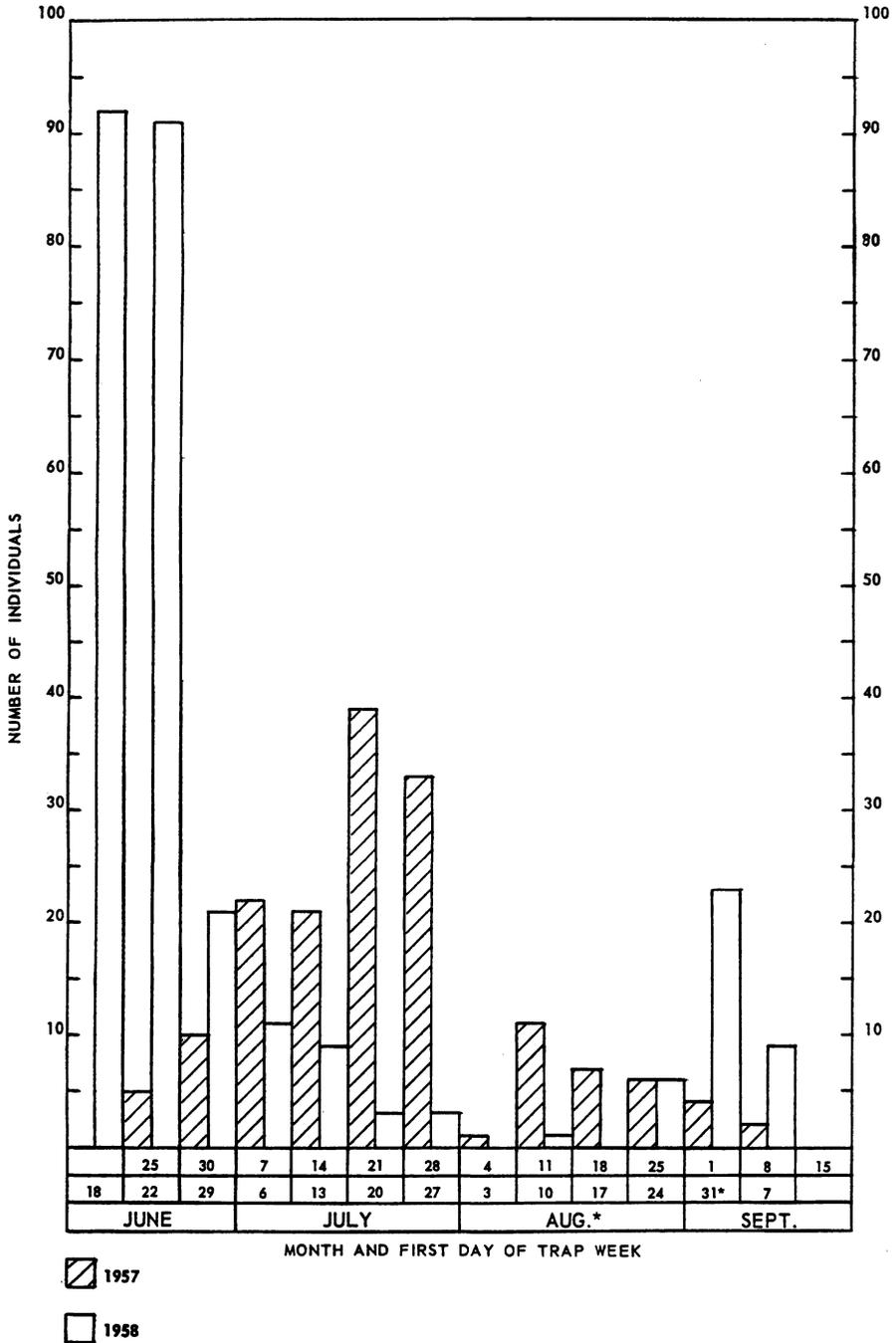
Fig. 186. Number of adult *Paralauterborniella* sp. taken weekly in 24 emergence traps in eight rice fields during two seasons.

Sublette (1960) lists only three additional individuals for California aside from those taken in the rice fields near Rio Linda, and one of those is a paratype from Bakersfield, California. In Lake Texoma of Oklahoma and Texas, however, Sublette (1957) observed that the adults of *Polypedilum digitifer* were much more numerous than *Polypedilum illinoense* and apparently had several generations per year. In that body of water the larvae occurred primarily on the sandy substratum of the shallow water near the shore line where they reached their peak in abundance in early May.

In the four years' work in rice fields during the present study only three adults of this species were taken and all were attracted to light. As no known larvae were encountered, this species could not be considered as definitely a part of the chironomid fauna of the rice fields. One male and one female were taken in 1957 and a single male was captured in 1958. On August 2, 1957, one male was taken in a light trap in operation in Field A from 8:30 p.m. until 9:30 p.m. The air temperature at 14 minutes after sunset, when the trap was started, was 84° F and by 9:30 p.m. it had dropped only two degrees. The wind was from the south with a velocity of 4 to 6 miles per hour. The single female was taken in Field C in a light trap started 32 minutes after sunset at 8:20 p.m. and run until 9:20 p.m. The air temperature when the trap was started was 71° F and 66° F at the conclusion of trapping. A south wind from 4 to 7 miles per hour was blowing. The single male taken in 1958 was from Field E. It was captured in the light trap started 20 minutes after sunset at 8:20 p.m. and run for one hour. The air temperature readings at the beginning and end of trapping were 79° F and 72° F, respectively. A slight wind from the south was blowing at a rate of 1 to 3 miles per hour.

Phaenopsectra profusa Townes. Adults of *Phaenopsectra profusa* have been collected in large numbers in Nevada and California as evidenced by the listing of the paratypes by Townes (1945). Few, however, were taken in the rice fields. One male of this species was reared from a larva taken in the mud of one of the seed dishes which had been placed in Field E on May 19 and which was removed for checking on May 26, 1958. This larva was a deep blood-red with a brown head and without ventral gills on the eleventh body segment. Soon after being placed in the rearing dish it built a tube of silk and felted algae and other debris. Then in the typical manner it began the undulating movements which brought aerated water and particles of food to it. The adult emerged on June 2, 1958, but could not free itself from the surface film and became water-soaked. It was saved as a slide mount. The other two males were taken by aerial net on August 25, 1958, in Field H near Davis. They were in flight over shallow open water protected from the wind by tall cat-tails. The wind was from the south 4 to 7 miles per hour, and the air temperature at 7:50 a.m. when these males were captured was 59° F. It was not determined why there were not more individuals of this species represented in the rice fields. The California localities given by Townes (*op. cit.*) all were colder, more highly oxygenated bodies of water than those encountered in the present study. Perhaps the lower water temperature was to some extent responsible for the isolated appearances of this species at the beginning and near the end of the rice season.

Tendipes (Tendipes) attenuatus (Walker). This is one of the best-known species of chironomids, since it is as Malloch (1915; p. 473) indicates, "Probably the commonest species of the genus." Townes (1945; p. 123) states, "The species breeds in a wide variety of lakes, ponds, rivers and streams and is the most abundant and widespread of our larger tendipedids." It was one of the few species whose larvae were found in the organic material of sewage oxidation ponds near Concord, California, by Usinger and Kellen (1955).

Under the name of *Tendipes decorus* Johannsen (1905), information concerning this species has appeared in many publications. Upon examining the type specimen in the Natural History Museum of London, Townes (1959) has synonymized *Tendipes decorus* with *(Chironomus) Tendipes attenuatus* Walker (1848).

Egg deposition by females of this species was not observed during this investigation. Two descriptions of the process indicate considerable variability. Ping (1917) noted that the egg mass was first deposited on the hind femora of the females where it was held for two or three minutes before being thrown down into the water. Females of *Tendipes attenuatus* (= *Chironomus cayugae* Johannsen) observed by Leathers (1922) alighted on small stones and thrust their abdomens into the water to attach their egg masses to submerged material.

As indicated earlier the egg masses of this species are variable in form. One taken on June 24, 1958, in Trap E together with several females of *Tendipes attenuatus* is pictured in figure 187. The narrowly elliptical eggs were located in the periphery of the mass with their long axes directed toward the center of the fig-shaped gelatinous envelope.

The difference in depth and the degree of movement of the water in the various parts of the rice fields had no apparent influence on the presence,
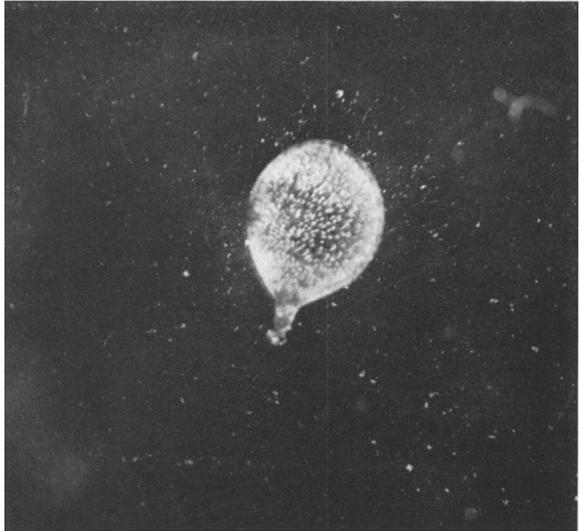

Fig. 187. Egg mass of *Tendipes attenuatus* (Walker), × 4.

absence, or abundance of larvae of *Tendipes attenuatus*. This agreed with the findings of Johannsen (1937b) who found the larvae common in various shallow ponds and streams in New York. Sublette (1957), in his study of the bottom fauna in Lake Texoma, observed that this species showed the least depth preference of any of the chironomids occurring in that body of water.

Early in the season, before the rice plants had emerged from the water, the numbers of larvae present in first-year and second-year fields were approximately the same. The environmental factor responsible for a greater number in any one field than in another appeared to be soil fertility. The larvae were especially abundant in those fields in which a dense cover crop had been plowed under prior to flooding and which was in the process of decay. Later in the season, as shown by table 7, the emergence of the adult midges was much greater from first-year fields than from the older fields. This is believed due directly to the difference in fertility between the new and old fields.

Within a rice field the larvae were widely distributed and were found wherever the substrate was of the proper consistency. This was one of the few species taken in emergence traps placed in dense rice growing in shallow standing water. The larvae were encountered in vegetation only when rooted plants carrying mud were pulled up from the bottom. Most of them inhabited the fine silty ooze forming the surface and upper 2 inches of the bottom. Few were taken in samples of coarser bottom material of rough sand and clods, and apparently none could penetrate the congealed rubbery adobe soil approximately 4 inches below the surface. The dependence of larval abundance on the type of bottom material present in various parts of the rice fields agreed with the finding of Sublette (1957) who noted that in Lake Texoma the larvae of this species were restricted to bottom areas of mud and sandy silt.

Tendipes attenuatus larvae both in rearing dishes and in the rice fields built silken tubes, the walls of which were heavily reinforced with bits of debris and algae. Most of the feeding was done inside these cases. It was not determined whether or not a filter-feeding net such as that described by Walshe (1947a and 1951b) was used by these larvae.

The structure of the pupal case spun by the last larval instar was not greatly different from the earlier larval tubes. It usually was somewhat shorter than the tubes of earlier instars and was enlarged at the anterior end.

The food of the larvae in the rice fields consisted of diatoms, algal debris, and other settled plankton particles forming the bottom ooze-film. It was not determined what proportion was eaten directly from the bottom by the larvae feeding around the mouth of their tubes and how much was carried into the tubes with the water currents created by the undulating movements of the larvae. Leathers (1922) found that the larvae which he studied in New York actually ate the material from the inner surface of their tubes, and expressed doubt that the larval undulating current brought much food into the tube. He observed that the greatest concentration of these larvae was correlated with the abundance of food consisting of diatoms and decaying grain. In Cedar Bog Lake of Minnesota, Lindeman (1941) considered these tube-dwelling larvae as primary browsers of the bottom ooze layer. Roback (1953) found only fine debris and sand in the intestines of larvae of *Tendipes attenuatus* from the Savannah River. Evidence that the larvae can thrive on food items

other than typical bottom material is provided by Tilbury (1913) who reared them using only finely ground leaves of the pondweed *Potamogeton* for food, and by Ping (1917) who fed larvae of this species *Spirogyra* in addition to finely ground leaves of *Elodea* and *Potamogeton*. Since diatoms were prominent in the food of these larvae in the present study, it would be of value to know if there was any correlation between the decaying cover crop of some of these rice fields and a greater amount of these microscopic plants. In the 1958 season when 187 adults were taken in the emergence traps, 93 were from Field G which had the heaviest cover crop, and 91 were from Field E, the next most fertile field. In several papers, Walshe (1948, 1950, and 1951a) and Ewer (1942) have pointed out that those species having blood pigment appear better able to survive anaerobic conditions than species without it. Further study should be conducted in the rice fields to determine whether it was an oxygen deficiency caused by the rotting vegetation which enabled *Tendipes attenuatus* larvae to gain a numerical advantage over other species in these fields or whether it was an increased food supply which was responsible. Lack of time prevented such an investigation by the writer.

Tendipes attenuatus is attacked by predators, parasites, and diseases in all of its life history stages. Few egg masses were seen in the rice fields, but Ping (1917) noted that often the fertilized eggs of this species were infested by a fungus disease which destroyed them.

The larvae of this species were eaten by many different predators in the rice fields. Some of the more important natural enemies were carp, dragonfly naiads, and both larvae and adult hydrophilid and dytiscid beetles. On June 18, 1958, at 9:45 a.m. a hydrophilid larva was observed feeding on a *Tendipes attenuatus* larva in Field G. The hydrophilid larva consumed the blood worm head first and continued forcing its prey into its foregut even when captured by the writer and held out of the water. Occasionally fungus growths were noted on the heads of larvae. On some larvae being reared these became dense enough to prevent feeding and to weaken them so that they failed to develop beyond the pupal stage.

Ectoparasites in the form of water mites apparently often attacked the pupae of this species because a number of newly emerged adults were observed to be mite-infested. Dr. Rodger Mitchell of the Department of Biology, University of Florida, identified specimens of these mites as either the family Pionidae or Arrenuridae. The mites remained on the adults attached to the intersegmental membranes of the abdomen and probably returned to the water upon the death of the midge.

The number of males of *Tendipes attenuatus* taken in emergence traps was much greater than that of the females. In 1957 when only 14 individuals were caught, there were nine males and five females. In 1958 there were 114 males to 73 females. Figure 188 shows that the peak emergence of the females instead of following that of the males actually was slightly ahead of it in 1958.

Swarming of the males of this species was observed several times in the rice fields. They were encountered only in the evening at sunset or slightly later. Perhaps early evening swarming and activity were the reasons why these large midges were among the first to appear when the light trap was started. Although some also were taken later in the evening, the majority were
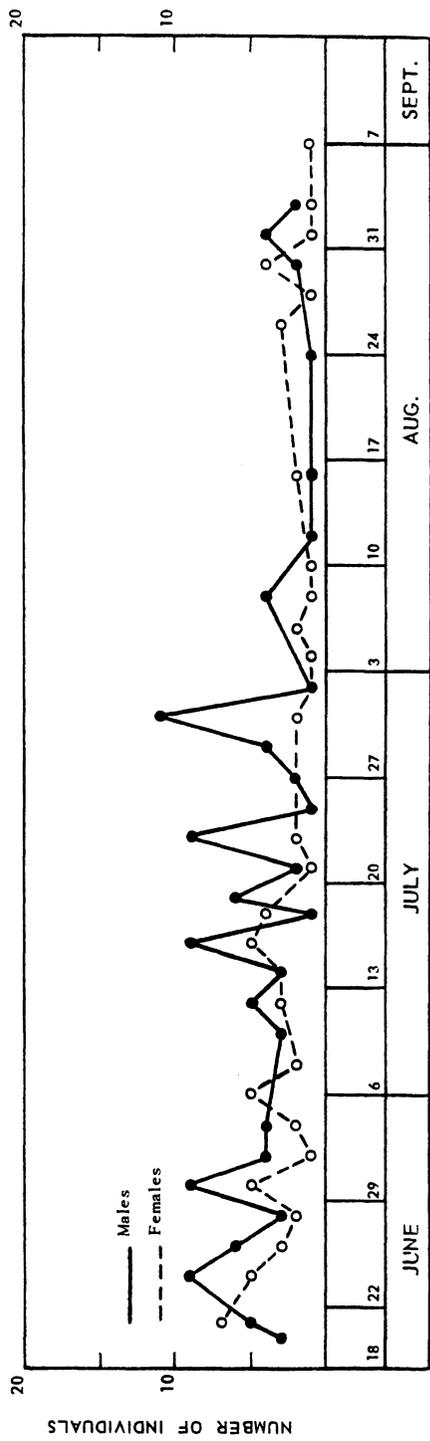
Fig. 188. Male and female *Tendipes attenuatus* taken weekly in 12 traps in four rice fields during the 1958 season.

captured shortly after sunset (table 8). Warm nights with temperatures of 80° F or above and without wind were optimum for the formation of large swarms of males. However, this species appeared to be more tolerant of wind than the smaller forms.

It was difficult to understand why only 14 individuals of such a common species were taken in the emergence traps during the 1957 season (fig. 189). Even if most of the adults had emerged prior to June 25 when the traps were placed in the field, later developing larvae should have accounted for more individuals than were taken. In 1958 most of the adults had emerged by the second week of July which was the time of peak emergence. Because the fields were drained early in September, there was no opportunity for a second generation to develop in the rice field. It is probable that there were two generations in the canals and ditches with permanent water. Miller (1941; table 12) indicates, however, that this species has but a single generation per summer in Costello Lake. In Cedar Bog Lake of Minnesota, Lindeman (1942a) found *Tendipes attenuatus* developing three generations per year. Thus it appears that the number of generations of this species which emerge each year is dependent upon the environment in which the larvae develop instead of being genetically fixed.

Tendipes (Tendipes) plumosus (L.). This species, the largest of the chironomids, was poorly represented in the rice fields. No larvae known to be of this species were taken from the fields and only three adults were captured in emergence traps. The fact that these three individuals were taken within two days of one another, and all in Field G, indicated an accidental establishment of a small population of larvae. Either a number of them were carried in with the water or a few eggs were deposited by a female which had emerged from the canal approximately one-half mile south of the field. This large canal had water in it throughout the year and *Tendipes plumosus* was known to breed in it.

The habitat of the rice field from which two adult males emerged on July 23, 1958, was shallow standing water near clumps of tall watergrass. A single female emerged on July 25, 1958, from the slow-moving water of the borrow pit. Under both traps the substrate was fine silty mud containing an abundance of decaying vegetation. As Mundie (1957) indicates, this species is generally considered most tolerant of anaerobic conditions and possibly this may explain its appearance in the field containing the greatest amount of decaying material.

More literature has been published concerning *Tendipes plumosus* than any other chironomid due to its large size and the fact that it is common both in Europe and North America. Townes (1945) indicates that this species normally breeds in larger rivers and eutrophic lakes and the larvae inhabit the soft mud usually at depths of 6 to 20 meters. According to Johnson and Munger (1930) two generations of adults emerged each year from the shallower water of Lake Pepin between Minnesota and Wisconsin. Lindeman (1942a) recorded three generations in the shallow Cedar Bog Lake. In water of greater depth, however, Mundie (1957) states that there is only a single generation.
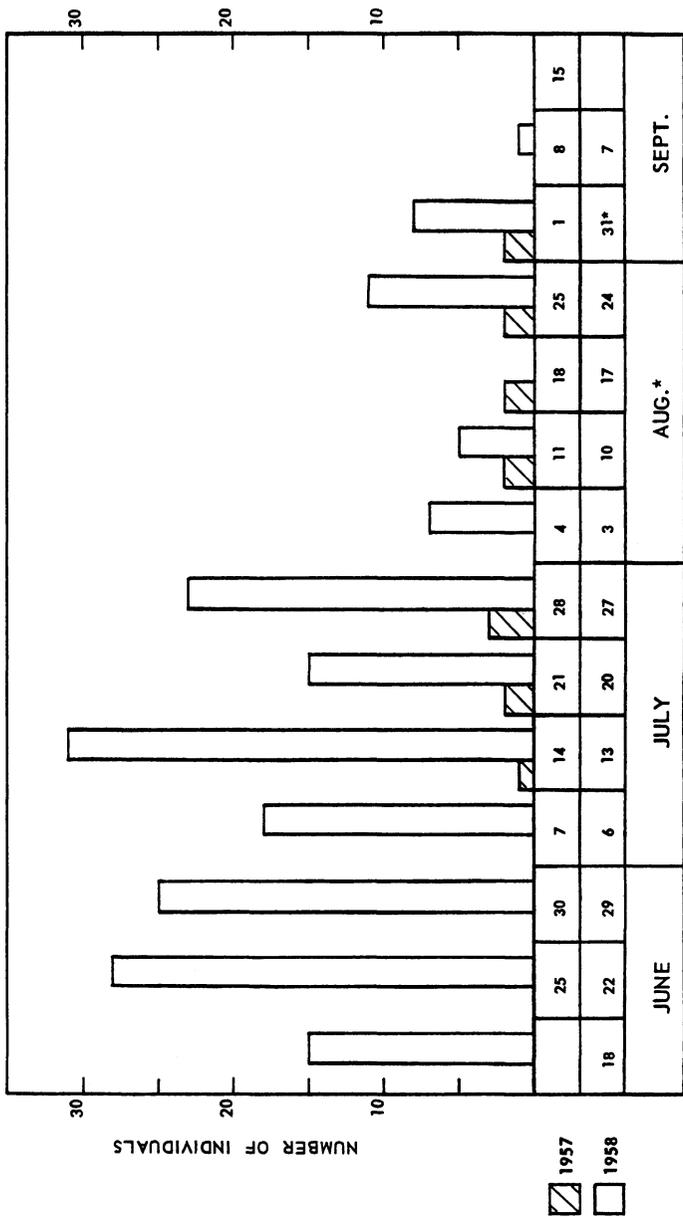
Fig. 189. Number of adult *Tendipes attenuatus* taken weekly in 24 emergence traps in eight rice fields during two seasons.

The relatively shallow water of rice fields and their temporary nature make it unlikely that this large species would ever become established in comparable numbers to those found in deeper permanent bodies of water.

Tendipes (Endochironomus) nigricans (Johannsen). This species probably was a fortuitous or chance inhabitant of rice fields. Although no adult was found, the presence of an empty pupal exuvia definitely identified indicated that an individual of this species had emerged from Field C on September 11, 1957. The emergence trap in which the pupal exuvia was found was in shallow standing water over clover fern and extremely sparse rice. Berg (1950) in a detailed discussion of the feeding habits of *Tendipes nigricans* larvae describes the leaf damage which they caused by feeding on *Potamogeton*. No evidence of such feeding was noted on the aquatic vegetation under or near the emergence trap which contained the pupal exuvia, thus this was judged to be an isolated individual which happened to get into this field from nearby more permanent water.

The only other member of this species which was captured in a rice field was a male which was taken at a light in Field A on July 16, 1957. The air temperature was 83° F and there was a southerly breeze of less than 1 mile per hour blowing. This individual was taken in an aerial net while in flight about the light trap.

Several adults were successfully reared from larvae taken in a large canal at the south edge of Field C. All of these larvae were inside common tule stems which were floating in the canal. However, not all of the floating stems contained larvae. There appeared to be certain necessary qualities which were observed consistently enough to predict the stalks in which larvae could be found. These must have been decayed and water-soaked to such an extent that if picked up by one end, they bent or broke of their own weight, yet they must have held enough air in the empty cells to cause them to float. The larvae had either gnawed through the softened epidermis or into the ends of these stems and had cleaned out spaces in which they constructed their silken galleries. Some food in the form of microscopic algae may have been carried into these cases by the water, but the digestive tracts of most of the larvae were full of bits of decayed tule stem and debris.

Tendipes nigricans larvae were taken in these stems from November to the middle of May, indicating that in California they overwinter in this microhabitat. Lindeman (1941) pointed out that this species may overwinter in the egg stage in Cedar Bog Lake of Minnesota. Berg (1950) believed, however, that in Third Sister Lake the larvae spent the winter under the ice.

Tendipes (Dicrotendipes) californicus (Johannsen). Adults of this species were taken in the rice fields in small numbers. It appeared to be a species which was fairly widespread, but not abundant anywhere.

Oviposition was not observed, and no eggs known to be those of this species were seen.

Of the 11 adults taken in the emergence traps in two years, eight were from first-year fields and only three from second-year fields.

Water depth and movement appeared to have slight direct effect upon the distribution of the larvae. They were found in shallow standing water as well as in the deeper moving water. Larvae were taken both in mud samples and on

submerged vegetation, but their presence was unpredictable. In late May and early June most of them were found on the surface of the mud, but as the submerged vegetation increased, it became the favored habitat. Most of the larvae were obtained from water nymph and the submerged ribbon-like leaves of burhead, but they were likely to be encountered on any aquatic vegetation which was coated with diatoms and algal debris. All of the emergence traps in which the adults of this species were taken were placed over some species of aquatic plant which was covered with periphyton.

The larvae constructed thick-walled algal tubes similar to those of *Tendipes decorus.* In contrast to the linear or parallel-sided larval cases, the pupation tube built by the last larval instar was fusiform or spindle-shaped in general outline.

Examination of the contents of the digestive tracts of a number of larvae showed that their food consisted of diatoms and bits of algal debris.

Because of the small population of this species in the rice fields, many questions concerning its ecology were unanswered.

Of the adults taken in the emergence traps, the males outnumbered the females five to three in 1957 and two to one in 1958. The emergences were too sporadic and widely separated to give the true conditions which must have existed for the species to survive.

As can be seen from figure 190, the emergence of the adults was distributed throughout the season with the third week of August showing the largest number of emergences. Probably only a single complete generation developed in one season.

Data from light trapping indicated the same sporadic appearance of adults in 1957 and their extreme scarcity in 1958. In 1957, *Tendipes californicus* was taken on only five nights out of twelve that the light trap was operated. These were: June 20 (one male and five females); August 2 (one male and one female; table 8); August 10 (two males); September 3 (one female); and September 8 (one male and four females). In 1958 the light trap was run on five nights from June 28 to August 31, but no *Tendipes californicus* were captured.

Tendipes (Dicrotendipes) modestus (Say). Only one male *Tendipes modestus* was taken from the rice fields. This individual emerged in Field C on July 21, 1957. It was taken from moving water over *Spirogyra* and water nymph. No statement concerning the habits of the immature stages in the rice fields can be made since no adults were successfully reared. In Iowa, Hauber and Morrissey (1945) found that this species bred in clear, shallow ponds or in shallow protected portions of streams where floating algae occurred. Muttkowski (1918) noted that *Tendipes modestus* was not an abundant species in Lake Mendota but was present in sandy bottom material. The adults apparently emerge early in the season for Bill (1932) recorded swarming males during the first week in May. No swarms of this species were seen during the present study.

Tendipes (Dicrotendipes) nervosus (Staeger). This species was represented in the rice fields by two individuals. A single male was taken on September 3, 1957, in Field C and another male was captured July 21, 1958, in Field G. These were both taken in moving water over submerged vegetation
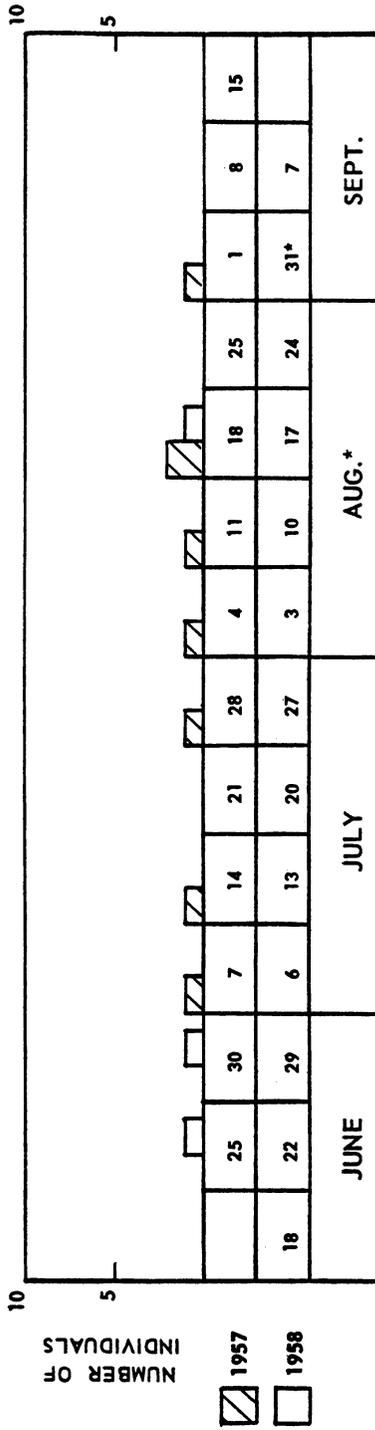
Fig. 190. Number of adult *Tendipes californicus* taken weekly in 24 emergence traps in eight rice fields during two seasons.

consisting of *Spirogyra,* some water nymph, and young arrowhead plants. A third representative of this species was captured in a light trap in Field A on June 20, 1957. This individual was an intersex which according to Dr. James E. Sublette[18] apparently had been parasitized by a merminthid nematode. A similar production of intersexes in *Chironomus plumosus* caused by parasitic nematodes of the genus *Parameris* was reported by Phillipp (1936).

No known larvae of this species were encountered, but the taking of the two newly emerged adults over aquatic vegetation agreed with the findings of Fellton (1940) that the larvae were almost restricted to green algal mats.

More study of the larval and pupal stages of the three species of the sub-genus *Dicrotendipes* is necessary, especially where they occur together, in order to be able to make accurate statements concerning their biology.

Tendipes (Cryptochironomus) chaetoala Sublette. Although *Tendipes chaetoala* bred in the rice fields and was often encountered, it was never abundant. The larvae were particularly difficult to find and only two were reared through to the adult stage. However, an examination of the emergence trap sites in which adults of this species were taken indicated a fairly wide distribution of the larvae. Most of the adults developed in the deeper moving water of the borrow pits, yet there were two examples from shallow, slow-moving or standing water.

This species appeared to be particularly well-established in the older fields. Of the 13 adults taken in emergence traps, 9 were from second-year fields and 4 from first-year fields. Results from light trapping also showed that *Tendipes chaetoala* was prominent in the chironomid fauna of older fields. The relatively large number of adults taken from Field H near Davis on August 4, 1958, was indicative of the apparent preference for this type of field.

Within the field this species was never encountered in dense rice, but was found in almost all other habitat types provided that some form of submerged vegetation was present. The plant species with which these larvae were most often associated were burhead, water nymph, and grass wrack. Larvae were found on all parts of these plants, but most were taken on the wrinkled, sub-merged leaves of burhead.

The larvae were tube dwellers and constructed somewhat loose, transparent silken tubes similar to those of the genus *Cricotopus*. In the rearing dishes, the larvae tended to move about outside of their tubes more than did most other tube-dwelling forms. The pupation tube constructed by the last larval instar as shown in figure 191 was roughly wedge-shaped. It was open at both ends and had masses of algal material adhering to it. The algae and debris had not been felted and woven directly into the walls of the pupal case as was done by some other *Tendipes* larvae.

Although not observed, it was believed that the larvae of this species were predatory feeders as well as browsers of periphyton. The basis for this was the close similarity of mouth parts of these larvae and those of *Tendipes tenuicaudatus* which will be discussed later. Since this was a tube-dwelling species, however, the diatoms and particles of algae observed in the alimentary

[18] Personal correspondence.

tracts of these larvae probably represented actual food eaten directly rather than that taken indirectly when eating their prey.

The attraction of the adults of *Tendipes chaetoala* to light indicated that they were active in the evening, but the only swarms observed were those seen in the morning hours. These were all small groups over open moving water of the channels and borrow pits. Usually they were mixed and included males of *Tanytarsus viridiventris* and *Tendipes tenuicaudatus*.

Although probably not typical of the actual proportion of the sexes of this species in the rice fields, the two seasons of emergence trapping showed nine females to only four males. As shown in figure 192 the adults emerged from the first week of July until the third week of September. Thus it is probable that only a single generation of this species was able to develop during one rice season.

Tendipes (Cryptochironomus) darbyi Sublette. This was an uncommon species. No known larvae were taken in the four years that the study was in progress. The four different emergence trap locations at which adults of this species were taken were all in the deeper water of the borrow pits. On July 21, 1958, however, a pupa believed to be that of *Tendipes darbyi* was found in an emergence trap in shallow water near a check bank in Field E. This trap was in total shade under a dense clump of watergrass.

All of the adults except one were taken from standing water. A single adult male captured on July 23, 1958, emerged from swiftly flowing water below a weir box in Field F. This individual was unable to completely free itself from the pupal exuvia and became water-soaked. It was mounted on a slide and the pupa of this species was associated with the adult on the basis of the
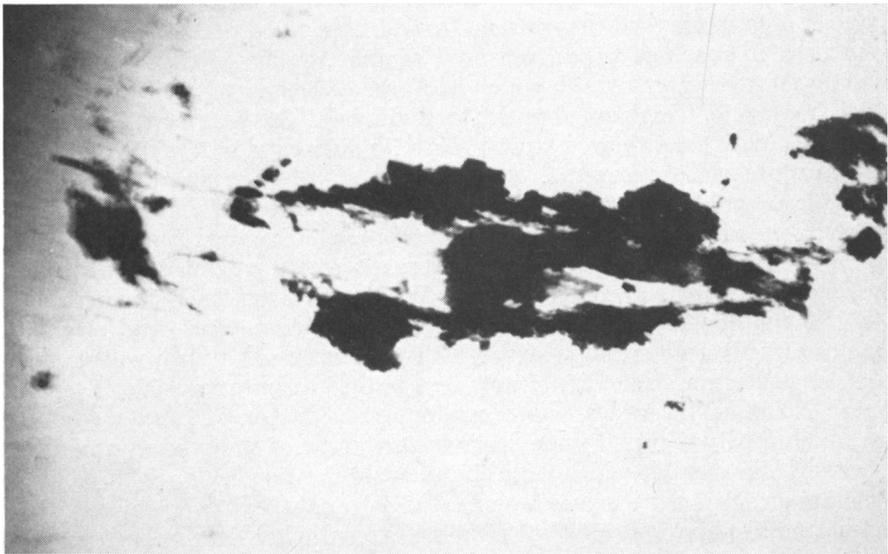

Fig. 191. Pupa of *Tendipes (Crytochironomus) chaetoala* Sublette in its short, silken pupation tube, × 12.5. Note mass of algae near right margin, which was dislodged from posterior end of the case by movement of anal fins.

unusual thoracic respiratory organs and conspicuous spines of the abdominal tergites of this damaged pupal exuvia. The pupa of this species matched closely the description incorrectly applied to the species *Tendipes* (= *Chironomus*) *fulvus* by Johannsen (1905; p. 224) and which Townes (1945) states should have been *Tendipes* (= *Harnischia*) *emorsa*.

Three adults were taken in first-year fields and three were from second-year fields. The microhabitat beneath the emergence traps in which this species was taken varied. Most individuals were trapped over a dense growth of water nymph and burhead, and all except one over some form of submerged vegetation. This exception was from the moving water of Field F over only the mud substrate.

Of the six adults captured in emergence traps, five were males and one was a female. The number of generations per season could not be determined because of the small number of adults which emerged in the traps. The first emergence recorded was on June 29 and the last of the season was on September 5.

Tendipes (Cryptochironomus) fulvus (Johannsen). This species was a proven resident of the rice fields but as with other related species it never developed large numbers of individuals. Most of the larvae occurred in deep standing or slowly moving water, but they were also present in the faster flowing waters and in shallow areas.

Seven of the 11 adults taken in the emergence traps were from first-year fields and three adults and a mature pupa were from second-year fields. Many of the emergence traps in which this species was captured were over plants, but it is believed that the larvae were actually in the ooze layer on the mud surface under the plants. This statement is based on the fact that six of the individuals trapped during the two seasons were from the mud substrate without any submerged vegetation. In addition, most of the larvae which were used in rearings were from mud samples. A few also were found in densely matted water nymph which had become coated with silt and brown algal fragments. This agreed with the findings of Sublette (1957) that the larvae of this species showed a preference for silty sand on the bottom of the littoral zones of Lake Texoma.

As far as could be determined from the single successful rearing and from observations of other larvae of this species in the laboratory, *Tendipes fulvus* larvae are free-living predators. They were often seen moving easily through the algae and debris in search of food. Wirth and Stone in Usinger (1956) state that most members of this genus (*Cryptochironomus*) feed on oligochaetes as well as other midge larvae. This was confirmed in the present study when oligochaete worms were clearly seen in the alimentary canals of several larvae. No midge larvae were noted among the food items of *Tendipes fulvus*, but undoubtedly they fed upon early instar larvae of *Tanytarsus* and other species of chironomids which were abundant in the rice fields.

Although the mature larvae became sluggish at the onset of pupation, they did not build pupation cases but remained free during the pupal stage. The length of the pupal stage was three days. None of the pupae examined in the present study agreed entirely in form with the characteristics given by Roback (1957) and implied by Johannsen (1937b; p. 39). However, the
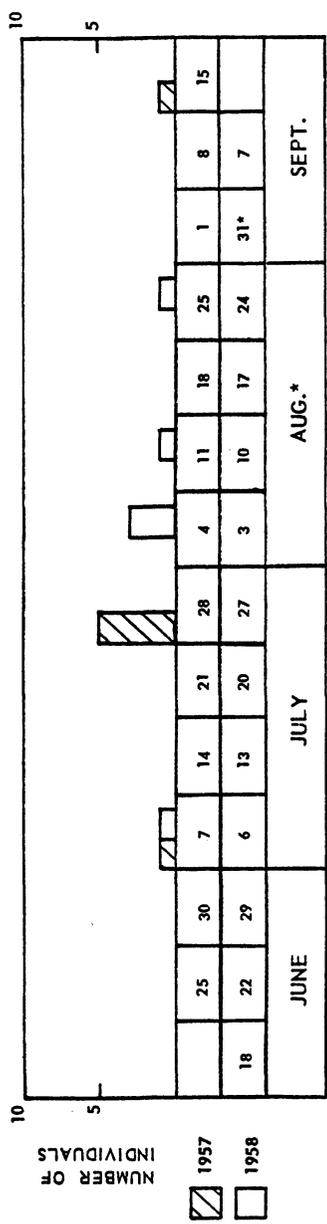
Fig. 192. Number of adult *Tendipes (Cryptochironomus) chaetoala* taken weekly in 24 emergence traps in eight rice fields during two seasons.
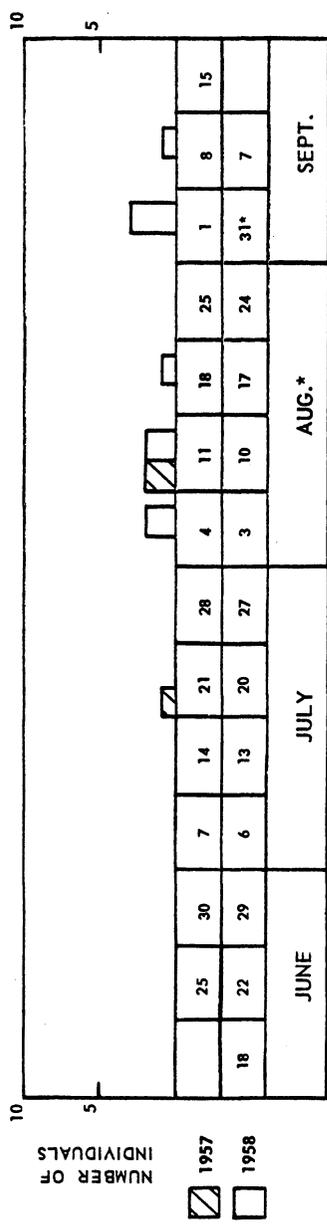

Fig. 193. Number of adult *Tendipes (Cryptochironomus) fulvus* taken weekly in 24 emergence traps in eight rice fields during two seasons.

genitalia of the adult males associated with these pupal exuviae were those of typical *Tendipes fulvus*. Instead of the elongate, cap-like cephalic tubercles as illustrated by Roback (1957; Plate 16, No. 348), the pupae in the present study had large, antler-like cephalic tubercles (fig. 122).

More adult males of this species were taken than females. In 1957, when only three individuals were taken, there were two males and one female. In 1958, six males and two females were taken. The sex of one pupa obtained was not determined.

The adults were readily attracted to light and as shown in table 8, they were active during the later hours as well as shortly after sunset. The adult males swarmed in the evening and in the morning, but appeared more sensitive to the wind than most other large midges. No large swarms were seen. Most contained from 20 to 30 individuals and usually were observed in protected areas, low over the water or on the leeward side of an old building.

As can be seen in figure 193 this species was late in emerging from the rice field, with the first record the third week in July. This late development would indicate that only one generation of this species developed during a rice season. Sublette (1957) noted that the adults emerged from Lake Texoma much earlier. He recorded them from May 4 to September 1.

Tendipes (Cryptochironomus) frequens (Johannsen). This species was not known definitely to be an inhabitant of the rice fields. It was somewhat surprising in view of the number of adults captured in and near the fields that no individuals actually were ever recorded from them. Occasional swarms of adults were seen over the open water of the rice checks both in the morning and evening throughout most of the summer.

The earliest record for this species was June 21, 1957, when several were taken in a light trap placed in Field A. During both 1957 and 1958 seasons most of the adults were observed during the second and third weeks of August. September 3, 1957, was the latest date of the season that they were seen. Many more were observed in 1957 than in 1958.

In 1957 this species was encountered in two of the first-year fields and one second-year field. In 1958 it was taken only in Field E, a first-year field.

Tendipes frequens usually was taken in mixed swarms with *Tendipes tenuicaudatus, Tendipes chaetoala,* and *Tendipes fulvus*. Occasionally they were found with *Cricotopus sylvestris* and *Cricotopus bicinctus* males.

Tendipes (Cryptochironomus) monochromus van der Wulp. Only two individuals correctly identified as this species were known to be actually from the rice fields. Probably there were others present, particularly females, which were incorrectly placed with *Tendipes tenuicaudatus*. These two species were extremely difficult to distinguish from each other. *Tendipes tenuicaudatus* was one of the more abundant species, whereas *Tendipes monochromus* was seldom encountered. Therefore, it is probable that misidentification errors favored the former species.

Oviposition by the females of this species was not observed in the present study nor were any egg masses found which could be associated with it. A fairly detailed description of the egg-laying process of this species is given by Fellton (1940) who has, according to Townes (1945), confused it with *Tendipes tenuicaudatus*. Fellton describes the egg masses as cylindrical in

shape and points out that the brownish eggs are arranged in a definite pattern.

No known larvae of this species were ever taken in the rice fields, and the larval and pupal stages were not successfully associated with the adult in the present investigation. Sublette (1957) was able to identify both the larvae and pupae of this species with the adults emerging from Lake Texoma and has indicated the differences between the immatures of this species and those of *Tendipes tenuicaudatus*. On the basis of the structure of the mouth parts and the wide range of distribution of the larvae, he believes *Tendipes monochromus* to be predatory in feeding habits. In the man-made lakes of New York City, Fellton (1940) observed that the larvae of this species were tube dwellers which were found in dense algae in the shallow portions of the lakes.

The preference by the larvae for submerged vegetation also was indicated in the rice fields. The two males captured in emergence traps were both from Field E in which no herbicide had been applied, hence there were large quantities of water weeds in the channels and borrow pits. The emergence traps in which these individuals were taken were over moving, deep, cool water containing the submerged leaves of burhead and arrowhead.

These two emergences occurred on widely separated dates, the first on June 30 and the other on September 11, 1958. A third male was taken by aerial net in Field E from a mixed mating swarm with *Tendipes tenuicaudatus* at 7:45 p.m. on August 21, 1958.

Tendipes (Cryptochironomus) tenuicaudatus (Malloch). This was one of the more abundant species of chironomids in the rice fields. As mentioned earlier the number of individuals recorded for this species may be higher than it should have been due to misidentification of some individuals of *Tendipes monochromus*.

Although no observations of egg masses or of oviposition were made in this investigation, it is probable that this phase of the life history of *Tendipes tenuicaudatus* is similar to that described by Fellton (1940) for *Tendipes monochromus*.

Water depth and movement appeared to be of little significance in the development of the larvae. They were taken more often in the deeper moving water of the borrow pits, but that was probably due more to the presence of plant material than to the water conditions, since several individuals were taken in the shallow standing water of Field F in the direct sunlight.

As can be seen in table 7 this species was one which was more abundant in second-year or older fields than in first-year fields. Within the field it was encountered in a variety of situations but always on some form of submerged vegetation. *Tendipes tenuicaudatus* was never recorded from a mud substrate devoid of plants.

Before discussing the ecological characteristics of the larvae, it should be pointed out that the labial plate of the individuals reared through to the adult stage in the present investigation (fig. 87) is unlike that illustrated for this species by Roback (1957; Plate 15; No. 329).

Tendipes tenuicaudatus larvae were not easily found. They seemed to be much less abundant than the number of adults emerging would indicate. They were never encountered in groups or concentrations as were some of

the other chironomid larvae. Solitary larvae were taken on a wide variety of submerged aquatic plants. Because of their tube-dwelling habits, they were more likely to be present on water nymph, grass wrack, *Chara*, or the ribbon-like leaves of burhead, all of which provided the maximum amount of surface area. In a study of the relationships of insects to aquatic plants in Michigan, McGaha (1952) records the larvae of this species on the submerged stems and leaves of *Myriophyllum exalbescens* which also is filamentous and much branched.

The silken larval tubes were transparent, loosely woven galleries similar to those of *Tendipes chaetoala* and the larvae of the genus *Cricotopus*. The pupation tubes were the same as those of *Tendipes chaetoala* (fig. 191).

Although the presence of diatoms and algal debris in the alimentary tracts of these larvae indicated that they were plant feeders, there was evidence in the present study that they also were predaceous. On August 2, 1958, upon placing a *Tendipes tenuicaudatus* larva in a rearing dish, it was observed that a fairly large oligochaete worm was working in the algae which was to serve as food for the chironomid larva. In attempting to remove it from the dish, the writer cut the worm in two. In a matter of seconds the midge larva had seized the wriggling anterior one third of the worm and swallowed it. Within four minutes it had eaten the posterior two thirds of the oligochaete. Although never observed feeding upon other chironomid larvae, the solitary nature of *Tendipes tenuicaudatus* was indicative of predatory food habits. Since young tube-dwelling larvae of several species of chironomids were abundant in the same microhabitat as *Tendipes tenuicaudatus*, it is probable that they constituted some of its food.

Attempts to rear *Tendipes tenuicaudatus* also contributed information concerning one of their natural enemies. On September 2, 1958, a fourth instar larva which had been placed in a rearing dish the night before was killed and eaten by a flatworm which somewhat resembled *Dugesia*.

Males and females were taken in the emergence traps in approximately equal numbers. In 1957 there were 19 males and 22 females and in 1958 there were 37 males and 31 females. Figures 194 and 195 show that the males emerged earlier than the females. In 1958 the peak emergence of the males on July 2 was four days ahead of that of the females.

Tendipes tenuicaudatus was one of the species most frequently seen swarming in the rice fields. The swarms seldom consisted of this species alone, but usually contained males of *Tanytarsus viridiventris*, *Tendipes chaetoala*, and *Tendipes frequens* as well. These were small groups which hovered over the weir boxes or open water in the corners of the checks. Most of the swarms were observed in the morning. However, the adults also were active in the evening as evidenced by the number taken at the light trap. Table 8 shows that more were attracted to light during the later hours than immediately after sunset. It is possible that this species was more tolerant of wind and lower air temperature than other midges.

Adults of this species emerged throughout most of the rice-growing season from June 18 until the second week of September (fig. 196). The emergence data from the 1958 season indicated that two generations would have developed had the season been extended. This did not happen, however, be-
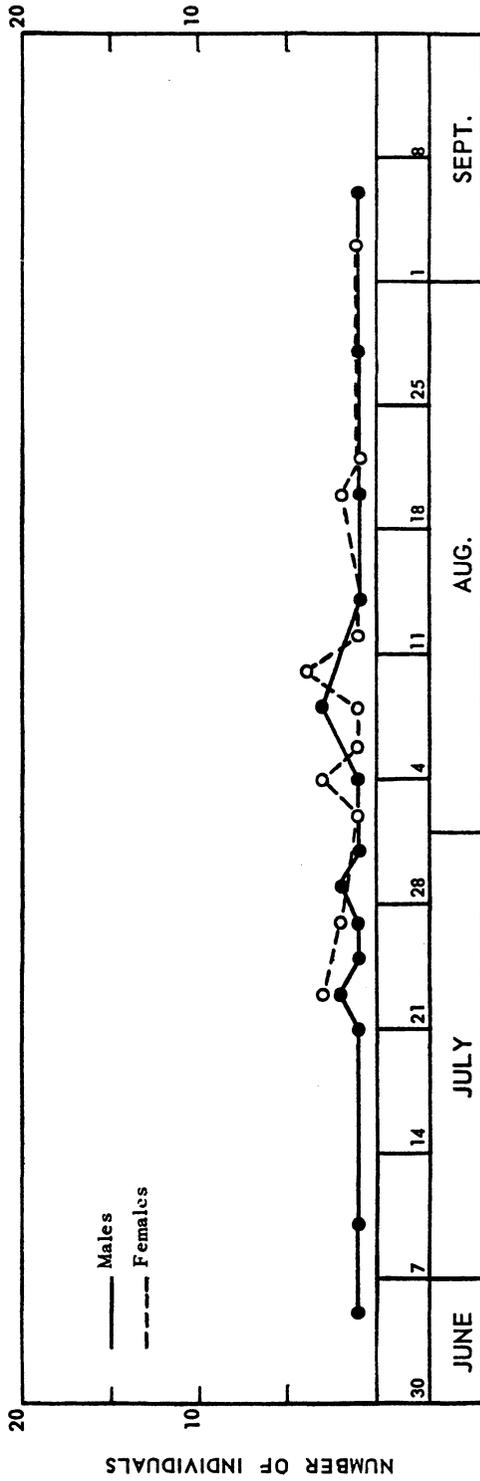
Fig. 194. Male and female *Tendipes* (*Cryptochironomus*) *tenuicaudatus* taken weekly in 12 traps in four rice fields during the 1957 season.
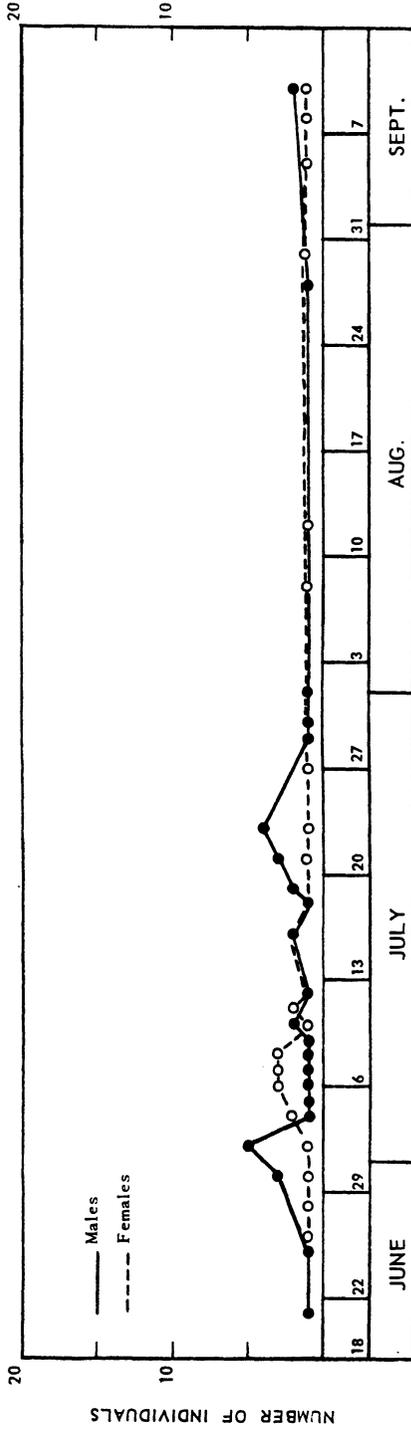
Fig. 195. Male and female *Tendipes* (*Cryptochironomus*) *tenuicaudatus* taken weekly in 12 traps in four rice fields during the 1958 season.
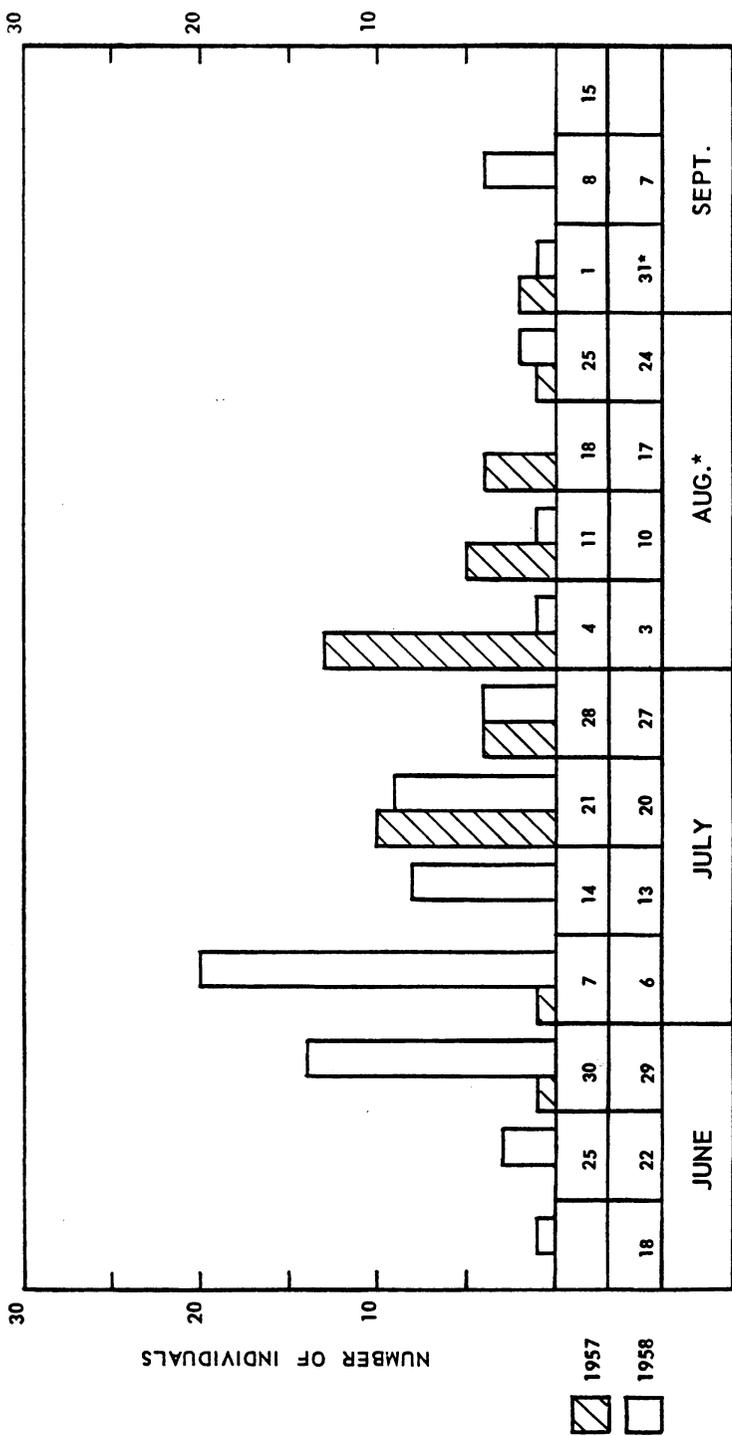
Fig. 196. Number of adult *Tendipes* (*Cryptochironomus*) *tenuicaudatus* taken weekly in 24 emergence traps in eight rice fields during two seasons.

cause the rice ripened rapidly, ending the season somewhat abruptly near
the middle of September. It is probable that there were two generations of
adults of *Tendipes tenuicaudatus* in the permanent water of the nearby canals
which contained aquatic vegetation. Miller (1941) recorded a single genera-
tion for this species in Costello Lake, but indicated that this was probably
the northern limit of its range and that farther south it could be expected
to have two generations per year.

Tendipes (Cryptochironomus) curtilamellatus (Malloch). This species
was not a proven inhabitant of the rice fields. In fact, it is apparently an
uncommon species in California. Townes (1945) lists no material from this
state. Wirth and Stone in Usinger (1956; p. 423) state for the entire group
of *Tendipes (Cryptochironomus)* [= *Harnischia* Kieffer], "No records are
available." Sublette (1960) lists only five of the adult males which were
taken in the present study.

These five individuals were all caught on June 26, 1957, from Field D near
Davis. Several were captured by aerial net from swarms of males. Due to a
strong south wind of 12 to 14 miles per hour, these swarms were close to the
ground and in a small area sheltered by a thicket of willows. The writer's
attention was first attracted to this spot by the unusually large number of
damselflies of the family Coenagrionidae feeding on some smaller insects.
Closer examination revealed the swarms of chironomids. Some of these males
were attracted to the light and were captured in the light trap which was
started at 8:55 p.m., 16 minutes after sunset. The air temperature at that
time was 79° F. By 9:55 p.m., when the trap was shut off, the temperature
had dropped to 73° F and the wind was blowing at the same velocity.

On July 5, 1957, a single male of this species was taken by light trap in
Field C. The trap was started at 9:00 p.m. when the air temperature was
80° F and an 8 to 10 mile per hour south wind was blowing. The time of
sunset was not recorded. By 10:00 p.m., when trapping was concluded, the
wind had died down to approximately 6 miles per hour and the air tempera-
ture had dropped to 76° F.

Nothing was learned concerning the biology of the immature stages of
Tendipes curtilamellatus in the present investigation. It seems probable, how-
ever, that this species was breeding in the shallower ditches and canals in
the vicinity of the fields. Miller (1941) found the larvae living in somewhat
comparable situations above the thermocline in Costello Lake.

Glyptotendipes (Phytotendipes) lobiferus (Say). This species has a wide
distributional range in North America, over most of which it is considered
one of the commoner chironomids. Therefore, it was somewhat surprising
that only two representatives of this species were taken in the rice fields.
Glyptotendipes lobiferus has been the subject of a number of investigations,
several of which consider its larvae together with those of *Tendipes decorus*
from the standpoint of habitat preference. Richardson (1921) regards the
two species as common in parts of the Illinois River. Both appeared somewhat
indifferent or moderately tolerant of the various environmental factors, par-
ticularly pollution. Similar findings were reported on these two species by
Alexander (1925) in his survey of the Salt Fork of the Vermilion River. The
ability of the larvae of three species of chironomids to tolerate extended

anaerobiosis was tested by Lindeman (1942*b*) in Cedar Bog Lake. He found a gradient of decreasing ability to tolerate the lack of oxygen from *Tendipes plumosus* to *Tendipes decorus* to *Glyptotendipes lobiferus* with the least tolerance range.

As previously indicated, *Tendipes attenuatus* (= *decorus*) was one of the more important members of the fauna of the rice fields. This fact, plus the presence in the rice fields of other chironomid larvae much less tolerant of oxygen deficiency than *Glyptotendipes lobiferus* was considered sufficient evidence for discarding the lack of oxygen as a reason for the scarcity of this species.

No egg masses of *Glyptotendipes lobiferus* were seen during the present study. These have been illustrated by Branch (1931) and described by Fellton (1940). The latter author, however, according to Townes (1945), had confused this and two other species of *Glyptotendipes* as a single species.

Both of the individuals taken during the present study were from the deeper water of the rice fields. One emergence trap was over standing water 2 feet deep and the other was at the edge of rapidly moving water 20 inches deep. Field E, in which both these adults were captured, was a first-year field, and both emergence traps in which this species was taken had burhead plants beneath them.

No larvae were encountered in the fields, but a number were collected from a deep canal south of Field C. In the rearing dishes these larvae were observed feeding by the characteristic filter-feeding method. This has been described in detail by Leathers (1922) and by Berg (1950) and for the larvae of *Glyptotendipes glaucus* by Burtt (1940). Leathers (1922) mentions that *Glyptotendipes lobiferus* also feeds directly from the mud surface, but this direct feeding was not seen during this study. The food consisted of diatoms and bits of algal debris large enough to be strained from the water by the silken nets spun across one end of the larval tubes. The water current through the tubes was created by the undulating movements of the larvae. In agreement with the findings of Burtt (1940) it was noted in the present investigation that the larvae exercised no selection as to the items collected in the net, but after a certain length of time ate the entire net and contents.

All of the larvae taken from the canal and used in the rearings were found in silken galleries inside the water-soaked, partially decayed stems of common tule. By several experiments, Leathers (1922) showed that the thickness and texture of the epidermis of the stems of water plants were the most important factors in determining whether or not the larvae could burrow into the plant tissues, and he noted that most of the larvae entered one end of a broken stem. The presence of most of the larvae near the ends of the tule stems in the present investigation agreed with these findings of Leathers (*op. cit.*). Another point of agreement was the wearing and the breaking of the labial teeth of the larvae in gnawing holes through the epidermis from the inside in order to admit water for filter-feeding.

Although the two adult males emerged from the same field, they did so at widely separated times. The first was taken on June 28 and the other on August 18, 1958. The complete absence of this species in the emergence traps in 1957 was difficult to explain, since they were regularly captured in the light trap.

Glyptotendipes lobiferus larvae have been reported from a wide variety of habitats. Muttkowski (1918) lists their habitats as "... varying from sand, gravel, and rocks, to plants and filamentous algae." Branch (1931) found these larvae inhabiting tubes of silt on *Chara,* and their relationships with several species of *Potamogeton* have been discussed in detail by Berg (1949 and 1950). The antagonistic extremes of habitat types which these larvae can successfully occupy are outlined by Lindeman (1942a). From the foregoing it appears that a limited larval tolerance of the environmental factors of the rice fields could hardly have been responsible for their scarcity in this ecosystem. It is possible that the limited flight range of the female midges may have been the actual reason that this species was absent from an apparently favorable habitat. From their study of swarming habits of mosquitoes and chironomids in Denmark, Nielsen and Greve (1950) state that the females of nematocerous Diptera tend to remain in the same small area all of their lives and lay their eggs in the same water from which they emerged. Additional work should be done on the ecology of this species making use of marked individuals.

Tribe Tanytarsini

Micropsectra nigripilus (Johannsen). This species was not known to be an inhabitant of the rice fields. The single representative taken from the vicinity of the fields during this study was a tube-dwelling larva on a floating cat-tail stem. This was obtained on May 5, 1958, from a ditch at the eastern edge of Field F. On May 16, 1958, an adult male emerged in the rearing dish. Apparently this species is more tolerant of low temperatures than most chironomids. On November 4, 1957, when the air temperature was 60° F and the water was 51° F and again on November 24, 1957, with air temperature of 58° F and water 51° F, a number of swarming males were captured which had recently emerged from a small pond in Carmichael, California.

Tanytarsus (Cladotanytarsus) viridiventris (Malloch). Despite the fact that no records of this genus in California were available prior to 1956 according to Wirth and Stone in Usinger (1956), *Tanytarsus viridiventris* was the third species from the standpoint of numbers taken in the emergence traps in the rice fields (table 5). None of the egg masses seen during this work could be identified definitely as those of *Tanytarsus viridiventris.* Since all of the egg masses of other species in the genus *Tanytarsus* were linear gelatinous ropes containing single rows of eggs, it was presumed that *Tanytarsus viridiventris* females produced similar strings of eggs. Normally these were oriented diagonally across the gelatinous envelope, but handling the mass disrupted this pattern (fig. 204).

Apparently the distribution of the larvae was not limited to any great extent by the water conditions, since adults were taken in emergence traps over shallow standing water as well as over deeper moving water (figs. 197, 198, 199, and 200). Four times as many adults of this species were taken by emergence traps from first-year fields than were captured in second-year fields (table 7). Within the individual fields, the larvae inhabited all the different microhabitats except those beneath the mud. Although not as abundant as elsewhere, this species was one of the few taken in traps placed in dense

Fig. 197. Standing water near edge of a first-year rice field
(Field C), with dense rice beyond the borrow pit.

Fig. 198. Trap C_3 located in shallow, standing water of a
first-year rice field (Field C).

rice. The larvae also were present in small numbers on the varied level stakes placed in the heavy stand of rice. Early in the season many of these larvae together with those of other species of *Tanytarsus* and of *Cricotopus* were found occupying the bladder-like masses of the alga, *Gloeotrichia,* which covered the water surface. The environmental factor, however, which appeared most important in contributing to large populations of this species was submerged vegetation. Fields A and E were not treated with herbicide, thus contained an abundance of burhead, arrowhead, and water plantain much of which was under water. These two fields also had the greatest number of adults entering the emergence traps with 79 and 107 individuals, respectively. All species of aquatic plants which provided underwater surface area were utilized by these larvae. Those plant species characterized by a diffuse growth pattern, such as water nymph, grass wrack, and *Chara,* or by a rosette of wrinkled leaves as burhead, supported the greatest number of *Tanytarsus* larvae.

In the field it was impossible to definitely distinguish the larvae of this species from those of other species of *Tanytarsus.* Even with the use of the microscope, the living individuals could be identified only tentatively. This species had the abdominal tubercle on the next to last abdominal segment well developed, and was generally shorter and more robust than the larvae of the other species of *Tanytarsus* present in the rice fields. The structure of the antennae (fig. 98) provided the best diagnostic characteristics of this species, but these were difficult to see on the extremely active larvae.

Fig. 199. Trap A_1 located in deep, rapidly moving water below a weir box in a first-year rice field (Field A).

In common with the other species of this genus, the larvae of *Tanytarsus viridiventris* were tube dwellers. The walls of the tubes were constructed of silk into which was woven felted algae and debris, thus they were almost opaque. Hauber (1944) indicates that all species of *Tanytarsus* which he observed produced this type of tube. The case illustrated in figure 206, although longer than those usually built by larvae of this species, is typical for the genus.

The pupation tube produced by the last larval instar was shorter than earlier larval cases and was somewhat constricted at each end, making it appear spindle-shaped. The openings at each end were smaller than those of the larval tubes. Lauterborn (1905) first observed this different pupation tube in which both ends were constricted and partially closed by a membranous operculum with a circular opening in it. Cavanaugh and Tilden (1930) consider the larval and pupation tubes of *Tanytarsus* the same, for they state that *Tanytarsus dissimilis* pupates in the larval tube, yet their photograph (Plate IX, fig. 11) shows a typical pupal case as contrasted with that of the larva (Plate XIII, fig. 3 of their publication).

Tanytarsus viridiventris larvae observed in the present study fed on diatoms, desmids, and algal debris which settled on the submerged aquatic vegetation. There was no evidence that these larvae ate anything other than the periphyton which coated any material submerged for a short period of time in most of the fields. Diatoms also were found to be the most important food item of *Tanytarsus dissimilis* by Cavanaugh and Tilden (*op. cit.*).

Fig. 200. Trap A_3 located in shallow, slowly moving water, over *Chara* and other aquatic vegetation in a first-year rice field (Field A).

Although no specific observations were made of predators attacking this species, probably many other members of the rice field community were dependent upon these larvae for food because of their abundance and sedentary tube-dwelling habits. A somewhat unusual enemy of *Tanytarsus dissimilis* was noted by Cavanaugh and Tilden (1930) who observed fresh-water snails eating the algal tubes of the larvae. In all instances the larvae escaped from the tubes, but they were deprived, at least temporarily, of their food and protection.

Taxonomic confusion of the immature stages of the various species of *Tanytarsus* prevented a detailed consideration of interspecific competition in the rice fields. This aspect of the ecology of the chironomids inhabiting rice fields should be thoroughly investigated in view of the number of species with apparently the same requirements which are living together.

During the two seasons of emergence trapping, almost twice as many females as males of this species were taken. In 1957, 108 females and 72 males were trapped. During the second season 109 females and 64 males were taken. The early-season emergence peaks of the two sexes coincided exactly for each of the two years. In 1957 this was on July 8 and in 1958 it was July 12 (figs. 201 and 202). Later in the season as the number of females trapped increased, there was less agreement in the time of emergence of the two sexes.

Many swarms of *Tanytarsus viridiventris* males were observed in the course of the present investigation. They varied in size from a few individuals to huge clouds of humming males. As has been indicated in the discussion of other species, the males of *Tanytarsus viridiventris* readily swarm in mixed groups with males of a number of different species. Although the largest swarms were seen on warm, relatively quiet evenings, *Tanytarsus viridiventris* males swarmed at various times during the day. For example, on May 2, 1958, at 3:25 p.m. a small swarm was discovered in a ditch north of Field E. This was a mixed group containing *Cricotopus bicinctus* males as well as those of *Tanytarsus viridiventris*. The air temperature was 74° F and a 10 to 12 mile per hour south wind was blowing. Consequently the midges were swarming down close to the water out of the wind. Other swarms were recorded in the morning hours from 7:30 to 11:00 a.m. often in bright sunlight. Many of these small morning swarms were attacked by damselflies of the family Coenagrionidae. Light intensity apparently was not a limiting factor in the swarming of this species, but wind velocity appeared to exercise a considerable effect. Gibson (1945) in a detailed study of chironomid swarming habits at Knostrop Sewage Works made similar observations.

On several occasions mating was observed in the large evening swarms. The copulating pairs did not remain in flight, but dropped to the ground where, after a few minutes, they separated. This was similar to the pattern of mating of *Spaniotoma minima* as discussed by Gibson (*op. cit.*).

As can be seen by figure 203, there appeared to be a single generation of this species during the 1957 rice season with the greatest emergence in the third week of July. The data for 1958, however, plus the fact that swarming males of this species were present near the rice fields in early May, indicated that under favorable conditions two generations of this species could develop per season.
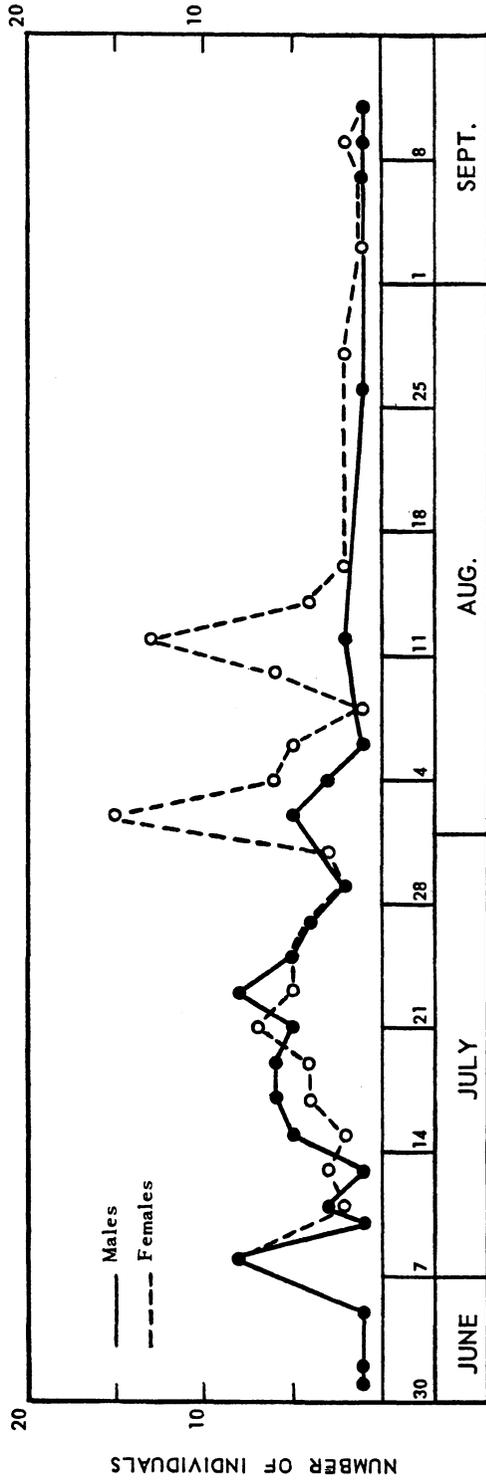
Fig. 201. Male and female *Tangytarsus viridiventris* taken weekly in 12 traps in four rice fields during the 1957 season.
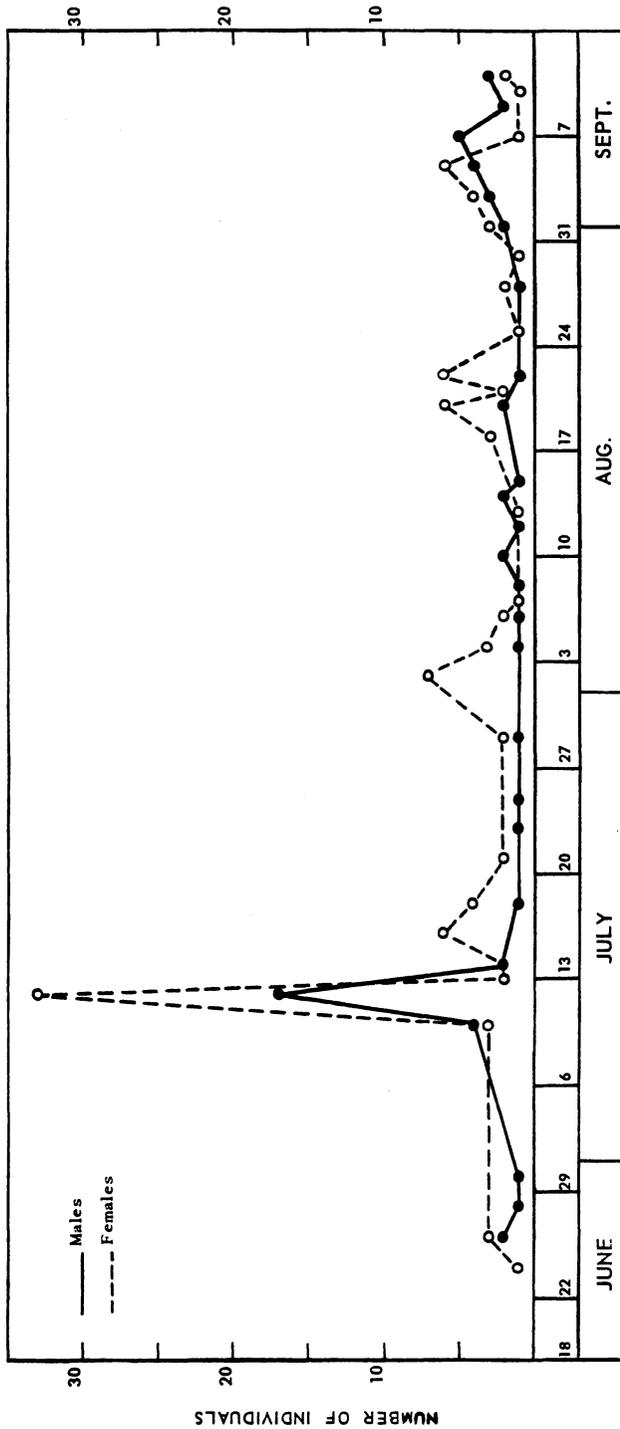
Fig. 202. Male and female *Tanytarsus viridiventris* taken weekly in 12 traps in four rice fields during the 1958 season.
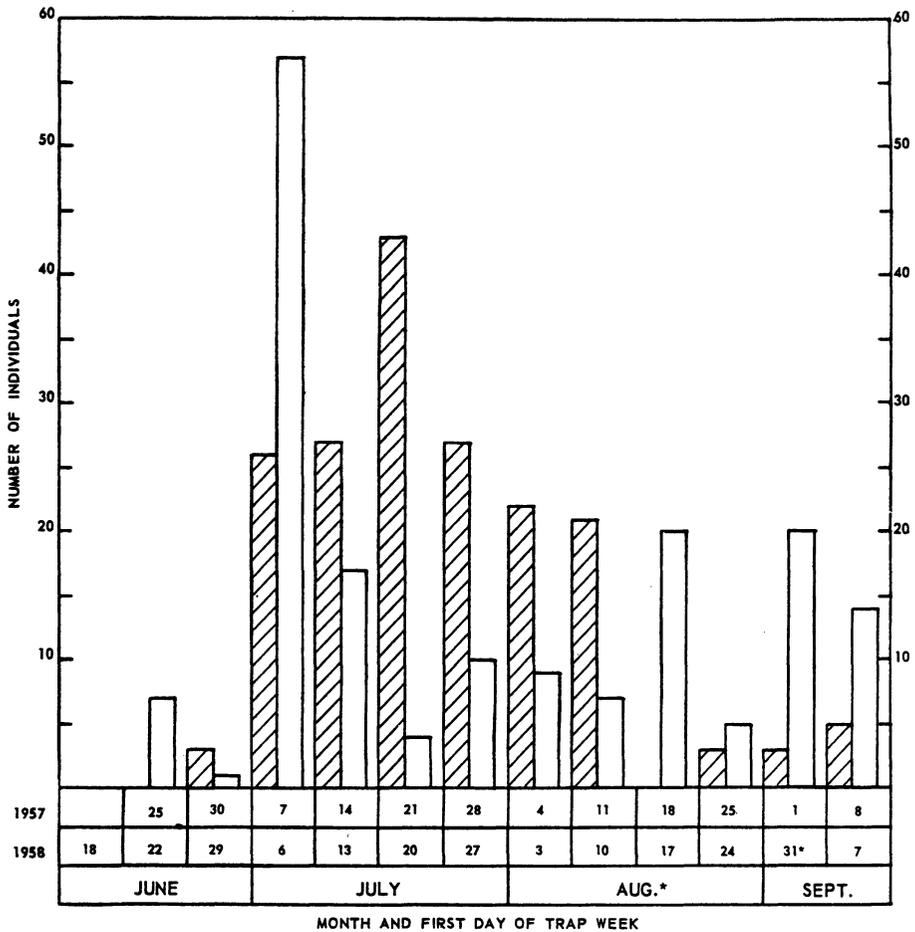
Fig. 203. Number of adult *Tanytarsus viridiventris* taken weekly in 24 emergence traps in eight rice fields during two seasons.

Tanytarsus (Rheotanytarsus) n. sp. 2. Based upon the present knowledge of the taxonomy of this species, it was poorly represented in the rice fields. No females ever were definitely identified; thus it is possible that there were actually a greater number of individuals of this species present than the data indicated. Only eight males were taken even though special emphasis was given throughout the study to the procurement of green males belonging to the genus *Tanytarsus*. All of these were captured in 1957 from Field C, a first-year field.

On July 15, the first male of this species was taken in an emergence trap at the edge of moving water approximately 14 inches deep over *Spirogyra* and young arrowhead plants. The second individual was taken at 8:10 a.m., August 16, from a mixed swarm of males including *Tanytarsus viridiventris, Cricotopus sylvestris,* and *Cricotopus bicinctus* which was over the rapidly flowing open water below a weir box. On August 21, at 8:00 a.m., a larger mixed swarm was encountered over shallow open water in the corner of the check on the northern edge of the field. Five males of this species were taken from this swarm together with several *Tendipes tenuicaudatus* and one male believed to be *Tanytarsus* n. sp. 5. The last record of this species was on September 13 when one male was taken in an emergence trap which had been in swiftly flowing water below a weir box over *Spirogyra* and other green algae. The water had been shut off, however, and when this specimen actually was taken there was only a puddle of water 3 inches deep under the trap with a large mass of algae resting on the mud substrate.

No known larvae or pupae of this species were seen, since it was not successfully reared and no pupal exuviae were found with the two adults taken in the emergence traps.

Tanytarsus (Tanytarsus) n. sp. 3. Although this species bred in the rice fields, its numbers were small. It was seldom encountered and little was learned concerning its biology. It was possible that some females of this species were misidentified as *Tanytarsus* n. sp. 5 since both species are green with brown markings. There was a considerable size difference, however, between the known males of *Tanytarsus* n. sp. 3 and the females of *Tanytarsus* n. sp. 5. The former species was larger as indicated by a wing length of 1.9 mm compared to 1.63 mm for *Tanytarsus* n. sp. 5. There was also a significant difference between the two forms in the leg ratio or the relative lengths of the tibiae and basitarsi of the forelegs.

A total of 17 males definitely identified as this species was taken in or near rice fields. This species was first taken in the present investigation on July 2, 1956, during the early survey collecting. At 9:15 a.m. on this date two males were flushed from rice and watergrass at the edge of a borrow pit in a field near Davis, California. There was no wind blowing and the air temperature was 72° F when these first two were captured in an aerial net. Three additional males were taken in the same manner in this Davis field; two were caught on July 10 and one on July 13.

The first and only known records of this species breeding in the rice field in 1957 were on July 17. Both were in Field C. One individual emerged into a trap placed in moving water 2 feet deep over water nymph and *Spirogyra.* The other was taken in an emergence trap at the edge of moving water 14 inches deep over arrowhead and *Spirogyra.* A third male of this species was captured on September 11, 1957, in Field B. This individual was taken by means of an aerial net from a mixed swarm of males of *Tendipes tenuicaudatus* and *Cricotopus bicinctus* at 7:52 a.m. The air temperature at this time was 58° F and a south wind of 1 to 4 miles per hour was blowing.

On June 24, 1958, four males were taken by aerial net as they were swarming over open water near a weir box in Field F. The time was 9:10 a.m., the air temperature was 68° F, and a strong south wind of 10 to 12 miles per

hour was blowing. The mixed swarm included, in addition to this species, *Tendipes tenuicaudatus, Cricotopus sylvestris,* and *Paralauterborniella* sp. They were low over the water so that the vegetation on the check bank protected them from the wind. Three males were captured in a similar mixed swarm in Field E at 8:55 a.m. on July 4, 1958. The wind was variable in direction 4 to 7 miles per hour and the air temperature was 75° F. This group was swarming over shallow, standing water in the corner of a rice check in which there was only sparse emergent vegetation consisting of few rice plants and some arrowhead. The water surface was almost entirely covered with *Gloeotrichia.* The only record of this species taken in an emergence trap in 1958 was the single male taken on July 10 in Field F. This emergence trap was in swift water 2 feet deep below a weir box and was placed over water nymph and some *Spirogyra.* The last individual taken was captured in flight over slowly moving water in a ditch at the north edge of Field H. It was taken on August 29, 1958, at 7:40 a.m. when the air temperature was 59° F and a light south wind of 1 to 3 miles per hour was blowing. It was not definitely determined that this male had recently emerged from the stream, but it appeared probable since other species such as *Cricotopus bicinctus* and *Tendipes tenuicaudatus* which were taken in the same sweep of the net were seen emerging from this moving water.

Although samples of aquatic vegetation and mud were taken from the water over which the adults of *Tanytarsus* n. sp. 3 had been captured, no larvae or pupae were successfully reared to associate the different life history stages with one another. The adult female also remained unknown; thus the manner of oviposition and characteristics of the egg masses were not recorded.

Tanytarsus (Tanytarsus) n. sp. 4. This species was extremely rare in the rice fields. In fact, the single record of its occurrence was questionable. This individual was a small light-green female taken on July 17, 1957, in Field C in an emergence trap in moving water of a borrow pit over sparse, partly emerged rice and *Spirogyra.* This specimen was sent to Dr. James E. Sublette for identification, and with some reservations, he has assigned it to *Tanytarsus* n. sp. 4. Because of the confusing similarities of the small green species in the genus *Tanytarsus,* green males were taken wherever encountered. The two males of *Tanytarsus* n. sp. 4, which were taken by the writer, were at least 12 miles from the nearest rice field. Both of them probably had developed from larvae living in the American River. One was taken by aerial net on August 9, 1957, in Carmichael, approximately 100 yards from the river, and the other was taken at a lighted window on the Sacramento State College campus. This individual was captured approximately 200 yards from the American River.

Tanytarsus (Tanytarsus) n. sp. 5. The small green female midges considered as *Tanytarsus* n. sp. 5 were by far the most numerous of all the species of chironomids inhabiting the rice fields (table 5). They have been assigned to this species because of their similarity in coloration, leg ratio, and wing length to a green male taken in Field C on August 21, 1957. This single individual was captured by means of an aerial net from a mixed swarm of *Tendipes tenuicaudatus* and *Tanytarsus* n. sp. 2 males over the shallow open water in the corner of a check at the northern edge of the field.

The green females were never actually associated with any males by taking them in copulation in mating swarms. Furthermore no males developed in any of the 38 successful rearings of this species. These findings indicated the possibility of a complete absence of the male sex in this species. Grimm (1871 reprinted from 1870) first reported on the condition of parthenogenetic paedogenesis occurring in the *Tanytarsus* (= *Chironomus*) *boiemicus* Kieffer. Edwards (1919) reviewed the phenomenon in the family and mentioned the production of all female adults from the parthenogenetically produced eggs of *Tanytarsus flexilis*. Previous investigations concerned with parthenogenesis have been summarized and additional examples have been given by Phillipp (1936). Johannsen (1937*b*) states that *Tanytarsus boiemicus* and *Tanytarsus dissimilis* also may reproduce parthenogenetically and in the latter species reproduction was also paedogenetic. In the present investigation parthenogenesis was first considered a plausible explanation for the absence of males on July 22, 1957, when an egg string was found in a rearing dish in which a dead, recently emerged female *Tanytarsus* n. sp. 5 was floating. Oviposition must have occurred some 48 hours earlier, because within an hour after they were discovered, 33 of the 35 eggs in the mass had hatched. Subsequently during this study four additional examples of oviposition by recently emerged, unmated females of this species were observed. In each instance the female had drowned and was floating in the rearing dish. The eggs deposited by female #328 which emerged on May 5, 1958, required three to three and one-half days to hatch. All the others hatched in two days' time. Several individuals were reared from the larvae which emerged from these eggs and, as expected, all developed into females. One of these adults, #620, also produced an egg mass upon emerging. Figure 205 shows the newly hatched larvae still within the gelatinous envelope of this egg string.

Oviposition by females of this species was observed frequently in the field during the early morning hours. It could not be determined that these small females extruded the egg masses on their hind tibiae as has been described for two other species. It was noted, however, that after they had dropped to the surface of the water, they appeared to bounce straight up into the air, indicating that they may have thrust the eggs from their hind tibiae. This manner of oviposition was probably responsible for drowning of the females as they attempted to fly in the small space above the water in the rearing dishes.

As previously indicated, the egg masses of this species were rope-like or linear in shape with a single row of eggs (fig. 204). Normally these were placed diagonally across the width of the gelatinous envelope.

The larvae of this species were the dominant chironomids of the rice fields. They were present in both the shallow and deeper areas and in standing as well as moving water. The distribution of the larvae on the varied level stakes which had been placed in the fields for one week indicated no preference for any particular depth.

Table 7 shows that almost three times as many adults of this species were taken in the emergence traps in first-year fields as were recorded from those of the second-year fields.
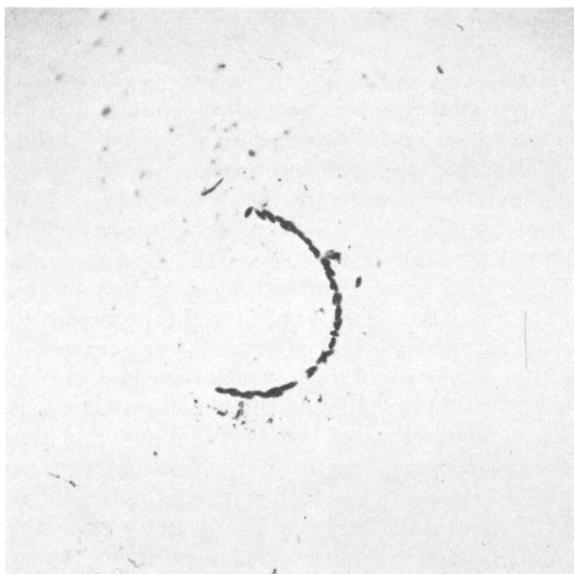
Fig. 204. Egg string of *Tanytarsus* n. sp. 5, × 10.
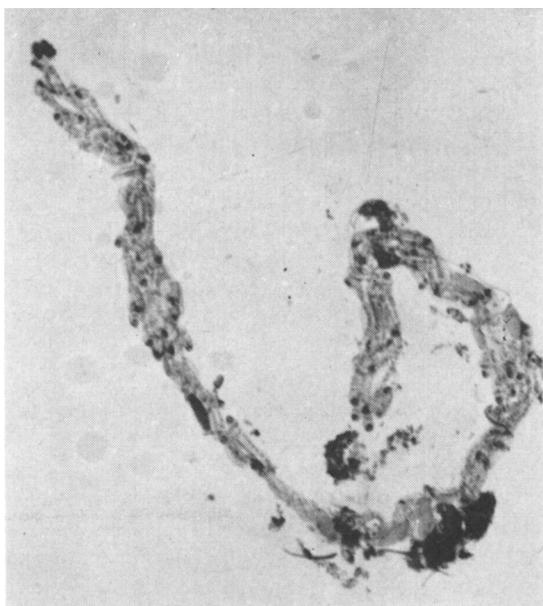
Fig. 205. Parthenogenetically developed larvae of *Tanytarsus* n. sp. 5 emerging from the gelatinous envelope which had surrounded the eggs, × 24.

Within a given field, the larvae were never found beneath the surface of the mud, and relatively few were present in the dense stands of rice. In all of the other habitats, however, they were extremely abundant. As with several other species considered earlier, larval numbers were closely related to the presence of submerged aquatic vegetation or any underwater objects which provided living space (fig. 207). This substrate preference combined with the fact that they reproduced parthenogenetically was believed responsible for the disproportionately high numbers of these midges captured in the emergence traps. The submerged portions of the traps, which were usually covered with diatoms, other unicellular algae, and debris, served as an ideal substrate for the development of many larvae. It was believed that in addition to the large number of these larvae which emerged from the egg masses deposited by the emerging adults, some tiny first instar larvae had crawled through the screening into the traps and completed their development.

The larvae were tube dwellers and constructed slender tubes of felted algae and debris which often were greatly elongated (fig. 206). New material usually was added to the end of the tube nearest a food source as indicated for *Tanytarsus dissimilis* by Cavanaugh and Tilden (1930), but unlike that species, *Tanytarsus* n. sp. 5 did not eat or remove the material from the end of the tube away from the food. This resulted in the production of long sinuous cases.

The pupation tubes were shortened fusiform or spindle-shaped structures the same as those described for *Tanytarsus viridiventris*.

Diatoms were by far the most important food item in the diet of these larvae. Desmids and other microscopic algae also were consumed as well as a considerable amount of debris gleaned from near the mouth of the tubes which the larvae inhabited. There was no evidence of this species feeding on the leaves or stems of higher plants. When the young larvae first emerged from the eggs, which they did by splitting the chorion longitudinally, they remained in the gelatinous envelope for approximately two and one-half hours. They appeared to be feeding on the gelatinous matrix, but this could not be determined with certainty. They may have been eating tiny particles of algae which had adhered to the sticky egg mass. Shortly after leaving the envelope, the larvae began spinning tubes of minute algal particles and silk which consequently were more transparent than those of older larvae. Most of the feeding of these first instar larvae was then done near the ends of these tubes. The undulation movements appeared to serve as a method of driving fecal pellets from the tube instead of bringing in particles of food.

It is probable that the larvae of this species because of their large numbers were eaten by all of the various aquatic predatory species in the rice fields. Figures 168 and 172 show that they were readily eaten by the larvae of *Pentaneura aequifasciata* and *Procladius culiciformis*. Undoubtedly many also were eaten by the larvae of several members of the subgenus *Cryptochironomus*. Both the adults and the larvae of the hydrophilid and dytiscid beetles fed extensively on these abundant tube-dwelling larvae.

Many of the larvae of *Tanytarsus* n. sp. 5 were attacked by a mold or fungus disease which often destroyed one or both antennae. It was believed that if left in the field most of these fungus-infested larvae would have died or
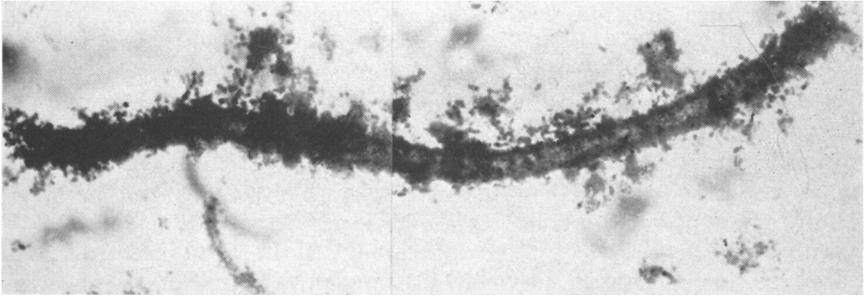
Fig. 206. Tube of silk and felted algae constructed by larva of *Tanytarsus* n. sp. 5, × 3.25. Note fecal pellets at each end of tube.

Fig. 207. Trap A_2 (foreground) and Trap A_3 (background) over aquatic vegetation in moving water, above a weir box in a first-year rice field (Field A).

have been more easily captured by predators. However, this phase of the ecology of the larvae was not given sufficient study to make a definite statement.

Whatever degree of interspecific competition may have existed between the immature stages of this species and other chironomids of the same microhabitat, certainly from the viewpoint of numbers present, *Tanytarsus* n. sp. 5 was the most successful.

The green female midges were readily attracted to light, and as shown by table 8 were most active in the early evening.

The emergence data for the 1957 season as shown by figure 208 were interpreted as the production of a single generation per season with the maximum emergence during the last week of July and the first week of August. The 1958 data, however, indicated more than one generation per season. The fields under investigation that season were flooded during the first week of May and by the middle of the month most of them supported extremely large populations of the larvae of *Tanytarsus* n. sp. 5 which were at least two weeks old. In view of this abundance early in the season, and the fact that the elapsed time of development under laboratory conditions ranged from 26 to 34 days, it was considered probable that under favorable field conditions several generations could develop during the 15 to 16 weeks that the fields were flooded.

Tanytarsus (Tanytarsus) n. sp. 6. This was one of the more important species of chironomids in the rice fields. It ranked fourth in the number of adults captured in the emergence traps (table 5).
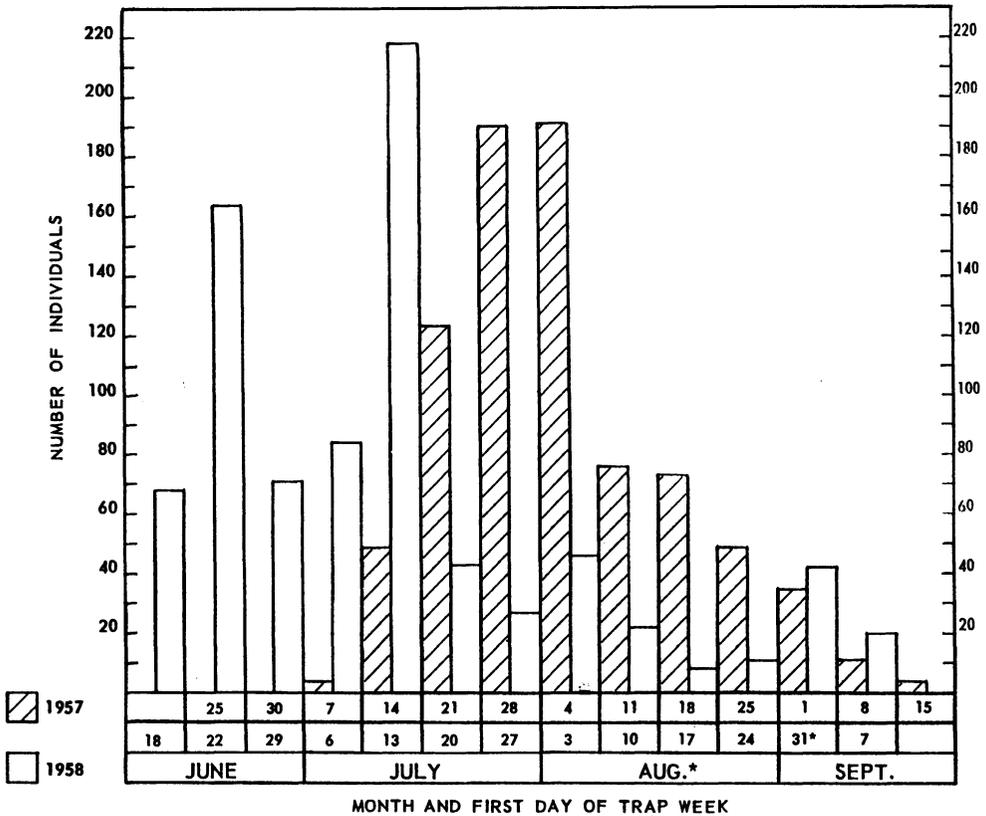
Fig. 208. Number of adult *Tanytarsus* n. sp. 5 taken weekly in 24 emergence traps in eight rice fields during two seasons.

Oviposition by the females of this species was not observed, but since the adults were most active during the morning and evening hours, oviposition was believed to occur at these times. No egg masses known to be from this species were encountered. From what has been stated and illustrated concerning the egg strings of other members of this genus, however, it appears unlikely that those of *Tanytarsus* n. sp. 6 should differ greatly in form and arrangement of eggs.

Apparently the larvae of this species developed equally well under various water conditions. They were found in shallow standing water as well as in that which was deeper and rapidly flowing.

Unlike most of the chironomids inhabiting rice fields, *Tanytarsus* n. sp. 6 was as abundant in second-year fields as it was in first-year fields (table 7). Most of the microhabitats within the fields were occupied by larvae of this species. Figures 209, 210, and 211 illustrate situations in which the *Tanytarsus* n. sp. 6 was noted most frequently. They were not present in the dense stands of rice and although plentiful on the surface of the mud, they were not often found beneath the surface. Walshe (1951*b*) states, however, that members of the subgenus *Tanytarsus* occur both on and below the surface of the mud. By far the greatest number were present on submerged vegetation such as *Chara*, water nymph, and the leaves of burhead. This species was one of the few which was taken over dense *Chara* which grew in the shallow waters of Field F where it received direct sunlight (fig. 13).

The larvae were tube-dwelling forms and constructed algal cases similar to those of *Tanytarsus* n. sp. 5, but usually not so long. These larvae were readily distinguished from the other two species of this genus, which were successfully reared, by their uniform pink color, slightly larger size, the presence of extremely long Lauterborn organs on the antennae (fig. 102), and by the fact that the tubercle on the next to last body segment was poorly developed. They were less active and were generally more reluctant to leave their tubes than the other species.

The pupation tube was similar to that described for *Tanytarsus viridiventris* and *Tanytarsus* n. sp. 5. The duration of pupation was from one to two days.

The food of the larvae consisted primarily of algal debris, but also included diatoms and desmids. These food items were picked from the substrate around the mouths of the tubes by the larvae. Often they extended their bodies out of the tubes for almost their entire length while maintaining attachment by the claws of the posterior prolegs.

Larvae of this species were attacked by the same predators preying upon the other members of the genus *Tanytarsus*. A larger proportion of these larvae was observed to be infested with fungus growths on their heads than was noted in other species of chironomid larvae.

During both seasons of emergence trapping, more males than females were captured. In 1957, 53 males and 34 females and in 1958, 85 males and 73 females were taken. As can be seen from figures 212 and 213, the two sexes emerged at almost the same times for both seasons.

Although a few males of this species were observed in small mixed swarms with *Tanytarsus viridiventris* during the morning hours, the larger swarms

Fig. 209. Trap B, located in clear, standing water in the corner of a check in a second-year rice field (Field B).

Fig. 210. Trap D_1 (partially obscured) located in turbid, standing water of a second-year rice field (Field D).

Fig. 211. Varied-level stake located in moving water below a weir box in a second-year rice field (Field H).

of *Tanytarsus* n. sp. 6 were encountered in the evening. On July 8, 1958, immediately after sunset the only instance of copulation by members of this species was recorded. This pair was in a large swarm over Field E. One member of the pair was actively flying, but the other appeared immobile with its head hanging downward. They were captured in an aerial net before it was learned whether the paired individuals of this species drop to the ground or remain in the air during copulation.

The pattern of emergence of the adults taken during 1957 indicated a single generation per season with the maximum number emerging in the third week of July (fig. 214). The early maximum emergence of the 1958 season, how-
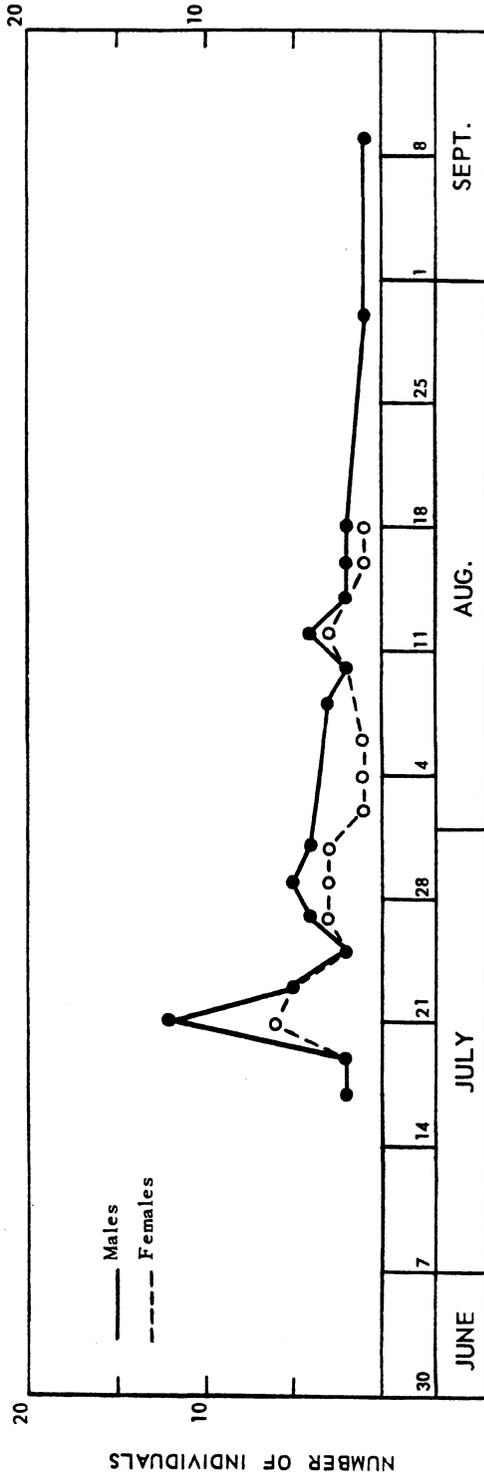
Fig. 212. Male and female *Tamytarsus* n. sp. 6 taken weekly in 12 traps in four rice fields during the 1957 season.
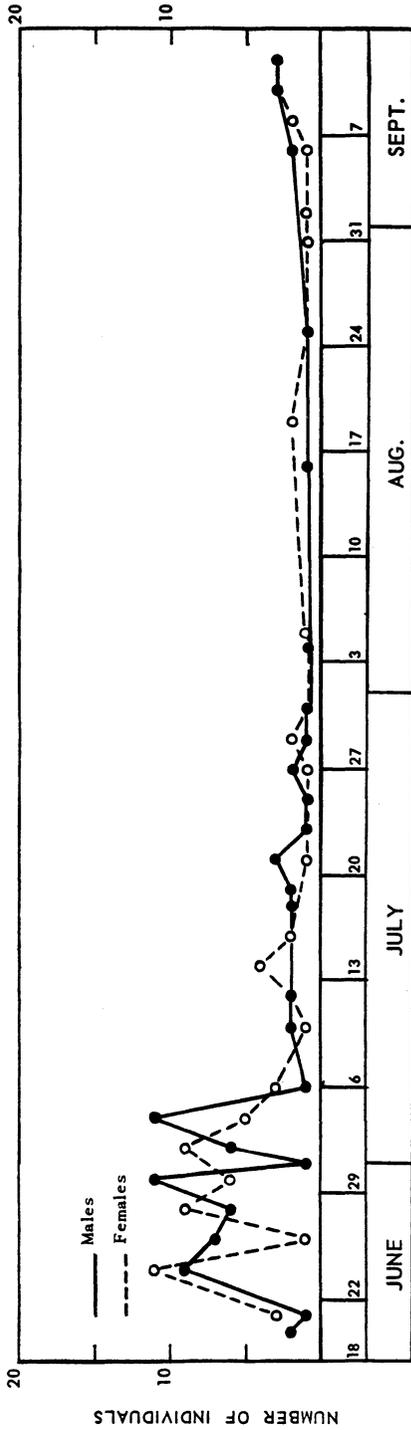
Fig. 213. Male and female *Tanytarsus* n. sp. 6 taken weekly in 12 traps in four rice fields during the 1958 season.

ever, indicated the possibility of a second generation in the first part of September. This probably occurred in the permanent bodies of water near the rice fields, but when the fields were drained at mid-September all of these developing larvae died.
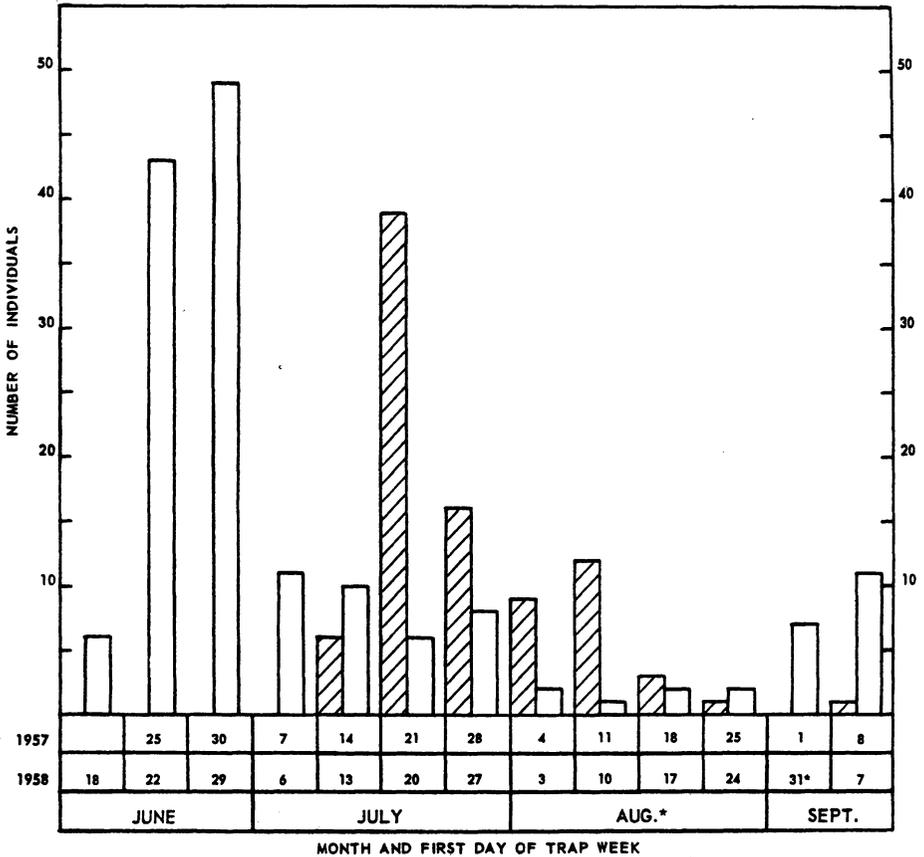

Fig. 214. Number of adult *Tanytarsus* n. sp. 6 taken weekly in 24 emergence traps in eight rice fields during two seasons.

THE ROLE OF MIDGE LARVAE IN RICE FIELDS
(SYNECOLOGY)

Although 30 species were represented, the dominant position maintained by chironomids in the rice fields was due to enormous numbers of relatively few species (table 9).

Soon after the fields were flooded in May, floating *Gloeotrichia,* the mud surface, and the upper 2 inches of the mud and ooze on the bottom were the principal microhabitats present. Many young larvae of the various species of *Tanytarsus, Paralauterborniella,* and *Cricotopus* comprised the primary consumers occupying the *Gloeotrichia* and the substrate surface microhabitats. These forms utilized diatoms and settled plankton particles as food and for tube construction. They were prey for a wide array of predaceous secondary consumers. Beneath the mud, the larvae of *Tendipes attenuatus* were the principal consumers of the material deposited in the ooze-film. The active predatory *Procladius culiciformis* larvae appeared well adapted to the three existing microhabitats and in each one were important secondary consumers.

Conditions on the surface of the ooze layer did not change appreciably during the season in the open water, but there was an over-all decrease in the larval population under the thick stands of rice. Although a few of the less plentiful predatory species such as *Pentaneura* sp. and *Tendipes fulvus* ranged into the mud, from the standpoint of species represented, the thin surface layer appeared to be the most stable microhabitat.

The emergence of the rice from the water and the increase of aquatic weeds in the channels and borrow pits were accompanied by a change in distribution of the midge larvae. In most of the fields at approximately this same time, the bladder-like clusters of *Gloeotrichia* and the algal mats of *Oedogonium* and *Mougeotia* were deteriorating. This left the submerged vegetation as the most important of the microhabitats. Included in this submerged plant material were several species of green algae which were used as food by many larvae. The isolated examples of *Cricotopus sylvestris* feeding on tissues of submerged or floating leaves of rice and burhead already have been mentioned under the discussion of that species. As can be seen in table 9, *Cricotopus sylvestris* was the only chironomid observed attacking higher plants in the rice fields. The principal contribution of these hydrophytes was that of providing additional substrate or supporting surface on which the larvae could feed and construct the tubes in which they lived. The common species which had previously occupied the floating *Gloeotrichia* and the mud surface now invaded this new microhabitat. Submerged vegetation also was the preferred habitat of *Tendipes tenuicaudatus, Corynoneura* n. sp., and *Tendipes californicus.* The latter two species were primary consumers of the periphyton and other settled phytoplankton on the higher plants. The free-living larvae of *Corynoneura* appeared to be completely dependent upon the presence of submerged aquatic vegetation for their existence in the rice fields. The *Tendipes tenuicaudatus* larvae ate a combination of food items. As tube-dwelling forms, much of their diet appeared to be the same as that of the primary consumers, but in contrast to these strict vegetarians, *Tendipes tenuicaudatus* larvae also were observed to prey upon oligochaete worms. The active preda-

TABLE 9

THE RELATIVE ABUNDANCE OF CHIRONOMID LARVAE IN VARIOUS MICROHABITATS OF RICE FIELDS

Taxonomic unit	Floating *Gloeotrichia*	Tissues of higher plants	Surface of submerged plants Moving water	Surface of submerged plants Still water	Surface of mud Sparse or no rice	Surface of mud Dense rice	Beneath mud Sparse or no rice	Beneath mud Dense rice
Tanypodinae								
Pentaneura two species	−	−	+	+	+	−	+	−
Procladius culiciformis	+	−	++	++	+++	−	+++	−
Orthocladiinae								
Cricotopus bicinctus	+	−	+++	+	+	−	−	−
Cricotopus sylvestris	++	+	+++	++	+	−	−	−
Psectrocladius n. sp. 2	−	−	+	?	−	−	−	−
Nanocladius n. sp.	−	−	+	−	−	−	−	−
Corynoneurinae								
Corynoneura n. sp.	+	−	+++	++	−	−	−	−
Chironominae								
Chironomini								
Pseudochironomus richardsoni	−	−	−	−	?	−	+	−
Paralauterborniella sp.	++	−	+++	+++	++	−	−	−
Tendipes attenuatus	−	−	−	−	+	−	+++	+
Tendipes plumosus	−	−	−	−	?	−	+	−
Tendipes nigricans	−	−	−	?	?	−	?	−
Tendipes californicus	−	−	++	++	++	−	+	−
Tendipes modestus	−	−	?	−	?	−	?	−
Tendipes nervosus	−	−	?	−	?	−	?	−
Tendipes chaetoala	−	−	+	+	−	−	−	−
Tendipes darbyi	−	−	?	?	?	−	?	−
Tendipes fulvus	−	−	−	+	+	−	+	−
Tendipes monochromus	−	−	?	−	−	−	−	−
Tendipes tenuicaudatus	−	−	+++	++	+	−	−	−
Glyptotendipes lobiferus	−	−	?	?	?	−	?	−
Tanytarsini								
Tanytarsus viridiventris	+	−	+++	++	++	+	−	−
Tanytarsus n. sp. 2	−	−	?	−	?	−	−	−
Tanytarsus n. sp. 3	−	−	?	?	?	−	−	−
Tanytarsus n. sp. 4	−	−	?	−	?	−	−	−
Tanytarsus n. sp. 5	++	−	+++	+++	++	−	−	−
Tanytarsus n. sp. 6	−	−	+++	+++	++	−	+	−

Legend: ? Under trap in which adult taken; no larva seen
    − Absent
    + Present
  ++ Moderately abundant
 +++ Abundant

tory larvae of *Procladius culiciformis,* however, were more important as secondary consumers in this microhabitat than any other predaceous forms of midge larvae.

A combination of two factors was believed responsible for the scarcity of larvae under dense stands of rice. One was the absence of open water over which females normally oviposited, and the other was the limited movement of the larvae in the sluggish water moving through the rice.

Apparently the rice fields provided conditions well within the tolerance range of these more abundant species because no direct correlations were

noted between the presence or absence of larvae and any of the physical factors of the environment tested. The variation in numbers of larvae supported by first-year fields in contrast to those of second-year fields was interpreted as being due to greater fertility of the first-year fields and a generally greater stabilization within the animal communities in the second-year fields. Studies by Platt (1915) and by Tressler *et al.* (1940) have shown that certain elements, such as nitrate, and general eutrophic or fertile conditions are necessary for the production of diatoms and other phytoplankton. The findings of the present investigation suggested that there may have been less of this necessary food material present in the second-year fields than in the more fertile new fields. Unfortunately a comparative study of diatom production in the different fields was not done, but, as stated earlier, there were indications of a scarcity of periphyton in the older fields. A report which indicated the importance of diatoms to insect larvae was that of Rudolfs and Lackey (1929) who attributed the death of mosquito larvae in certain cedar swamps to a lack of diatoms and other food items.

The abundance of fresh-water snails in second-year fields utilizing the same food as the chironomid larvae was believed to be partly responsible for the smaller number of these insects in the older fields. Although no quantitative sampling was done, there also appeared to be more crayfish, carp, and bull frogs in the second-year fields. Apparently a carry-over of some basic factor in the soil produced a more stabilized pond-type habitat during the second season that a field was planted in rice.

In an aquatic habitat classification such as that listed by Eggleton (1939) a rice field perhaps should be classified between a marsh of the lenitic series and a slowly flowing creek in the lotic series. The list of species of chironomids which were dominant in rice fields agreed most nearly with the pond fauna of Roback (1957). In a comparative study of chironomid larvae from ponds and streams, Walshe (1948) found that those species from ponds had a much wider range of tolerance for dissolved oxygen and greater thermal resistance than did the stream forms. It appears that this intermediate environment of the rice fields did not approach the critical levels of the different environmental factors of these common and widespread pond forms until the water was turned off near the end of the season.

DISCUSSION OF INJURY TO RICE BY LARVAE

Chironomid larvae have been known to damage rice in two ways. One form is the injury to the leaves which has been observed in different fields annually for several years.[19] This damage, which usually is confined to the leaves of slow-growing rice in the borrow pits, has been described under the discussion of *Cricotopus sylvestris* (Fabr.). The other type of larval damage affects the germinating seed rice. The feeding larvae destroy the soft apical meristem of the developing seedling as it emerges from the seed coat and in many instances they burrow into the seed at the point at which the seed coat was ruptured. Risbec (1952) observed this type of destruction of rice seedlings by *Cricotopus trifasciatus* Panzer in France. As mentioned earlier, losses of rice

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[19] From conversation with Dr. W. H. Lange, Jr., Department of Entomology, University of California, Davis, California.

seedlings from this form of injury were reported in 1953 and 1954 near Stockton, San Joaquin County.[20] At that time larvae taken from germinating rice seeds were identified as *Cricotopus sylvestris* (Fabr.). Later examination of some of the larvae taken out of the rice grains showed that in addition to *Cricotopus sylvestris*, larvae of *Tanytarsus* n. sp. 5 and *Paralauterborniella* sp. also had invaded the seeds.

Seed sample trays were placed in the four fields under investigation in 1958 in an attempt to learn the extent of the damage to germinating rice caused by midge larvae. As previously mentioned under "Materials and Methods," each sample tray contained three dishes of viable seeds and three dishes of heat-killed nonviable seeds. The sample trays were placed in the three fields north of Sacramento on May 19, 1958, approximately two weeks after flooding and ten days after the field had been seeded. On May 23, 1958, approximately two weeks after flooding and one week after seeding, the sample was placed in Field H near Davis. At intervals of one, two, and three weeks, two dishes, one of viable and one of nonviable seeds, were removed from each plot. These were taken to the laboratory and the seeds were examined for evidence of damage by the larvae. Unfortunately the sample tray in Field F north of Sacramento was removed by the owner of the field and dumped on the check bank after being in place for one week. However, the results of all four plots after the first week, and of the three remaining plots for the subsequent examinations were consistent. In all there was a high percentage of germination of the viable seed. All of the dishes contained large numbers of larvae. These were predominantly *Tendipes attenuatus* with *Procladius culiciformis* second in abundance under the mud in the dishes. Several species of *Tanytarsus, Paralauterborniella* sp., and *Cricotopus sylvestris* larvae occupied tubes on the surface of the mud, the edges of the dishes, and even on the outer surface of the rice seeds, but there was no invasion of any of the seeds. At the first week's examination the heat-killed seeds had a definite odor of fermentation which became worse as the seeds burst and deteriorated. Even in these damaged seeds, there was no sign of larval invasion.

SUMMARY AND CONCLUSIONS

A review of the literature revealed no studies in this country and relatively few in Europe and Asia concerned with chironomids and their relationships in rice fields. Several investigations have dealt with the immature stages in shallow ponds and marshes which were similar in some respects to rice fields. The latter aquatic environment, however, differed from typical ponds or marshes because of the variable and continual flow of the water, the extremely dense emergent vegetation, and the fact that the rice fields were flooded during the summer months whereas intermittent ponds and marshes contained water only during the winter and early spring. The conditions of water movement in rice fields were most closely approximated by those of stream backwaters, yet this natural habitat did not completely duplicate the combination of environmental factors of the temporarily flooded fields. Consequently the present study was initiated in order to obtain information concerning the family Chironomidae in this unique aquatic environment.

[20] Personal correspondence with Mr. R. S. Baskett, Farm Advisor of San Joaquin County, California.

The field work of this study was conducted in rice fields of the southern Sacramento Valley. The water used in most of the fields was pumped from the Sacramento River. Although subject to slight variation, this water was moderately hard with pH values ranging from 6.9 to 7.2. Results of comparative tests showed that variations in total hardness and pH of water from different fields were more dependent upon the original source of water than on seasonal changes occurring within each field.

Water temperature readings followed the same seasonal trend in all fields. The greatest fluctuations were observed immediately after flooding. The highest maximum readings were recorded near the end of June and early in July. Following these, the water temperatures gradually declined until the fields were drained in September.

From early May until the rice emerged from the water, the rice fields resembled large shallow lakes with masses of bladder-like *Gloeotrichia* floating on the surface. The dissolved oxygen values of the water were highest at this time. Photosynthetic activity of phytoplankton was largely responsible for the observed dissolved oxygen cycle. This was indicated by the decrease in oxygen following the growth of rice and other vegetation which shaded the water, and by the fact that the diurnal fluctuation of the dissolved oxygen values was greater than that observed throughout the season.

Plankton movement in rice fields was essentially the same as that recorded for sluggish streams.

A considerable variation in soil fertility existed between the different fields. First-year fields were consistently more fertile than older fields. Apparently this difference in fertility was responsible for the variation in species of aquatic and semiaquatic plants occurring in fields of different ages. Although a greater number of species of algae was recorded from first-year fields than from second-year fields, a similar succession in species occurred in both. No evidence of algal toxicity was observed. Results of chemical analysis of water showed no correlation between several chemical constituents and the age of the field.

First-year fields supported both a greater number of species and a greater number of individual chironomids than did the older fields. No correlation was found between field age and any of the physical-chemical properties of the water. It was concluded that the more fertile first-year fields provided more food for the developing larvae than did the older fields. In addition, it was believed that possibly the fauna of the first-year fields was less stabilized or fixed than that of the second-year fields. Thus the species which became established faced less competition for the different ecologic niches within these new fields than they did in the older fields.

Several taxonomic difficulties were encountered in the present investigation. These all involved the confusion of two or more species in their different life history stages. A thorough taxonomic study of such groups as the *Pentaneura* complex, the *Paralauterborniella* complex, and the larval stages of the subgenus *Dicrotendipes* is needed. This should utilize larval chromosome or biochemical characteristics and relate these to morphological differences.

A key to the adults of the 36 species of midges which were taken in or near the rice fields is included in the present work. Of this number, 12 species

either were new or had only manuscript names at the time the study was conducted. Thirty species were definitely recorded from the rice fields. Eighteen of these were considered rare because fewer than 20 individuals of each were taken from the fields in two seasons of work. Keys are presented to the species of those larvae and pupae which were reared to adults. The key to the pupae also includes those species determined by relating the pupal exuviae in the emergence traps to the adults which had emerged from them.

The rice fields became populated with chironomids both by larvae which were carried by the water at the time of flooding and from eggs deposited by females which had emerged from neighboring canals. Early in the season larvae of several species occupied all the microhabitats and were found in fairly uniform numbers throughout a field. Many of the smaller tube-dwelling forms were inside the *Gloeotrichia* and on the decaying cover crop as well as the surface of the mud. Larger species of "blood worms," particularly *Tendipes attenuatus*, dominated the subsurface mud and ooze. Active predators such as *Procladius culiciformis* larvae also were present in these different microhabitats feeding on the tube-dwelling species.

When the rice emerged from the water there was no longer a uniform distribution of larvae. During the rest of the season most of them occurred on and under the submerged vegetation in the relatively open water of the channels and borrow pits. Individuals were seldom taken from beneath the dense rice. It was believed that some open water was necessary for successful oviposition by the adult females.

There was evidence of a temporal difference in the activities of the adults in that several species were attracted to light much later than most other species of chironomids. Mating swarms of most species were observed in the evening twilight and in the early morning hours. Swarms containing several species were common at both times. Some of the smaller species swarmed in the bright sunlight during the day. The difference between the observed altitudes of swarms of larger midges and those of the smaller species was interpreted as a greater tolerance of wind by the larger, higher flying forms.

No correlation was found between the water temperature and either the number of species or the number of individuals which emerged during the rice season. From the evidence recorded in this study, any relationship between water temperature and numbers of midges emerging was believed to be indirect.

A direct correlation was observed between the amount of submerged aquatic plant material and the abundance of chironomids. Neither host specificity nor any obligatory food relationship was noted. The principal importance of this underwater vegetation appeared to be the provision of surface area or additional living space.

Although populations of midge larvae dominated the various microhabitats of the rice fields, only 12 species were responsible for this position of prominence. By far the most numerous of these were the tube-dwelling species of the tribe Tanytarsini in the subfamily Chironominae. These were primary consumers whose numbers were largely dependent upon the crop of diatoms and other phytoplankton which collected as periphyton on the surface of the submerged aquatic plant material and the bottom. Another reason for the

abundance of *Tanytarsus* larvae was the parthenogenetic development observed in at least one species. Four species of active, free-living larvae were known predators. There was evidence that some members of the subgenus *Cryptochironomus,* although tube dwellers, were also partly predaceous in food habits. The difference in time of development and emergence of the adults appeared to minimize competition between the larvae of the two species in the genus *Cricotopus.* However, the question of interspecific competition among several chironomids existing in the same microhabitats was unanswered.

Seed tests conducted in this study showed no larval damage or invasion of rice seeds by any of the species inhabiting the rice fields. *Cricotopus sylvestris* was the only species observed feeding on the tissues of higher plants. These larvae channeled into the leaves of late emerging rice and caused considerable damage to the individual plants. As long as the leaves remained prostrate and floating upon the water surface, they were subject to attack. This harmful activity usually was not extensive because it was confined to those plants growing in the thin soil and deeper water of the borrow pits. However, the larvae of *Cricotopus sylvestris* apparently thrive in the cold water early in the rice season and conceivably could cause considerable economic loss if the rice were planted earlier than usual or if abnormally cool weather retarded its growth.

All the larvae and pupae remaining in the fields after they were drained died of desiccation. All of the species represented in the rice fields overwintered as larvae in the canals and ditches where they occupied microhabitats similar to those utilized during the summer in the fields.

The fact that most of the species of chironomids taken in rice fields were represented by a small number of individuals indicated that it was relatively difficult for them to become established. The few species responsible for the large populations were common, widely distributed forms. Most were characterized by extensive ranges of tolerance for different environmental factors present in ponds or other standing water. Thus, they encountered few difficulties in this intermediate type of temporary environment. They were able to become established as soon as the fields were flooded and to occupy most of the microhabitats with little or no competition from the more sedentary or less tolerant forms.

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