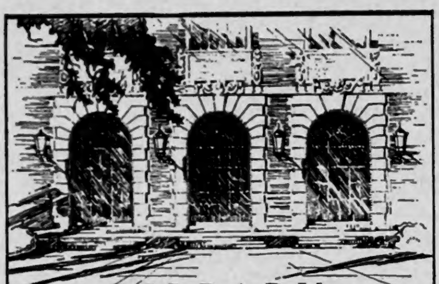

May, 1958

BULLETIN

of the

ILLINOIS NATURAL HISTORY SURVEY

HARLOW B. MILLS, *Chief*

Contents and Index

Volume 26

1953–1955

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STATE OF ILLINOIS

WILLIAM G. STRATTON, *Governor*

DEPARTMENT OF REGISTRATION AND EDUCATION

VERA M. BINKS, *Director*

Urbana, Illinois

STATE OF ILLINOIS
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Illinois Natural History Survey

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*Employed on co-operative projects with one of several agencies: University of Illinois, Illinois Agricultural Extension Service, Illinois Department of Conservation, United States Army Surgeon General's Office, United States Department of Agriculture, United States Fish and Wildlife Service, United States Public Health Service, and others.

This paper is a contribution from the Section of Publications and Public Relations.

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EMENDATIONS

Page 7, column 2, lines 30 and 31. This observation is incorrect. The subimagoes alight to shed their skins.

Page 55, column 1, line 30. *For* There are two long caudal filaments *substitute* There are three long caudal filaments.

Page 144, column 2, page 146, and following pages, *Metreturus*. *Metreturus* is a synonym of *Acanthametropus* Tshernova, described in Russia in 1948. The publication in which the description appeared was not available in the United States at the time Dr. Burks wrote *The Mayflies of Illinois*.

Page 287, column 2, line 9 below tables. For *Endoconiodiophora* substitute *Endoconidiophora*.

Page 308, column 2, line 10 of text matter. *For* Orthropidae *substitute* Orthoperidae.

Page 413, column 1, line 22. For *Virburnum* substitute *Viburnum*.

Page 420, table 14. For *Croton glandulosus* substitute *Croton glandulosus* var. *septentrionalis*.

Page 424, table 14. For *Solidago missouriensis* substitute *Solidago missouriensis* var. *fasciculata*.

Page 440, column 2, line 18. *For* weed *substitute* wort.

Volume 26, Article 1 Urbana, Illinois May 1953

BULLETIN
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The Mayflies, or Ephemeroptera, of Illinois

B. D. BURKS

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*Employed by the Illinois Department of Conservation and assigned to the Natural History Survey for administrative and technical supervision.

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This paper is a contribution from the Section of Faunistic Surveys and Insect Identification.

(58256—3M—10-52) 2

FOREWORD

ALMOST a century ago, Benjamin D. Walsh, the first State Entomologist of Illinois, became interested in the mayflies or shadflies of the area about his home in Rock Island. Since his first observations and writings concerning these insects, a great deal has happened to the Illinois environment, and great advances have been made in our knowledge of this interesting part of our native fauna. The following treatise by Dr. B. D. Burks, formerly of the Natural History Survey, brings our knowledge of this group up to date.

Mayflies are of importance to people in many ways. One of the most obvious is the swarming and massing of some species in such strategic places as river bridges, where at times the bodies of countless millions form barriers or hazards to traffic. But these dramatic occurrences are far from the most important aspects of the lives of mayflies.

As a part of the biological complex of our waters, for all mayflies are aquatic in their developmental stages, these insects find their most important place in human economy and interest. They are an important link in converting microscopic food organisms and vegetable detritus into units large enough and of proper character to be of value to our predatory fishes. This fact has been employed by fly tiers in the design of certain artificial lures intended to be attractive to certain fishes.

Furthermore, mayflies may be characteristic of certain types of waters. Dr. Burks has listed a dozen different habitats, with species typical of each. This association of insect with habitat is of importance to all workers interested in our fresh waters, as the mayfly species which are present in a given body of water may indicate the condition of that water and therefore its usefulness for domestic or industrial purposes. When Walsh studied the mayfly populations in the Rock Island area, he found a considerably different species complex from that existing in the area now. In spite of much careful collecting in the Rock Island vicinity, Dr. Burks could recover only 8 of the 31 species which Walsh recorded from there. This recovery represents only about 26 per cent of the mayfly fauna present before the damming, dredging, siltation, and addition of pollutants which characterize these waters now. It was necessary to extend the search into less modified waters in order to rediscover some of the other species with which Walsh was familiar.

And then there is the peculiarness, the uniqueness, of this archaic group of insects, of interest to all who profess a delight in nature. In this group, as seldom found in an aggregation of related animals, there is a great divergence from that which we consider to be the accepted pattern. The morphology of mayflies is reminiscent of the morphology of insects which disappeared many millions of years ago and which are now known only through fossil remains. The adult stage has become a mere vestige, lasting usually but a very few days at the most. The life span is consumed almost entirely by the developmental stages under water. All of the eating is done during this growth period; the adults have useless mouthparts and digestive systems. Of all of the winged insects, mayflies are the only ones which shed their skins after they have developed wings with which they can fly. And a few species reproduce their kind without ever attaining the true adult stage!

Thus, we find that mayflies are important not alone to harassed highway maintenance men and press photographers. They are much more so to those entrusted with the well-being of our fish populations, those interested in the public health and other values in inland waters, and those interested in the peculiarities of nature.

Dr. Burks, who prepared the following treatise, obtained the B.A. degree in 1933, the M.A. in 1934, and the Ph.D. in 1937, all from the University of Illinois. On July 1, 1937, he joined the staff of the Natural History Survey. But for short leaves during which he assisted at the United States National Museum, and leave for military service, he remained in the employ of this Survey until May 21, 1949. At that time, he resigned to take a position in the Division of Insect Identification with the United States Department of Agriculture in Washington, D. C.

A number of people have been of assistance in the preparation of this manuscript. We are especially indebted to Dr. Carl O. Mohr for his excellent illustrations, to Mrs. Elizabeth Maxwell for the preparation of many of the line drawings, and to Mrs. Leonora K. Gloyd for her careful and painstaking work in the later stages of preparation of the manuscript for publication.

For permission to use figs. 88, 188–192, 218, and 300, most of them redrawn without appreciable change from Traver in *The Biology of Mayflies,* we are indebted to the Comstock Publishing Company. For loan of critical material for study, we are grateful to Dr. Henry Dietrich of Cornell University, Dr. Joseph C. Bequaert of the Museum of Comparative Zoology, Harvard University, Dr. C. E. Mickel of the University of Minnesota, and Mr. W. J. Brown and Mr. G. P. Holland of the Canadian National Museum.

HARLOW B. MILLS, *Chief*
Illinois Natural History Survey
Urbana, Illinois

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The Mayflies, or Ephemeroptera, of Illinois

B. D. BURKS

MAYFLIES or shadflies are a group of insects constituting the order Ephemeroptera. In the young or nymphal stages, they live in the water of ponds, lakes, or streams, where they can be found under rocks or logs, in the mud at the bottom, or occasionally swimming about. When the nymphs are full grown, they come to the surface of the water and transform into free-flying aerial insects. As such, they are familiar to many fishermen and nature lovers.

In Illinois, a few large, conspicuous forms come to general attention every year when they emerge on warm midsummer evenings in enormous numbers from our larger lakes and rivers. However, these constitute only a relatively small part of the mayfly fauna of the state. Other forms are to be found emerging at various times of the year from all the relatively permanent and unpolluted bodies of water, including ponds, lakes, brooks, creeks, and rivers.

The mayfly may be distinguished readily from all other aquatic insects. The nymph has a definite head, thorax, and abdomen. It has three pairs of well-developed legs, a pair of gills on each of the middle abdominal segments, and either two or three long "tails" (called caudal filaments) extending from the posterior end of the body. It more closely resembles the stonefly nymph than any other nymph but differs from it in having gills on the middle abdominal segments.

Unlike most insects, the mayfly typically has two winged stages. It is the only existing insect that molts after getting functional wings. The first winged stage is called the *subimago,* which is actually a subadult stage; soon after it is formed this subimago (in most species) molts to form the true *adult* or reproductive stage, sometimes called the *imago.* In a very few species, noted later, which never develop to the adult, the female lays her eggs while in the subimago stage.

The subimago is very similar to the adult in appearance, but the body and all appendages are incased in a transparent skin or pellicle. The adult has its mouthparts and alimentary system represented by only minute, distorted vestiges; it usually has two pairs of extremely thin and papery, triangular wings (the posterior pair being much smaller, or lacking in a few species), which are held upright and not folded above the back when the insect is at rest. As in the nymph, the adult has two or three long, well-developed caudal filaments; if the median one appears to be lacking, it will be found on close examination to be represented by at least a small rudiment.

There are over 550 different species of mayflies known for North America north of Mexico. This report includes 48 genera and 222 species, with Illinois records of 126 species, 15 of which are described as new.

Importance of Mayflies

Although, at times of unusual abundance, the adults of a few species may swarm to lights and become an expensive nuisance in towns and cities near rivers and lakes, mayflies are, on the whole, harmless and gentle creatures. Some species apparently do not even indulge in the activity of swarming. The nymphs are likewise innocuous except in two exotic species of *Povilla.* One species of this genus, found in the East Indies, bores into wood submerged in fresh water, often seriously weakening or destroying piles and other wood structures; the other, occurring in the Belgian Congo, bores into freshwater sponges.

Occasionally, over a period of years, adult mayflies have caused damage in certain local areas. Unusual hordes of these insects may leave the water on the first suitable day after adverse weather conditions, or other

PHOTOGRAPH FROM WORLD WIDE PHOTOS.

Fig. 1.—The picture above was published in the *Chicago Daily News* on July 8, 1946. It carried the legend: "May flies stop motorists. Lawrence Rutz stops his truck on the west channel bridge at La Crosse, Wis., yesterday to clear May flies from the front of the vehicle. The insects got so thick they obstructed the view of the driver, clogged radiators and made roadway of the bridge slippery."

rare circumstances, have interfered with the normal rhythm of successive-day emergence. A few of the larger species have

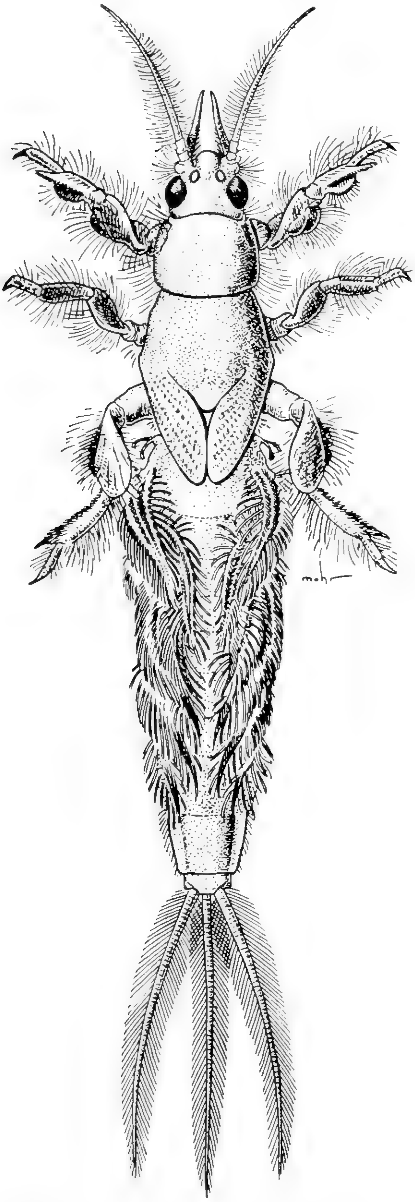


Fig. 2.—Nymph of *Hexagenia limbata.*

been known to form dense clouds and to settle in great drifts over roads, bridges, and streets. These fragile insects die within a few hours, and when occurring in such hordes their dead bodies may clog ventilator ducts and sewers and may also cause temporary traffic difficulties, fig. 1. On July 23, 1940, the Associated Press carried the following dispatch:

"Sterling, Ill.—Shadflies that in some places piled to a depth of four feet blocked traffic over the Fulton-Clinton highway bridge for nearly two hours last night.

"Fifteen men in hip boots used shovels and a snow plow to clear a path. The bridge appeared to be covered with ice and snow. Trucks without chains were unable to operate until most of the flies had been shoveled into the Mississippi river."

In both aquatic and terrestrial stages, figs. 2 and 3, mayflies achieve their chief importance as food for other animals. They are preyed upon by birds, fish, amphibians (frogs and salamanders), spiders, and many predaceous insects. It is as a natural food for fish that they are of primary economic value.

The first extensive observations on the role of mayflies as fish food were made by Forbes (1878–1888). They were based on examinations of the stomachs of Illinois fishes. Since the observations by Forbes, many contributions to this subject have been made by many authors, but no attempt is made here to collate the material in the limnological literature.

In general, it has been found that the diet of fishes consists of the most readily available suitable food. Consequently, fish of the same species in a body of water will be found to have quite different organisms in their stomachs at different seasons of the year. At certain times of year, mayflies are abundant in lakes or streams, and at these times are readily eaten by fish. Both adult and nymphal mayflies are eaten by the fish, the adults either when molting at the surface of the water, or when alighting later to lay eggs.

Mayflies have been found in the stomachs of most species of the larger Illinois fishes, including all the sport fishes, such as crappies, bass, and various other types of sunfish. There is little doubt that fish of many species feed extensively on mayflies, and that, at times of great mayfly emergence, the fish of a considerable number of species subsist chiefly on these insects.

That fish will consume mayfly nymphs readily was shown in an interesting way in New Zealand. The New Zealand mayflies had evolved over a long period in streams which did not contain game fishes. As a result, the nymphs of such forms as *Oniscigaster wakefieldi* McLachlan, instead of remaining concealed beneath rocks and debris as our American mayflies do, swam freely in the open water. Shortly after the turn of the century, brown trout and rainbow trout were introduced into the New Zealand streams to provide game fishing. The trout ate the mayfly nymphs in such numbers that within about 20 years the once extremely abundant mayflies had become almost extinct. Tillyard (1926:64) states, "The introduced trout have greatly reduced this once abundant fauna [of mayflies] and some species are now extinct, or nearly so . . . . The mayfly fauna of Australia and New Zealand is not specialized to hold its own against the introduced brown and rainbow trout and is rapidly being reduced to a minimum."

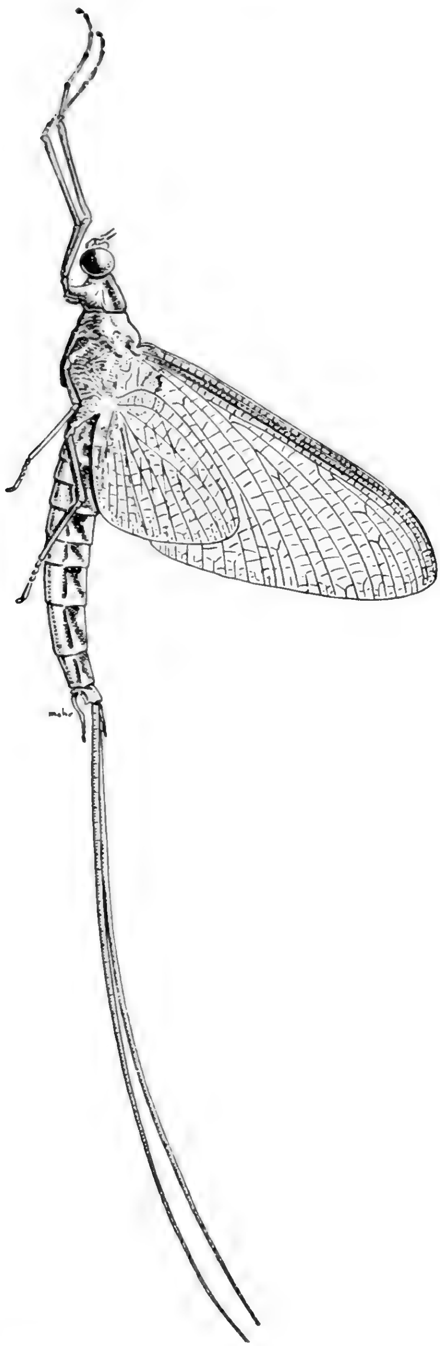


Fig. 3.—Adult male of *Hexagenia limbata.*

Habitat Preference

Some species of mayflies may develop in a variety of situations, but most species are restricted to definite types of aquatic habitats. The various types of mayfly habitats found in Illinois and the species which have been observed to be characteristic of them are as follows:

1. Large, relatively slow rivers, such as the Mississippi, Ohio, and Illinois: *Hexagenia bilineata* and *limbata, Pentagenia vittigera, Tortopus primus, Potamanthus myops* and *verticis,* and *Ephoron leukon* and *album.*

2. Moderate-sized, fairly rapid rivers, such as the Kankakee, fig. 4, and Rock: *Hexagenia rigida* and *limbata, Potamanthus myops* and *verticis, Ephoron leukon* and *album, Ephemerella dorothea, invaria,* and *simplex, Baetisca bajkovi, Pseudiron centralis, Siphloplecton interlineatum, Stenonema* spp., and *Heptagenia* spp.

3. Small rivers or creeks with fairly rapid flow, such as the Salt Fork River and Lusk Creek: *Ephemera simulans, Hexagenia atrocaudata, Ephemerella frisoni* and *needhami, Baetisca laurentina, obesa,* and *bajkovi, Oligoneuria ammophila, Paraleptophlebia praepedita* and *ontario, Ameletus lineatus, Isonychia sicca, bicolor,* and *rufa, Centroptilum walshi* and *rufostrigatum, Baetis spinosus, propinquus, harti, pygmaeus, frondalis, pallidulus,* and *intercalaris, Pseudocloeon punctiventris, dubium, parvulum,* and *veteris, Stenonema* spp., and *Heptagenia* spp.

4. Sluggish creeks or small rivers with a great deal of silt, constituting the majority

of the streams in central Illinois: *Stenonema tripunctatum.*

5. Permanent or semipermanent brooks with rapid flow, such as the spring-fed stream in the Botanical Gardens near Elgin or the spring-fed tributaries of Lusk Creek and Gibbons Creek in southern Illinois, fig. 5: *Paraleptophlebia moerens* and *praepedita* and *Baetis vagans.*

6. Relatively permanent ponds, many of which are found in Lake, Cook, and Du Page counties, almost always in woods: *Callibaetis skokianus, ferrugineus, and fluctuans.*

7. Temporary ponds, which are commonly found in central Illinois in the springtime: *Leptophlebia nebulosa* and *cupida.*

8. Small, temporary pools, usually along the margins of streams, which have greatly reduced current or no current: *Siphlonurus marshalli, Tricorythodes* spp., *Caenis ridens* and *hilaris, Leptophlebia cupida, Habrophlebiodes americana, Callibaetis fluctuans,* and *Cloeon mendax, rubropictum,* and *simplex.*

9. Stagnant bodies of water, such as the vegetation-choked backwaters of streams or bogs: *Caenis simulans.*

Fig. 4.—Kankakee River at Aroma Park. Habitat of *Ephemerella needhami, Baetisca bajkovi* and *laurentina, Pseudocloeon dubium, Baetis spinosus, Stenonema integrum* and *bipunctatum.*

Fig. 5.—Gibbons Creek at Herod, from which *Ameletus lineatus* emerges in early spring. In late spring, *Baetis herodes* and *Leptophlebia cupida* emerge here. *Stenonema tripunctatum* emerges here throughout spring and summer months.

10. Large lakes, represented by Lake Michigan: *Ephemera simulans.*

11. Small, relatively shallow glacial lakes, such as those found in Lake County: *Ephemerella lutulenta* and *temporalis.*

12. Small, temporary brooks, which flow into larger streams in late winter and early spring. This type of stream may furnish a habitat favorable for an occasional small nymph of *Stenonema* or *Caenis* but no mayfly has been found to mature in such a place. Stoneflies and craneflies, however, often occur abundantly in these streams.

Another category might have been made for the various bodies of impounded water which now exist in considerable numbers in central and southern Illinois, but no mayfly can be said to be characteristic of such bodies of water. Mayflies that occur in such waters indicate the ecological characteristics of the individual impoundments. Some of these impoundments are stagnant and produce large flights of *Caenis simulans* only; others apparently have the characteristics of a large, slow river, and produce flights of *Hexagenia bilineata* or *limbata.*

Life History

Mayfly nymphs require a relatively long time to develop from egg to full-grown nymph. The shortest known length of nymphal life is in species of the genus *Callibaetis* which, in summer, mature from egg to adult in 5 to 6 weeks. Some of the smaller baetines require 4 to 5 months, a length of time that results in the production each year of two waves of adults for a species, one in early spring, the other in late summer or early autumn. Some, as was shown by Murphy (1922) for *Baetis vagans,* have a complex, overlapping series of broods. The summer brood matures in 6 months, the winter brood in 9. The large ephemerids, such as *Hexagenia,* figs. 2 and 3, require 2 years to mature; the annual appearance of a given species in a locality is due to overlapping broods of the species. Many other mayflies, such as *Stenonema* and *Heptagenia,* emerging as they do year after year in the same locality at about the same dates, may be inferred to require 1 year to mature from egg to adult.

During nymphal life, the developing mayfly passes through a very large number of instars. *Baetis vagans,* which has a relatively short nymphal life of 6 to 9 months, passes through 27 instars (Murphy 1922). Other mayflies, such as *Callibaetis,* have been estimated to go through about 20 nymphal instars (Needham *et al.* 1935:15).

Stenonema possibly has 30 nymphal instars. *Hexagenia,* with its 2-year life cycle, has an unknown but quite large number of nymphal instars. Mayfly nymphs have been observed to grow relatively little during each stadium.

The developing adult wings, eggs, and genitalia can clearly be seen inside the later nymphal instars. Feeding terminates with the next to the last nymphal instar. When the last nymphal instar is reached, development of the adult structures is almost complete. During the last instar, the nymph is quiescent, and the alimentary canal degenerates rapidly. The vestigial mouthparts and short antennae of the adult can clearly be seen developed beneath the nymphal cuticle.

In such forms as *Hexagenia,* the mature nymph when ready to molt comes to the surface of the water, the nymphal skin splits rapidly, and the subimago emerges quickly. The subimago rests for a short time on the shed nymphal skin, which floats like a raft. Then it is ready to take flight for a place of safety. The whole process requires only about 2 minutes. This molt from the nymph to the subimago represents a very dangerous time in the life of the mayfly. Many mature nymphs, as they are swimming to the surface of the water to molt, and many more subimagoes while resting on their nymphal skins, are devoured by fish. Some, even as they take flight, fall prey to fish that jump out of the water to catch them. Some of the mayflies that elude their fish enemies at this time are likely, as they flutter up from the surface of the water, to be eaten by birds.

In other mayflies, such as *Isonychia, Ameletus,* and *Siphlonurus,* the nymph crawls out of the water onto stones, sticks, or other convenient objects, the nymphal skin splits, and the subimago emerges fairly slowly, the process requiring 3 to 5 minutes. The empty nymphal exoskeleton is left clinging to the support where the subimago emerged.

If the shed last nymphal skin is examined, it will be found to contain, almost intact, the nymphal structures for which the adult has no use. The nymphal mouthparts are complete and still contain some of the musculature in only a partly disintegrated state. The nymphal gills also are intact, even in such forms as *Isonychia,* which retain gill rudiments in the adult.

The subimaginal stage in most mayflies normally lasts 1 or 1½ days. This is subject to some prolongation at low temperatures. *Siphlonurus marshalli* requires 2½ days when the daytime temperature is from 45 to 50 degrees F. When daytime temperatures rise to 70 degrees F., the imago appears in 1½ days. During the subimaginal stage, almost 25 per cent of the body weight is lost, probably due principally to losses of water through evaporation and respiration. It can be shown that subimagoes must lose water before the adults can emerge, as subimagoes kept in a too-moist atmosphere are never able to emerge as adults. On the other hand, water loss must not be too rapid, or the subimagoes will die without producing the adults. My experience in rearing mayflies has been that relative humidity is the most critical single factor in the maturing of subimagoes to adults.

In some mayflies, such as *Ephoron, Tortopus,* and *Caenis,* the subimago stage is greatly abbreviated. In them, the subimaginal skin or pellicle is shed almost immediately after the emergence from the nymph. In *Ephoron* and *Tortopus,* which do not have functional legs in the adults, the males shed the subimaginal skins in flight, but the females remain as subimagoes. In *Caenis simulans,* I have observed the subimaginal pellicle to be shed in flight, but Needham (Needham *et al.* 1935:99) states that in *Caenis* sp. the subimagoes alight to shed the subimaginal skin. The observations probably were made on different species of the genus. At any rate, in the females of all species of *Caenis* which have been observed, the subimaginal pellicle is only partly shed, but in the males it is shed completely.

In the great Papuan mayfly of the East Indies, *Plethogenesia papuana* (Eaton), both males and females remain subimagoes, never attaining the adult stage. However, of the many preserved specimens of this species I have seen, the subimaginal pellicle is differentiated from the enclosed adult structures. The same is true of the subimago females of our American species of *Ephoron* and *Tortopus* which, as has already been mentioned, do not attain the ultimate adult stage.

By the time the subimago stage is reached, the eggs and sperm are already mature and can be stripped from subimagoes and mixed in normal saline solution, by which fertilization is accomplished. Nymphs can be hatched from these fertilized eggs. This has been done successfully with several species of mayflies, among them *Hexagenia limbata* and *bilineata* and *Isonychia bicolor.* During the subimago state, the degeneration of the alimentary tract becomes almost complete. This tract then becomes, in the adult male, fig. 3, only an air-filled and transparent sac which serves to make the body buoyant. In the female, the degenerated digestive tract is crowded and depressed by the eggs but, as eggs are expelled, it becomes inflated again, possibly aiding in the expulsion. It is the bursting of these inflated digestive tracts that produces the familiar popping noise living mayfly adults make when they are stepped on.

Most mayflies spend the subimago state resting in the shade among plants near water. In many species, the subimaginal pellicle is shed in the early evening hours and in others during the night. It is left behind as an extremely delicate and fragile skin adhering to the support the subimago has occupied. After this molt, adults of most species continue to rest quietly among the concealing vegetation until the next sundown; then the males swarm, mating occurs, and the females deposit all their eggs before midnight. In such forms as *Caenis* and *Ephoron,* which shed the subimaginal pellicle immediately after emerging from the nymphal stage, mating and egg laying occur within a very few hours of emergence, at most during the same night. In these forms, the total winged life is thus but a few hours. In most mayflies, however, the life in the winged stages endures for 2 or 3 days at summer temperatures. There are records in the literature of its being prolonged to 5 or 6 days, but such length of life is unusual, except in the females of *Callibaetis* and *Cloeon.* In these forms, the female adults have been observed to live from 1 to 3 weeks.

Mayflies deposit their eggs in the water in a number of different ways. In many baetines, such as *Baetis intercalaris,* the female crawls beneath the surface to oviposit on stones or other objects on the bottom. This phenomenon is often referred to in the literature, and I have observed it several times in Illinois. In many genera, such as *Ameletus, Siphlonurus,* and *Leptophlebia,* and in some species of *Stenonema,* the female flies near the surface of the water and dips the end of the abdomen into it at intervals, by this action permitting a few eggs to be washed off at a time, much as in the oviposition of some dragonflies. In other genera, such as *Ephemerella,* the female extrudes all the eggs during flight, and temporarily holds them in a mass beneath the recurved tip of the abdomen. As she flies along near the surface of the water, she darts quickly down to break the surface film momentarily, and drops the entire packet of eggs into the water. The eggs sink instantly and adhere to rocks or other objects on the bottom.

The female of other mayflies, such as *Heptagenia,* flies a short distance above the surface of running water, and then alights on the surface for a few seconds, permitting the current to carry her a short distance downstream. During this time, she extrudes a few eggs, which are washed into the stream. Then she flies up from the surface for a few minutes, returning again to it to deposit more eggs. This alternate flying and dropping of eggs continues until the female is spent, or, as I have seen so often happen, until some bird or fish eats her.

In most of the large Ephemeridae, such as *Hexagenia,* the female simply alights flat on the surface of the water, with wings outspread, and extrudes all the eggs at once in two elongate packets. These eggs sink almost instantly, and the female remains on the surface until she drowns or, more likely, is eaten by a fish.

The eggs of most mayflies hatch in from 1 to 2 weeks, depending on temperature, and nymphal development begins at once. In a few genera, however, such as *Ameletus* and *Siphlonurus,* the eggs, deposited in the spring, do not hatch until the following February or March. The long period before hatching is due to the fact that, during the summer and fall, the breeding sites for these genera become completely dry. The eggs of these genera evidently can tolerate such desiccation. Clemens (1922) pointed out this phenomenon for *Ameletus ludens* in New York, and his findings agree well with my own field observations made in Illinois.

Mayfly eggs are of a great variety of forms (Smith 1935: 67), but, characteristically, most possess long, coiled, adhesive filaments which serve to attach them to stones or other objects in the water.

Some mayflies, such as *Ameletus ludens* and *lineatus,* normally are parthenogenetic, males being either unknown or extremely rare. Some, such as species of *Callibaetis* and *Cloeon dipterum,* are said to be ovoviviparous. Edmunds (1945: 170) and Berner (1941: 32) have observed a process approximating ovoviviparity in species of *Callibaetis.* They found that the eggs are retained within the abdomen of the fertilized female for several days, during which time the embryos develop. Then, when the female alights on the surface of a suitable body of water, she expels the eggs, and the nymphs hatch within a few minutes.

Food Habits

With very few exceptions, the nymphs are herbivores or scavengers, living on vegetable detritus and microscopic aquatic organisms, principally diatoms. A few, such as those of *Isonychia,* are partly predaceous, eating apparently almost anything that comes within their grasp, including other mayflies. Others, such as the supposed nymph of *Anepeorus,* fig. 394, and the nymph of *Metreturus pecatonica,* fig. 312, have long, sharp mandibles which indicate that they are entirely predaceous in habit. In the subimago and adult stages, mayflies do not feed.

Emergence Peaks

The adults of many species consistently appear year after year in the same localities on about the same dates for those localities. The species of *Callibaetis,* which develop in ponds and woodland pools, emerge continuously throughout the open growing season from April to October, but they usually have a peak of emergence in late May or early June. Some species of *Baetis,* developing in small, well-aerated streams and along the margins of small rivers, have two peaks of emergence in a season, in late April or May and in August or September. Other species of *Baetis* have three peaks of emergence, in May, July, and September.

In *Hexagenia bilineata,* which develops in large, slow rivers such as the Mississippi and Ohio, the adults emerge in late June, in July, or, rarely, in August. The swarms which appear in mid-July are the largest. *H. limbata,* which may be found in the largest rivers but which prefers somewhat smaller ones such as the Kankakee or Illinois, emerges in greatest numbers in late June or July. *H. rigida,* restricted to fairly rapid, well-aerated rivers such as the Rock and Kankakee, appears in greatest numbers in June. *Pentagenia vittigera,* which seems to prefer large, slow rivers but is also known to develop in smaller numbers in a great variety of streams, emerges in greatest numbers in July or early August but never in such tremendous numbers as does *Hexagenia. Ephemera simulans,* which inhabits lakes with considerable wave action as well as fairly sluggish streams, emerges in greatest numbers in early June. It should be noted, however, that occasional specimens of all these larger ephemerines are to be taken from April to October.

Dispersal

Mating usually occurs between males and females from the same brood of a species, and oviposition most often is carried out in the same body of water in which the individuals have developed. From this fact, it would seem that the chances are rather small that new genetic factors will be introduced into a given mayfly population by cross-breeding with other populations. However, on exceptionally warm, humid summer evenings, females still carrying their egg masses will sometimes be found late at night flying to lights that are located several miles from any body of water in which they could have developed as nymphs. At times, the flight range of fertilized females may thus be fairly long. Evidently by means of long flights of such females, mayflies are able to establish themselves in new breeding grounds fairly far removed from their places of origin. As an example, a large swarm of adults of *Hexagenia bilineata* was observed to emerge from Lake Glendale, an impounded body of water in Pope County, on June 18, 1942. *H. bilineata* ordinarily is a large-river species, common in the Ohio River, 12 air-line miles from Lake Glendale. The Ohio River is the nearest known source of this species. Adults from the Ohio evidently had flown the 12 miles to Lake Glendale in the summer of 1940 and established a colony of nymphs there. The valve in the dam which formed Lake Glendale was closed in the autumn of 1939. This artificial lake is not, however, a very suitable place for the development of *bilineata*, and that species is not known to have developed there subsequently.

Many adult females of *Tortopus primus* were taken in a trap light in Urbana, on August 13, 1943. These females still carried their eggs. There is no locality where this species is known to breed within a radius of 20 miles from Urbana. The most likely source of this typically large-river species was the Vermilion River, 30 air-line miles away, or the Wabash River in Indiana, almost 50 miles away.

Fig. 6.—*Siphlonurus marshalli* adult being removed from a rearing pan.

Rearing Mayflies

Although the classification of the mayflies is based almost entirely on the adults, it is the nymphs which are most often taken in aquatic collecting or limnological work. In many instances, the generic and specific differences are much more distinct in the nymphs than in the adults. In order to be certain of their identity, it is necessary to rear the adults from the immature forms, but for most purposes of identification the association of mature nymph and adult is adequate.

The length of nymphal life is so long and the nymphs are so frail that usually mayflies cannot be reared from eggs to adults without great loss of life. If mature or nearly mature nymphs whose wingpads show signs of darkening can be collected for the purpose of rearing, the number of deaths can be greatly reduced. Such nymphs are in the last instar, or at most only a molt or two removed from it.

Mayflies which spend all or the latter part of their nymphal existences in still water can be easily and successfully reared from a late instar to the adult form in shallow pans. Such mayflies are *Callibaetis, Siphlonurus, Leptophlebia, Paraleptophlebia, Stenonema, Heptagenia,* all the Caenidae, most Ephemeridae, and some species of *Baetis*.

The rearing pans may be circular, flat-bottomed, enameled pans approximately 10 inches in diameter and 4 inches deep. A large, flat rock should be put in each pan and water from the place where the nymphs were collected added to a depth of not over 1 inch. The rock should be of a size to project partly above the water and thus provide a place on which an adult may emerge, fig. 6. A few rotting leaves or other detritus from the water where the nymphs were found should also be added to each pan to provide food. Care must be taken to have the pan, rock, and water all at the same temperature as the water from which the nymphs were collected.

The nymphs may be taken from the pool or stream with a dipnet, or simply picked off rocks or other objects submerged in the water. They must be handled with the greatest care, as they are easily injured, always with fatal results. They may be kept in glass jars or cap vials partly filled with water until they can be transferred to the rearing pans. These temporary storage jars or vials must be kept cool, preferably by being partly immersed in the water where collecting is being done.

An effort should be made to sort the nymphs to species, using the obvious characters that can be seen with a hand lens. Part of each collection of a species should be preserved in alcohol at the time the other specimens are placed in the pans for rearing. An accession number should be given to each lot of specimens so that the adults, when secured, can unquestionably be associated with their nymphs.

The rearing pans containing the nymphs should be covered with a screen-wire or cheesecloth top to provide a place for the adults to rest after they have emerged and, also, to prevent their escape. The pans can be transported to any convenient and suitable place for observation, but must be kept cool and protected from the direct rays of the sun. An outdoor, open-air insectary, if cool and shaded, is an ideal place for them. A cool basement also will serve. Many of the mayflies for this report were reared at the fish hatchery of the Illinois Department of Conservation at Spring Grove, Illinois.

If more than a day or two elapses between the time the living nymphs are collected and the time subimagoes begin to appear, it is advisable to change the water in the rearing pans. This can be done by dipping out part of the water in each pan and replacing it with aerated, unchlorinated water of the same temperature.

When the subimagoes emerge, each specimen should be removed to a cap vial or other similar glass jar in which one moderate-sized green leaf has been placed. The cap of this container must not make an air-tight seal. The subimago has to lose water during the subimaginal stage, but the loss must not be too rapid. The leaf will maintain the humidity at a satisfactory level, while the loose cover on the container will permit the loss of water vapor by diffusion. If water is allowed to condense on the inside of the container, the subimago will almost certainly die without shedding the subimaginal pellicle.

The subimaginal skin will be shed usually within 24 to 36 hours, although, at very low temperatures, the subimago stage may last 2 or 3 days. When the adults emerge, they should be killed and mounted on pins. Notes should be made on the colors of the eyes and body of each specimen at the time of its death. The shed nymphal and subimaginal exuviae should be preserved in alcohol and be given the same lot accession numbers as the respective preserved nymphs.

The reared adults should be studied carefully to determine if all the specimens in each lot actually are of but a single species. The nymphs associated with each lot should also be studied critically at this time to determine if a pure culture of a single species is represented. The nymphs, the nymphal and subimaginal exuviae, and the adults should now be clearly and permanently labeled in such a way that there will never be doubts, in the future, as to the correct association of nymphal and adult specimens.

Some mayflies, such as *Isonychia, Ephemerella, Ameletus,* some species of *Baetis,* and *Baetisca,* cannot be reared successfully in pans. However, they can be reared in screen-wire cages partly submerged in the waters in which the nymphs live. When the subimagoes appear in these cages, they can be removed to cap vials, where the adults will emerge. The only real disadvantage of this method is that it requires that much time be spent in the field and makes difficult the finding of the shed nymphal skins intact.

Phillips (1930) was able to rear most of the New Zealand mayflies in laboratory aquariums, but I have had very poor results in my attempts to rear Illinois mayflies by this method.

In the past, many associations of nymphs and adults have been made by the process of relating adults taken by sweeping vegetation around bodies of water with mature nymphs found in those waters at the same time. This method has led to so many misassociations that it should be followed only as a last resort, and the results should always be viewed with suspicion.

Collecting and Preserving

Both nymphs and adults must be collected very carefully if intact specimens are to be secured. The most valuable adult specimens are those reared from nymphs. Rearing not only yields a definite association of the nymph and the adult form but makes possible a collection of well-preserved specimens.

Collecting at lights will yield the largest number of adults. Although usually specimens taken at light traps are in very poor condition, some very worth-while Illinois records have been secured by these devices. Careful sweeping of the vegetation near bodies of water will yield much valuable adult material. Subimagoes secured by the same means should be placed in cap vials so that the adults can emerge a day or so later.

Experience has shown that adult mayfly specimens are best preserved dry, on pins. Each specimen may be pinned through the thorax from dorsum to venter with the wings spread in the conventional manner for entomological specimens, or it may be pinned on the side, with the wings to the left, the pin being inserted through the pleura of the thorax. The latter method is the more rapid, and the specimens, although perhaps not so neat in appearance, are more easily handled for study and can be stored in smaller space.

The wings may be spread during the drying process, without the use of a conventional spreading board, in the following manner. A square piece of 50-pound ledger paper, as large as the maximum wing expanse, when placed on the pin above the specimen will serve to hold the wings outspread at the proper angle during the 2 or 3 days required for drying. Another piece of the same weight paper of equivalent width, but twice as long, pushed up on the pin from below, will serve to hold the caudal filaments and fore legs at the proper extension. Extremely small specimens, such as those of most species of *Caenis,* may be mounted on card points.

If a long series of adult mayflies is available, it is desirable to preserve some dry and some in ethyl alcohol. Dry specimens retain their color characters longer than those preserved in alcohol. Specimens I have seen that were collected by Benjamin D. Walsh of Rock Island, Illinois, and preserved dry for more than 80 years show most of the color characters fairly well. In alcohol, the colors fade so rapidly that 10-year-old specimens in many genera are almost impossible to identify. Specimens in 85 per cent alcohol retain their color longer than those in 70 per cent alcohol, but, after storage in 85 per cent alcohol for several years, specimens become so hardened that it is almost impossible to make satisfactory slide mounts of the genitalia. Although alcohol is not satisfactory in some respects, it provides an easy method of preservation and permits compact storage of large series taken at one time and place, and, in some instances, is better for the study of structural characters.

No matter how preserved, the adult specimens are extremely fragile and must be handled with the greatest care. Specimens, whether dry or in alcohol, should be stored so that they are not exposed to the direct rays of sunlight, as light quickly bleaches them.

If it is ever desirable to preserve subimagoes, they may be preserved in 70 per cent ethyl alcohol, as the colors of subimagoes are usually unimportant. Then, at any later date, the adult genitalia of such specimens may be dissected out of the subimaginal pellicles and be cleared and mounted in the same fashion as those from any adult specimens.

Nymphal specimens may be picked from rocks or other objects in the water or collected from the water itself by careful dipping with an aquatic dipnet. In running water, large numbers of specimens may be secured if a seine or dipnet is held in the current and the rocks, gravel, and other objects on the bottom upstream from the net are carefully turned over. The nymphs will release their holds on these objects and the current will carry them into the net.

Nymphs and exuviae are best preserved in 70 per cent ethyl alcohol. Preserving mixtures containing acetic acid or glycerin should be avoided, as they eventually make the specimens so soft that the parts will not hold together. Glycerin also eventually turns mayflies almost pitch black. Formalin hardens specimens so much that it should not be used.

Collections of specimens in alcohol, if in vials with cork stoppers, will almost certainly have many losses due to evaporation of the alcohol. The use of red rubber stoppers in the vials will greatly reduce evaporation, but, even with the best care, specimens will occasionally be found to have dried out. Many dried specimens can, however, be partially restored by careful treatment with trisodiumphosphate (Van Cleave & Ross 1947). This method of restoration often makes it possible to identify nymphs which formerly had to be discarded.

Study Preparations

For a study of the male genitalia, slide mounts of these structures must be prepared with special care. I have used the following procedures in material examined in this report.

The entire mayfly is first relaxed and the caudal filaments removed but saved in case it should be necessary to study them later. Then the apex of the abdomen is cut off and cleared in cold 10 per cent potassium hydroxide for a period of 6 to 12 hours. After this treatment the dissection is placed in distilled water and any undisintegrated muscle or abdominal contents are carefully teased out with fine dissecting needles. The preparation is transferred first to 50 per cent ethyl alcohol and then through two changes of 70 per cent alcohol, being left in each not less than 15 minutes. A few drops of acidulated acid fuchsin are added to the last change of 70 per cent alcohol, and after a minimum of 15 minutes the preparation is removed to 95 per cent alcohol. In this alcohol the tenth tergite and the bases of the caudal filaments are dissected off so that they will not obscure the structure of the penis lobes in the finished slide. The genitalia are then left in the 95 per cent alcohol until all excess stain has been washed away.

The preparation is mounted, directly from the 95 per cent alcohol, in balsam. The latter is a special medium made by diluting standard, filtered Canada balsam with 10 per cent turpentine. A small drop of this medium is put on the slide and the stained genitalia preparation placed in it; the transferring is done with a hooked dissecting needle, not a pipette. This turpentine mounting medium dries slowly enough to allow ample time for orienting the dissection correctly on the slide. Each specimen is mounted with the genital forceps down, care being taken to mount all dissections as nearly as possible in the same position, for the structures of the penis lobes of a single species may look quite different if seen from different angles. The preparation is then placed in a dust-tight box to dry. It should be examined at intervals over a period of several days and the dissection straightened, if necessary, with a dissecting needle. The coverslip is not put on until the preparation is almost completely dry.

In this paper, the drawings of the male genitalia were, except in Leptophlebiidae, made from the dorsal aspect, that is, with the penis lobes above the genital forceps. In the Leptophlebiidae, the genitalia were drawn from the ventral aspect, so as better to show the ventral appendages of the penis lobes.

In many instances, it is necessary to make dry mounts of the adult wings so that the venation can be studied critically. If the adult specimen is preserved in alcohol, the mount can be made directly, but, if the specimen is dry, it must first be relaxed. The wings from the alcoholic specimen or relaxed dry specimen are then carefully dissected off with dissecting needles or knives. As these wings are extremely fragile, the operation must be done with great care. The wings can easily be removed by severing the muscles at the base of each wing.

The detached wings are carefully washed in a watchglass containing 70 per cent alcohol to remove any dust or debris. It may be necessary to use a fine camel's-hair brush to remove all the dust; the brushing must be done very carefully, else the fragile wings will be torn.

Next a drop or two of 70 per cent alcohol is placed on a clean microscope slide and the wings are floated onto it. They should be spread and arranged symmetrically, dissecting needles being used for the manipulation. Then, before the alcohol evaporates, a square, No. 1 thickness coverslip is put on. Coverslips three-fourths inch or seveneighths inch square will serve for most mayfly wings. The weight of this coverslip will serve to hold the wings flat and in place as the alcohol evaporates.

When most of the alcohol has evaporated, but the wings are still slightly damp, a narrow strip of gummed paper is moistened and affixed along each of the lateral margins of the coverslip. The strips of paper serve to hold the coverslip in place during the drying process. After the mount is completely dry (it is best to let the preparation stand 24 hours to be sure it is dry), strips of gummed paper are affixed to the top and bottom margins of the coverslip to make a permanent mount. Gummed paper having animal glue should be used, as it can be relied upon to adhere tightly to the polished glass surfaces for years. These slide preparations may then be studied and stored, as are the balsam mounts of the genitalia. They must, however, always be handled carefully, as the wings are most fragile after they are thoroughly dry.

Literature

The mayflies, in contrast with many other insect groups, are fairly well known for the world as a whole. The great majority of specimens of adults from anywhere in the world can be placed generically with the keys of Ulmer (1933, 1939). Generic keys to the nymphs of the world are not so readily available, but Ulmer (1940) keyed out many nymphs, and most of the faunal papers cited below include keys to nymphs as well as adults. The excellent monograph of Eaton (1883–1888) still serves for the generic and specific identification of the adults and nymphs of many forms from all parts of the world.

A great many papers have been published which include keys and descriptions of the species of a single country or region. Klapálek (1909), Ulmer (1924*a*), and Schoenemund (1930) published keys and descriptions for the German and central European species of mayflies. Kimmins (1942) treated the British species, Perrier (1934) the French, Grandi (1941–1951) the Italian, and Lestage (1928 *et seq.*) the Belgian. Chernova (1940) described and keyed the nymphs of the Russian species.

Barnard (1932, 1940) published on the South African species, Lestage (1925*b*) cataloged and described part of the North African species, and Ulmer (1930) published a paper on some Abyssinian species. Chopra (1927) published a comprehensive paper on the Indian species, while Traver (1939) considered species endemic to the Himalayan region. Phillips (1930) published a revision of the New Zealand species. Ulmer (1924*c*, 1939–1940) described the East Indian and Philippine species, Lestage (1921, 1924*b*) treated the species of Indo-China, while Ulmer (1926*a*) published a large paper on the species of China, and Uéno (1931) treated those of the Japanese fauna.

Traver (1938) published a work on the mayflies of Puerto Rico; she also (1944) treated many of the species of Brazil. Ulmer (1938) treated the Chilean species. Needham & Murphy (1924), Ulmer (1942–1943), and Traver (1946–1947) published major contributions on the South American and Central American species. Spieth (1943) made some taxonomic notes on several species from Surinam and other Neotropical localities.

The majority of the species of mayflies occurring in North America north of Mexico can be identified with the keys and descriptions of Traver (1935*a*). Despite the fact that some of the keys and many of the descriptions in her paper were compiled from the literature, and that various other workers have not agreed with her conclusions on a number of points, her work nevertheless remains the greatest single contribution yet made to the study of North American mayflies. This paper is especially valuable in that it brings together the great number of descriptions of North American species that appeared in the nearly 50-year period between 1888 (the time that Eaton's monograph was published) and 1935. McDunnough (1921–1943) published a long series of extremely valuable papers containing descriptions and illustrations of a great many of the North American species of mayflies. Berner (1940–1950) studied and keyed out the Florida species.

This list of works just cited does not, of course, constitute a complete bibliography of the world literature on mayfly classification, but it will serve to indicate the present extent of the comprehensive literature.

The Walsh Species

Benjamin D. Walsh became interested in mayflies and related insects about the year

Table 1.—Mayfly species described by Benjamin D. Walsh in 1862 and 1863, and status of lectotypes designated by Nathan Banks from specimens collected by Walsh and deposited by Herman A. Hagen in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

WALSH SPECIES	MCZ TYPE NO.	CONDITION	LABEL
SPECIES DESCRIBED IN 1862			
Baetis sicca	11248, ♂	Good	*B. sicca* ♂ Rock Island Walsh 672
*Potamanthus odonatus**	—	—	—
*Palingenia vittigera**	—	—	—
Palingenia flavescens	11252, ♂	Good	Rock Island Walsh 675
Palingenia pulchella	11251, ♂	Bleached; genitalia gone	Rock Island Walsh 677
Palingenia terminata	11253, ♂	Good	Rock Island Walsh 679
Ephemera flaveola	11210, ♂	Good	*E. flaveola* Rock Island Walsh 688
Ephemerella excrucians	11213, ♂	Good; genitalia on slide	*Ephemerella excrucians* ♂ Rock Island Walsh 691
*Ephemerella consimilis**	—	—	—
*Cloe ferruginea**	—	—	—
*Cloe fluctuans**	—	—	—
Cloe dubia	11214, ♂	Genitalia broken	Rock Island Walsh 700
Cloe mendax	11215, ♀	Faded	Rock Island Walsh 697
SPECIES DESCRIBED IN 1863			
Baetis interlineata	Undesignated	Good	*Baetis femorata* Say Rock Island 1863
*Pentagenia quadripunctata**	—	—	—
Heptagenia simplex	11250†	—	—
*Heptagenia cruentata**	—	—	—
Heptagenia maculipennis	11249, ♂	Badly broken	*maculipennis* ♂ Rock Island Walsh 683
Ephemera myops	11209**	—	—
Cloe propinqua	11218, ♂	Good	*Cl. propinqua* Walsh Rock Island, not Hagen 667

* Type material missing.
† Should be disregarded; see McDunnough 1929:179 and page 184 below.
** Should be disregarded, as specimen was collected in 1864.

1860. He amassed a large collection of mayflies, principally from and near his home at Rock Island, Illinois. He also collected a few specimens from Coal Valley Creek, a tributary of the Rock River, in Rock Island County; from the Des Plaines River near Chicago; and from southern Illinois, along the Ohio River. He preserved all the specimens dry, on pins, and made careful notes on the colors of the specimens while they were still alive or very shortly after their death.

By 1862, Walsh had segregated these mayfly specimens to genera and species, basing his determinations principally on Hagen's *Synopsis of the Neuroptera of North America* (1861). He published the results of these studies in 1862. In his paper, he described 26 species of mayflies, of which he considered 13 to be new; 7 he identified as species previously described by Say or Pictet, and the remaining 6 he questionably referred to species described by Say, Walker, or Hagen. He also described two new genera of mayflies in his paper.

Shortly after the publication of this work, Walsh sent duplicate specimens of most of these species to Hagen, then living and working in Koenigsberg, Prussia. Hagen examined these specimens and returned critical notes to Walsh concerning them. These notes were published (Hagen 1863) along with Walsh's further observations on the species, in the light of Hagen's comments (Walsh 1863). In this latter paper, Walsh described three additional new genera and five new species; he also provided new names for two species he had misidentified in his first paper.

Hagen did not return Walsh's duplicate specimens to him, but added them to his own collection. Walsh sent specimens of additional species to Hagen in 1864; these Hagen added to his collection. Later, in 1870, Hagen brought his collection to the United States and deposited it in the Museum of Comparative Zoology, Harvard University. In the meantime, Walsh had died, in 1869, and his collection, containing the types of all his mayflies, was deposited in the Chicago Academy of Sciences. In 1871, this collection was completely destroyed in the great Chicago fire. As a result, the specimens of Walsh's species in the Hagen collection, still preserved at the Museum of Comparative Zoology, became the sole remaining authentic representatives of those species.

It should be noted that, although the true types of Walsh's species are destroyed, most of the specimens of Walsh material now in the Museum of Comparative Zoology may be considered to be cotypes. Some specimens, however, were collected by Walsh after the descriptions were published, as is shown by the specimen labels, and these specimens are only autotypes. Lectotypes for most of Walsh's species of mayflies have been designated by Nathan Banks. A number of workers, myself included, have studied these specimens. Table 1 gives a list of the species described by Walsh and the present status of the lectotypes.

In addition to the species listed in table 1, the Museum of Comparative Zoology collection includes specimens determined and labeled by Walsh as *Baetis arida* Say, *B. alternata* Say, *Potamanthus cupidus* Say, *Palingenia limbata* Pictet, *Palingenia bilineata* Say, *Palingenia interpunctata* Say, and *Baetisca obesa* Say. All were collected by Walsh at Rock Island.

In collecting material for the present Illinois report on mayflies, we made a great effort to secure good series of all the Walsh species from the type locality. The results were somewhat disappointing, as, of the 31 species described or identified by Walsh, we were able to secure only 8 at Rock Island, even with intensive collecting. This is not surprising when it is realized that the rivers around Rock Island are now quite different than they were in Walsh's time. In the 1860's the Mississippi and Rock rivers at Rock Island were large, rapid rivers (Walsh 1863: 202). Since Walsh's time, extensive dredging, channel straightening, and damming operations have greatly reduced the rapidity of flow of these rivers. As a result, the Mississippi River at Rock Island is now ecologically more like a lake than a rapid river, and the Rock River is extremely sluggish. Changes in the rivers have produced a corresponding change in the local mayfly fauna.

In Walsh's time, also, it was the annual practice, in spring, to float log rafts down the Rock and Mississippi rivers to the saw mills located in Rock Island (Walsh 1862: 372; 1863: 202). These rafts originated in the pine forests of Wisconsin and Minnesota. Walsh noticed that large numbers of mature mayfly nymphs were brought down the river to Rock Island with these rafts. The nymphs, in the accumulated debris of the rafts, crawled out on the logs to molt. Walsh collected much of his material from these log rafts. Needless to say, this source of specimens long since has disappeared from Rock Island.

Although we collected only 8 of Walsh's species at Rock Island, we ultimately secured 27 of his 31 species by searching in other localities. Most of the specimens we took at various points on the Rock River upstream from Rock Island, notably at Prophetstown, Dixon, Sterling, Oregon, and Rockford. Some also we took in southern Illinois at Mount Carmel, on the Wabash River.

Of the Walsh species which have not been collected again in Illinois, *Ephemerella excrucians* has recently been reared in northern Michigan (Leonard 1949: 158). *E. consimilis,* based on a very brief, comparative description, and unrepresented in the Museum of Comparative Zoology collection, has of necessity remained unrecognized. Walsh identified Rock Island specimens as questionably belonging to two species described by other authors: *Baetis debilis* Walker and *Cloe unicolor* Hagen. The former has been shown by Eaton (1885: 253) to be a misidentification, but exactly what species Walsh had cannot now be determined. The latter was an identification of a Hagen species which is itself unrecognizable today. As we lack the original material, what species Walsh ascribed to the name *unicolor* cannot be ascertained with any degree of certainty.

External Morphology

The external features of both nymph and adult mayfly are described in detail in *The Biology of Mayflies* (Needham *et al.* 1935). Only those characters used in identification of Illinois species are mentioned here.

Many of the morphological structures which have proved useful in classification are shown in fig. 7 of a generalized mayfly adult and in fig. 8 of a generalized nymph. The terminology for the adult thorax is essentially the same as that used by Velma Knox (1935). The location of the various margins and areas of the wings is illustrated in figs. 7 and 9. The disc of the wing is the middle part, bounded roughly anteriorly by R_1 and posteriorly by Cu, but not including the marginal or extreme basal areas. The spines on various parts of the penis valves which have proved of diagnostic value, and their locations, are shown in fig. 10, of the generalized male genitalia.

All mayfly nymphs are strictly aquatic and respire by means of gills, which vary greatly in size and form in different species. Typically, there is one pair of gills on each of the first seven abdominal segments. They may be lamelliform (platelike), filiform (threadlike), or a combination of these two forms, figs. 51–55, 91*a–d*, 96, 113, 172, 199, and others.

When mayflies first emerge as winged insects, in the subimago stage, the surfaces of the semiopaque wings are covered with microtrichia; the wing margins and the caudal filaments are clothed with numerous long, slender setae. Beneath the subimaginal pellicle the adult eyes, legs, genitalia, and caudal filaments can be seen, contracted and wrinkled. Most mayflies remain in this stage about a day before shedding the subimaginal pellicle. Immediately following, the legs in most species and the caudal filaments become greatly lengthened and the eyes of the males greatly expanded; the wings are clear and hyaline, and they lack microtrichia and marginal setae. In a few mayfly adults, the legs are aborted, while, in some others, they are so greatly reduced as to be useless. Although mayflies typically have two pairs of wings, the anterior pair being much the larger, there are some species in which the hind wings are lacking.

In most adults, the compound eyes occupy the greater part of the head and, in the males of most species, the eyes are larger and closer together on top of the head than in the females. In the males of some genera, the eyes are greatly expanded and each is divided into an upper and lower portion, which may be further differentiated by size and color, figs. 255–257. In the nymphs, the compound eyes show a considerable range in size and position but none shows the high degree of development exhibited in adults.

The colors of the compound eyes of the male as given in the species descriptions and keys are those of the eyes while the specimens were still alive or had been dead only a short time. In mayflies, such as *Baetis,* which have divided eyes, the color of the upper portion of each eye is the significant one; the lower portion, as is well known, is a day-eye, with pigmentation so extensive that this part of the eye appears black. In such forms as *Stenonema* and *Heptagenia,* occasional specimens are to be found in which the entire eye is completely black, before death as well as after. These specimens should be disregarded, as this blackening is apparently due to the corneal layer of the eye separating from the hypodermis. After specimens have been killed and are thoroughly dry, the colors the eyes had in life disappear completely.

The other color characters as given in the descriptions in this report are, wherever possible, those of fresh, dry specimens. All colors fade or change somewhat within a few days after death of the specimens, regardless of the method of preservation; however, this loss of color is relatively slight in dry specimens stored away from the light. Specimens preserved in 70 per cent alcohol soon change color almost completely, becoming, after a few months, only a dull tan or yellow, even though the color in life may have been of various shades from dark brown to white. On dry specimens, the salient features of the color pattern are relatively permanent, but the delicate tints of red, green, gray, or yellow of fresh specimens eventually disappear or become scarcely discernible.

The system of nomenclature for wing veins used by Traver (1935*a*:119) has been followed in this report. It may be noted that this differs from the system of Tillyard (1923) in several respects. For instance, the branched, convex vein in the center of the fore wing called MA by Tillyard is called R_{4+5} in this report. The branches have been named M_1 and M_2 by Ulmer (1933, pls. I, II) and 6 and 6^1 by Eaton (1883, pls. I–XXIII). The vein R_{4+5} is of greatest importance, as it is the best landmark that can be used in identifying the veins of the mayfly fore wing. Once it has been located (except in the greatly specialized Oligoneuriidae), all other veins anterior and posterior to it can quickly be located.

Traver considered R_{4+5} to be a branch of R_s, whereas Tillyard believed it to be a

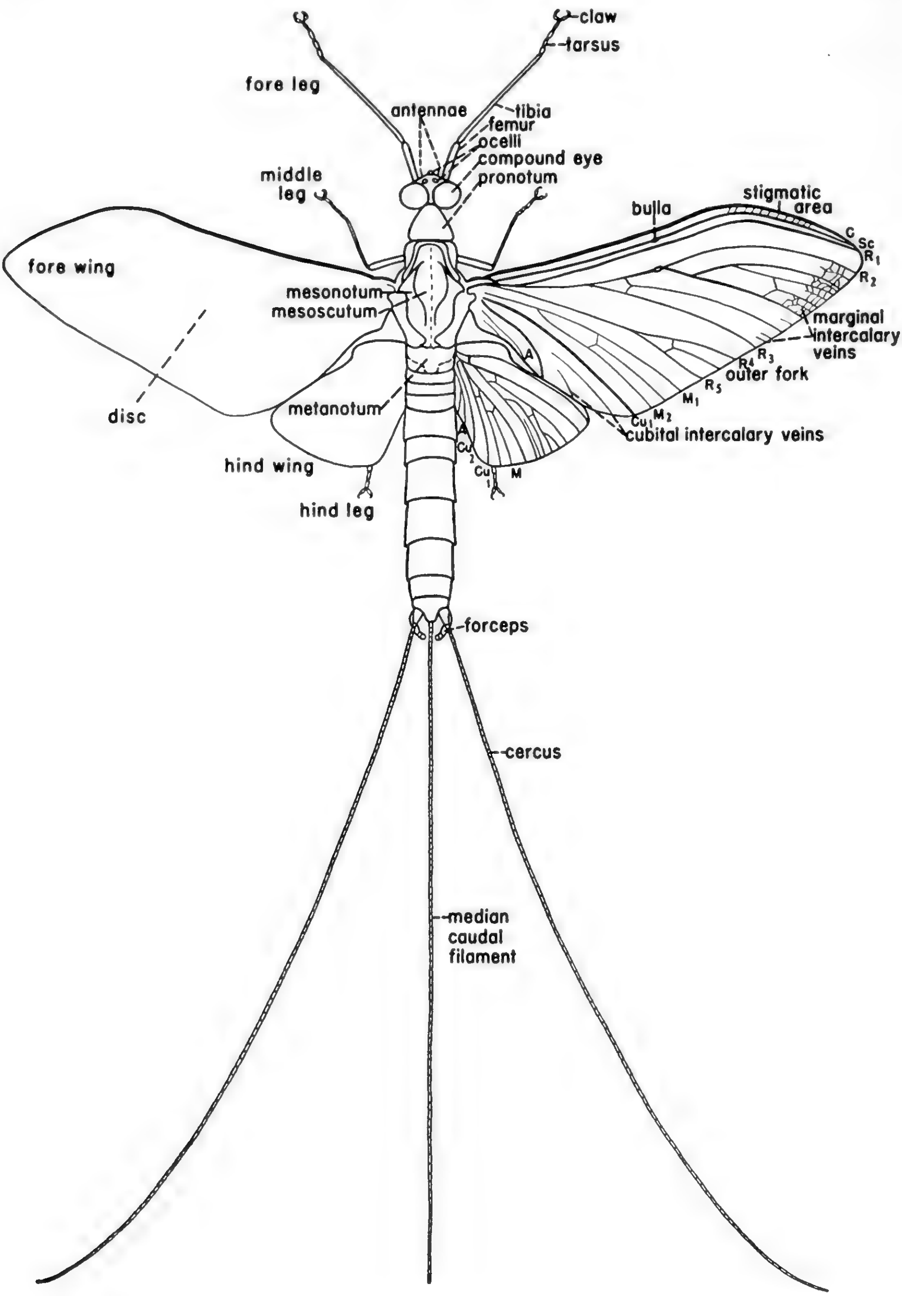
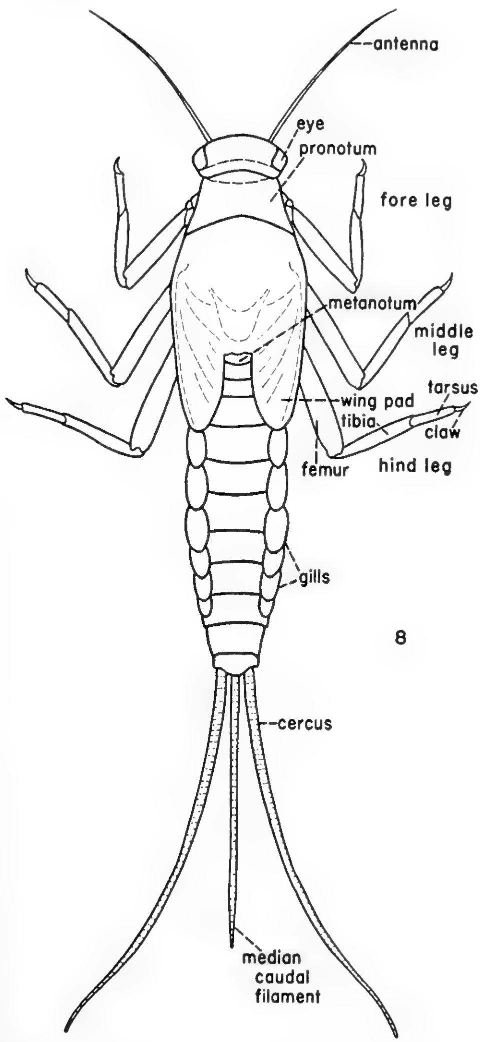


Fig. 7.—Generalized mayfly adult male, showing structures used in classification.

branch of M. Actually, as good a case can be made for considering this vein a branch of R_s as of M. It is not clearly joined to either, but sometimes appears to arise nearer the stem of R than of M. The poorly developed axillary sclerites of the mayfly wing give no conclusive evidence either way. Such being the case, I have decided to follow Traver's system, in which this vein is considered to be a branch of R_1, as her system was used consistently in *The Biology of Mayflies* (Traver 1935*a*). This work has been, and is most likely to continue for many years to be, the standard reference work on North American mayflies.

It should further be noted that the veins called M_1 and M_2 by Traver have been called Cu_1 and Cu_2 by Ulmer, MP by Tillyard, and branches of vein 7 by Eaton. The veins Cu_1 and Cu_2 of Traver's system correspond to 1st and 2nd anal veins of Ulmer's, Cu_1 and Cu_2 of Tillyard's, and veins 8 and 9 of Eaton's.

In mayfly literature, it is frequently stated



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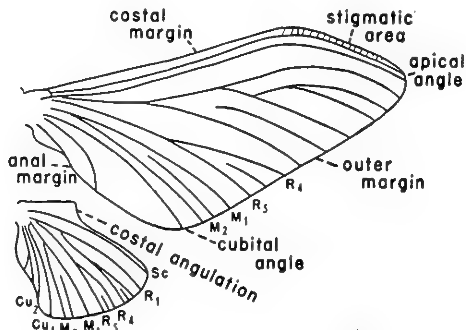

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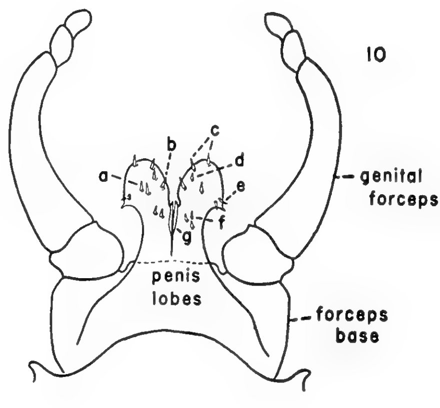

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Fig. 8.—Dorsal aspect of generalized mayfly nymph, showing structures used in classification.
Fig. 9.—Generalized mayfly wings, showing principal veins and areas used in classification.
Fig. 10.—Generalized mayfly male genitalia, showing structures used in classification: *a,* discal spines; *b,* subapical spines; *c,* apical spines; *d,* apicomesal spines; *e,* lateral spines; *f,* basal spines; *g,* mesal spines.

that the median caudal filament is wanting, but actually this filament is simply reduced to a minute, unsegmented or partly segmented vestige. In all adult mayflies there is at least some indication of it. The outer caudal filaments are the cerci.

An arbitrary system for the designation of sizes of specimens has been followed in this report. The size of an adult specimen is taken to be the length of the body without the head or fore legs and without the caudal filaments. Specimens having such a body length of 5 mm. or less are called small, those from 6 to 10 mm. long are called medium, and those over 1 cm. long are designated as large. The length of the body in nymphs is without the head or caudal filaments, and the sizes given refer to mature nymphs, that is, ones with dark wingpads.

Identification of Sexes

The adult male mayfly is easily recognized by the presence of a pair of forceps, or claspers, near the apex of the ninth sternite, as well as by two shorter structures, the penes, between the arms of the forceps. The forceps, except in the subfamily Campsurinae, are segmented, and both forceps and penes vary greatly in size and form, figs. 60–67. These same structures can be seen through the pellicle of the subimago and of the mature nymph, although in these two stages they are soft and less sclerotized than in the adult. They are not fully expanded in the subimago, and much less developed in the nymph.

In the female, the posterior margin of the ninth abdominal sternite is rounded, simple, and without prominent processes or additional structures. In a few genera, the female possesses a rudimentary ovipositor.

Classification

The order Ephemeroptera is one of the most archaic of winged insect groups. It is not closely related to any other order but, as Tillyard (1917) points out, certain points of resemblance give some slight evidence of a very ancient connection with the Odonata. These points of resemblance, not common to other orders, are the presence of only one wing axillary, the inability to fold the wings backward or downward over the abdomen, and the retention of abdominal gills in Ephemeroptera and in a few primitive nymphs of Odonata (*Cora* and *Pseudophaea*). The fossil record indicates that the two orders were already differentiated in the Upper Carboniferous Period but were then more closely related than they are today (Tillyard 1917: 6).

At the time Eaton wrote his *Revisional Monograph* (1883–88), the mayflies were considered to constitute the single family Ephemeridae. However, several years earlier Eaton (1869: 132) had indicated that the family Ephemeridae could be subdivided into three major divisions, based on the habits and structures of the nymphs: (1) the burrowing forms with tusked mandibles, (2) the flat, crawling forms, and (3) the rather long, slender, free-swimming forms. In the *Revisional Monograph,* he divided the adults into three groups; these groups somewhat paralleled the divisions he had previously suggested, based on the nymphs. He further subdivided these three groups into 13 generic types; the three groups were not named as taxonomic categories.

Banks (1900: 246) published a classification of the mayflies, considering them to represent but the one family Ephemeridae, but dividing this family into seven tribes: Baetiscini, Polymitarcini, Leptophlebini, Siphlurini, Ephemerini, Baetini, and Caenini.

Needham (1901: 419) published a key to the nymphs of the family Ephemeridae and indicated that this family could be divided into three subfamilies, the Ephemerinae, Heptageninae, and Baetinae. Needham mentions (1905:29, footnote) that this key indicated subdivisions of the Ephemeridae into subfamilies which were very similar to those given in a manuscript key prepared earlier by C. A. Hart for use by students at the University of Illinois.

A few years later, Needham (1905: 22) published a revised key to the family Ephemeridae in North America. In this key, which included both nymphs and adults, he again divided the Ephemeridae into the three subfamilies Ephemerinae, Heptageninae, and Baetinae. These three subfamilies corresponded only very roughly to the three groups into which Eaton had divided the family Ephemeridae in his classification.

Klapálek (1909) then published a greatly expanded classification of the mayflies, based on German species, dividing the order into

10 families; Palingeniidae, Polymitarcidae, Ephemeridae, Potamanthidae, Leptophlebiidae, Ephemerellidae, Caenidae, Baetidae, Siphlonuridae, and Ecdyonuridae. These families he placed in the order Ephemerida. It may be noted that Klapálek's classification bears considerable resemblance to the earlier classification of Banks (1900:246), and, as Ulmer (1920*a*: 98) remarks, the 10 families in Klapálek's classification correspond almost exactly to 10 of the unnamed subdivisions of the family Ephemeridae that Eaton had indicated in his monograph.

Ulmer (1914), in a new classification of the German mayflies, added the family Oligoneuriidae.

Bengtsson (1917) added the family Ametropidae to the classification and changed the name of the Ecdyonuridae of Klapálek's classification to the Heptageniidae. The same year, Lestage (1917) published a classification of the Palearctic mayfly nymphs in which he used only the families Ephemeridae, Heptageniidae, Baetidae, Oligoneuriidae, and the new family Prosopistomatidae.

Three years later, Ulmer (1920*a*: 99) published a revised classification for the mayflies of the world in which he combined the essential features of all the preceding classifications. He elevated the three subfamilies of Needham's classification to suborders, with 14 families beneath them, but no subfamilies. Ulmer's classification was arranged as follows:

Suborder Ephemeroidea
  Family Palingeniidae
  Family Polymitarcidae
  Family Ephemeridae
  Family Potamanthidae
Suborder Baetoidea
  Family Leptophlebiidae
  Family Ephemerellidae
  Family Caenidae
  Family Baetidae
  Family Oligoneuriidae
  Family Prosopistomatidae
Suborder Heptagenioidea
  Family Baetiscidae
  Family Siphlonuridae
  Family Ametropodidae
  Family Ecdyonuridae
    (Heptageniidae)

A few years later, Handlirsch (1925: 415) published a much more conservative classification for the mayflies of the world. In this he placed all the forms in one family, but employed a number of subfamilies and tribes, as follows:

Family Ephemeridae
  Subfamily Siphlurinae
    Tribe Siphlurini
    Tribe Ametropodini
    Tribe Ecdyurini
  Subfamily Baetiscinae
  Subfamily Prosopistomatinae
  Subfamily Baetidinae
  Subfamily Caenidinae
  Subfamily Leptophlebiinae
    Tribe Ephemerellini
    Tribe Leptophlebiini
  Subfamily Ephemerinae
    Tribe Ephemerini
    Tribe Potamanthini
    Tribe Polymitarcini
    Tribe Palingeniini
  Subfamily Oligoneuriinae

Ulmer (1933) later revised his classification of 1920 but made no changes in the arrangement of suborders and families. The same year, Spieth (1933) published a paper on the phylogeny of mayflies. His conclusions, based on a study of adult wings and male genitalia and nymphal gills and mouthparts, were that the North American mayflies represented four superfamilies and eight families, as follows:

Superfamily Siphlonuroidea
  Family Siphlonuridae
  Family Heptageniidae
  Family Baetidae
Superfamily Ephemeroidea
  Family Leptophlebiidae
  Family Ephemeridae
  Family Ephemerellidae
Superfamily Caenoidea
  Family Caenidae
Superfamily Baetiscoidea
  Family Baetiscidae

Two years later, *The Biology of Mayflies* (Needham *et al.* 1935) appeared. In this work the mayflies were divided into three families (the three subfamilies of Needham's earlier classification) and 17 subfamilies:

Family Ephemeridae
  Subfamily Palingeniinae
  Subfamily Ephoroninae
  Subfamily Ephemerinae
  Subfamily Potamanthinae
  Subfamily Campsurinae
  Subfamily Neoephemerinae
Family Heptageniidae
  Subfamily Heptageninae

Family Baetidae
- Subfamily Oligoneurinae
- Subfamily Ametropinae
- Subfamily Metretopinae
- Subfamily Siphlonurinae
- Subfamily Baetiscinae
- Subfamily Ephemerellinae
- Subfamily Leptophlebiinae
- Subfamily Caeninae
- Subfamily Baetinae
- Subfamily Prosopistomatinae

The supergeneric classification of the mayflies which I have adopted here does not coincide exactly with any of the previous classifications, although it more closely agrees with the classification of Banks (1900) than with that of any other author. I do not believe that all mayflies can be divided into only three main categories without introducing an unjustifiably large number of exceptions into the characterization of each of those three main divisions. Although the mayflies are an extremely archaic group, we still have living representatives of many of the diverse branches that have arisen within the order during its long history. As has been shown by Tillyard (1925, 1932), the mayflies reached their maximum abundance in the Permian Period and have declined since. In the long period from the Permian to the present, many quite distinct types of mayflies have arisen, all of which evidently represent considerable divergence from the Permian mayfly prototype. Characteristics of this ancestral mayfly type are discussed by Tillyard (1932) and Carpenter (1933).

In our present-day mayfly fauna, we retain representatives of many of these diverse lines of mayfly evolution. The family classification should, as much as possible, reflect these degrees of divergence from the ancestral mayfly prototype. Certainly there are more than 3, and, in my opinion, there are at least 11 distinct lines of descent. I have accordingly distributed our Illinois mayflies among 10 families; the eleventh, Prosopistomatidae, is not represented in North America. This family classification has been arrived at through an evaluation of all available characteristics in nymphs and adults. The conspectus of the supergeneric classification followed here is given below:

Order Ephemeroptera
- Family Ephemeridae
  - Subfamily Campsurinae
  - Subfamily Potamanthinae
  - Subfamily Ephoroninae
  - Subfamily Ephemerinae
  - Subfamily Palingeniinae
- Family Neoephemeridae
- Family Caenidae
- Family Ephemerellidae
- Family Baetiscidae
- Family Prosopistomatidae
- Family Oligoneuriidae
- Family Leptophlebiidae
- Family Baetidae
  - Subfamily Siphlonurinae
  - Subfamily Isonychiinae
  - Subfamily Baetinae
- Family Ametropidae
- Family Heptageniidae

It must be admitted that varying degrees of relationship are indicated among some of these families. The Caenidae almost certainly arose from an ephemerid ancestor, as is shown by the still existing but extremely rare interstitial forms which are placed here in the Neoephemeridae. The point of divergence, however, of the Caenidae from the ephemerid stem must have been quite remote. The Ephemerellidae, Oligoneuridae, Baetiscidae, and Prosopistomatidae apparently have no near relatives in the recent fauna. The Leptophlebiidae possibly arose from the same stem which produced the Baetidae, although the similarity between the two is slight. On the other hand, the Heptageniidae and the Baetidae must have arisen from an ancestor common to both of these families; the rare but still existing interstitial forms between these two families indicate this probable relationship.

The forms here included in the Baetidae admittedly represent rather widely divergent types. The Siphlonurinae contain quite archaic forms that (Spieth 1933: 329) probably arose very early from the Permian mayfly prototype, while the Baetinae contain greatly reduced adult forms that probably arose much later. The baetine and siphlonurine nymphs are, however, quite similar, and most adult baetine structures can be derived by simple reduction from corresponding adult structures in the Siphlonurinae. The divided compound eyes of the adult male baetines, on the other hand, seem to be strikingly different from the eyes of the siphlonurines, but actually the beginnings of the development of this divided eye


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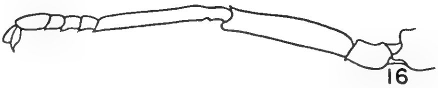
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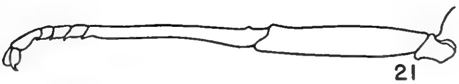
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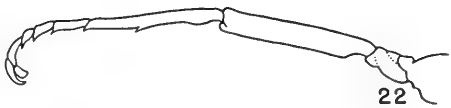
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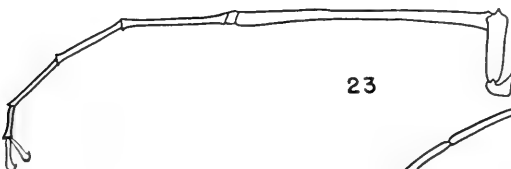
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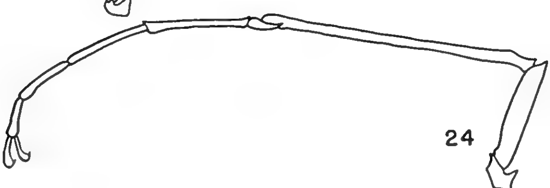
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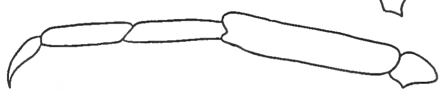
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Fig. 11.—*Caenis simulans*, hind leg of adult male.

Fig. 12.—*Brachycercus lacustris*, hind leg of adult male.

Fig. 13.—*Tricorythodes atratus*, hind leg of adult male.

Fig. 14.—*Neoephemera purpurea*, hind leg of adult male.

Fig. 15.—*Callibaetis fluctuans*, hind leg of adult male.

Fig. 16.—*Ephemerella needhami*, hind leg of adult male.

Fig. 17.—*Stenonema pulchellum*, hind leg of adult male.

Fig. 18.—*Isonychia sicca*, hind leg of adult male.

Fig. 19.—*Heptagenia* sp., hind leg of adult female.

Fig. 20.—*Siphlonurus alternatus*, hind leg of adult female.

Fig. 21.—*Leptophlebia nebulosa*, hind leg of adult male.

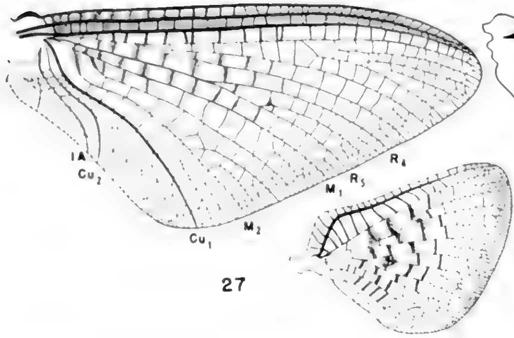
Fig. 22.—*Siphloplecton interlineatum*, hind leg of adult male.

Fig. 23.—*Ephoron leukon*, fore leg of adult male.

Fig. 24.—*Ephemera simulans*, fore leg of adult male.

Fig 25.—*Siphloplecton interlineatum*, hind leg of mature nymph.

Fig. 26.—*Ameletus lineatus*, hind leg of mature nymph.



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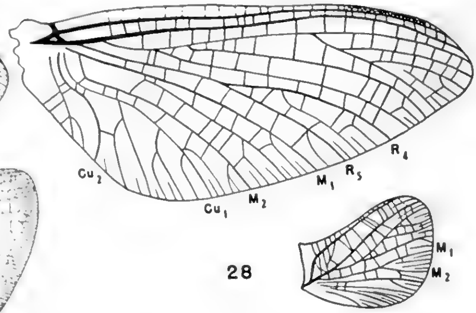

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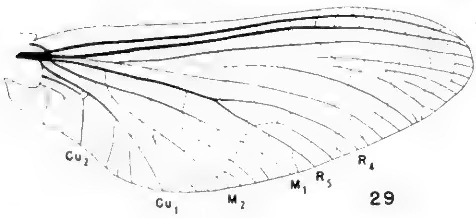

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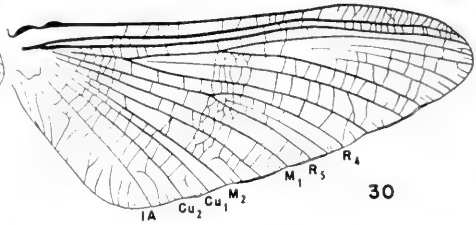

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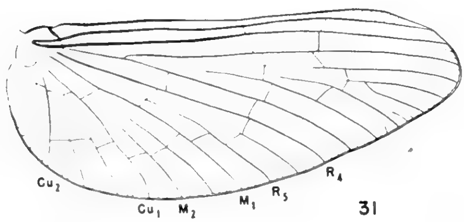

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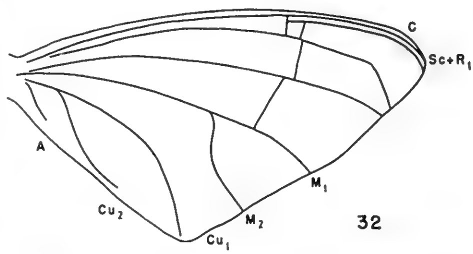

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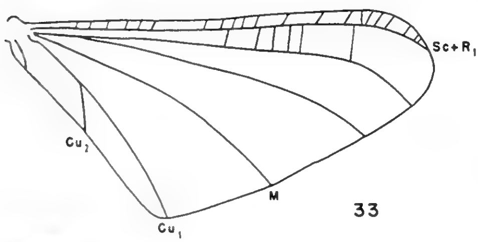

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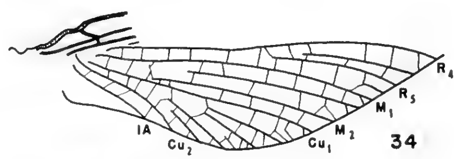

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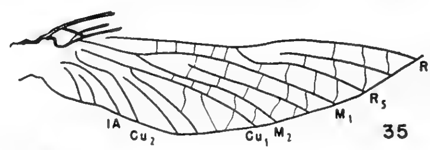

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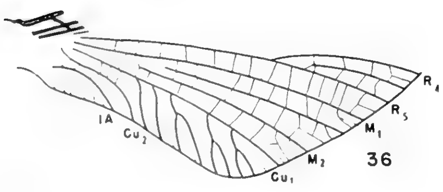

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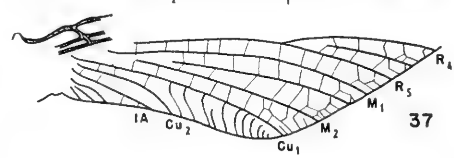

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Fig. 27.—*Hexagenia bilineata*, wings.

Fig. 28.—*Neoephemera purpurea*, wings.

Fig. 29.—*Ephemerella lutulenta*, fore wing.

Fig. 30.—*Baetisca obesa*, fore wing.

Fig. 31.—*Baetis propinquus*, fore wing.

Fig. 32.—*Lachlania saskatchewanensis*, fore wing. (After Ide.)

Fig. 33.—*Oligoneuria anomala*, fore wing. (After Eaton.)

Fig. 34.—*Siphloplecton basale*, posterior half of fore wing.

Fig. 35.—*Paraleptophlebia praepedita*, posterior half of fore wing.

Fig. 36.—*Isonychia rufa*, posterior half of fore wing.

Fig. 37.—*Siphlonurus quebecensis*, posterior half of fore wing.

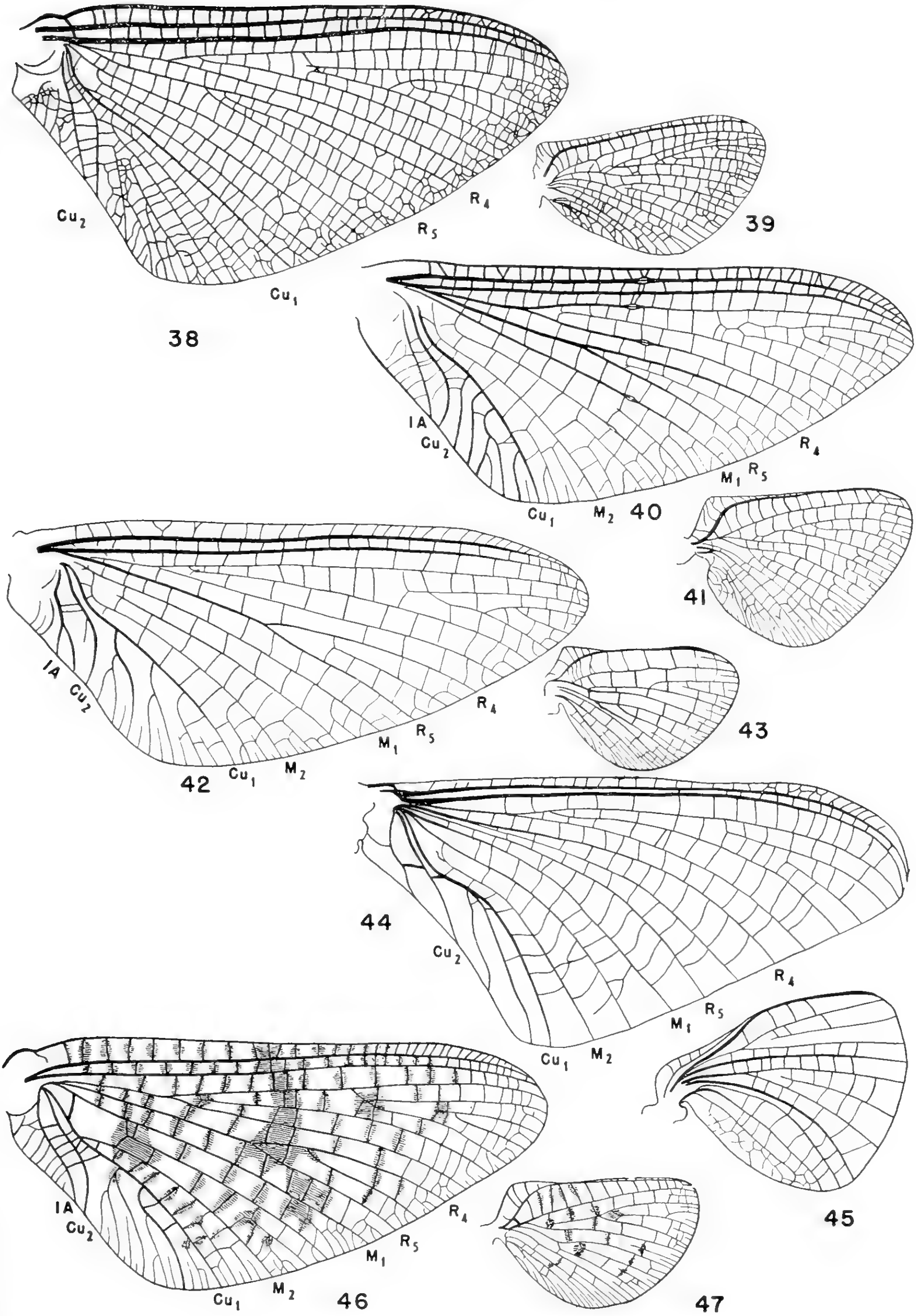


Fig. 38.—*Ephoron leukon,* fore wing.
Fig. 39.—*Ephoron leukon,* hind wing.
Fig. 40.—*Pentagenia vittigera,* fore wing.
Fig. 41.—*Pentagenia vittigera,* hind wing.
Fig. 42.—*Potamanthus verticis,* fore wing.
Fig. 43.—*Potamanthus verticis,* hind wing.
Fig. 44.—*Tortopus primus,* fore wing.
Fig. 45.—*Tortopus primus,* hind wing.
Fig. 46.—*Ephemera simulans,* fore wing.
Fig. 47.—*Ephemera simulans,* hind wing.

can be seen clearly in the living adult male siphlonurines.

KEY TO FAMILIES

Adults

1. Lateral ocellus in both sexes extremely large in comparison with a compound eye; each ocellus approximately one-half as large as a compound eye. . . . . **Caenidae,** p. 43
   Lateral ocellus in males never more than one-tenth as large as a compound eye; in females lateral ocellus not more than one-fourth as large as a compound eye 2
2. Vein Sc of fore wing wanting or united with R_1, figs. 32, 33 . . . . **Oligoneuriidae,** p. 79
   Vein Sc of fore wing present as a separate vein extending from base to apex of wing, figs. 27–31 3
3. Cubital intercalary veins entirely absent, crossveins in disc of fore wing weak and netlike, fig. 30. . . . . . **Baetiscidae,** p. 75
   Cubital intercalary veins present, crossveins in disc of wing not netlike, figs. 27–29, 31 4
4. Hind tarsus with five clearly differentiated segments, true first tarsal segment not fused with tibia, figs. 17, 19 . . . . **Heptageniidae,** p. 151
   Hind tarsus with only three or four clearly differentiated segments, figs. 14–16, 18, 20–22 5
5. Vein M_2 of fore wing sharply bent near base, figs. 27, 28, running parallel with vein Cu_1 in this area 6
   Vein M_2 of fore wing straight throughout its length, figs. 30, 31, 34–37, or curved no more than in fig. 29 7
6. Costal crossveins of fore wing in area basad of bulla partly or almost completely atrophied; veins M_1 and M_2 of hind wing separating distad of the center of wing; fig. 28 . . . . **Neoephemeridae,** p. 42
   Costal crossveins in both fore and hind wings well developed; veins M_1 and M_2 of hind wing separating proximad of center of wing; figs. 27, 38–47 . . . . **Ephemeridae,** p. 27
7. Fore wing with one or two long intercalary veins between M_2 and Cu_1, fig. 29. . . . . **Ephemerellidae,** p. 55
   Fore wing without long intercalaries between veins M_2 and Cu_1, figs. 34–37. 8
8. Vein Cu_2 of fore wing angularly bent toward inner wing margin, figs. 35, 185–192. . . . . . **Leptophlebiidae,** p. 81
   Vein Cu_2 of fore wing straight or evenly curved, figs. 31, 34, 36, 37 9
9. Cubital intercalary veins of fore wing consisting of one or two pairs of long, parallel veins, free marginal veinlets always absent, fig. 34; hind wings invariably present. **Ametropidae,** p. 144
   Cubital intercalary veins of fore wing either a series of short, slightly sinuate veins extending from vein Cu_1 to inner wing margin, figs. 36, 37; or cubital intercalaries one or two long, basally detached veins accompanied by free marginal veinlets, figs. 31, 220–222; hind wing sometimes absent. . . . . **Baetidae,** p. 97

Mature Nymphs

1. Gills on abdominal segments 1–6 concealed under carapace-like projection of thoracic notum, fig. 181 . . . . **Baetiscidae,** p. 75
   Abdominal gills not concealed under carapace-like projection of thoracic notum. 2
2. Second abdominal segment bearing a pair of operculate or lidlike gills which cover gills on segments 3–6; gills lacking on segment 7; figs. 88, 96, 113, 114. 3
   Second abdominal segment not bearing a pair of operculate gills which cover more posterior gills; operculate gills, if present, borne by segment 4; gills present on segment 7. 4
3. Operculate gills fused on meson, connate; a hooklike, median spine at posterior margin of abdominal tergites 6–8, fig. 88. . . . . **Neoephemeridae,** p. 42
   Operculate gills not fused on meson; abdominal tergites 6–8 without hooklike spines, figs. 96, 113, 114. . . . . **Caenidae,** p. 43
4. Gills of first abdominal segment large and situated on the venter, fig. 184. . . . . **Oligoneuriidae,** p. 79
   Gills of first abdominal segment dorsal, or first abdominal segment without gills. . 5
5. Gills always absent from second abdominal segment and sometimes absent from third segment, also. . . . . **Ephemerellidae,** p. 55
   Gills present on abdominal segments 1–7. 6
6. Tibia of hind leg shorter than hind tarsal claw, figs. 301, 312; or claw at least six times as long as wide at its widest point, fig. 25. . . . . **Ametropidae,** p. 144
   Tibia of hind leg as long as, or longer than, hind tarsal claw, figs. 26, 247, 254, 266, 385; claws relatively thick. 7
7. Each mandible with a projecting tusk, visible from dorsal aspect, figs. 2, 55, 59. 8
   Mandibles without projecting tusks. . . . 9
8. Gills relatively broad, biramous, with margins ciliate, figs. 51–54. . . . . **Ephemeridae,** p. 27
   Gills slender, filamentous, and bare. . . . . **Leptophlebiidae,** p. 81
9. Head flattened dorsoventrally, prognathous, eyes dorsal, and labrum mostly or completely concealed under projecting anterior margin of head, figs. 360, 383–386, 390, 394, 395 . . . . **Heptageniidae,** p. 151
   Head hypognathous, eyes lateral, or, if prognathous, labrum completely ex-

posed, figs. 199, 212, 240, 247, 254, 266, 298 10

10. Cerci uniformly clothed with short setae, figs. 199, 212 . . . . **Leptophlebiidae,** p. 81

Cerci bearing a dense row of setae only on the mesal margin of each, fig. 298 . . . . **Baetidae,** p. 97

EPHEMERIDAE

The family Ephemeridae, as defined here, corresponds to the families Ephemeridae, Polymitarcidae, and Potamanthidae in the classification of Ulmer (1933: 195), except that *Neoephemera,* included by Ulmer in the Ephemeridae, is excluded from this family and placed in a new family, Neoephemeridae. The classification of the Ephemeridae used here is identical with that of Traver (1935*a*: 240), except for her inclusion of *Neoephemera* in this family.

The Ephemeridae include the largest mayflies occurring in Illinois. These are the mayflies that on warm summer evenings commonly emerge in enormous numbers from our larger rivers and lakes, and cover bridges and water-front buildings.

The wings of adult ephemerids have extremely numerous crossveins, and, except in *Tortopus* and *Campsurus,* a band of fine, short veinlets along the outer margin of each wing, figs. 38–43, 46, 47. In the fore wing, vein Cu_1 is sinuate near the base, and the posterior branch of vein M_2 is curved so as to be approximately parallel with Cu_1 in the basal area. The basal costal crossveins are well developed, and the stigmatic crossveins usually are not anastomosed. In many ephemerids, each compound eye in the males is divided into a dark lower portion and a light-colored upper portion, but the facets usually are the same size in each portion of the eye. The eye of the male in some species is not much larger than the eye of the female. The fore tarsus in the males has five segments, the basal one very short, figs. 23, 24. The hind tarsus in both sexes has only four clearly differentiated segments. In *Tortopus,* the middle and hind legs are nonfunctional and almost completely degenerated; in *Ephoron* the legs are reduced somewhat and are nonfunctional.

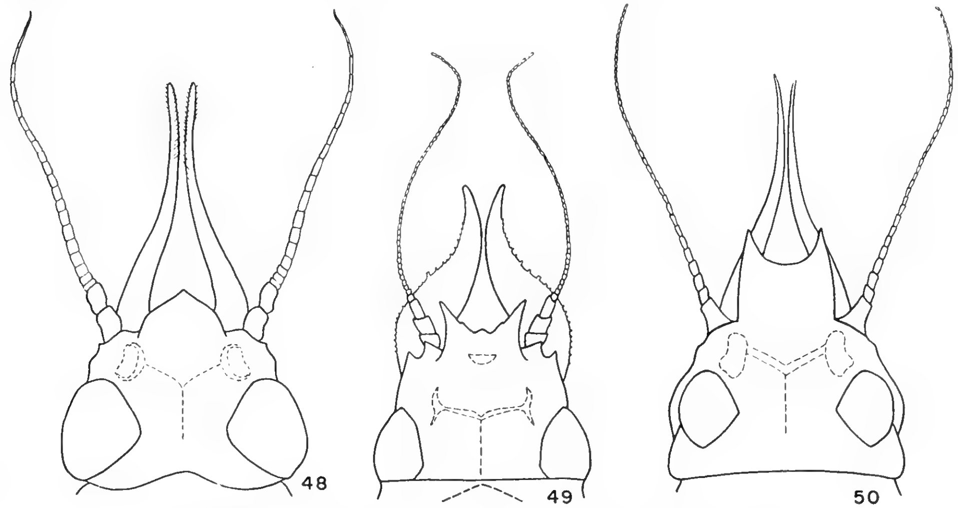


Fig. 48.—*Hexagenia bilineata,* doral aspect of head of nymph.
Fig. 49.—*Pentagenia vittigera,* dorsal aspect of head of nymph.
Fig. 50.—*Ephemera simulans,* dorsal aspect of head of nymph.

The nymphs of all ephemerids are provided with mandibular tusks and a row of completely exposed, biramous gills on either side of the abdomen, figs. 2, 55, 59. These nymphs live in the sand, gravel, or silt on the bottoms of our larger streams and lakes. Although they remain almost completely buried most of the time, they can sometimes be seen swimming freely in fairly deep water near shore. They have been observed to swim with a characteristic darting and undulating motion at about a foot beneath the surface. The periods in which the nymphs swim freely in the water may be near the time of molting. Nymphs in an aquarium were observed to leave the sand in the bottom, swim about in the water, and, after molting, re-bury themselves in the sand.

KEY TO SUBFAMILIES

ADULTS

1. Veins Sc and R_1 of fore wing curved posteriorly and continued around apical angle of wing; marginal veinlets wanting, fig. 44. Middle and hind legs of both male and female completely atrophied beyond trochanter, or femur, tibia, and tarsus degenerated to mere membranous flaps; male forceps unsegmented, fig. 60 .... **Campsurinae,** p. 28
   Veins Sc and R_1 of fore wing straight at apexes; marginal veinlets present, figs. 38, 40, 42, 46. Middle and hind legs beyond trochanter not atrophied or degenerated to membranous vestiges; male forceps segmented, figs. 61–63, 65–67 2
2. Marginal veinlets of fore wing extremely numerous; cubital intercalary veins straight, not attached at bases to Cu_1, fig. 38 .... **Ephoroninae,** p. 32
   Marginal veinlets of fore wing relatively few in number; cubital intercalary veins sinuate, attached at bases to Cu_1, figs. 42, 46 3
3. First anal vein of fore wing forked near wing margin, fig. 42 .... **Potamanthinae,** p. 30
   First anal vein of fore wing not forked, fig. 46 .... **Ephemerinae,** p. 35

MATURE NYMPHS

1. Gills lateral, fig. 55 .... **Potamanthinae,** p. 30
   Gills dorsal, figs. 2, 59 2
2. Head without a frontal process .... **Campsurinae,** p. 28
   Head with a frontal process, figs. 2, 59 .. 3
3. Mandibular tusks upcurved .... **Ephemerinae,** p. 35
   Mandibular tusks downcurved .... **Ephoroninae,** p. 32

CAMPSURINAE

The subfamily Campsurinae, as defined here, corresponds to the first section of the family Polymitarcidae in the classification of Ulmer (1933: 197). It includes only *Tortopus* and the very closely related genus *Campsurus* in the Nearctic region. Together, these two genera include about 50 species in South America and Central America, but only 4 species of campsurine mayflies have been described or identified from America north of Mexico. Of these, 2 occur in Texas only, another cannot be identified at present, and the fourth is quite generally distributed in eastern North America. The nymphs are unknown for the Nearctic species.

KEY TO GENERA

ADULTS

Middle and hind legs reduced to functionless, membranous vestiges, but with all leg-parts still discernible .... **1. Tortopus**
Middle and hind legs completely aborted beyond the trochanters .... **2. Campsurus**

1. *TORTOPUS* Needham & Murphy

Tortopus Needham & Murphy (1924:23).

In the adults, the fore wing has veins C and Sc recurved around the apical angle of the wing, fig. 44; the veinlets along the apical wing margin are absent, vein M is forked at the wing base, and there are two long, cubital intercalary veins. The fore leg in the males is developed normally, but the middle and hind legs, as well as all of the legs in the females, are reduced to small, nonfunctional semimembranous vestiges, which, however, have all leg-parts still discernible. The females never molt to the imago stage, but mate and lay their eggs as subimagoes. In adults of both sexes, gill stumps are retained along the lateral margins of the abdomen. The median caudal filament is vestigial in the males, but is well developed in the females.

It has, unfortunately, not been possible as yet to find the nymphs of *Tortopus* in Illinois. The nymphs are presumed to be burrowing forms, relatively close in structure to the nymphs of *Campsurus*. Characteristics for the latter have been given by Needam & Murphy (1924:13) and Ulmer (1920*b*:17).

Tortopus primus (McDunnough)

Campsurus primus McDunnough (1924*a*:7).
Campsurus incertus Traver (1935*a*:286).
Campsurus manitobensis Ide (1941:155).

As has been pointed out before (McDunnough 1926:185; Traver 1935*a*:288), this species may be a synonym of *Palingenia puella* Pictet (1843: 145). The type of *puella* has not, so far as is known, been located and compared with recently collected material. Pictet's description was apparently drawn from a single mutilated female specimen, almost certainly a subimago. The species *puella* can probably never be identified with certainty. For the present, the name *primus* may be used for the species.

MALE.—Length of body 10–14 mm., of fore wing 9–12 mm. Body of living specimen snow-white, with wings white and costal margin of each fore wing faintly shaded with bluish gray. Antennae and apical tarsal segments of each fore leg shaded with bluish gray.

Fore leg with femur and tibia approximately equal in length, first tarsal segment one-third as long as tibia, second to fifth tarsal segments equal in length, each twice as long as first segment; longer of two tarsal claws as long as fifth tarsal segment, shorter claw two-thirds as long as longer one. Middle and hind legs greatly reduced, but all parts still represented by small, membranous vestiges. Genitalia, fig. 60, with two characteristically broad, flat penis lobes.

FEMALE.—Length of body 13–17 mm., of fore wing 16–22 mm. Body of living specimens snow-white, but often with a faint, longitudinal band of grayish brown on meson of pronotum and on dorsum of ab-

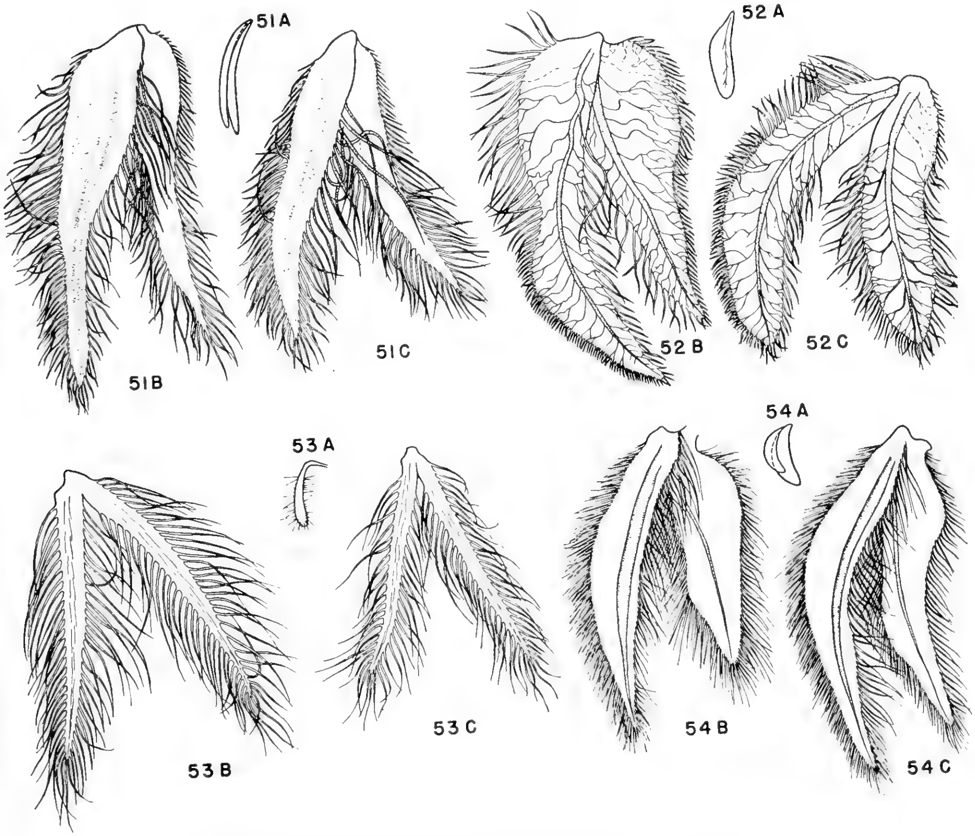


Fig. 51*A*.—*Hexagenia limbata*, gill of first abdominal segment.
Fig. 51*B*.—*Hexagenia limbata*, gill of fourth abdominal segment.
Fig. 51*C*.—*Hexagenia limbata*, gill of seventh abdominal segment.
Fig. 52*A*.—*Ephoron leukon*, gill of first abdominal segment.
Fig. 52*B*.—*Ephoron leukon*, gill of fourth abdominal segment.
Fig. 52*C*.—*Ephoron leukon*, gill of seventh abdominal segment.
Fig. 53*A*.—*Potamanthus myops*, gill of first abdominal segment.
Fig. 53*B*.—*Potamanthus myops*, gill of fourth abdominal segment.
Fig. 53*C*.—*Potamanthus myops*, gill of seventh abdominal segment.
Fig. 54*A*.—*Pentagenia vittigera*, gill of first abdominal segment.
Fig. 54*B*.—*Pentagenia vittigera*, gill of fourth abdominal segment.
Fig. 54*C*.—*Pentagenia vittigera*, gill of seventh abdominal segment.

domen. Mesoscutum of thorax with three longitudinal, obscure, brown lines which converge toward scutellum. Dorsal meson of metathorax vaguely stained with grayish

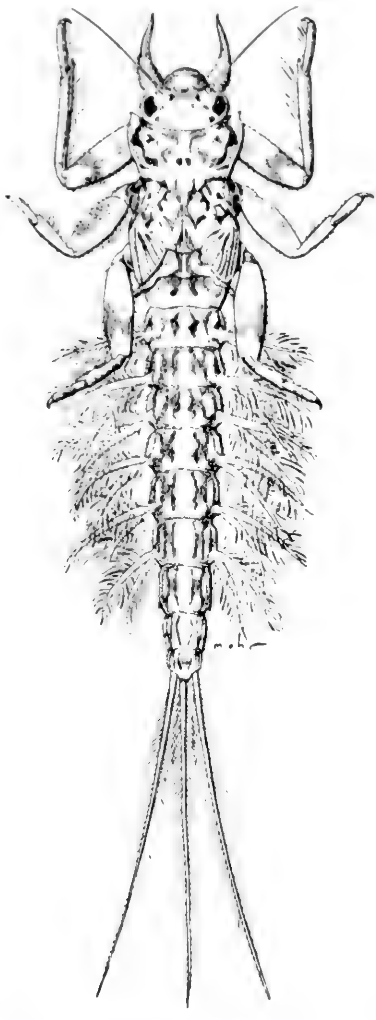


Fig. 55.—*Potamanthus* sp., mature nymph, dorsal aspect.

brown. All legs greatly reduced, semimembranous, nonfunctional.

Known from Alabama, Arkansas, Georgia, Illinois, Kansas, Manitoba, Missouri, Nebraska, Ontario, and Tennessee. Develops in large, slow rivers.

Illinois Records.—ALTON: Aug. 29, 1913, 2♀. BLOOMINGTON: C. C. Adams, 10♀. CHAMPAIGN: Sept. 21, 1892, C. A. Hart, 1♀. ELIZABETHTOWN: at light, July 14, 1948, Mills & Ross, 1♀. GRAND TOWER: Aug. 14, 1898, C. A. Hart, 73♂. HAVANA: Aug. 10, 1889, C. A. Hart, 1♀; White Oak Creek, Aug. 14, 1896, C. A. Hart, 3♀. MOMENCE: Aug. 16, 1938, Ross & Burks, 1♀. OQUAWKA: Sept. 26, 1947, H. H. Ross, 30♀. QUINCY: Aug. 10, 1889, C. A. Hart, 1♀. SHAWNEETOWN: Oct. 3, 1942, Frison & Ross, 1♀. URBANA: at light, Aug. 23, 1943, H. B. Petty, 5♀; Sept. 20, 1909, 2♀.

2. *CAMPSURUS* Eaton

Campsurus Eaton (1868: 83).

The adults of *Campsurus* differ from those of *Tortopus* mainly in the structure of the legs; the middle and hind legs in both sexes in *Campsurus* are completely aborted beyond the trochanters. The difference in the wing venation between the two, described by Needham & Murphy (1924: 23) when they defined the genus *Tortopus*, is not reliable, according to Ulmer (1942:108).

Campsurus decoloratus (Hagen) (1861: 43), known from Texas and Mexico, and *circumfluus* Ulmer (1942:110), described from Texas, are the only known Nearctic species. *C. puella* (Pictet) (1843: 145), described from Louisiana, has been tentatively placed in *Campsurus*, but is at present unidentifiable.

POTAMANTHINAE

The subfamily Potamanthinae corresponds to Ulmer's family Potamanthidae (1933: 199). It has only one Nearctic genus.

3. *POTAMANTHUS* Pictet

Potamanthus Pictet (1845: 208, pl. 25).

The adults are fairly large, whitish mayflies with the vertex and the dorsum of the thorax light reddish brown. The marginal intercalary veins of the wings are not netlike, fig. 42. In the fore wing, the basal part of vein M_2 is more strongly curved to the rear than is vein Cu_1, fig. 42, and the first anal vein is forked near the wing margin. In the hind wing, the costal projection is acute and veins M_1 and M_2 diverge near the wing base. The middle and hind legs of the adults are functional. The male genitalia, fig. 61, have the penis lobes broad, flattened, and almost completely fused on the meson; each arm of the forceps has three segments. The nymphs, fig. 55, are sprawlers, with the gills extended laterally. The median caudal filament is well developed in the nymphs and in the adults of both sexes.

Adult specimens of *Potamanthus* should be studied when freshly killed, as the faint color markings fade rapidly after death. This fading occurs much more rapidly in alcoholic than in dried specimens.

Reliable specific characters for the nymphs of this genus have not been found.

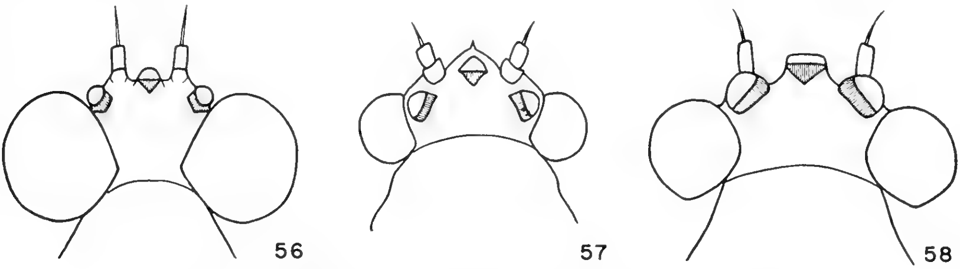


Fig. 56.—*Potamanthus verticis*, dorsal aspect of head of adult male.
Fig. 57.—*Potamanthus myops*, dorsal aspect of head of adult male.
Fig. 58.—*Potamanthus distinctus*, dorsal aspect of head of adult male.

KEY TO SPECIES

ADULTS

1. Abdomen usually entirely unmarked, occasionally each abdominal segment with a faint, minute, pink spot on either side; crossveins in fore wing hyaline in each sex; compound eyes of male small, fig. 57 .... **1. myops**
   Abdomen with large, well-marked, lateral, salmon-pink spots or stripes 2
2. Abdomen with lateral stripes; fore wing in each sex with black crossveins; compound eyes of male moderate in size, fig. 58 .... **3. distinctus**
   Abdomen with lateral spots 3
3. Female with crossveins of each fore wing black, male with those crossveins hyaline, or with only a few of the anterior crossveins black; compound eyes of male large, fig. 56 ....**2. verticis**
   Both male and female with all crossveins of each fore wing black; compound eyes of male small, as in fig. 57 .... **4. neglectus**

1. *Potamanthus myops* (Walsh)

Ephemera myops Walsh (1863:207).
Potamanthus medius Banks (1908:259).

A study of the type of *medius* leaves no doubt in my mind that it represents the same species as the one we have been calling *myops*. In the Museum of Comparative Zoology there is a specimen labeled as the type of *myops*, but it was collected a year after the description was published and cannot, therefore, be the type. It is, however, a specimen determined as *myops* by Walsh himself, and is in agreement with the present-day concept of the species.

MALE.—Length of body 10–13 mm., of fore wing 11–14 mm. Compound eyes small, fig. 57; wings completely hyaline, with no crossveins black; abdomen without lateral, salmon-pink spots or stripes, or, rarely, with small, faint, lateral spots discernible in living specimens; caudal filaments with articulations usually slightly darkened with red-brown or pink.

FEMALE.—Length of body 11–13 mm., of fore wing 12–14 mm. Eyes same size as in male; wings with no crossveins black; abdomen without lateral, salmon-pink spots or stripes; caudal filaments with articulations usually slightly darkened with red-brown or pink.

Known from Illinois, Indiana, Iowa, Kansas, Michigan, and Wisconsin. Develops in large and moderate-sized rivers.

Illinois Records.—Adult specimens, collected June 6 to August 17, are from Aurora (Fox River), Champaign, Dixon (Rock River), East Dubuque (Mississippi River), Effingham, Freeport, Galesburg, Homer, Kankakee, Monmouth, Monticello, Muncie, Oakwood, Oregon, Peoria, Rockford, Rock Island, Rockton, Sterling, and Urbana.

2. *Potamanthus verticis* (Say)

Baetis verticis Say (1839:42).
Ephemera flaveola Walsh (1862:377).

The type of Say's species is lost, but both male and female types of Walsh's species are in the Museum of Comparative Zoology. By common consent, the identity of this species has long been based on the characters of Walsh's species, although Say's name has priority. There is at present no reason for changing this practice, as is mentioned below under *neglectus*.

MALE.—Length of body 7–9 mm., of fore wing 8–10 mm. Compound eyes large, fig. 56; wings with all crossveins hyaline or, in occasional specimens, with a few anterior crossveins of each fore wing darkened; abdomen with a row of salmon-pink spots on either side; cerci and median caudal filament with articulations darkened.

FEMALE.—Length of body 8–10 mm., of fore wing 9–11 mm. Compound eyes small, each less than half the size of eye of male; wings with crossveins darkened; abdomen with a row of salmon-pink spots on either side; cerci and median caudal filament with articulations darkened.

Known from the midwestern and northeastern states. Develops in large and moderate-sized rivers.

Illinois Records.—Adult specimens, collected May 2 to August 16, are from Antioch, Aurora, Bloomington, Champaign, Dixon (Rock River), Foster (Mississippi River), Hardin (Illinois River), Kankakee, Keithsburg, Mount Carmel, Oregon, Prophetstown (Rock River), Quincy, Rockford, Rock Island, Rockton, Savanna (Mississippi River), South Beloit, Sterling, Warsaw (Mississippi River), Wilmington, Yorkville.

3. *Potamanthus distinctus* Traver

Potamanthus distinctus Traver (1935*a*:280).

The crossveins of the fore and hind wings are black in both sexes; the fore wing is 11 mm. long; there is a reddish-tan stripe on the vertex, pronotum, and the anterior part of the mesonotum; the abdomen has a salmon-pink stripe on either side; and the articulations of the cerci and the median caudal filament are darkened. The compound eyes of the male are moderately large, fig. 58.

Known from New York and Ohio.

4. *Potamanthus neglectus* Traver

Potamanthus neglectus Traver (1935*a*:282).

In describing this species, Traver mentioned that it might eventually prove to be a synonym of *verticis*. There is, however, nothing in the original description of Say's species that would conclusively decide the matter; if *neglectus* were to be placed as a synonym of *verticis*, it would then be necessary to resurrect from synonymy the name *flaveola* for that species at present being called *verticis*. I prefer to follow McDunnough (1926:186) in considering *flaveola* a synonym of *verticis*, as there is no strong reason for not doing so, and the present known distribution of the species involved is in agreement with that practice. *P. verticis* was described from Indiana, and *flaveola* was described from Illinois; the species now going under the name *verticis* occurs in the midwestern and northeastern states. *P. neglectus* is known only from the Atlantic Seaboard.

The crossveins in the wings in both sexes are darkened; the length of the fore wing of the male is 8–9 mm.; there is a reddish-brown median stripe on the vertex of the head, on the pronotum, and on the mesonotum; the abdomen has a row of salmon-pink spots on either side; the caudal filaments have the articulations darkened; the compound eyes of the male are small, as in *myops*, fig. 57.

Known from Maryland, New York, and Pennsylvania.

EPHORONINAE

The subfamily Ephoroninae includes only one genus in the Neartic region, *Ephoron*. As used here, this subfamily corresponds to the second section of the family Polymitarcidae in Ulmer's classification (1933:197).

4. *EPHORON* Williamson

Ephoron Williamson (1802:71).
Polymitarcys Eaton (1868:84).

The adults of *Ephoron* are fairly large, snow-white mayflies with all legs of the females and the middle and hind legs of the males greatly reduced and functionless. The females do not molt to the adult stage, but mate and lay their eggs as subimagoes. The costal and subcostal areas of the fore wing are grayish purple; otherwise the wings are snow-white. These wings, fig. 38, have extremely abundant crossveins and netlike marginal intercalaries suggesting the archaic orthopteroid archedictyon. The cubital intercalaries of the fore wing consist of three or four long, straight veins, the posterior one of which is attached to the anal wing margin by a series of confused, short, and irregular veinlets. The hind wing has a blunt costal angulation. In the fore leg of the males, fig. 23, the tarsus is normally developed but the femur is quite short. In the females, the median caudal filament is well developed, while, in the males, it is reduced to a minute rudiment.

The nymphs, fig. 59, have prominently toothed, downcurved mandibular tusks; the gills have short, relatively inconspicuous marginal ciliae, figs. 52*B*, 52*C*.

Reliable characters for separating the females to species have not yet been found.

KEY TO SPECIES

ADULT MALES

Mesonotum dark brown; apicolateral angle of each penis lobe rounded, fig. 66 .... **1. leukon**
Mesonotum light yellow, shaded with tan; apicolateral angle of each penis lobe acute, fig. 67 .... **2. album**

MATURE NYMPHS

Gills on abdominal segments 2–6 with lateral tracheal branches pigmented, figs. 52*B*, *C*, 59 .... **1. leukon**
Gills on abdominal segments 2–6 with lateral tracheal branches hyaline .... **2. album**

1. *Ephoron leukon* Williamson

Ephoron leukon Williamson (1802:71).
Polymitarcys albus of authors, misidentification.

Rearing work and field observations carried on here in Illinois show that the mature nymphs of this species, when ready to transform, migrate to the shores of the large rivers in which they develop. At dusk, they congregate in the shallow water or even in the wet mud at the edge of the water. The subimagoes emerge there, leaving their cast nymphal skins floating on the shallow water or partly submerged in the mud. These subimagoes take flight at once, and the males molt to the adult stage almost immediately. Molting occurs in the air, during flight, as the legs are nonfunctional. The adults then disperse to mate and lay their eggs. All the adults that emerge during one evening are, apparently, dead by the following morning. The length of adult life I observed for this species in Illinois was about one hour. My observations do not agree with those of Howard (Needham 1905:60; 1920:285), also made in Illinois. However, Howard's observations were made on a mixture of individuals belonging to the genera *Ephoron* and *Potamanthus*. My observations on *leukon* agree closely with those made by Ide (1937*a*:25) on this species in Ontario.

MALE.—Length of body 12–14 mm., of fore wing 11–13 mm. Vertex of head light yellow, shaded with very dark gray between ocelli; anterodorsal area of mesonotum dark brown, metanotum a lighter brown; legs light yellowish to snow-white (in freshly killed specimens), with each fore femur and tibia stained with purplish gray; abdomen white, with variable areas of gray shading

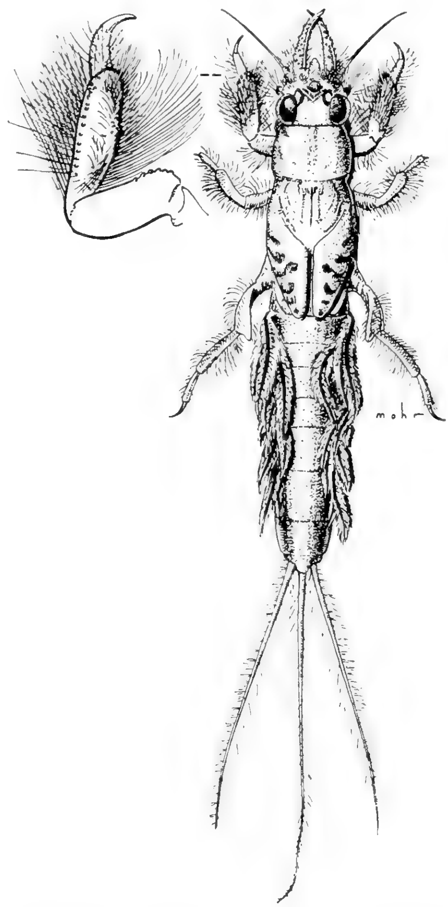


Fig. 59.—*Ephoron leukon*, mature nymph, dorsal aspect. Small figure at left represents enlargement of fore leg to show detail.

on apical tergites; penis lobes, fig. 66, with lateral angles relatively blunt, slightly downcurved; each cercus stained with gray-lavender near base, color paling to snow-white toward apex.

The nymph, fig. 59, was described by Ide (1935*a*:113).

Known from central, eastern, and northeastern states and southeastern Canada. Most of the older published records of *album*

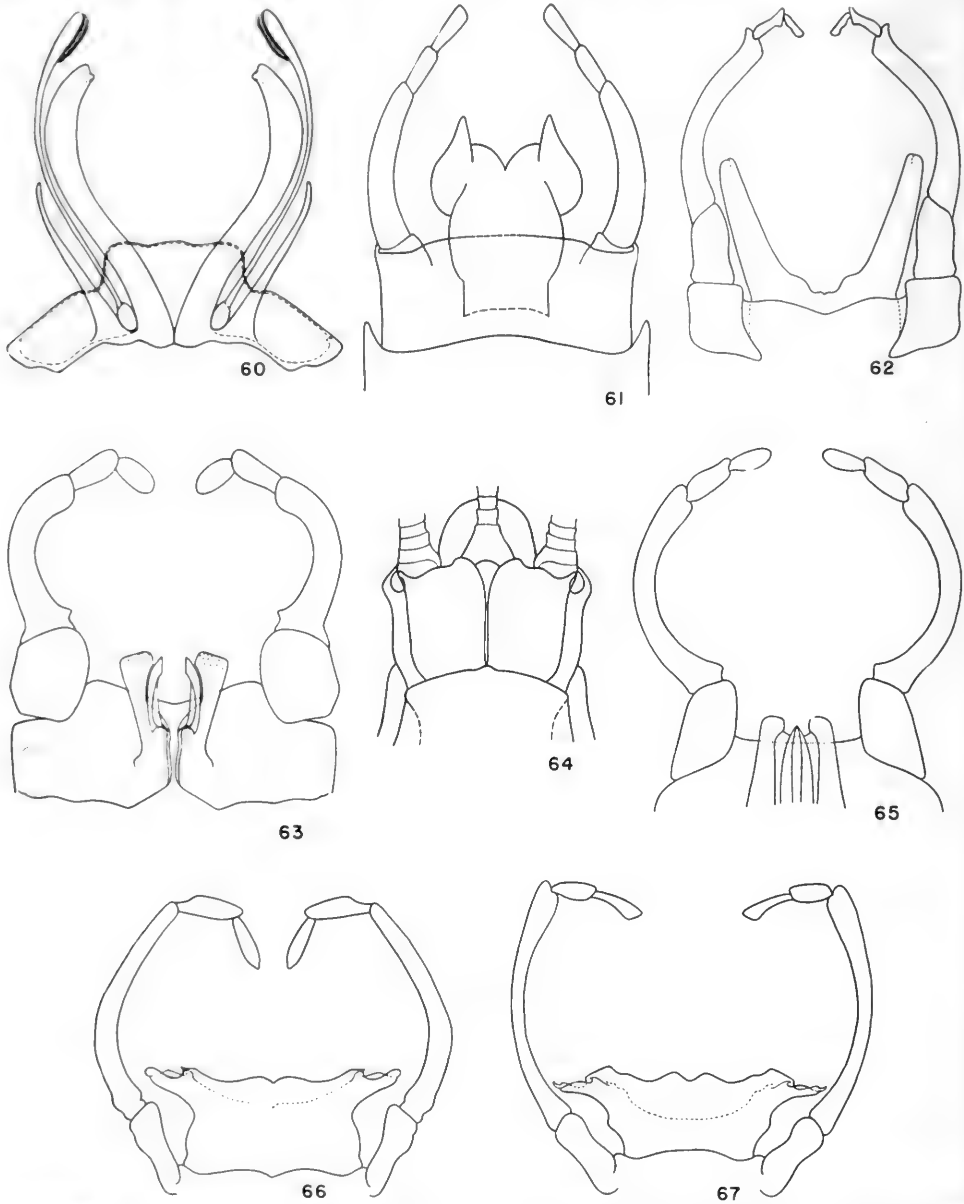


Fig. 60.—*Tortopus primus*, male genitalia.
Fig. 61.—*Potamanthus myops*, male genitalia.
Fig. 62.—*Pentagenia vittigera*, male genitalia.
Fig. 63.—*Ephemera simulans*, male genitalia.
Fig. 64.—*Pentagenia vittigera*, apex of female abdomen, ventral aspect.
Fig. 65.—*Ephemera varia*, male genitalia.
Fig. 66.—*Ephoron leukon*, male genitalia.
Fig. 67.—*Ephoron album*, male genitalia.

for the eastern states should be referred to *leukon*. Develops in large and moderate-sized rivers.

Illinois Records.—Specimens, collected June 9 to September 24, are from Bloomington, Champaign, Cleveland (Rock River), Como (Rock River), Dixon (Rock River), Golconda, Havana, Homer, Kankakee, Lyndon (Rock River), Mahomet (Sangamon River), Milan, Muncie, Oakwood, Prophetstown, Rock Island, Rockton (Rock River), Roscoe (Rock River), Savanna (Mississippi River), Sterling (Rock River), Urbana, West Salem, and Wilmington.

2. *Ephoron album* (Say)

Baetis alba Say (1824:305).
Polymitarcys albus (Say) in part. Eaton (1883:47).

MALE.—Length of body 9–12 mm., of fore wing 8–11 mm. Vertex of head light yellowish, shaded with purplish gray between ocelli; entire dorsum of thorax light cream colored, almost white, sutures faintly shaded with tan; legs white to pale yellow, with each fore femur and tibia stained with purplish gray; abdomen snow-white, apical tergites faintly yellowish; genitalia, fig. 67, with penis lobes having lateral angles acute, slightly upcurved. Each cercus stained with gray near base, blending into snow-white toward apex.

The nymph was described by Edmunds (1948*a*: 12).

Known from the north-central and northwestern states. Develops in large and moderate-sized rivers.

Illinois Records.—FOSTER: Mississippi River, July 11, 1939, B. G. Berger, 2♂. KANKAKEE: at light, Aug. 4, 1936, Frison & Burks, 2♂; Aug. 15, 1938, H. H. Ross, 1♂; Aug. 16, 1938, Ross & Burks, 3♂. MOMENCE: at light, Aug. 5, 1938, Burks & Boesel, 1♂; Aug. 16, 1938, Ross & Burks, 25♂. PROPHETSTOWN: July 7, 1925, T. H. Frison, 5♂. ST. CHARLES: Fox River, July 8, 1948, Ross & Burks, 1♂. WILMINGTON: at light, Aug. 3, 1937, Ross & Burks, 18♂.

EPHEMERINAE

The subfamily Ephemerinae, as defined here, corresponds to the family Ephemeridae in Ulmer's classification (1933:198). It includes the genus *Hexagenia*, whose members are the largest and commonest of Illinois mayflies. They are also the most important mayflies in the state when considered as food for the fishes of our larger lakes and streams.

In the adults, the middle and hind legs are well developed and functional. The marginal intercalary veins of the wings are not netlike. The cubital intercalary veins of each fore wing consist of two to four long, slightly sinuate, forked veins attached to Cu_1 and extending to the wing margin, figs. 27, 40, 46. The median caudal filament may be well developed, greatly reduced, or vestigial.

In the nymphs, figs. 2, 48–50, the frontal process is well developed and the mandibular tusks are strong. When the nymph is alive, the gills are held curved over the abdominal tergites.

KEY TO GENERA

ADULTS

1. Fore wing with crossveins at and posterior to bulla crowded and darkened so as to form a path extending half way across wing, fig. 46 . . . . **5. Ephemera**
   Fore wing with crossveins in region of bulla not so arranged as to form a path extending across wing, figs. 27, 40 . . . 2
2. Median caudal filament reduced but relatively well developed; in female, median caudal filament four-fifths to five-sixths as long as each cercus; in male, one-fifth to one-sixth as long as cercus . . . . **6. Pentagenia**
   Median caudal filament vestigial: in each sex, reduced to only four to nine small, poorly defined segments . **7. Hexagenia**

NYMPHS

1. Head with a more or less dome-shaped anterior projection between bases of antennae, figs. 48, 68–72 . . . . **7. Hexagenia**
   Head with a two-pronged anterior projection between bases of antennae, figs. 49, 50 2
2. Mandibular tusk with dorsolateral angle smooth, rounded, fig. 50 . . **5. Ephemera**
   Mandibular tusk with dorsolateral angle carinate and toothed, fig. 49 . . . . **6. Pentagenia**

5. *EPHEMERA* Linnaeus

Ephemera Linnaeus (1758:546).

The adults are large, relatively slender-bodied mayflies, usually with spotted wings and an abdominal color pattern made up of dark longitudinal stripes and blotches on a very pale yellowish background. In the males, the fore leg is almost as long as the body. The fore wing, fig. 46, has the crossveins at and posterior to the bulla crowded together so as to form a path extending halfway across the wing. The median caudal filament in both sexes is as long as each cercus. The cerci and the median caudal filament are extremely long—each more than twice as long as the body.

In the nymphs, the frontal process of the head has a conspicuous, sharply projecting angle at each lateral margin, fig. 50. The mandibular tusks are long, slender, and smooth, with a few small, toothlike rasps on the outer side near the base. The apex of the labial palp is broad and truncate.

KEY TO SPECIES

Adults

1. Abdomen creamy white, without dark markings . . . . **1. guttulata**
   Abdomen yellowish or tan, with longitudinal, dark brown markings 2
2. Hind wing with small, dark clouds surrounding discal crossveins, making wing appear spotted; genitalia with penis lobes relatively broad, fig. 63 . . . . **2. simulans**
   Hind wing not spotted, discal crossveins not surrounded by dark clouds; genitalia with penis lobes relatively narrow, fig. 65 . . . . **3. varia**

Mature Nymphs

1. Abdomen without color markings on venter . . . . **1. guttulata**
   Abdomen with longitudinal color markings on venter 2
2. Hind wingpad with dark color pattern indicated . . . . **2. simulans**
   Hind wingpad without indication of color pattern . . . . **3. varia**

1. *Ephemera guttulata* Pictet

Ephemera guttulata Pictet (1843:135).

The wings appear to be almost solid brown because of the dense, dark red-brown pigmentation around and between the crossveins; abdomen uniformly pale cream, without a darker color pattern, contrasting markedly with the very dark wings; cerci and median caudal filament tan to brown, with articulations very dark brown. Distinctive genitalia of male figured by Needham (1921, pl. 81, fig. 58) and others.

Known from New York, Pennsylvania, and Quebec.

2. *Ephemera simulans* Walker

Ephemera simulans Walker (1853:536).
Ephemera natata Walker (1853:551).
Ephemera decora Walsh (1862:376).

Male.—Length of body 10–12 mm., of fore wing 11–13 mm. Thorax mostly dark red-brown, with relatively small, light tan areas on pro- and mesopleuron; each fore leg dark red-brown, middle and hind legs tan to yellow; fore wing and hind wing, figs. 46, 47, each with dark brown spots in discal area. Abdomen yellow to tan, with dark red-brown markings: each tergite with a pair of lateral dark blotches; each of apical three tergites with a pair of submedian, longitudinal, lateral stripes; sternites with longitudinal, lateral stripes, and a pair of submedian, longitudinal spots on each sternite; penis lobes, fig. 63, relatively wide; caudal filaments dark yellow-brown, with articulations darkened.

Female.—Length of body 11–13 mm., of fore wing 12–14 mm. Color pattern same as in male, but dark areas and spots relatively less extensive; legs light tan or yellow, fore legs shaded with light red-brown; caudal filaments light yellow, with brown articulations.

Known from the northeastern and central states and eastern Canada. This is one of the commonest mayflies in the Chicago region. It emerges along the lake front in enormous numbers every summer. The nymph is found near the shores of lakes having considerable wave action and in moderate-sized rivers and creeks.

Illinois Records.—Cedar Lake: Oct. 21, 1882, 3 nymphs. Chicago: July 31, 1887, C. A. Hart, 3♂, 3♀; July, 1916, 1♂; July 8, 1937, Frison & Ross, 43♂, 18♀. Eddyville: Lusk Creek, May 16, 1947, B. D. Burks, 1♀. Evanston: July 17, 1938, G. T. Riegel, 2♂; July 9, 1939, G. T. Riegel, 1♂; July 22, 1942, J. S. Ayars, 2♂. Homer: June 30, 1925, T. H. Frison, 1♂; June 10, 1926, T. H. Frison, 9♀; June 30, 1927, Frison & Glasgow, 9♂, 11♀; Oct. 3, 1946, L. J. Stannard, 2 nymphs. Kankakee: June 12, 1931, Frison & Mohr, 2♂, 3♀; June 5, 1932, Frison & Mohr, 2♂; May 31, 1938, Burks & Mohr, 3♂, 1♀;

June 15, 1938, Ross & Burks, 1 ♀. McHENRY: June 3, 1943, Ross & Sanderson, 1 ♀. MUNCIE: June 29, 1919, 1 ♂; May 25, 1941, Ivabel Johnson, 1 ♀. OAKWOOD: June 6, 1925, T. H. Frison, 18 ♂, 1 ♀; June 9, 1926, Frison & Auden, 81 ♀; June 14, 1935, C. O. Mohr, 1 ♀; June 5, 1948, Burks & Sanderson, 5 ♂, 1 ♀; June 23, 1948, B. D. Burks, 3 ♂. SOUTH BELOIT: July 2, 1931, Betten, Frison, & Ross, 1 ♂, 1 ♀.

3. *Ephemera varia* Eaton

Ephemera decora Hagen (1861:38), not Walker. Misidentification.
Ephemera varia Eaton (1883:69).

The types of this species are in the Museum of Comparative Zoology.

The fore wing in the adults has the same fundamental color pattern as that in *simulans,* although the dark-colored areas are relatively smaller; the hind wing in *varia,* however, lacks the dark spots entirely. The thorax is relatively lighter colored than the thorax of *simulans;* the fore leg of the male is dark yellow, the base and apex of the tibia brown; the middle and hind legs are light yellow, almost white. The penis lobes, fig. 65, are relatively narrower than those in *simulans,* fig. 63.

Known from Connecticut, Maine, Michigan, New Hampshire, New York, Ontario, and West Virginia.

6. *PENTAGENIA* Walsh

Pentagenia Walsh (1863:196).

The adults of *Pentagenia* are large, cream-colored mayflies, each with a conspicuous, dark brown, longitudinal band on the dorsum of the thorax. In the males, the eyes, which are almost contiguous on the meson, are larger than those of any other member of the family Ephemeridae. Each fore leg in the males is relatively short, about one-half as long as the body, and only slightly longer than the middle and hind legs; the legs in the females are quite similar to those in the males. The wing venation, figs. 40, 41, is typical for the subfamily. The median caudal filament in both sexes is reduced in length.

In the nymphs, fig. 49, the frontal projection of the head has a stout prong at each lateral margin, the mandibular tusks are short and stout, bearing irregular teeth along each dorsolateral margin; and the apical segment of the labial palp is a broad, somewhat scoop-shaped triangle.

KEY TO SPECIES

ADULTS

Caudal filaments uniformly light yellowish or white; abdominal sternites unmarked............................... **1. vittigera**
Caudal filaments brown, with narrow, yellowish band at each articulation; abdominal sternites marked with brown lines.. **2. robusta**

1. *Pentagenia vittigera* (Walsh)

Palingenia vittigera Walsh (1862:373).
Pentagenia quadripunctata Walsh (1863:198).

MALE.—Length of body and of fore wing 15–18 mm. Head and body generally cream colored, with dorsum of thorax marked with brown and entire dorsum of abdomen occupied by a conspicuous, dark brown, longitudinal band; legs light yellowish, almost white, with variable, vague gray shading at articulations; wings hyaline, C, Sc, and R of fore wing light yellow, and crossveins in this area yellowish, other veins and crossveins hyaline; fore wing often with four black dots in a row extending across wing from bulla toward posterolateral angle of wing; abdominal sternites unmarked; genitalia, fig. 62, and caudal filaments very light yellow, almost white.

FEMALE.—Length of body 18–25 mm., of fore wing 18–23 mm. Colored as in male; apical abdominal sternite with a median, V-shaped notch on apical margin, fig. 64.

Known from Arkansas, Illinois, Iowa, Kansas, Minnesota, Missouri, Tennessee, and Texas. Although this species in Illinois is never so abundant as the species of *Hexagenia,* the adults of *vittigera* occur in considerable numbers throughout the summer along our larger rivers. Apparently, *vittigera* develops only in large rivers.

Illinois Records.—Specimens, collected from June 6 to September 20, are from Anna, Bloomington, Cairo, Carbon Cliff, Carbondale, Carlyle, Centralia, Champaign, Chicago, Dixon, Elizabethtown, Freeport, Gibson City, Golconda, Grafton (Illinois River), Harrisburg, Havana, Keithsburg, McConnell (Rock River), Meredosia (Illinois River), Mount Carmel, Murphysboro, Oquawka, Peoria (Illinois River), Pere

Marquette State Park, Poplar Bluff, Quincy (Mississippi River), Rock Island, Rockton (Rock River), Rosiclare, Shepherd, Urbana, and Waukegan.

2. *Pentagenia robusta* McDunnough

Pentagenia robusta McDunnough (1926: 185).

All crossveins in wings tan; no pigmented dots in fore wing. Abdominal sternites marked with longitudinal, brown lines, and terminal two sternites mostly brown; caudal filaments brown, with yellowish articulations.

Known only from Ohio.

7. *HEXAGENIA* Walsh

Hexagenia Walsh (1863: 197).

The various members of this genus are the commonest Illinois mayflies, as well as the largest. The eyes in the adult males are large, but never quite so large as in *Pentagenia vittigera,* and are always separated on the meson by at least a small space. Each fore leg in the males is approximately as long as the body. In the fore wing, the crossveins near the bulla are not crowded, fig. 27, as they are in *Ephemera,* fig. 46. The median caudal filament is reduced to a mere vestige in both sexes.

In the nymphs, fig. 2, the frontal process is dome-shaped, conical, or truncate; the lateral angles are never produced anteriorly as spines or prongs. The upcurved mandibular tusks are long, slender, and smooth, entirely lacking rasplike teeth. The apical segment of the labial palp is broad, with a median apical point.

My views of specific limits in this genus correspond in the main with those of Spieth (1941*b*: 233); I have not, however, followed him in recognizing subspecific segregates within the species *limbata* and *munda.*

It is not advisable to attempt to name single female specimens, unassociated with males; the characters given below for females apply to typical specimens only.

KEY TO SPECIES

Adults

1. Males 2
   Females 7
2. Apex of each penis lobe reflexed, fig. 73; first segment of forceps shorter than penis lobe ....**6. recurvata**
   Apex of each penis lobe not reflexed, figs. 74–78; first segment of forceps longer than penis lobe 3
3. An anteapical protuberance on mesal margin of each penis lobe (dorsal view), fig. 78 ....**2. bilineata**
   No anteapical protuberance on mesal margin of each penis lobe, figs. 74–77....4
4. Apexes of penis lobes sharply incurved, fig. 75 ....**3. limbata**
   Apexes of penis lobes arcuate, figs. 74, 76, 77 5
5. Penis lobes short and blunt, fig. 77...... ....**1. atrocaudata**
   Penis lobes elongate, figs. 74, 76.......6
6. Penis lobes tapered gradually to apexes, fig. 74 ....**5. rigida**
   Penis lobes abruptly constricted at about midlength, fig. 76 ....**4. munda**
7. Membrane of wings uniformly stained with brown pigment, and lacking darker spots or areas at costal margin of fore wing, posterior margin of hind wing, or in disc of either of these wings........ ....**6. recurvata**
   Wing membrane hyaline, yellowish, or very light tan, and always with some darker areas or spots in wings.......8
8. Hind wing with a broad, reddish or purplish-brown band at posterior margin, fig. 83..............**1. atrocaudata**
   Hind wing either without darkened posterior margin or with a relatively narrow, sometimes discontinuous, dark brown band at posterior margin, figs. 82, 84–87........................9
9. Hind wing with membrane hyaline, veins hyaline, and discal crossveins black, figs. 86, 87; abdomen white or cream colored, with dorsal color pattern of dull red markings..........**5. rigida**
   Hind wing with membrane hyaline, yellowish, or light tan, with veins partly or entirely yellowish or tan, and crossveins black or brown both in discal and marginal areas of wing; abdomen yellow, tan, or light brown, with brown color pattern.....................10
10. Hind wing with a continuous, dark brown band at posterior margin and two relatively large, brown spots in disc of wing; each discal crossvein surrounded by a small, brown cloud, fig. 82....... ....**2. bilineata**
    Posterior margin of hind wing without brown band, fig. 85, or often with an irregular, discontinuous one, fig. 84; no large, brown spots in disc of wing... ....**3. limbata, 4. munda**

Mature Nymphs

1. Each gill of first pair composed of a single filament...............**6. recurvata**
   Each gill of first pair composed of two or more filaments...................2
2. Frontal process of head truncate at apex and with a small mesal indentation, fig. 70...............**1. atrocaudata**
   Frontal process of head rounded or angled on meson, figs. 68, 69, 71, 72........3

3. Frontal process of head dome shaped, fig. 69 . . . . **3. limbata**
   Frontal process of head angled on meson at apex, figs. 68, 71, 72 4
4. Mid-tarsal claw slender, long, fig. 79; frontal process of head bluntly angled on meson, broad at base, fig. 72 . . . . **5. rigida**
   Mid-tarsal claw broadened near base, figs. 80, 81; frontal process of head as in figs. 68, 71 5
5. Frontal process of head relatively narrow, and with straight lateral margins, fig. 71; mid-tarsal claw slender near tip, fig. 81 . . . . **4. munda**
   Frontal process of head wider, and with curved lateral margins, fig. 68; mid-tarsal claw thick near tip, fig. 80 . . . . **2. bilineata**

1. *Hexagenia atrocaudata* McDunnough

Hexagenia atrocaudata McDunnough (1924*b*: 92).

MALE.—Length of body 22–24 mm., of fore wing 23–25 mm. Eyes large, almost contiguous on meson of head. Dorsum and sternum of thorax mostly very dark red-brown, pleura with yellow and light red areas. Fore wing hyaline, with all veins and crossveins very dark red-brown, costal interspace red-brown, no conspicuous, discal, dark spots present; hind wing, fig. 83, hyaline, veins and crossveins dark, no discal, dark spots present, outer margin with a broad, purplish or reddish-brown band. Abdominal tergites mostly dark red-brown, with small, yellowish streaks or spots on dorsal meson and at lateral margins; genitalia, fig. 77, with short and blunt penis lobes.

FEMALE.—Length of body 23–25 mm., of fore wing 24–25 mm. Colored much as in male, but brown areas slightly smaller and lighter colored; wings as in male.

NYMPH.—Length of mature specimen 25 mm. Frontal process of head, fig. 70, truncate at apex and with a small mesal indentation.

Known from Georgia, Illinois, Indiana, Maryland, Michigan, Missouri, New York, North Carolina, Ohio, Ontario, Pennsylvania, Virginia, and West Virginia. Develops in relatively cool, rapid creeks and smaller rivers.

Illinois Records.—MOMENCE: Aug. 21, 1936, Ross & Burks, 1 ♀; Aug. 22, 1936, 1 ♂. RICHMOND: Aug. 15, 1938, Ross & Burks, 1 ♂. WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 2 ♀.

2. *Hexagenia bilineata* (Say)

Baetis bilineata Say (1824: 303).
Hexagenia bilineata falcata Needham (1921: 292; pl. 81, fig. 62).

MALE.—Length of body 14–20 mm., of fore wing 14–18 mm. Eyes separated on meson of head by a space one-half as wide as width of one eye. Thorax mostly red-brown; fore wing hyaline, veins red-brown, crossveins darker, several prominent, brown spots in disc of wing, costal interspace tinted with red-brown; hind wing, fig. 82, with several prominent, discal, brown spots. Abdomen, when viewed from side without magnification, appears to have two parallel, longitudinal, dark brown bands; penis lobes, fig. 78, beaked.

FEMALE.—Length of body 18–22 mm., of fore wing 20–22 mm. Color of body and wings as in male, but generally slightly lighter; parallel, longitudinal, color bands of abdomen not so obvious.

NYMPH.—Length 25–35 mm. Frontal process of head, fig. 68, relatively broad, with curved margins; mid-tarsal claw thick near tip, fig. 80.

Known from the District of Columbia, Mississippi River valley, Maryland, and Virginia. Develops usually only in large, relatively slow rivers, but sometimes develops also in impounded bodies of water.

Illinois Records.—Specimens, collected from June 6 to September 16, are from Alton, Cairo, Decatur, Elizabethtown, Fulton, Glendale, Grafton, Hardin, Harrisburg, Havana, Kankakee, Mahomet, Meredosia, Milan, Monticello, Mound City, Murphysboro, Oregon, Peoria, Pontiac, Prophetstown, Quincy, Ripley, Rockford, Rock Island, Rockton, Rosiclare, Savanna, Springfield, Venedy Station, and Wilmington.

3. *Hexagenia limbata* (Serville)

Ephemera limbata Serville *in* Guérin (1829: 384; pl. 60, figs. 7–9).
Palingenia occulta Walker (1853: 564).
Palingenia viridescens Walker (1853: 550).
Baetis angulata Walker (1853: 564).
Hexagenia variabilis Eaton (1883: 55).
Hexagenia venusta Eaton (1883: 54).
Hexagenia mingo Traver (1931*b*: 597).
Hexagenia pallens Traver (1935*a*: 271).

MALE.—Length of body 16–21 mm., of fore wing 13–19 mm. The compound eyes separated on meson by a space slightly nar-

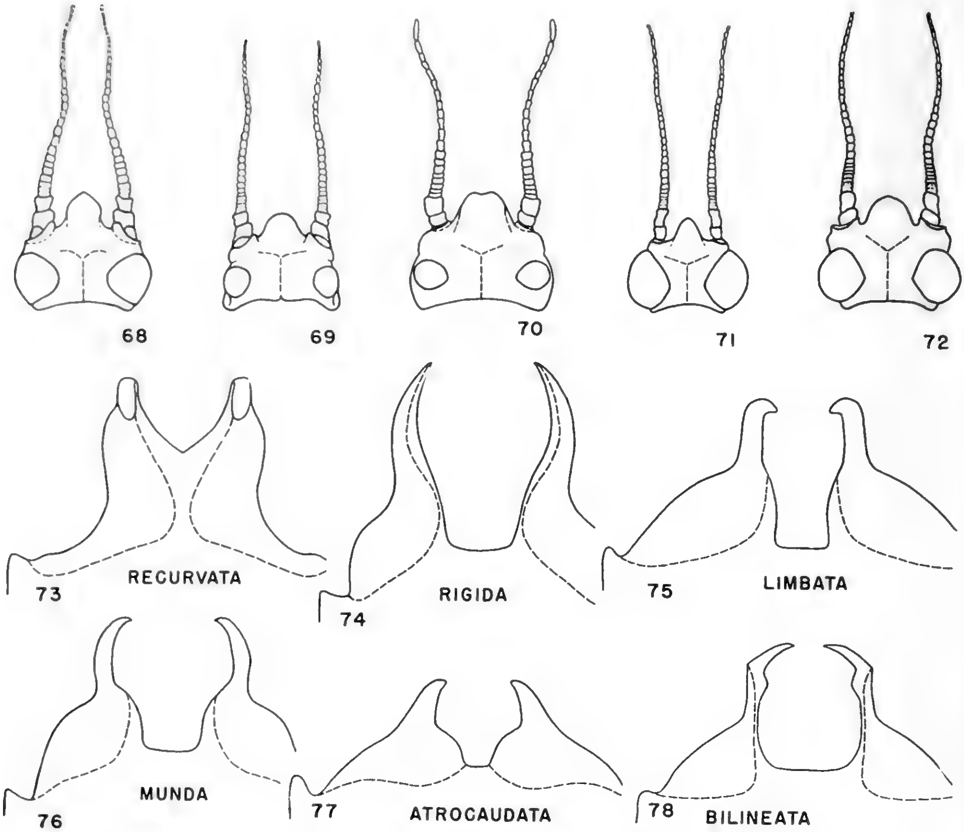


Fig. 68.—*Hexagenia bilineata,* dorsal aspect of head of nymph.

Fig. 69.—*Hexagenia limbata,* dorsal aspect of head of nymph.

Fig. 70.—*Hexagenia atrocaudata,* dorsal aspect of head of nymph.

Fig. 71.—*Hexagenia munda,* dorsal aspect of head of nymph.

Fig. 72.—*Hexagenia rigida,* dorsal aspect of head of nymph.

Fig. 73.—*Hexagenia recurvata,* penis lobes.

Fig. 74.—*Hexagenia rigida,* penis lobes.

Fig. 75.—*Hexagenia limbata,* penis lobes.

Fig. 76.—*Hexagenia munda,* penis lobes.

Fig. 77.—*Hexagenia atrocaudata,* penis lobes.

Fig. 78.—*Hexagenia bilineata,* penis lobes.

rower than diameter of one eye. Thorax typically mostly dark red-brown, varying to light brown; fore wing hyaline or faintly stained with yellow or tan, costal interspace shaded with red-brown, usually several prominent, brown spots in disc of wing; outer margin of hind wing usually with a conspicuous brown band. Abdominal tergites typically marked with dark brown lateral triangles and lighter brown mesal ones, sternites varying from almost completely unmarked to having a conspicuous row of dark mesal triangles; genitalia, fig. 75, with penis lobes hook shaped at apexes.

Female.—Length of body 22–24 mm., of fore wing 20–22 mm. Colored much as in male, but generally lighter, some individuals almost completely yellow, darkest individuals never so dark as darkest males; fore wing usually lacking discal spots; hind wing, figs. 84, 85, without discal spots, posterior margin with or without brown band, this band, when present, discontinuous.

Nymph.—Length 23–30 mm. Frontal process of head dome shaped, fig. 69.

Known from the Mississippi and Missouri river valleys, eastern states, and southern Canadian provinces. Develops in a great variety of waters: small to large creeks, small to large rivers, small lakes, and bodies of impounded water.

Illinois Records.—Specimens, collected from June 4 to September 15, are from Anna, Antioch, Beardstown, Bloomington, Carbondale, Champaign, Channel Lake, Decatur, Dixon, Elgin, Fisher, Fox Lake,

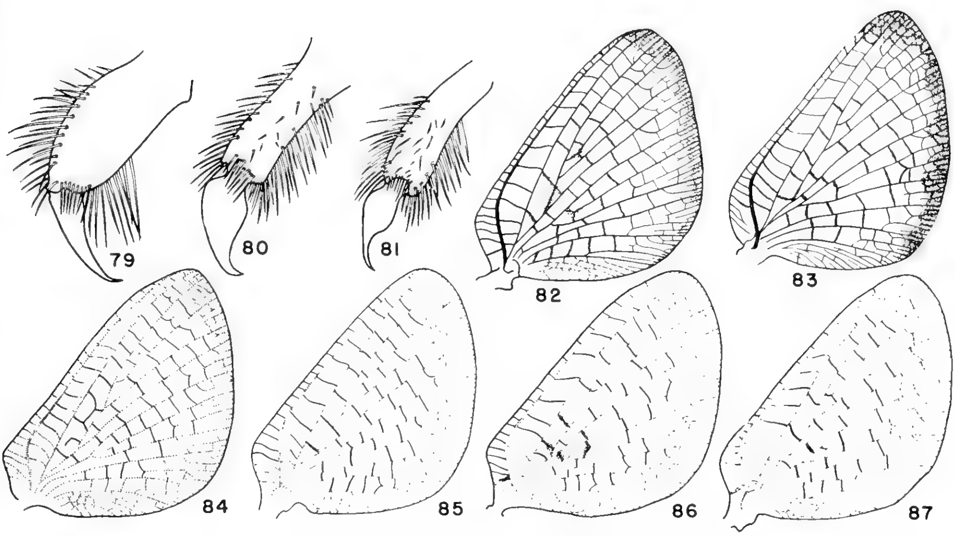


Fig. 79.—*Hexagenia rigida*, claw of middle leg of mature nymph.
Fig. 80.—*Hexagenia bilineata*, claw of middle leg of mature nymph.
Fig. 81.—*Hexagenia munda*, claw of middle leg of mature nymph.
Fig. 82.—*Hexagenia bilineata*, hind wing of female.
Fig. 83.—*Hexagenia atrocaudata*, hind wing of female.
Fig. 84.—*Hexagenia limbata*, dark phase, hind wing of female.
Fig. 85.—*Hexagenia limbata*, light phase, hind wing of female.
Fig. 86.—*Hexagenia rigida*, dark phase, hind wing of female.
Fig. 87.—*Hexagenia rigida*, light phase, hind wing of female.

Freeport, Giant City State Park, Gilman, Glen Ellyn, Grayslake, Havana, Homer, Kankakee, Kickapoo State Park, Laclede, La Salle, McHenry, Mahomet, Momence, Monticello, Morris, Mount Carmel, Murphysboro, New Milford, Oakwood, Oregon, Peoria, Poplar Bluff, Quincy, Rantoul, Richmond, Rockford, Rock Island, Roodhouse, Rosecrans, Springfield, Spring Grove, Urbana, and Waukegan.

4. *Hexagenia munda* Eaton

Hexagenia munda Eaton (1883:53).
Hexagenia affiliata McDunnough (1927*c*:119).
Hexagenia carolina Traver (1931*b*:601, 616).
Hexagenia elegans Traver (1931*b*:594).
Hexagenia marilandica Traver (1931*b*:599).
Hexagenia orlando Traver (1931*b*:608).
Hexagenia rosacea Traver (1931*b*:607).
Hexagenia weewa Traver (1931*b*:605).
Hexagenia kanuga Traver (1937:29).

This species is distinguishable from *limbata* only in the male and the nymph. Male genitalia, fig. 76, have penis lobes in form of elongate, shallow hooks. Nymph has a relatively narrow, straight-margined frontal process, fig. 71; mid-tarsal claw slender near tip, fig. 81.

Known from the northeastern, central, and southeastern states; it is extremely rare in Illinois, possibly an adventive. Apparently normally develops in small lakes.

Illinois Record.—Monticello: April 11, 1934, 1 ♂.

5. *Hexagenia rigida* McDunnough

Hexagenia bilineata falcata Needham (1921:292; pl. 81, fig. 65).
Hexagenia rigida McDunnough (1924*b*:90).

MALE.—Length of body 18–24 mm., of fore wing 16–20 mm. Eyes separated on meson by a space equal to diameter of one eye. Thorax mostly dark red-brown; fore wing hyaline, costal interspace stained with brown, veins and crossveins dark brown; hind wing with prominent discal spots, outer margin usually with brown band. Abdomen with extensive, dark red-brown color pattern on yellow- or red-brown background; penis lobes, fig. 74, elongate, almost straight.

FEMALE.—Length of body 18–28 mm., of fore wing 18–24 mm. Background color of body white or light cream; dorsal abdominal pattern dull red, venter entirely white; hind wing with membrane and veins hyaline, and crossveins black, figs. 86, 87. This is the only species of *Hexagenia* so colored.

Nymph.—Length of body of mature specimen 22–28 mm. Apex of frontal process of head bluntly angled on meson, broad at base, fig. 72; mid-tarsal claw elongate, slender, fig. 79.

Known from Illinois, Iowa, Kansas, Manitoba, Michigan, Missouri, New Brunswick, New York, Ohio, Oklahoma, Ontario, Pennsylvania, Quebec, and Vermont. Develops in moderate-sized rivers that have a fairly rapid flow.

Illinois Records.—Specimens, collected from April 26 to September 6, are from Aroma Park, Aurora (Fox River), Beardstown, Chicago, Dixon (Rock River), Homer, Kankakee (Kankakee River), Libertyville, Mahomet, Momence, Oakwood, Oregon, Prophetstown, Rockford, Rockton (Rock River), Roscoe (Rock River), Rosiclare, South Beloit, White Heath, and Wilmington.

6. *Hexagenia recurvata* Morgan

Hexagenia recurvata Morgan (1913:395).

This species has the wing membranes so heavily tinted with dark brown that freshly killed specimens appear to have almost black wings. The dorsum of the thorax is mostly very dark brown, but the abdomen is mostly light yellow, with relatively small, darker markings; the male genitalia are distinctive, fig. 73, as the penis lobes have their apexes recurved. The nymph differs from all others in the genus in having the first pair of abdominal gills single.

Known from Maine, Massachusetts, Michigan, New York, North Carolina, Ontario, Quebec, and West Virginia.

NEOEPHEMERIDAE new family

This family includes a single North American genus, *Neoephemera,* which I am segregating from the Ephemeridae. Although the adults of *Neoephemera* show considerable similarity to the typical ephemerids, the nymphs are very similar to the caenid type. This indicates that *Neoephemera* is an interstitial form. Rather than include it in either the Ephemeridae or the Caenidae, necessitating the inclusion of a number of exceptions in the characterization of each family, I believe *Neoephemera* can better be considered as representing a distinct family. Ulmer (1933:199) placed *Neoephemera* in the family Ephemeridae, as did Traver (1935*a*:289). In describing the new Javanese genus *Neoephemeropsis,* Ulmer (1939:481, 483; 1940:606) pointed out that it is a near relative of the American genus *Neoephemera* and placed it in his family Potamanthidae. *Neoephemeropsis* almost certainly belongs in the family Neoephemeridae. The European form that is known as *Caenis maxima* Joly (1870:144) probably also belongs here.

8. *NEOEPHEMERA* McDunnough

Neoephemera McDunnough (1925*b*:168).
Oreianthus Traver (1931*a*:103).
New synonymy.

In the adults of this genus, the fore wing, fig. 28, has the basal costal crossveins weak or entirely absent, the stigmatic crossveins partly anastomosed, vein M_2 slightly curved toward vein Cu_1 near the wing base, two long, forked, cubital intercalary veins, and vein 1A with one to three crossveins extending from it to the anal wing margin. The hind wing has an acute marginal projection, and veins M_1 and M_2 diverge near the center of the wing. The median caudal filament is well developed in both sexes. It may be noted that, in *Neoephemeropsis,* the median caudal filament is rudimentary in both sexes.

The nymphs, fig. 88, are typically caenid in type, although each possesses two pairs of wingpads. Each tarsal claw is long, slender, and edentate, fig. 92. There is a minute, median, backward-projecting spine on the posterior margin of dorsum of the metathorax and on each of abdominal tergites 1–2 and 6–8. Each gill of the pair on the first abdominal segment is minute, single, and filiform, fig. 89*B*; on second segment elytroid, connate, covering the gills of the four following abdominal segments, and bearing a ventral tuft of filaments, fig. 89*A*; on segments 3–6, fig. 89*C*, similar in form to the corresponding gills in *Caenis,* fig. 91*D*, but differing in that each dorsal, platelike gill has a ventral tuft of filaments near the base. The median caudal filament is well developed and all three caudal filaments are uniformly clothed with short spines. In

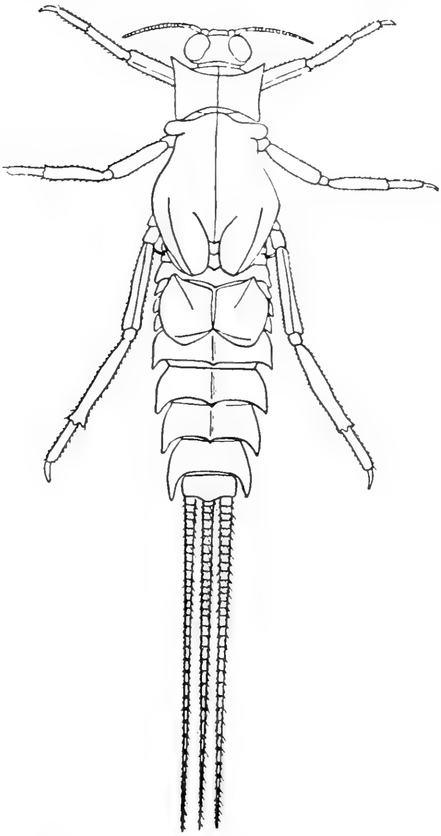


Fig. 88.—Nymph of *Neoephemera purpurea.* (From Traver. Figure used by permission of the Comstock Publishing Company, Ithaca, New York.)

the Javanese *Neoephemeropsis,* each cercus is also clothed, on the mesal side, with a dense comb of long setae, and the median caudal filament bears such a comb of long setae on either side.

There are two described species of *Neoephemera* in North America. *N. bicolor* McDunnough (1925*b*:168) is known from Michigan, Quebec, and Georgia; *purpurea* (Traver) (1931*a*: 103; 1937: 34) is known from Florida, Georgia, North Carolina, and South Carolina.

CAENIDAE

This family corresponds to the subfamily Caeninae of the family Baetidae in Traver's classification (1935*a*: 629), and to the family Caenidae in Ulmer's classification (1933: 206).

The members of the Caenidae are among the most distinct of the mayflies. In most species, the individuals are small, but some attain a body length of 6 or 7 mm. The adult females are slightly larger than the males, but otherwise they are almost identical in appearance; even the compound eyes of one are not larger than those of the other. In both sexes, each lateral ocellus is at least one-half as large as one of the compound eyes. The thorax is greatly developed, while the abdomen is relatively small and contracted, giving these mayflies a rather thickset appearance. The fore wing is white, being quite cloudy or milky, the costal margins tinged with grayish lavender; the marginal ciliae are numerous, even in the imago stage. In all genera, the wings characteristically have very few crossveins, and, except in *Leptohyphes,* they are quite broad in the anal region, figs. 97, 98. The hind wing is wanting except in the subimago stage of the genus *Leptohyphes.* Each tarsus has five segments, figs. 11–13. The abdomen is somewhat broad and flattened dorsoventrally, with the posterolateral angles of each segment obliquely produced. There are three well-developed caudal filaments, and the individual segments making up these filaments are relatively longer than in most mayflies. In the subimagoes, the filaments bear prominent setae, but in the adult males they are bare. The adult females retain, partly or completely, the subimaginal filaments. Especially in the females, the subimaginal exuviae are often only partly shed.

In the hairy nymphs, figs. 96, 113, 114, the head is hypognathous and the body somewhat flattened dorsoventrally. The tarsal claws are relatively large and long, figs. 93–95. The lateral margins of the abdominal segments are produced as spines or plates. The first abdominal segment has either a pair of single, filamentous gills or none. The gills borne by the second abdominal segment are operculate, completely covering the gills on segments 3–6. There are three well-developed caudal filaments; the cerci bear setae on all sides.

KEY TO GENERA

ADULTS

1. Fore wing with very few crossveins and with median intercalary vein extending to wing base, fig. 97; male genital forceps with only one segment, fig. 108. . 2

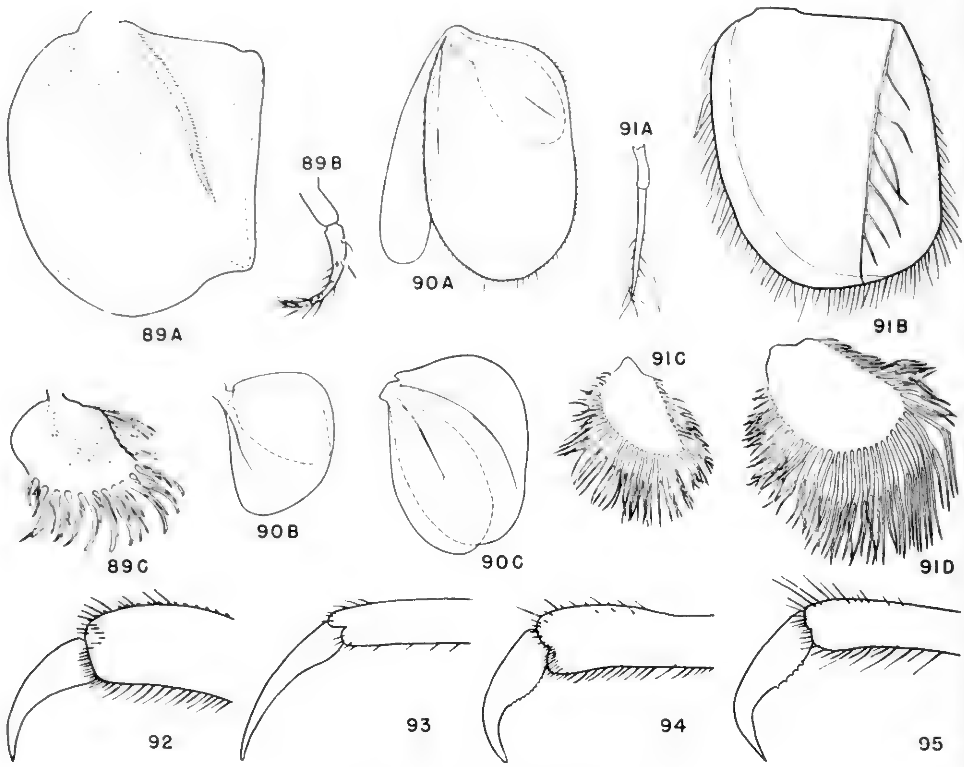


Fig. 89*A*.—*Neoephemera purpurea,* elytroid gill.
Fig. 89*B*.—*Neoephemera purpurea,* gill of first abdominal segment.
Fig. 89*C*.—*Neoephemera purpurea,* gill of fourth abdominal segment.
Fig. 90*A*.—*Tricorythodes atratus,* elytroid gill.
Fig. 90*B*.—*Tricorythodes atratus,* gill of sixth abdominal segment.
Fig. 90*C*.—*Tricorythodes atratus,* gill of fourth abdominal segment.
Fig. 91*A*.—*Caenis* sp., gill of first abdominal segment.
Fig. 91*B*.—*Caenis* sp., elytroid gill.
Fig. 91*C*.—*Caenis* sp., gill of sixth abdominal segment.
Fig. 91*D*.—*Caenis* sp., gill of fourth abdominal segment.
Fig. 92.—*Neoephemera purpurea,* claw of middle leg of mature nymph.
Fig. 93.—*Brachycercus lacustris,* claw of middle leg of mature nymph.
Fig. 94.—*Caenis* sp., claw of middle leg of mature nymph.
Fig. 95.—*Tricorythodes atratus,* claw of middle leg of mature nymph.

Fore wing with relatively numerous cross-veins and with median intercalary vein extending only halfway to wing base, fig. 98; male genital forceps with three segments, fig. 101 3

2. Prosternum twice as broad as long, fore coxae being widely separated on venter .... **10. Brachycercus**

Prosternum at least twice as long as broad, fore coxae being close together on venter .... **11. Caenis**

3. Fore wing broadest in the anal region, fig. 98; subimago without hind wing .... **9. Tricorythodes**

Fore wing more elongate and narrow, broadest in the center; subimago with hind wing.......... **12. Leptohyphes**

Mature Nymphs

1. First abdominal segment without gills; each operculate gill borne by second abdominal segment triangular, fig. 96, or elongate-oval; operculate gills well separated on mid-dorsal line of abdomen.......................... 2

First abdominal segment bearing a pair of single, filamentous gills; each operculate gill borne by second abdominal segment semiquadrate, these operculate gills meeting or overlapping on mid-dorsal line of abdomen, figs. 113, 114.................................. 3

2. Operculate gills triangular, fig. 96...... .... **9. Tricorythodes**

Operculate gills elongate-oval.......... ....**12. Leptohyphes**

3\. Head bearing occipital and frontal tubercles, fig. 113.......**10. Brachycercus**

Head without tubercles, fig. 114........ ....**11. Caenis**

9. *TRICORYTHODES* Ulmer

Tricorythodes Ulmer (1920*a*: 51).

The species of *Tricorythodes* consist of small, fragile mayflies which resemble *Caenis* in habitus, but differ considerably in diagnostic characteristics. *Tricorythodes* is a New World genus related to *Tricorythus* of the Palearctic and African regions. *Tricorythodes* and *Tricorythus* are distinguished in the adults by the characteristics of the legs. In the former, the legs are long and slender; in the latter, they are short and less slender.

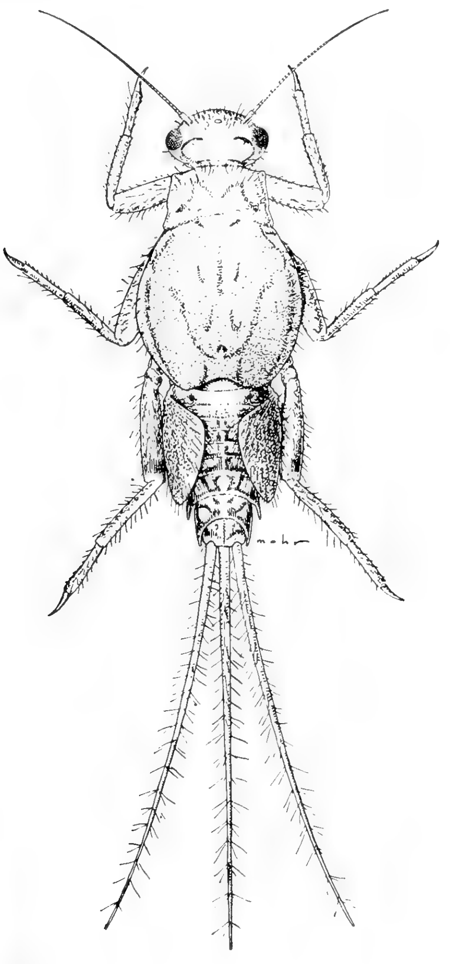
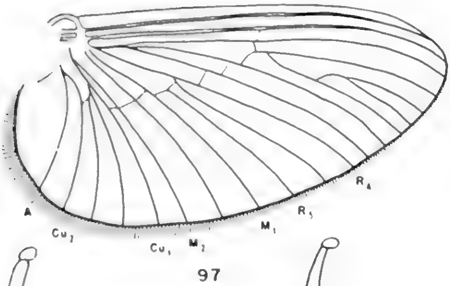


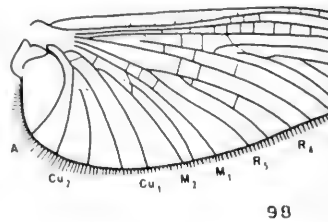
Fig. 96. — *Tricorythodes atratus*, mature nymph, dorsal aspect.

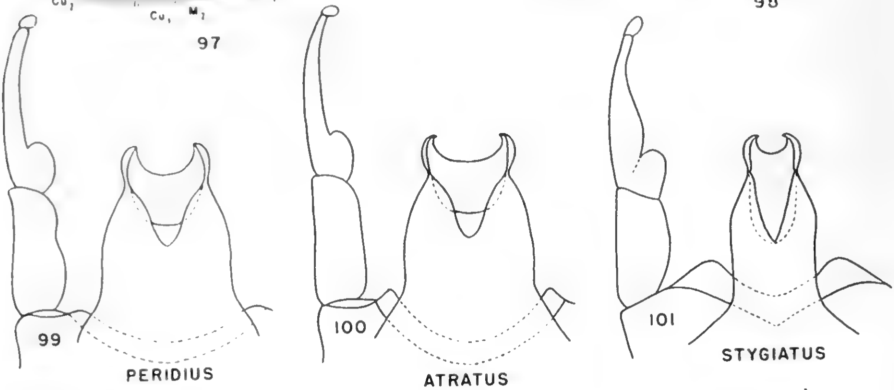
In the Illinois species of *Tricorythodes*, each adult has a pair of tubercles near the posterior margin of the vertex of the head. Each antennal pedicel in both sexes is two or three times as long as the scape; the flagellum is enlarged near the base and is four or five times as long as the pedicel. In the adult males, the fore leg is as long as the body, the fore femur is one-half as long as the fore tibia, and the fore tibia is one and one-half times as long as the fore tarsus; the second tarsal segment is one-half as long as the tibia and as long as tarsal segments 3–5 combined. In the fore wing, fig. 98, there are relatively numerous crossveins; veins R_4 and R_5 diverge in the center of the wing, and vein M_2 and the median intercalary arise some distance distad of the wing base. The posterior margin of the male genital forceps base has a wide, median excavation. Each arm of the forceps, figs. 99–101, has three segments; segment 1 is columnar, segment 2 has a bulbous, median enlargement at the base, and segment 3 is minute. The penis lobes are fused on the meson almost to the apexes, much as in some species of *Ephemerella*. In the adult females, the caudal filaments are as long as those of the males, and these female caudal filaments usually retain the subimaginal setae only at the apexes.

The nymphs, fig. 96, have smooth heads lacking tubercles. Each antenna is almost twice as long as the head and pronotum, when measured in dorsal aspect. The legs are relatively longer than in *Caenis*, fig. 114, but shorter than in *Brachycercus*, fig. 113; each claw is relatively long, hooked at its apex, and has a ventral row of denticles, fig. 95. Abdominal segment 1 lacks gills; segment 2 bears a pair of subtriangular, operculate gills, each of which has an additional, ventral, membranous plate; each of segments 3–6 bears a pair of double, platelike gills. All gills, fig. 90, have the margins entire. The three caudal filaments are relatively long and stout, and they have a whorl of setae at each articulation.

I have observed the subimagoes of *Tricorythodes atratus* to shed the subimaginal







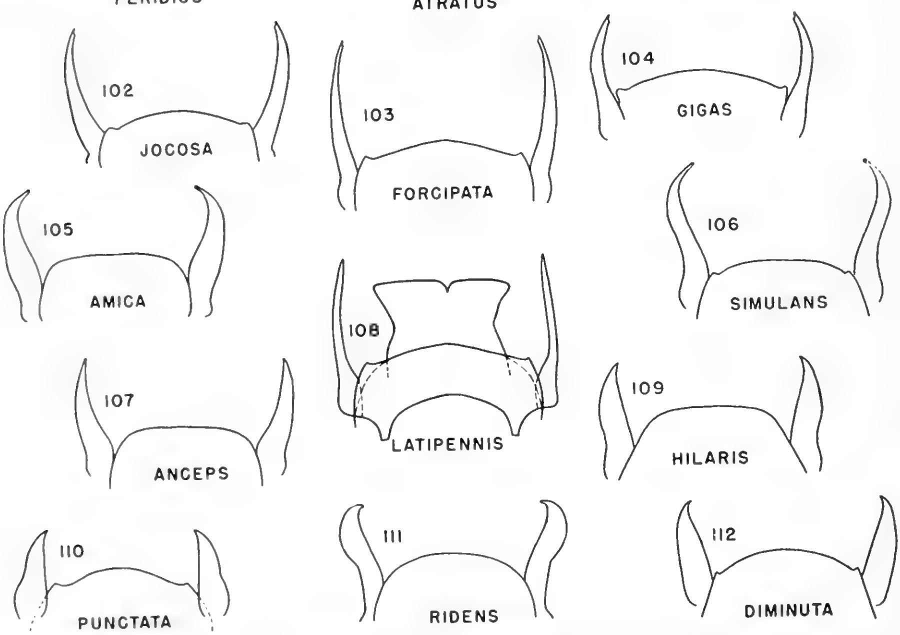


Fig. 97.—*Brachycercus lacustris,* fore wing.
Fig. 98.—*Tricorythodes atratus,* fore wing.
Fig. 99.—*Tricorythodes peridius,* male genitalia.
Fig. 100.—*Tricorythodes atratus,* male genitalia.
Fig. 101.—*Tricorythodes stygiatus,* male genitalia.
Fig. 102.—*Caenis jocosa,* penis lobes.
Fig. 103.—*Caenis forcipata,* penis lobes.
Fig. 104.—*Caenis gigas,* penis lobes.
Fig. 105.—*Caenis amica,* penis lobes.
Fig. 106.—*Caenis simulans,* penis lobes.
Fig. 107.—*Caenis anceps,* penis lobes.
Fig. 108.—*Caenis latipennis,* male genitalia. (After McDunnough.)
Fig. 109.—*Caenis hilaris,* penis lobes.
Fig. 110.—*Caenis punctata,* penis lobes.
Fig. 111.—*Caenis ridens,* penis lobes.
Fig. 112.—*Caenis diminuta,* penis lobes.

pellicle during flight; it is quite possible that all species of the genus do likewise.

The first-described Nearctic species in this genus, *allectus* (Needham) (1905: 47), is now virtually unidentifiable. It cannot be placed from the characters given in the original description alone. The types are, furthermore, either lost, or represented by only a few fragments. These fragments of specimens are not certainly the types, but might be; in any event, they are not in good enough condition to serve as a basis for an identification of the species.

Reliable characteristics for the separation to species of females and nymphs of this genus have not yet been found.

KEY TO SPECIES

ADULT MALES

1. Wings with all crossveins hyaline; antennal scape black......**1. stygiatus**
   Wings with anterior crossveins brown; antennal scape white or yellow, tinged with red-brown....................2
2. Vertex of head black........**2. atratus**
   Vertex of head mostly light yellow...... ....**3. peridius**

1. *Tricorythodes stygiatus* McDunnough

Tricorythodes stygiatus McDunnough (1931*e*:267).

MALE.—Length of body 2.5–3.0 mm., of fore wing 3.5–4.0 mm. Head black, compound eyes and ocelli black; each antennal scape black, pedicel tan, flagellum yellow. Pronotum black, mesonotum very dark brown, metanotum yellow-brown; meso- and metapleura dark red-brown, with vague, black markings near wing bases; thoracic sternum dark red-brown; all coxae black; femora black, with red shading and with vague, longitudinal, yellow streaks; tibiae white, mottled with black and red-brown over basal three-fourths; tarsi white or gray; wings hyaline, anterior longitudinal veins brown. Abdominal tergum black; tergites 3–7 lighter near lateral margins: sternites dull yellow, suffused with gray, and with a median, black mark at posterior margin of each sternite; caudal filaments white, shaded with gray near bases. Genitalia, fig. 101, yellow to white, with penis lobes relatively narrow and median indentation at posterior margin of forceps base relatively narrow and shallow.

Known from Illinois, Michigan, New Brunswick, and Quebec. Develops in almost stagnant eddies along large streams.

Illinois Record.—WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 4♂.

2. *Tricorythodes atratus* (McDunnough)

Tricorythus atrata McDunnough (1923: 39).

It is quite possible, as McDunnough (1931*e*:265) has said, that *atratus* is the same as *allectus* (Needham 1905:47), although the characters given in the original descriptions are not quite identical. As was remarked above, the specimens at present taken for the types of *allectus* are not in good enough condition to serve as a basis for an identification of the species. It is preferable at present to use *atratus* for the species, as that name is based on a detailed description, and the types are well preserved and available for study.

MALE.—Length of body 3.0–3.5 mm., of fore wing 3.5–4.5 mm. Head black, compound eyes black, each antenna yellow or white, with faint, gray shading at base of pedicel. Pronotum black, becoming brown at lateral margins; mesonotum and metanotum dark brown, pleura lighter brown, sternum dark brown; coxae and trochanters dark gray; femora gray, with black shading, subapical area of each with red-brown shading; fore tibia brown, with median, black shading, middle and hind tibiae white, with black shading in middle, fore tarsus gray; middle and hind tarsi white; wings hyaline, veins Sc and R_1 shaded with gray, anterior veins and crossveins brown. Abdomen yellow-gray or white; tergites 1 and 2 completely shaded with black, tergites 3–7 black only on meson and at posterolateral angles, apical tergites covered by black shading; sternites yellowish gray, with a median, black mark at posterior margin of each sternite; caudal filaments white, shaded with gray near bases. Genitalia, fig. 100, white or light yellow, with penis lobes relatively wide and apical, median excavation of forceps base relatively wide and deep.

Known from Illinois, Michigan, and Quebec. Develops in almost stagnant eddies of larger streams.

Illinois Records.—MILAN: Rock River, June 4, 1940, Mohr & Burks, 1♂. OREGON: at light, July 18, 1927, Frison & Glasgow, 1 ♂. ROCKTON: Rock River, June 11, 1948, Burks, Stannard, & Smith, 1 ♂. WILMINGTON: at light, Aug. 3–4, 1937, Ross & Burks, 70 ♂; Aug. 6, 1947, Burks & Sanderson, 3 ♂.

3. *Tricorythodes peridius* new species

This species agrees with *atratus* in having the antennae almost completely white, in having a subapical, red-brown band on each of the femora, which are extensively shaded with black, and in having abdominal segments 3–7 shaded with black only on the dorsal meson and at the posterolateral angles of the tergites. The two differ in that *peridius* is larger and generally much lighter in color, with the vertex of the head mostly yellow instead of entirely black, as in *atratus*; in *peridius*, also, the apical margin of the genital forceps base has a relatively broad, shallow median excavation.

MALE.—Length of body 4.0–4.5 mm., of fore wing 4.5–5.5 mm. Head yellow-brown, shaded with black near posterior margin of vertex; eyes and ocelli black; antennae white, each usually shaded with tan and black on pedicel. Pronotum completely shaded with dark gray, mesonotum and metanotum brown, pleura slightly lighter brown, venter same color as mesonotum at lateral margins, color paling to white on meson; all coxae and trochanters dark brown; femora light brown, shaded with black, and with a subapical, red-brown band on each; fore tibia gray, middle and hind tibiae light yellow or white, with black shading in middle; fore tarsus light gray, middle and hind tarsi white; wings hyaline, veins Sc and R_1 shaded with gray, veins and crossveins in anterior half of each wing brown. Abdomen mostly light yellow or white, tergites 1 and 2 washed with gray. Tergites 3–7 shaded with gray on meson and at lateral margins, apical tergites uniformly washed with gray; sternites faint gray-tan, often almost white; caudal filaments white, basal four to six segments of each filament shaded with gray. Genitalia, fig. 99, white, with vague, gray shading along lateral margins of structures, apical margin of forceps base with a broad, shallow median indentation.

Holotype, male.—Wilmington, Illinois, at light, Aug. 6, 1947, Burks & Sanderson. Specimen in alcohol.

Paratypes.—ILLINOIS: Same data as for holotype, 11 ♂. ST. CHARLES: at light, July 8, 1948, Ross & Burks, 1 ♂. All specimens in alcohol.

10. *BRACHYCERCUS* Curtis

Brachycercus Curtis (1834: 122).
Oxycypha Burmeister (1839: 796). In part.
Eurycaenis Bengtsson (1917: 186).

The species of *Brachycercus* consist of small mayflies with broad thoraxes. All species have the mesonotum and metanotum various shades of brown, and the head, pronotum, and abdomen white, with black or gray markings. Each antennal pedicel is markedly long, three times as long as the scape. In both sexes, each lateral ocellus is two-thirds as large as one of the compound eyes. The wing venation, fig. 97, does not

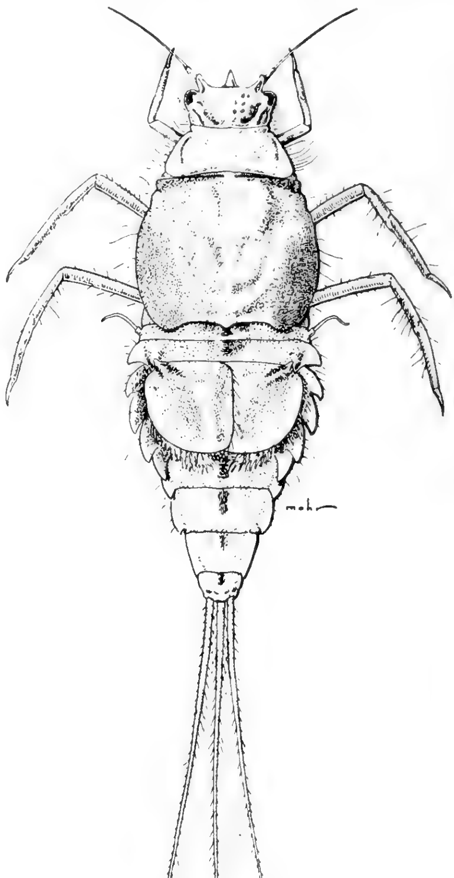


Fig. 113.—*Brachycercus lacustris*, mature nymph, dorsal aspect.

differ significantly from that of *Caenis*: veins R_4 and R_5 diverge relatively close to the wing base, veins M_1 and M_2 and the median intercalary vein all arise at the wing base, and there are relatively few crossveins. The legs are long and slender, with the femora very little stouter than the tibiae; legs conspicuously more slender than in *Caenis*. The abdomen in the males is about as long as the thorax, while, in the females, the thorax is slightly shorter than the abdomen. The segments of the abdomen bear long and filamentous, lateral projections. The male genital forceps base bears a pair of accessory lateral projections; otherwise the male genitalia are similar to those of *Caenis*. The posterior margin of the terminal abdominal sternite in the females is evenly rounded from margin to margin. The caudal filaments of the males are much longer than those of the females.

The nymphs, fig. 113, are flattened, heavy-bodied forms with conspicuously long, slender legs and tuberculate heads. Each antennal pedicel is three times as long as the scape, and the flagellum is as long as the head and pronotum combined. The tarsal claws are long, slender, and entirely without ventral denticles, fig. 93. The lateral margins of the abdominal tergites are produced as broad, flat, and thin projections. The first abdominal segment bears a pair of single, filamentous gills; the gills of abdominal segment 2 are operculate and semiquadrate; and the gills borne by segments 3–6 are single, the margins of each gill being provided with a fringe of long filaments.

Reliable characteristics for the separation to species of females and nymphs of this genus have not yet been found.

KEY TO SPECIES

ADULT MALES

Abdominal tergites white, entirely without black markings................**1. prudens**

Abdominal tergites white; a black, transverse line at posterior margin on each of the apical tergites, and traces of a median, longitudinal, black line on each of the middle and apical tergites................**2. lacustris**

1. *Brachycercus prudens* (McDunnough)

Eurycaenis prudens McDunnough (1931*e*:264).

MALE.—Length of body and of fore wing 3 mm. Head below antennae yellow; vertex shaded with brown, and with a median, longitudinal, black line, lateral areas near ocelli dark gray-brown. Pronotum light yellow, almost white, with dark brown shading on median area of posterior margin; fore coxa vaguely shaded at base and apex with brown, fore femur gray-brown, fore tibia gray at base; mesonotum yellow-brown, with faint, dark brown shading on dorsal sutures; each pleuron and sternum of meso- and of metathorax light yellow-brown; metanotum yellow-brown; middle and hind legs white, with coxae sometimes slightly shaded with gray-brown. Abdomen entirely light yellow, almost white, either entirely without darker markings or with faint, pinkish-brown shading at posterior margins of caudal tergites; genital forceps long and flat, faintly gray in color; caudal filaments white.

FEMALE.—Length of body and of fore wing 3.5 mm. Coloration identical with that of male except that mesonotum is a slightly darker brown, and middle and hind coxae are extensively shaded with brown.

Known from Illinois, Kansas, and Saskatchewan. Apparently develops in large rivers.

Illinois Records.—SAVANNA: at light, July 20, 1892, Hart, Forbes, & McElfresh, 7♂. SHETLERVILLE: at light, Aug. 10, 1898, C. A. Hart, 4♂, 1♀.

2. *Brachycercus lacustris* (Needham)

Caenis lacustris Needham (1918:249).
Eurycaenis pallidus Ide (1930*b*:218), not Tschernova. Name preoccupied.
Brachicercus idei Lestage (1931*a*:119). New name for *pallidus* Ide.

Caenis lacustris was described from nymphs only, and the types have been lost. I follow Lyman (1944:3) in placing *idei* as a synonym of *lacustris*.

MALE.—Length of body 4–5 mm., of fore wing 4.5–6.0 mm. Head, pronotum, and abdomen white, meso- and metathorax light brown; each of the apical abdominal tergites marked with a transverse, black line at posterior margin, and traces of a median, longitudinal, dorsal, black line present on middle and posterior tergites; fore leg shaded with brown, other legs white; claspers of genitalia tan, and penis lobes white; caudal filaments white.

Known from Michigan, Minnesota, New York, Ohio, and Ontario; should eventually be found to occur in Illinois.

11. *CAENIS* Stephens

Caenis Stephens (1835:61).
Oxycypha Burmeister (1839:796). In part.
Ordella Campion (1923:518). New name, unnecessarily proposed.

The species of *Caenis* consist of small, predominantly white mayflies with shadings of purplish gray. These mayflies often emerge in enormous numbers, filling the air like snowflakes.

Each antennal pedicel in the adults of both sexes is approximately twice as long as the scape. The vertex of the head lacks tubercles. The fore coxae are close together on the venter; each fore leg in the males is as long as the body, with the tibia twice as long as the femur and slightly longer than the tarsus. In most species, there is a pair of submedian, dark brown spots on the pronotum. In each wing, there are very few crossveins, as in fig. 97 of *Brachycercus lacustris;* vein M_2 and the median intercalary vein extend to the wing base, and the cubital intercalary veins are long and relatively straight. The marginal ciliae are well developed in the adult wings; the subimaginal pellicle covering the wings is often only partly shed. The wings are whitish hyaline, with gray-purple shading in the first three interspaces and on veins Sc and R_1. Each abdominal segment bears a pair of long, lateral ciliae in the subimago; these ciliae are reduced to small, lateral projections in the adult. The posterior margin of the male genital forceps base is slightly convex; each forceps has only one segment. The penis lobes are fused on the meson; each lobe is broad and flat, and slightly widened at the apex, fig. 108. In both sexes, the three caudal filaments are well developed, those of the males being the longer; these filaments are entirely white in all Illinois species.

In the nymphs, the body is quite flat, with the pronotum narrower than the mesonotum. The nymph shown in fig. 114 to illustrate this genus has been drawn somewhat distended in order to show the structure of the abdomen; when the nymph is alive, the abdomen is more compact than it is represented in this figure. The head is smooth, lacking tubercles. As measured in dorsal aspect, each antenna is twice as long as the head and pronotum combined. The legs are relatively short and stout; the claws are small and slender, and have extremely minute ventral denticles, fig. 94. The first abdominal segment bears a pair of prominent, single, filamentous gills, fig. 91*A*; the gills borne by the second segment are single, quadrate, and operculate, fig. 91*B*. The gills borne by segments 3–6 are single and plate-like, each gill having the margins deeply fissured to produce a marginal fringe of long filaments; each filament is secondarily divided near the tip to produce two or three smaller filaments, figs. 91*C*, 91*D*. The three caudal filaments are relatively stout, with a whorl of three to five setae at each articulation.

I have observed the subimagoes of *simulans* to shed the subimaginal exuviae during

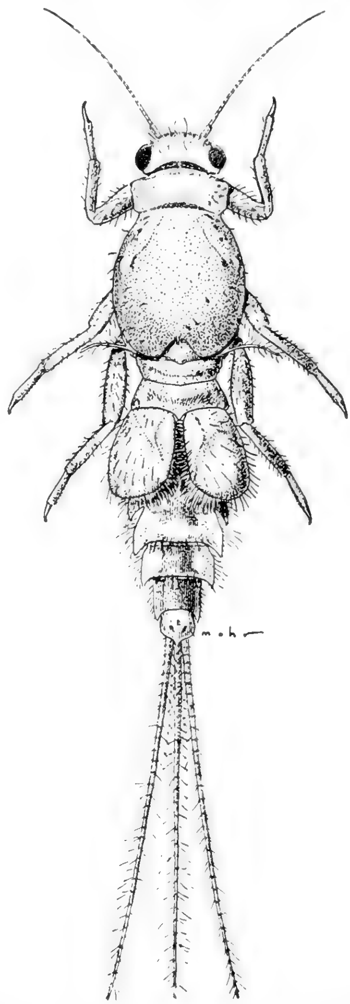


Fig. 114.—*Caenis simulans*, mature nymph, dorsal aspect.

flight, almost immediately after emerging from the nymphs.

Most adult specimens of *Caenis* intended for study should be killed with cyanide and mounted dry on pins or points; a few specimens of a series may also profitably be preserved in alcohol for ease in studying the genitalia. The colors of the specimens in alcohol fade seriously, but the characters of the male genitalia can be seen plainly in uncleared specimens preserved in alcohol. The male genitalia of dry specimens can be cleared in KOH for study, but the clearing technique is difficult. Specimens of *Caenis* are both small and fragile, which makes them difficult to handle without breakage during staining and clearing operations.

A revision, based on adult specimens of this difficult genus, was made by McDunnough (1931*e*); all subsequent North American workers have leaned heavily on his work. Specific characteristics for females and nymphs of *Caenis* have not been found.

KEY TO SPECIES

ADULT MALES

1. Vertex of head entirely and uniformly shaded with dark gray 2
   Vertex of head partly or completely white or pale yellow 5
2. Hind femur freckled with numerous, minute, black dots .... **1. punctata**
   Hind femur without numerous, minute, black dots; white, with an apicodorsal black spot or subapical black band .. 3
3. Apex of hind femur completely encircled by a black band .... **2. diminuta**
   Apex of hind femur with only a dorsal black spot 4
4. Genital forceps short and stout, fig. 105; body and fore wing each only 2 mm. long .... **3. amica**
   Genital forceps moderately long and curved, fig. 106; body and fore wing each 3.5–4.0 mm. long .... **4. simulans**
5. Abdomen lacking spiracular dots or streaks 6
   Abdomen with spiracular dots or streaks 7
6. Mesonotum light red-brown; genital forceps short, fig. 107, apexes straight; vertex of head almost entirely white, shaded with purplish gray only at margins and near ocelli .... **5. anceps**
   Mesonotum light yellow; genital forceps moderately long, fig. 111, apexes hooked; vertex of head heavily shaded with purplish gray near ocelli, light only in center .... **6. ridens**
7. Abdominal segments 7–9 only with gray-brown spiracular streaks; segments 1–6 without spiracular dots or spots .... **7. hilaris**
   Abdominal segments 1–6 with spiracular dots or spots 8
8. Vertex of head almost entirely white, with purplish-gray shading present only at anterior and posterior margins and occasionally near lateral ocelli; length of body 2 mm. .... **8. gigas**
   Vertex of head dark gray-purple in entire anterior two-thirds, posterior third light yellow or white; length of body 3 mm. or more 9
9. Length of body 3 mm.; genital forceps of relatively moderate length and stout, fig. 102 .... **9. jocosa**
   Length of body 4 mm.; genital forceps relatively long and slender, fig. 103 .. .. **10. forcipata**

1. *Caenis punctata* McDunnough

Caenis punctata McDunnough (1931*e*:259).

MALE.—Length of body and of fore wing 3 mm. Vertex of head completely covered with purplish gray; mesonotum yellow-brown; fore femur with dark purplish-gray shading in middle and near apex; middle and hind femora peppered with minute, black dots, each also with a dark gray band near apex; abdomen pale yellow, almost white, with extensive gray shading on tergites; spiracular marks present on all abdominal segments; each sternite with a pair of black, lateral dashes, sternites 1–6 each with a pair of sublateral, black dots, and sternites 7–9 each with two pairs of sublateral, black dots; genital forceps, fig. 110, short and stout.

Known from New York, Ontario, Quebec, and Wisconsin.

2. *Caenis diminuta* Walker

Caenis diminuta Walker (1853:584).

MALE.—Length of body and of fore wing 3 mm. Vertex of head slightly but uniformly shaded with gray; mesonotum dark chestnut brown; fore femur shaded with gray and with a darker, transverse band near apex; fore tibia uniformly shaded with faint gray; middle and hind femora white, with a black band encircling each near apex; abdomen white, with extensive gray shading on tergites 1–6; spiracular dots present on segments 1–8 or –9; sternites 2–6 each with a pair of slender, lateral, black lines; two pairs of minute dots sometimes present on each abdominal sternite, those on sternites 7–9 always darker than anterior ones; genital forceps, fig. 112, short, stout, and markedly divergent.

Known from Florida, Georgia, Ontario.

3. *Caenis amica* Hagen

Caenis amica Hagen (1861:55).

MALE.—Length of body and of fore wing 2.0 mm. Vertex of head completely covered by dark gray shading; mesonotum yellow-brown; fore femur extensively shaded with dark gray, middle and hind femora each with a black, subapical, dorsal spot; abdominal tergites lightly shaded with gray, and spiracular dots present on abdominal segments 1–7 or –8; genital forceps, fig. 105, short and relatively slender.

Known from Maine, Maryland, Missouri, North Carolina, New York, and West Virginia.

4. *Caenis simulans* McDunnough

Caenis simulans McDunnough (1931*e*:263).

This is by far the commonest Illinois species of *Caenis*.

MALE.—Length of body and of fore wing 3.5–4.0 mm. Head below antennae yellow, vertex completely covered with dark purplish-gray shading; antennae yellow. Pronotum light yellow, with dark purple-gray shading at margins and on dorsal meson; each fore coxa shaded with grayish brown, fore femur gray, with a black apicodorsal spot, fore tibia and tarsus light gray; meso- and metanotum chestnut brown, darker brown shading present on median dorsal suture or mesoscutum, just dorsad of wing bases, and at posterior ends of outer parapsides; apex of mesoscutum shaded with gray; gray shading present near either lateral margin of metanotum; each pleuron chestnut brown, with dark gray shading around coxal cavities and light gray shading over prealar bridge; middle and hind legs white, with a black streak on outer side of each trochanter, and on dorsal side of each femur at base and near apex. Abdomen white or faintly stained with yellow, tergites 1–6 heavily shaded with dark gray, tergites 7–9 with gray shading in basolateral areas; black stigmatic dots or spots usually present on abdominal segments 1–9, these markings sometimes obsolete on segments 8 and 9; each sternite typically with a black spot near either lateral margin and another black spot on meson, in addition to a pair of minute, sublateral, black dots on each of sternites 1–7 and a pair of sublateral, black dots on each of sternites 8–10; genital forceps, fig. 106, long and slightly bowed.

FEMALE.—Length of body and of fore wing 4.0–5.5 mm. Coloration almost identical with that of male except that fore femur is light yellow, without gray shading, but with apicodorsal spots preserved; fore tibia and tarsus light yellow rather than gray, and median, black spots of abdominal sternites wanting or only faintly indicated.

Known from the northern states and Canada. Develops in nearly or quite stagnant water; it evidently tolerates considerable pollution.

Illinois Records.—Specimens, collected May 3 to August 19, are from Antioch, Banner, Beach, Chester, Fox Lake, Golconda, Havana, Herod, Kankakee, Momence, Oakwood, Palos Park, Prophetstown, Richmond, Rosecrans, Serena, Spring Grove, Sterling, Wadsworth, and Zion.

5. *Caenis anceps* Traver

Caenis anceps Traver (1935*a*:645).

MALE.—Length of body and of fore wing 2 mm. Vertex of head mostly white, with anterior and posterior margins edged with gray-purple, and with gray-purple shading near lateral ocelli; mesonotum light red-brown; fore femur shaded with gray at apex, and fore tibia shaded with gray at base; middle and hind femora white, with a minute, black, dorsal dot near apex of each; abdomen entirely white, without markings of any kind; genital forceps, fig. 107, short and straight.

Known from Missouri and New York.

6. *Caenis ridens* McDunnough

Caenis ridens McDunnough (1931*e*:256).

MALE.—Length of body and of fore wing 2 mm. Head white, vertex lightly shaded with gray-purple, this shading darker near lateral and anterior ocelli, median area of vertex relatively pale; antennae white. Pronotum white, with minute, purplish gray-shaded area at each anterolateral angle; gray-purple shading present around each fore coxal cavity and on fore coxa; fore leg white, fore femur faintly shaded with gray at apex, fore tibia gray; meso- and metanotum pale yellow, with light purplish brown shading on median, longitudinal line of mesoscutum and on apex of mesoscutellum; pleuron light yellow, with purplish brown shading around coxal cavities; all thoracic sternites white; middle and hind legs entirely white. Abdomen white, without spiracular spots or streaks; genital forceps, fig. 111, stout and moderately long.

FEMALE.—Length of body and of fore wing 2.5–3.0 mm. Head almost entirely white, with faint gray shading extending across middle of vertex only; fore femur with gray shading at apicodorsal angle; abdominal tergites 1 and 2 each with a pair of sublateral, transverse dark spots.

Known from Illinois, Kansas, Michigan, Ontario, and Wisconsin. Develops apparently in eddies in small rivers.

Illinois Records.—AURORA: at light, July 17, 1927, Frison & Glasgow, 22♂, 4♀. LAKE FOREST: J. G. Needham, 1♀ (Traver 1935*a*: 653). OAKWOOD: at light, July 10, 1927, Frison & Glasgow, 53♂, 21♀.

7. *Caenis hilaris* (Say)

Ephemera hilaris Say (1839:43).

MALE.—Length of body and of fore wing 2.0–2.5 mm. Head white, faint lavender shading present on vertex near lateral ocelli; antennae white. Pronotum white, with faint gray-brown shading at each anterolateral angle; a fairly large, gray-brown spot present on outer side of each fore coxa; fore leg white, with gray shading at apex of femur; meso- and metanotum light yellow, with a prominent, gray-brown spot near apex of mesoscutellum, this spot often extending forward onto mesoscutum; meso- and metapleura white, with vague gray-brown shading around coxal cavities; all thoracic sternites white; middle and hind legs white, with a black spot on dorsal side near apex of each femur. Abdomen white, with gray shading on first tergite and prominent, gray-brown spiracular lines on tergites 7–9; genital forceps, fig. 109, short and stout.

FEMALE.—Length of body and of fore wing each 2.5–3.0 mm. Coloration identical with that of male except that vertex of head is slightly darker, each fore femur has a dorsoapical, black spot, and spiracular lines may be present on tergites 5 and 6 as well as on apical tergites.

Known from the eastern and central states. Develops in eddies of moderate-sized and large rivers.

Illinois Records.—DIXON: June 27, 1935, DeLong & Ross, 17♂. ELIZABETHTOWN: June 22, 1932, Dozier & Park, 9♀. FOSTER: Mississippi River, July 22, 1939, B. G. Berger, 8♀. FULTON: July 20, 1927, Frison & Glasgow, 2♂. HOMER: Aug. 10, 1925, T. H. Frison, 2♀. JACKSON ISLAND, in Mississippi River opposite Hannibal, Mo.: Sept. 6, 1940, G. T. Riegel, 1♂, 12♀. KANKAKEE: Aug. 16, 1938, Ross & Burks, 3♂, 5♀. MACKINAW: July 4, 1939, Ivabel Johnson, 3♀. MOMENCE: Aug. 16, 1938, Ross & Burks, 3♂. MONTEZUMA: at light, Oct. 9, 1931, C. O. Mohr, 36♀. OQUAWKA: Sept. 26, 1947, H. H. Ross, 18♂, 36♀. OREGON: at light, July 18, 1927, Frison & Glasgow, 290♂, 21♀; July 2, 1946, Burks & Sanderson, 54♂, 70♀. ROCK ISLAND: 1♂ (Walsh 1862: 381). SAVANNA: Mississippi River, July 23, 1892, S. A. Forbes *et al.,* 1♀.

8. *Caenis gigas* new species

This species resembles *hilaris* in being very small and having the vertex of the head almost entirely white. The two differ in that *gigas* has spiracular dots or streaks on abdominal segments 2–9 rather than on segments 7–9 only, as in *hilaris*; *gigas* also has longer and more slender genital forceps than does *hilaris*.

MALE.—Length of body and of fore wing each 2 mm. Head white, vertex white, with a narrow, gray-purple line at anterior and posterior margins, occasionally faint, gray-purple shading present on vertex near lateral ocelli; antennae white, each pedicel twice as long as scape, flagellum five times as long as pedicel. Pronotum white, with purplish shading at margins; propleura and sternum white; each fore coxa shaded with purplish gray at base, fore femur almost completely shaded with gray, fore tibia gray, tarsus white, with purplish gray shading at articulations; mesonotum light yellow-brown and with a narrow line of gray shading at principal sutures; mesopleura yellow-brown, with fairly extensive, gray-purple shading, mesosternum white; wings hyaline, costal shading typical for genus; metathorax white, with gray shading around coxal cavities; middle and hind legs white, shaded on coxae and on dorsal sides, near apexes, of femora. Abdomen white, tergites with extensive, dark gray shading on median area and at posterior margins of tergites 1–6; tergite 7 with gray shading covering median and anterolateral areas; tergite 8 with gray shading in anterolateral areas; tergite 9 with a black median spot; spiracular marks present on segments 2–9, those on segment 7 largest; a black mark present near middle of each lateral margin of sternites 2–9; genital forceps, fig. 104, slender, almost straight; caudal filaments white.

Female.—Length of body 2.5–3.0 mm., of fore wing 3.0–3.5 mm. Color as in male, except that fore femur is gray, shaded only on ventral side near base and dorsally near apex; fore tibia white.

Holotype, male.—Giant City State Park, Illinois, at light, August 6, 1946, Mohr & Sanderson. Specimen in alcohol.

Allotype, female.—Same data as for holotype. Specimen in alcohol.

Paratypes.—Illinois: Same data as for holotype, 7♂, 33♀; same locality: July 5, 1944, Sanderson & Leighton, 46♀; Aug. 22, 1944, 2♂, 15♀. Hamilton: Aug. 30, 1931, Ross & Mohr, 62♂. Herod: July 8–11, DeLong & Ross, 25♂, 36♀. All specimens in alcohol.

9. *Caenis jocosa* McDunnough

Caenis jocosa McDunnough (1931*e*: 260).

Male.—Length of body and of fore wing 3 mm. Head below antennae, and on posterior third of vertex, light yellow; anterior two-thirds of vertex shaded with purplish gray; antennae pale yellow, almost white. Pronotum light yellow, with black shading at lateral margins and on dorsal meson; area around fore coxal cavities, and on outer side of each coxa, shaded with black, fore femur shaded with gray, this shading darker near base and on dorsal side near apex of femur, fore tibia light gray; mesonotum yellow-brown, shaded with dark brown on dorsal, longitudinal, median line and at apex of mesoscutum; mesoscutellum shaded with gray at apex; metanotum yellow-brown, with dark brown shading on meson; pleuron yellow-brown, shaded with black around coxal cavities; thoracic sternum light yellow, almost white; middle and hind legs light yellow, with a black streak on the outer side of each trochanter and a black apicodorsal spot on each femur. Abdomen very light yellow, tergites 1–7 shaded with gray; spiracular marks present on segments 1–7 or –8, sometimes these marks wanting on segments 3 or 4; abdominal sternites pale yellow, with a pair of lateral, black streaks on each sternite 1–5 and a pair of black dots on each of the more posterior sternites; genital forceps, fig. 102, relatively long and slender.

Female.—Length of body and of fore wing each 4 mm. Coloration identical with that of male except that fore femur is white, with gray shading in middle and near apex, and that thorax has more extensive, black or gray shading and little or no dark brown shading.

Known from the northeastern and midwestern states and southeastern Canadian provinces. Possibly a pond species.

Illinois Records.—Anna: May 6, 1925, T. H. Frison, 2♂, 22♀. Homer: at light, Aug. 10, 1925, T. H. Frison, 1♂, 3♀.

10. *Caenis forcipata* McDunnough

Caenis forcipata McDunnough (1931*e*: 257).

This species, described from Ontario and Quebec, may eventually be shown to be a synonym of *latipennis* Banks, described from the state of Washington. The male genitalia of the two species are virtually identical, figs. 103, 108.

Male.—Length of body and of fore wing 4 mm. Head below vertex light yellow, almost white; anterior two-thirds of vertex dark gray, posterior third light yellow; antennae white, apex of each pedicel slightly darkened. Pronotum light yellow, shaded with purplish gray at margins; prosternum white, with black lateral margins; each fore femur shaded with dark gray, with a black apicodorsal spot, fore tibia gray; meso- and metanotum and pleuron dark yellow-brown; sternum white; middle and hind femora white, with a subapical, dorsal, black spot on each. Abdomen pale yellow; tergites 1–7 heavily shaded with dark gray, stigmatic marks present on segments 1–7 or –8; sternites pale yellow, with paired, gray dots faint; genital forceps, fig. 103, long and slender.

Female.—Length of body and of fore wing 4.0–4.5 mm. Coloration identical with that of male except that the yellow-brown of the mesonotum is lighter and the gray shading of the fore femur is less extensive.

Known from Illinois, Manitoba, Michigan, New York, Ontario, Quebec, and Wisconsin. Possibly a pond species.

Illinois Records.—Antioch: Channel Lake, June 15, 1928, T. H. Frison, 1♂. Shawneetown: May 11, 1935, C. O. Mohr, 2♂. STERLING: at light, May 21–22, 1925, D. H. Thompson, 5♂.

12. *LEPTOHYPHES* Eaton

Leptohyphes Eaton (1882:208).

This genus formerly was thought to be restricted to South America and Central America; I have, however, seen specimens, referable to *Leptohyphes,* which were collected at lights in San Antonio, Texas.

Species of the genus *Leptohyphes* consist of small or medium-sized, fragile mayflies which closely resemble the other members of the family Caenidae. The fore leg in the males is shorter than the body, and the hind leg is slightly longer than the fore leg. The fore wing is constricted in the cubito-anal region, as in mayflies with two pairs of wings; veins R_4 and R_5 diverge at or near the center of the wing, and vein M_2 and the median intercalary vein arise at a point some distance distad of the wing base. The hind wing, persisting in the subimagoes, usually has a very long, thin costal projection; there always is a pair of thin, membranous projections arising near the wing bases and extending along the lateral margins of the mesoscutellum. The male genitalia consist of a pair of 3-segmented forceps and a pair of slender, apically diverging penis lobes. There are two long caudal filaments; the middle one is vestigial.

In the nymphs, which are flattened and sprawling forms having relatively short, thickset legs and edentate claws, the pronotum typically is rectangular, with the anterolateral angles acute. Two pairs of wingpads are present. The abdominal gills are borne at the lateral margins of segments 2–6; the first pair is elongate-oval and elatroid, covering the following pairs of gills; the lateral margins of the abdominal segments are produced as broad, shelflike projections having the posterolateral angles acute. There are three well-developed caudal filaments.

EPHEMERELLIDAE

The family Ephemerellidae, as it is here treated, is identical with the subfamily Ephemerellinae of the family Baetidae of Traver (1935*a*:562) or the family Ephemerellidae of Ulmer (1933:204). In my opinion, this group of mayflies is sufficiently different from all others to require segregation as a distinct family. The ephemerellids are quite a homogeneous group and as far diverged from the fossil ephemerid prototype (Tillyard 1932) as are the Ephemeridae or Heptageniidae. It may be noted that, although the ephemerellids are world-wide in distribution, they were first recognized as a distinct group by Walsh in 1862, on the basis of a study of specimens he had collected at Rock Island, Illinois.

Although ephemerellids are one of the commonest mayfly groups in the northern and western states and are represented there by a large number of interesting species, they are relatively uncommon in Illinois. They seem to require for their development either somewhat rapid, clear streams which are cool throughout the year or small, clear lakes. Such bodies of water are rather rare in this state, but a few suitable habitats are provided by Nippersink Creek in McHenry County, the Rock River in Winnebago and Ogle counties, the Kankakee River in Kankakee County, the Salt Fork River in Vermilion County, Lusk Creek in Pope County, and some of the lakes in Lake County. A few ephemerellids have been taken in the Wabash River at Mount Carmel, but, in general, the Wabash River does not provide a habitat favorable for their development. They seem to have disappeared completely from the Mississippi and Rock rivers at Rock Island, although they obviously were fairly common there in the early 1860's when Walsh collected and described the genus *Ephemerella* and two species from that locality.

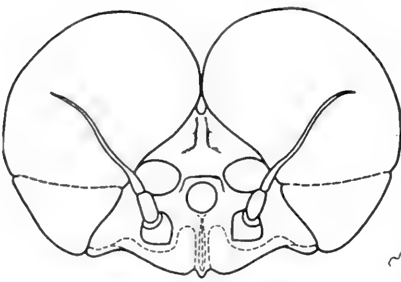
The ephmerellids offer an excellent example of a common mayfly phenomenon: the nymphs are more easily collected and more readily separated to species than the adults. The nymphs can be found at almost any time during the spring or summer months by turning over rocks and debris in the streams or lakes in which they live. The adults have a length of life of only 3 or 4 days, are strong fliers and rather difficult to net, and have a high mortality rate when being reared from the nymphs. Opportunities for obtaining adults of a given species are thus relatively few. As a consequence, most American mayfly collections include a great many more nymphal than adult specimens of ephemerillids. The Illinois Natural History Survey collection, for example, has only a few dozen adults but hundreds of nymphs.

In the Nearctic region, the family Ephemerellidae includes one genus, *Ephemerella*.

13. *EPHEMERELLA* Walsh

Ephemerella Walsh (1862:377).
Drunella Needham (1905:42).
Chitonophora Bengtsson (1908:243; 1909:6).
Torleya Lestage (1917:366).
Timpanoga Needham (1927:108).
Eatonella Needham (1927:108).

This genus now includes more than 80 Nearctic species, only 11 of which have, so far, been taken in Illinois. Quite a few more species of *Ephemerella* might, however, eventually be found to occur in the smaller streams in the northern tier of Illinois counties. For that reason, a number of extralimital, northern species of *Ephemerella* have been included in the keys and discussions given below.



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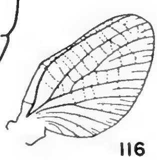

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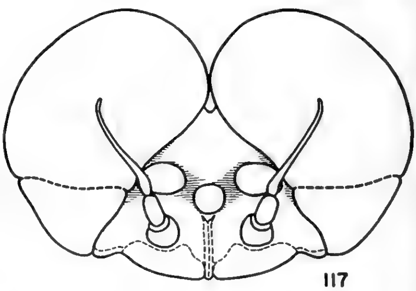

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Fig. 115.—*Ephemerella argo*, head of adult male, anterior aspect.
Fig. 116.—*Ephemerella lutulenta*, hind wing of adult.
Fig. 117.—*Ephemerella ora*, head of adult male, anterior aspect.

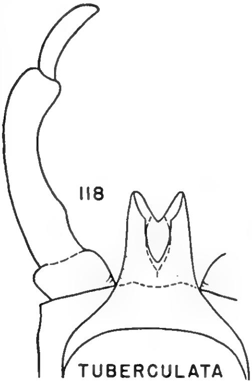
In each fore wing of the *Ephemerella* adults, the costal crossveins are entirely wanting or a few apical ones are very weakly indicated, the stigmatic crossveins are weak and usually slightly anastomosed, and all other crossveins are weak, fig. 29. All the longitudinal veins are well indicated. Vein Cu_2, at mid-length, is bent at right angles toward the wing margin. The hind wing, fig. 116, has a subangulate costal projection and weak crossveins.

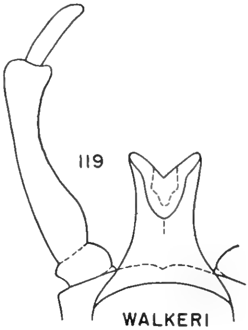
In adult males, the large compound eyes are almost or quite contiguous on the dorsal meson and each is rather indistinctly divided, figs. 115 and 117, with the ventral portion smaller and darker than the dorsal portion. In both sexes, the hind tarsus has four clearly differentiated segments, the basal three of which are short and approximately equal in length; the apical segment is usually as long as the basal three combined. Each arm of the male genital forceps has three segments, the basal one short, broad, and usually indistinctly set off from the distal ones; the second segment is long and somewhat bowed; and the third segment is usually minute, although it is fairly long in a few species. The penis lobes invariably are fused at the base on the meson; in most species, this mesal fusing extends almost to the tips of the penis lobes. There are three long caudal filaments.

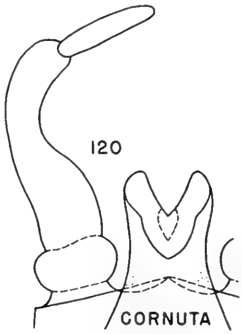
The nymphs, figs. 172 and 173, are more or less flattened dorsoventrally. In each, the head is relatively small, and the body is often as broad across the middle abdominal segments as across the thorax. The integument in the *Ephemerella* nymphs is more heavily sclerotized than it is in most mayfly nymphs. In many species of *Ephemerella*, the nymphs are provided with prominent dorsal spines and tubercles. In some western species, the nymphs have each an ingenious, ventral, abdominal sucker-disc that permits them to cling to rocks in the rapid streams in which they live. In various species, the abdomen bears either four or five platelike gills; the second segment is invariably without gills. The first pair of platelike gills sometimes forms a sort of operculum which covers the more caudal pairs of gills. Structures of the individual gills of two species of *Ephemerella* are shown in figs. 170 and 171. There are three well-developed caudal filaments.

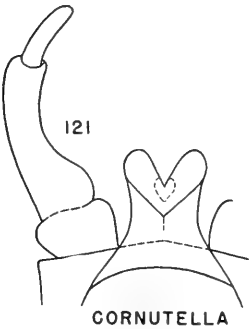
In the figures of male genitalia included here, ventral spines borne by the penis lobes are shown by broken lines; dorsal spines are shown by unbroken lines. These stout spines borne by the penis lobes occur in three positions on the lobes: apical, near or at the apex near the meson; lateral, at or near the outer lateral margin of each penis lobe a short distance from the apex; and basal, approximately midway between base and apex of the penis lobe; see fig. 10.

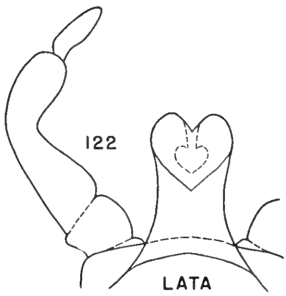
The following keys to the genus *Ephemerella* do not include the species *consimilis* Walsh, described in 1862, from Rock Island, Illinois. No authentic Walsh material of this species is known to exist, and the species cannot be identified from the description alone. Extensive collecting in and around Rock Island has failed to turn up any speci-

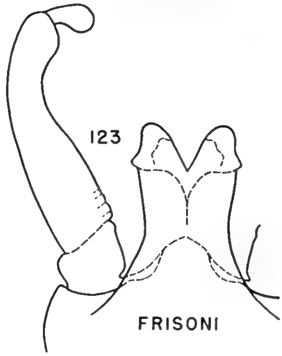


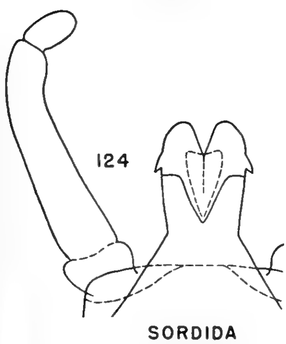


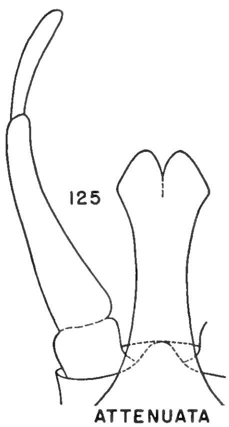












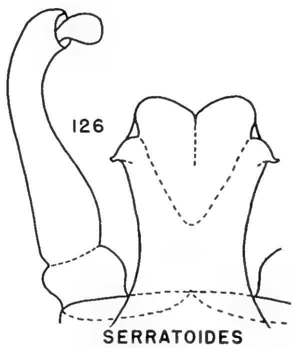


Fig. 118. — *Ephemerella tuberculata,* male genitalia.
Fig. 119.—*Ephemerella walkeri,* male genitalia.
Fig. 120.—*Ephemerella cornuta,* male genitalia.
Fig. 121.—*Ephemerella cornutella,* male genitalia.
Fig. 123.—*Ephemerella frisoni,* male genitalia.
Fig. 124.—*Ephemerella sordida,* male genitalia.
Fig. 125.—*Ephemerella attenuata,* male genitalia.
Fig. 126.—*Ephemerella serratoides,* male genitalia.
Fig. 122.—*Ephemerella lata,* male genitalia.

mens that could be assigned to this species. It may be noted, however, that the streams around Rock Island are today quite different than they were in Walsh's time. The genotype, *excrucians*, also described from Rock Island and not found to occur there now, has recently been located and reared in northern Michigan.

Examination of the lectotype of *Cloe quebecensis* Provancher (1876:267), now deposited in the Provincial Museum, Quebec, shows that the species was described from a female specimen of the genus *Ephemerella*. This species was transferred by Provancher to *Heptagenia* the year following its description (1878:127). At the present state

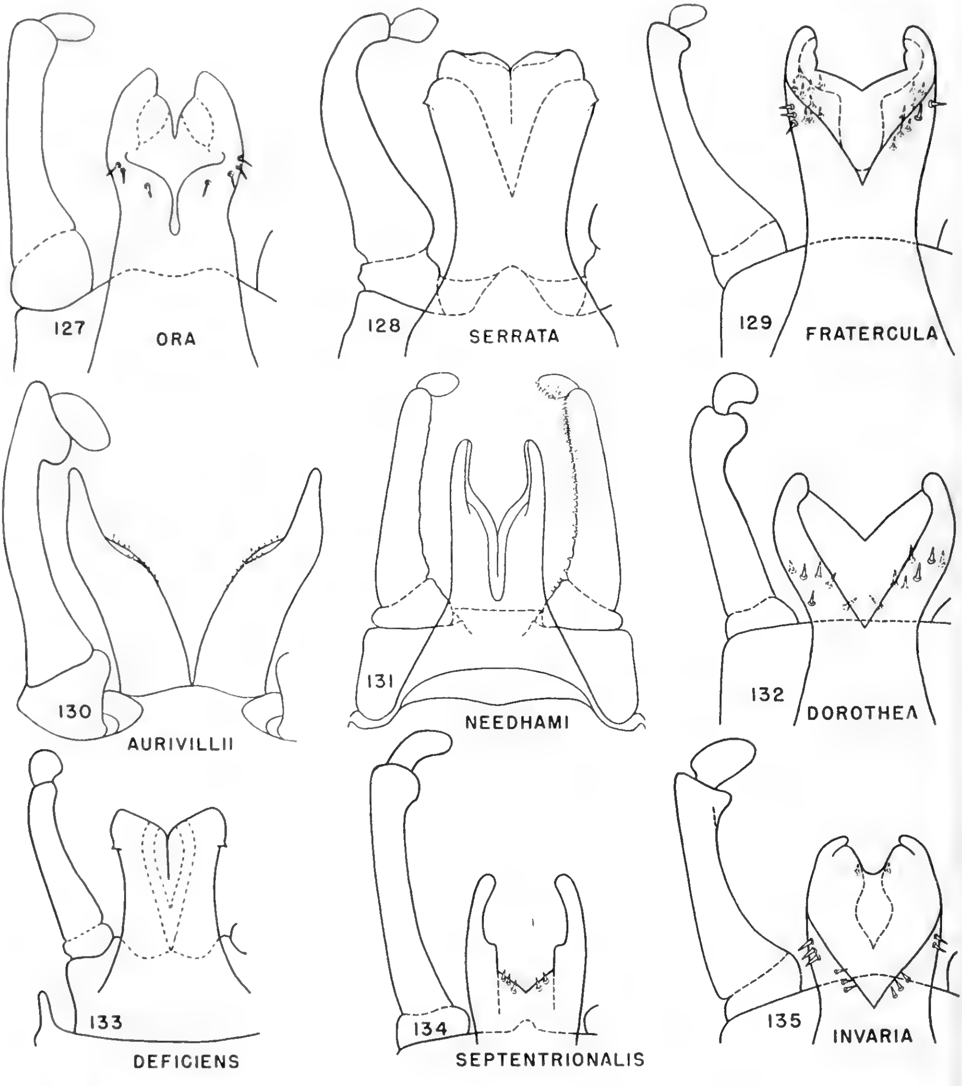


Fig. 127.—*Ephemerella ora*, male genitalia.
Fig. 128.—*Ephemerella serrata*, male genitalia.
Fig. 129.—*Ephemerella fratercula*, male genitalia.
Fig. 130.—*Ephemerella aurivillii*, male genitalia.
Fig. 131.—*Ephemerella needhami*, male genitalia.
Fig. 132.—*Ephemerella dorothea*, male genitalia.
Fig. 133.—*Ephemerella deficiens*, male genitalia.
Fig. 134.—*Ephemerella septentrionalis*, male genitalia. (After McDunnough.)
Fig. 135.—*Ephemerella invaria*, male genitalia.

of our knowledge of the species in the genus *Ephemerella,* this female type specimen of *quebecensis* cannot be placed even to species group. Specific characters for the females of this genus have not yet been found.

KEY TO SPECIES

ADULT MALES

1. Third segment of genital forceps long and slender: six times as long as broad, fig. 125 . . . . **33. attenuata**
   Third segment of genital forceps shorter and more stout: never more than four times as long as broad, usually as broad as long, figs. 118, 122, 123, 136, 150 2
2. Third segment of forceps three or four times as long as broad, figs. 118–122 . . 3
   Third segment of forceps less than twice as long as broad, sometimes only as long as broad, figs. 123, 124, 126–138 . . 7
3. Second segment of forceps relatively short and subangulate, with a sharp and deep mesal constriction, fig. 122 . . . **1. lata**
   Second segment of forceps relatively long and more evenly curved, not having a sharp and deep mesal constriction, figs. 118–121 4
4. Outer surface of hind femur with numerous small, black dots 5
   Outer surface of hind femur without black dots 6
5. An arcuate, transverse row of four black dots present on each abdominal sternite . . . . **2. tuberculata**
   Abdominal sternites without transverse rows of black dots . . . . . . **3. walkeri**
6. Second segment of forceps only three times as long as basal segment, fig. 121; fore wing only 6–7 mm. long . . . . **4. cornutella**
   Second segment of forceps four times as long as basal segment, fig. 120; fore wing 9 mm. long . . . . **5. cornuta**
7. Penis lobes broadened near apexes and bearing a pair of subapical, lateral tubercles, figs. 123, 124, 126 8
   Penis lobes not broadened near apexes and not bearing a pair of subapical, lateral tubercles; either not expanded near apexes, or, if so, bearing several dorsal or ventral spines, figs. 132, 135–138 12
8. Abdominal tergites 2–7 white (in freshly killed specimens), with a pair of small, brown, lateral dots or streaks on each tergite . . . . **6. frisoni**
   Abdominal tergites tan or brown 9
9. Caudal filaments white, with articulations not darkened . . . . **7. sordida**
   Caudal filaments with at least basal articulations darkened with red or brown 10
10. An arcuate, transverse row of four black dots present on each abdominal sternite . . . . **9. serratoides**
    Abdominal sternites without transverse rows of black dots 11
11. Genital forceps strongly bowed, fig. 128; abdominal sternites light tan, with dark brown, longitudinal streaks near each lateral margin . . . . **8. serrata**
    Genital forceps more nearly straight, fig. 133; abdominal sternites uniformly shaded with tan, lacking lateral, dark brown, longitudinal streaks . . . . **10. deficiens**
12. Penis lobes with a deep, median, apical notch, lateral margins projected posteriorly as relatively narrow processes, as in figs. 130–132, 134–138, 145 . . . 13
    Penis lobes with only a very shallow, median, apical notch, lateral margins not produced posteriorly, figs. 139–144, 146–150; penis lobes never bearing stout spines 23
13. Penis lobes entirely without spines, fig. 131; upper face red-brown, with area below antennae bright yellow . . . . **11. needhami**
    Penis lobes provided with spines, as in figs. 130, 132, 134–138 14
14. Penis lobes divided on meson to level of bases of genital forceps; numerous, minute spines borne by mesal surface of each penis lobe, fig. 130 . . . . **12. aurivillii**
    Penis lobes not divided on meson to level of bases of forceps; penis lobes bearing relatively few, large spines, figs. 132, 134–138 15
15. Lateral processes of penis lobes long and slender, extended straight, fig. 134 . . . . **13. septentrionalis**
    Lateral processes of penis lobes short, curved inward at apexes, figs. 132, 135–138 16
16. Second segment of genital forceps not suddenly swollen at apex, figs. 127, 137, 138 17
    Second segment of genital forceps suddenly swollen at apex, figs. 129, 132, 135, 136, 145 19
17. Penis lobes short and broad, with each lobe bearing two or three dorsal spines, three or four ventral spines, and two or three apical spines, fig. 138 . . . . **14. argo**
    Penis lobes narrower and more elongate, with spines arranged differently, figs. 127, 137 18
18. Dorsum of thorax tan and yellow; compound eyes of living insect pinkish tan . . . . **15. ora**
    Dorsum of thorax deep reddish brown; compound eyes of living insect yellow . . . . **16. excrucians**
19. Caudal filaments entirely white, with articulations not darkened . . . . **17. dorothea**
    Caudal filaments with at least basal articulations darkened 20
20. Wings with veins brown . . . . **18. subvaria**
    Wings with veins and crossveins hyaline, or costal longitudinal veins faintly tinged with light yellow 21
21. Penis lobes without apical, submesal spines; each lobe bearing two to three

dorsal spines and seven to nine ventral spines, fig. 129 . . . . **19. fratercula**

Penis lobes with at least one pair of apical, submesal spines; each lobe bearing four to six dorsal spines in basal area, figs. 135, 145 22

22. No ventral spines on penis lobes in basal area, fig. 135 . . . . **20. invaria**

One to three ventral spines on each penis lobe in basal area, fig. 145 . . . . **21. rotunda**

23. Penis lobes showing, from lateral aspect, a large, ventral, subapical enlargement, figs. 140, 141 . . . . **22. prudentalis**

Penis lobes lacking a ventral, subapical enlargement 24

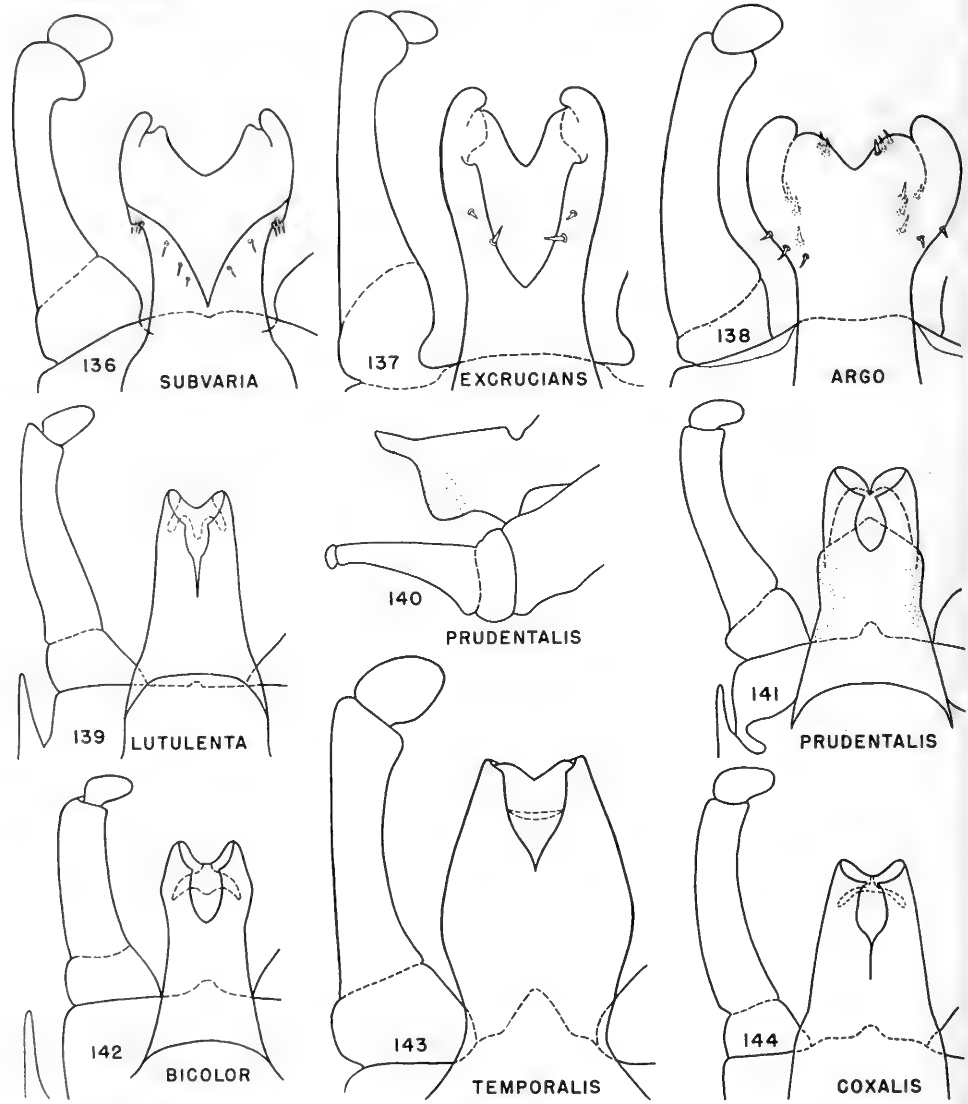


Fig. 136.—*Ephemerella subvaria,* male genitalia.
Fig. 137.—*Ephemerella excrucians,* male genitalia.
Fig. 138.—*Ephemerella argo,* male genitalia.
Fig. 139.—*Ephemerella lutulenta,* male genitalia.
Fig. 140.—*Ephemerella prudentalis,* lateral aspect of male genitalia. (After McDunnough.)
Fig. 141.—*Ephemerella prudentalis,* dorsal aspect of male genitalia. (After McDunnough.)
Fig. 142.—*Ephemerella bicolor,* male genitalia.
Fig. 143.—*Ephemerella temporalis,* male genitalia.
Fig. 144.—*Ephemerella coxalis,* male genitalia. (After McDunnough.)

24. Legs and abdomen having extremely numerous, minute black dots scattered over surfaces . . . . **23. lutulenta**
    Legs and abdomen not having black dots scattered over surfaces 25
25. Penis lobes short, extremely stout, enlarged near bases to form a vase-shaped structure, fig. 143 . . . . **24. temporalis**
    Penis lobes not vase shaped, figs. 144, 146–150 26
26. Caudal filaments white, articulations not darkened . . . . **25. coxalis**
    Caudal filaments either entirely dark gray or brown, or light and with darkened articulations 27
27. Penis lobes with lateral margins evenly, sinuately enlarged toward apexes, and maximum width of apical portion as great as maximum width of basal portion, fig. 146 . . . . **26. simplex**
    Penis lobes with lateral margins not evenly and sinuately enlarged toward apexes, and maximum width of apical portion less than maximum width of basal portion, figs. 142, 147–150 . . . 28
28. Penis lobes with a subangulate, preapical enlargement on either side, figs. 142, 147 29
    Penis lobes with a rounded, preapical enlargement on either side, fig. 150, or lobes with lateral margins parallel near apexes, figs. 148, 149 30
29. Caudal filaments white, with articulations red . . . . **28. bicolor**
    Caudal filaments gray, with articulations dark gray or black . . . **29. verisimilis**
30. Penis lobes with rounded, preapical, lateral enlargements, fig. 150 . . . . **30. minimella**
    Penis lobes with lateral margins subparallel near apexes, figs. 148, 149 . . 31
31. Penis lobes constricted (or narrower) in apical third, and inner, apical angles of peritreme acute, as in fig. 148; caudal filaments yellow-brown near bases, color blending into white at apexes, and articulations black . . **31. funeralis**
    Penis lobes constricted in slightly more than basal half, and inner, apical angles of peritreme blunt, fig. 149; caudal filaments light yellow, with articulations red-brown . . . . **32. aestiva**

MATURE NYMPHS

1. Platelike gills present on abdominal segments 3–7, figs. 165, 166, 172, 173;

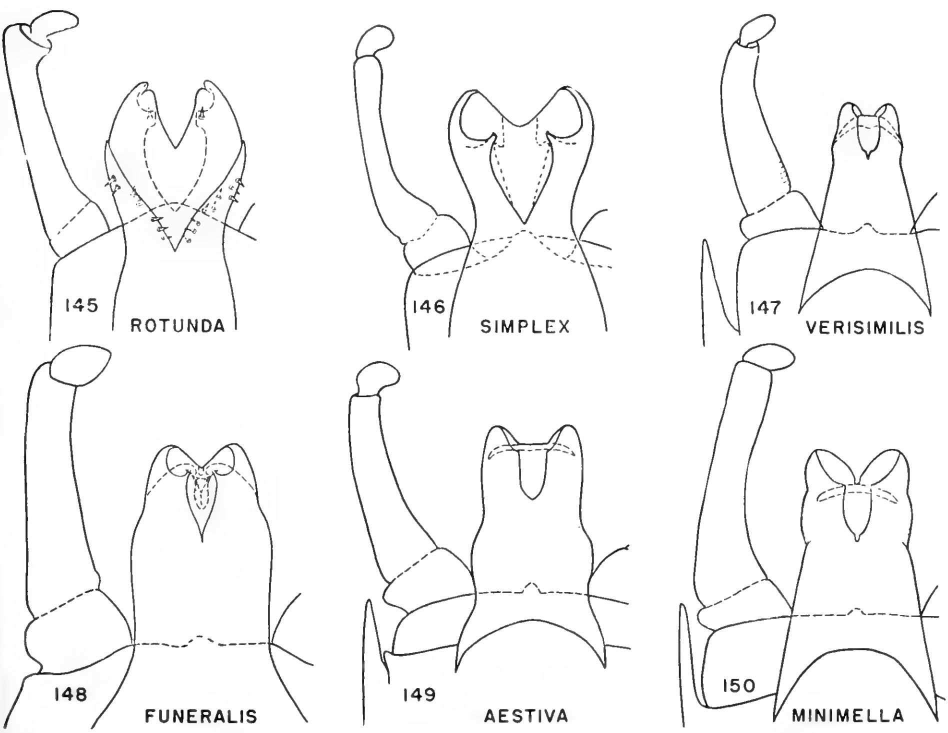


Fig. 145.—*Ephemerella rotunda*, male genitalia.
Fig. 146.—*Ephemerella simplex*, male genitalia.
Fig. 147.—*Ephemerella verisimilis*, male genitalia.
Fig. 148.—*Ephemerella funeralis*, male genitalia.
Fig. 149.—*Ephemerella aestiva*, male genitalia.
Fig. 150.—*Ephemerella minimella*, male genitalia. (After McDunnough.)

filamentous gills absent on first abdominal segment..................2

Platelike gills present on abdominal segments 4–7, figs. 162–164; filamentous gills present on first segment.......4

Frontal shelf of head without such a notch..............................8

8. Frontal shelf with a pair of small, triangular, lateral projections, fig. 156.............................**1. lata**

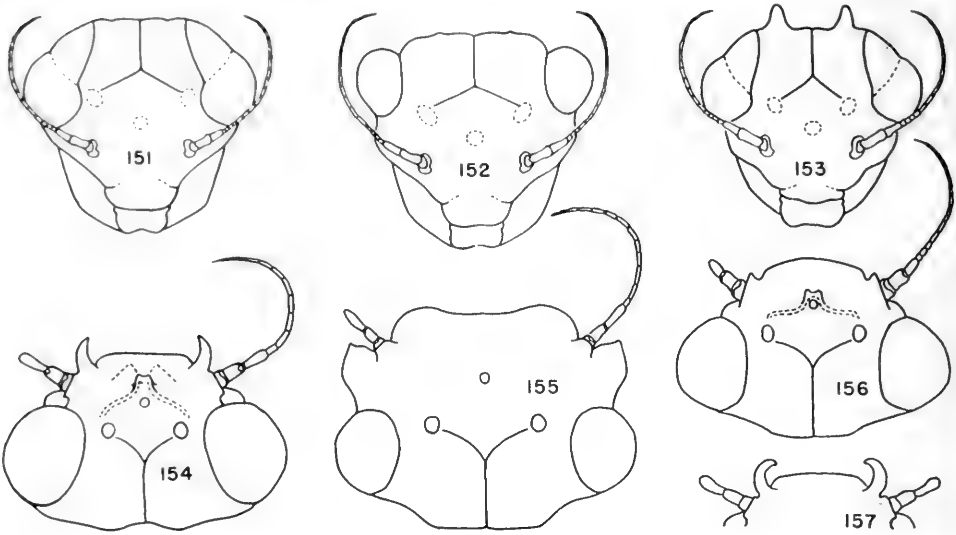


Fig. 151.—*Ephemerella bicolor*, head of mature male nymph, anterior aspect.
Fig. 152.—*Ephemerella bicolor*, head of mature female nymph, anterior aspect.
Fig. 153.—*Ephemerella temporalis*, head of mature nymph, anterior aspect.
Fig. 154.—*Ephemerella cornuta*, head of mature nymph, dorsal aspect.
Fig. 155.—*Ephemerella walkeri*, head of mature nymph, dorsal aspect.
Fig. 156.—*Ephemerella lata*, head of mature nymph, dorsal aspect.
Fig. 157.—*Ephemerella cornutella*, frontal shelf of head of mature nymph, dorsal aspect.

2. Fore femur not enlarged and toothed on anterior margin, figs. 161, 172, 173..3

Fore femur enlarged and toothed on anterior margin, fig. 160............6

3. Apical half of caudal filaments clothed with short spines, fig. 172; maxillary palps reduced or entirely wanting, figs. 167, 169.....................10

Apical half of caudal filaments clothed with long hairs, fig. 173; maxillary palps well developed, fig. 168......14

4. Gill on abdominal segment 4 operculate, fig. 164; maxillary palps wanting, fig. 169...............................5

Gill on abdominal segment 4 semioperculate, figs. 162, 163; maxillary palps present, as in fig. 168..............29

5. Occipital tubercles wanting in male, vestigial in female, figs. 151, 152....22

Occipital tubercles well developed in both sexes, although larger in females than in males, fig. 153..................23

(*WALKERI* Group)

6. Occipital tubercles present, as in fig. 153..................**2. tuberculata**

Occipital tubercles absent............7

7. Frontal shelf of head with a notch beneath each antennal base, fig. 155.... ....**3. walkeri**

Frontal shelf with a pair of conspicuous, lateral horns, figs. 154, 157..........9

9. Body of mature nymph 6–7 mm. long; frontal horns so curved inward as to be almost semicircular, fig. 157.......... ....**4. cornutella**

Body of mature nymph 9–10 mm. long; frontal horns not so markedly incurved, fig. 154..................**5. cornuta**

(*SERRATA* Group)

10. Maxillary palps entirely wanting, fig. 169....................**10. deficiens**

Maxillary palps present, although reduced in size, fig. 167............11

11. Prothorax with a pair of small, dorsal, submedian tubercles near posterior margin....................**8. serrata**

Prothorax lacking dorsal tubercles.....12

12. Head, thorax, and legs clothed with long hair......................**7. sordida**

Head, thorax, and legs not clothed with long hair.......................13

13. Caudal filaments black at bases, tips light yellow or white; each abdominal sternite with a pair of dark, lateral streaks and a row of four black dots.. ....**9. serratoides**

Caudal filaments entirely light yellow or white, fig. 172; each abdominal sternite with a pair of dark, lateral streaks only .... **6. frisoni**

(*INVARIA* Group)

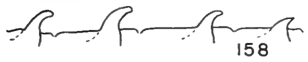
14. Abdominal tergites with a double row of erect, conspicuous tubercles .... **11. needhami**
Abdominal tergites either entirely without paired dorsal tubercles, or with small to minute ones, figs. 165, 166, 173....15

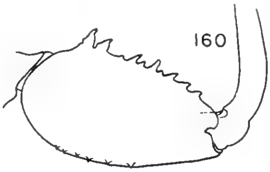
15. Legs markedly long and slender, spider-like.............**13. septentrionalis**
Legs not markedly long and slender...16

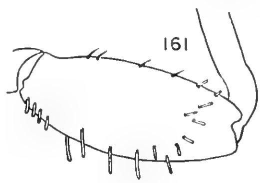
abdominal tergites 5 and 6 mostly brown.........................18

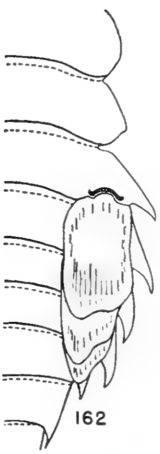
18. Dorsum of mesothorax freckled with pale dots in addition to the usual 16 relatively large, pale spots...**17. dorothea**
Dorsum of mesothorax uniform deep brown, with relatively large, pale spots only.............**16. excrucians**

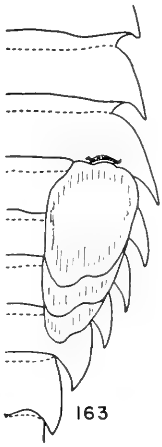
19. Lateral spines of apical abdominal tergites well developed, those of eighth segment twice as long as wide at base; hind leg with tibia longer than femur ....**12. aurivillii**

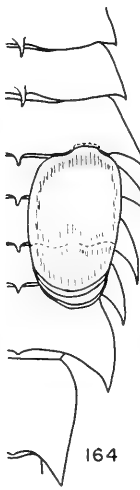


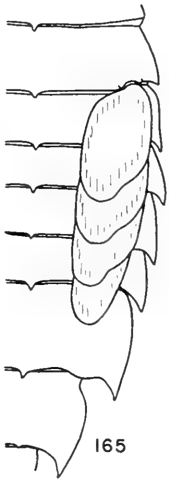












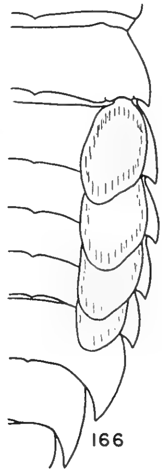


Fig. 158.—*Ephemerella lutulenta,* dorsal tubercles of basal abdominal segments of mature nymph, lateral aspect.

Fig. 159.—*Ephemerella coxalis,* dorsal tubercles of basal abdominal segments of mature nymph, lateral aspect.

Fig. 160.—*Ephemerella cornuta,* fore femur of mature nymph.

Fig. 161.—*Ephemerella needhami,* fore femur of mature nymph.

Fig. 162.—*Ephemerella simplex,* right side of abdomen of mature nymph, dorsal aspect.

Fig. 163.—*Ephemerella lita,* right side of abdomen of mature nymph, dorsal aspect.

Fig. 164.—*Ephemerella temporalis,* right side of abdomen of mature nymph, dorsal aspect.

Fig. 165.—*Ephemerella subvaria,* right side of abdomen of mature nymph, dorsal aspect.

Fig. 166.—*Ephemerella rotunda,* right side of abdomen of mature nymph, dorsal aspect.

16. Paired dorsal tubercles of abdomen entirely lacking.....................17
Abdomen with at least rudimentary paired dorsal tubercles...................19

17. Lateral margin of eighth abdominal tergite sinuate, fig. 173; abdominal tergites 5 and 6 almost completely white........ ....**14. argo**
Posterior two-thirds of each lateral margin of eighth abdominal tergite straight;

Lateral spines of apical abdominal tergites not so well developed, those of eighth segment as long as broad at base; hind leg with tibia equal to or shorter than femur................20

20. Dorsal abdominal tubercles greatly reduced, almost obsolete...**20. invaria**
Dorsal abdominal tubercles distinct, figs. 165, 166.........................21

21. Dorsal abdominal tubercles relatively

well developed, fig. 165; abdominal tergites lacking pale spots at bases of tubercles .... **18. subvaria**
Dorsal abdominal tubercles more reduced, fig. 166; abdominal tergites having a pale spot at base of each tubercle .... **21. rotunda**

(*BICOLOR* Group)

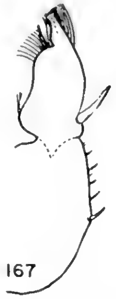
22. Distance between rows of dorsal abdominal spines suddenly increased on segment 5 .... **28. bicolor**
Distance between rows of dorsal abdominal spines uniformly increasing from segments 1 to 7 .... **30. minimella**
23. Distance between dorsal abdominal spines on segment 5 less than length of that segment at median line 24
Distance between dorsal abdominal spines on segment 5 equal to or greater than length of that segment at median line 25
24. Rows of dorsal abdominal tubercles parallel, fig. 164 ...... **24. temporalis**
Rows of dorsal abdominal tubercles converging posteriorly ... **22. prudentalis**
25. Posterolateral spine of abdominal segment 3 well developed, its length twice as great as width at base 26
Posterolateral spine of abdominal segment 3 reduced, its length only as great as width at base 28
26. Posterolateral spine of abdominal segment 9 slightly incurved; lateral margin of segment 9 almost straight .... **31. funeralis**
Posterolateral spine of abdominal segment 9 straight; lateral margin of segment 9 clearly convex 27
27. Dorsal abdominal tubercles of segments 1–3 long and slender, fig. 158 .... **23. lutulenta**
Dorsal abdominal tubercles of segments 1–3 short and blunt, fig. 159 .... **25. coxalis**
28. Distance between rows of dorsal abdominal spines increasing from segments 2 to 7 .... **29. verisimilis**
Rows of dorsal abdominal spines almost parallel .... **32. aestiva**
29. Paired dorsal tubercles present on occiput, thorax, and abdomen ... **33. attenuata**
Dorsal tubercles wanting on occiput, thorax, and abdomen 30
30. Second and third abdominal tergites with posterolateral angles produced as spine-like projections, fig. 163 ...... **27. lita**
Second and third abdominal tergites with posterolateral angles not produced, fig. 162 .... **26. simplex**

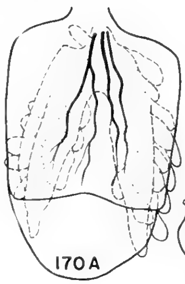
WALKERI Group

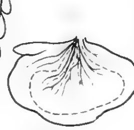
1. *Ephemerella lata* Morgan

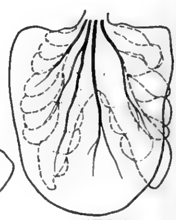
Ephemerella lata Morgan (1911:112).
Ephemerella inflata McDunnough (1926:187).

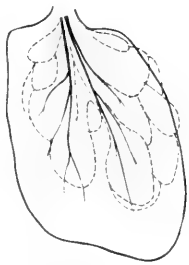
MALE.—Length of body and of fore wing 6–7 mm. Body generally very dark brown, almost black, with abdominal tergites slightly lighter in color than thorax. Wings hyaline, with most veins and crossveins hyaline, veins near costal margin of fore wing very light yellow. Genitalia with penis lobes fused almost to tips, penial spines lacking; second forceps segment short and subangulate, with a sharp median constriction, fig. 122; and

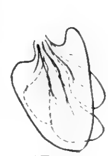












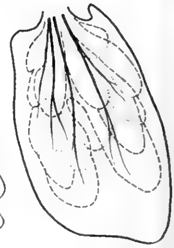


Fig. 167.—*Ephemerella frisoni*, maxilla of mature nymph.
Fig. 168.—*Ephemerella needhami*, maxilla of mature nymph.
Fig. 169.—*Ephemerella deficiens*, maxilla of mature nymph.
Fig. 170*A*.—*Ephemerella temporalis*, gill of fourth abdominal segment.
Fig. 170*B*.—*Ephemerella temporalis*, gill of seventh abdominal segment.
Fig. 170*C*.—*Ephemerella temporalis*, gill of fifth abdominal segment.
Fig. 171*A*.—*Ephemerella needhami*, gill of third abdominal segment.
Fig. 171*B*.—*Ephemerella needhami*, gill of seventh abdominal segment.
Fig. 171*C*.—*Ephemerella needhami*, gill of fifth abdominal segment.

third forceps segment three times as long as wide.

NYMPH.—Head and body without dorsal spines and tubercles. Frontal shelf of head with a pair of small, triangular projections, fig. 156. Fore femur enlarged and toothed on anterior margin.

Known from Maine, Michigan, New York, North Carolina, and Quebec.

2. *Ephemerella tuberculata* Morgan

Ephemerella tuberculata Morgan (1911:112).

MALE.—Length of body and of fore wing 8–9 mm. Body generally very dark red-brown, with middle abdominal tergites usually yellow-brown. Wings hyaline, veins slightly grayish or gray-brown. Genitalia with penis lobes fused almost to tips, penial spines lacking, and inner angles of peritreme acute, fig. 118; second forceps segment evenly bowed from base to apex, a slight inner enlargement near base; third forceps segment four times as long as wide.

NYMPH. — Head with frontal shelf notched below bases of antennae, and with a pair of horns on vertex. Each fore femur enlarged and toothed on anterior margin. Thorax and abdomen with dorsal, paired tubercles.

Known from Maryland, New York, North Carolina, Ontario, Quebec, and Tennessee.

3. *Ephemerella walkeri* Eaton

Baetis fuscata Walker (1853: 570). Name preoccupied.
Ephemerella walkeri Eaton (1884:129). New name.
Ephemerella bispina Needham (1905:43).
Ephemerella fuscata (Walker). McDunnough (1931*d*:214); Traver (1935*a*:600).

MALE.—Length of body and of fore wing 7–8 mm. Body generally dark brown, with abdominal tergites slightly lighter toward lateral margins. Wings hyaline, veins slightly stained with yellow. Genitalia with penis lobes fused almost to tips, spines wanting, and inner angles of peritreme blunt, fig. 119; second forceps segment only slightly bowed, with an inner enlargement near base; third forceps segment four times as long as wide.

NYMPH.—Head with a broad frontal shelf having a notch beneath each antennal base, fig. 155; vertex lacking tubercles. Each fore femur enlarged and toothed at anterior margin. Prothoracic tubercles small and represented by a single pair laterally; dorsal abdominal tubercles minute.

Known from Indiana, New Brunswick, Ontario, and Quebec.

4. *Ephemerella cornutella* McDunnough

Ephemerella cornutella McDunnough (1931*b*:82; 1931*d*:211).

MALE.—Length of body and of fore wing 6–7 mm. Body generally very dark brown, abdominal tergites somewhat lighter on mesal area. Wings hyaline, veins slightly tinged with faint yellow; crossveins almost invisible. Genitalia, fig. 121, with penis lobes fused almost to tips, penial spines wanting; second segment of forceps relatively short and straight, an inner enlargement near base; third segment four times as long as wide.

NYMPH.—Frontal shelf of head with a pair of strongly incurved, lateral horns, fig. 157. Fore femur enlarged and bearing teeth on anterior margin. Head, thorax, and abdomen without dorsal tubercles or spines.

Known from Georgia, New Brunswick, New Hampshire, New York, North Carolina, Nova Scotia, Quebec, and West Virginia.

5. *Ephemerella cornuta* Morgan

Ephemerella cornuta Morgan (1911:114).

This species differs from *cornutella* only in that the length of body and of fore wing of male are 9–10 mm. each, second forceps segment of male genitalia is relatively longer and more bowed, fig. 120, and frontal shelf of head of nymph bears a pair of horns which are relatively less incurved, fig. 154.

Known from Connecticut, Maine, New Hampshire, New York, North Carolina, Pennsylvania, Quebec, and Tennessee.

SERRATA Group

6. *Ephemerella frisoni* McDunnough

Ephemerella frisoni McDunnough (1927*a*:10).

MALE.—Length of body and of fore wing 5.0–6.5 mm. Head dark brown, eyes tan; antennal pedicel tan, flagellum brown. Thoracic notum dark brown, lateral areas, near wing bases, tan; venter dark brown;

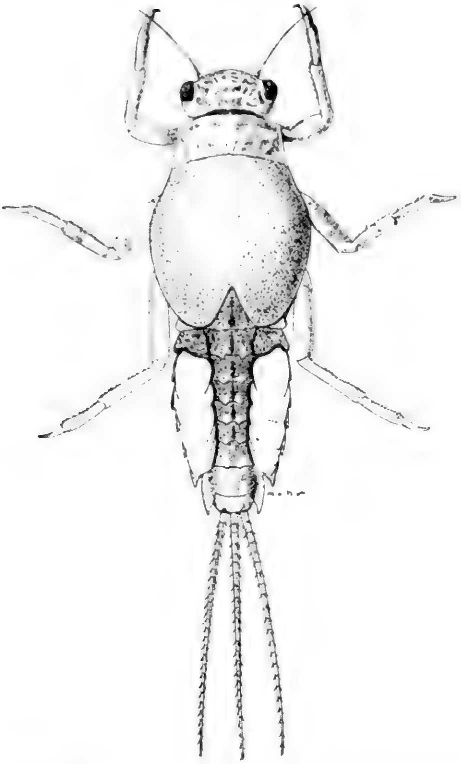


Fig. 172. — *Ephemerella frisoni*, mature nymph, dorsal aspect.

fore femur light brown, fore tibia and tarsus and all of middle and hind legs white; wings hyaline, with brown stain at base of each wing, each fore wing milky in stigmatic area. Abdominal tergites 1–7 and anterior half of tergite 8 white, usually with a fine, median, dorsal, brown line and a pair of small, brown, lateral marks on each tergite; posterior half of tergite 8, and tergites 9 and 10, light brown; abdominal sternum white, usually with a pair of lateral, brown dots on each sternite; caudal filaments entirely white, articulations not darkened. Genitalia, fig. 123, white, with forceps faintly shaded with tan.

Nymph.—Fig. 172. Length of body 5.0–6.5 mm., of caudal filaments 2.5–3.5 mm. General color light yellowish tan, sometimes almost white, with small and variable brown markings.

Vertex of head, dorsal area of pronotum, and (usually) basal area of front wingpads with irregular, light brown markings; apexes of femora and bases of tibiae usually shaded with light brown; a minute, dark brown dot present at apicoventral angle of each trochanter. Dorsal part of abdominal tergites fairly uniformly shaded with light brown in area not covered by gills, elongate, dark brown markings along line of inner dorsal margins of gills and on median dorsal line; abdominal venter rather uniformly shaded with light tan, this shading freckled with light yellow or white dots; a minute, dark brown dot present near lateral margin of each abdominal sternite, these dots forming a sublateral row on either side of abdominal venter; basal half of each posterolateral projection of sternites shaded with tan; each caudal filament with a single tan crossband usually present near base.

Head and thorax without tubercles; maxillary palps present, but somewhat degenerated, fig. 167; each tarsal claw with six to eight denticles; posterolateral angles of abdominal segments 4–9 produced, bluntly pointed; posterior margin of second abdominal tergite with a pair of extremely small, submedian tubercles; tergites 3–7 with these tubercles relatively well developed; eighth tergite with tubercles greatly reduced, but discernible, tubercles wanting on ninth tergite; pairs of tubercles converging slightly from tergites 3 to 7, rudimentary tubercles more widely spaced on tergite 8; abdominal segments 1 and 2 without gills, segments 3–7 bearing platelike gills; caudal filaments with relatively few, short setae at each articulation, these setae not longer nor more dense in apical than in basal area of filaments.

Known from Illinois and Missouri. Develops in fairly rapid creeks or small rivers.

Illinois Records.—Muncie, Stony Creek: June 8, 1927, T. H. Frison, 1 N; May 22, 1942, Ross & Burks, 1 ♂. Oakwood, Salt Fork River: June 6, 1925, T. H. Frison, 1 ♂; June 9, 1926, Frison & Auden, 3 ♂; May 21, 1928, T. H. Frison, 4 N; June 29, 1929, T. H. Frison, 2 N; June 14, 1935, C. O. Mohr, 6 N; May 21, 1936, Mohr & Burks, 3 N; June 11, 1936, C. O. Mohr, 9 N; May 22, 1942, Ross & Burks, 5 N.

7. *Ephemerella sordida* McDunnough

Ephemerella sordida McDunnough (1925*c*:42; 1931*d*:205).

Male.—Length of body 4.5–5.0 mm., of fore wing 5–6 mm. Body very dark brown, almost black, with abdominal sternites somewhat lighter; wings hyaline, all veins only very slightly darker than membrane. Caudal filaments white throughout. Genitalia, fig. 124: penis lobes with a pair of prominent, lateral tubercles, second forceps segment slightly bowed, and third forceps segment as broad as long.

NYMPH.—Head, thorax, and legs conspicuously hairy; maxillary palp present, but reduced; fore femur not toothed on anterior margin, but bearing a few spicules; abdominal tergites with a double row of submesal, papillate protuberances; caudal filaments bearing only short spines throughout their length.

Known from Ontario and Quebec.

8. *Ephemerella serrata* Morgan

Ephemerella serrata Morgan (1911:109).

MALE.—Length of body and of fore wing 5–6 mm. Thorax yellow-brown, abdominal tergum red-brown, and abdominal venter yellow-brown, without transverse rows of black dots. Wings hyaline, tinged with brown at bases, and veins faintly shaded. Genitalia, fig. 128, with penis lobes fused almost to tips, and a lateral tubercle present on each penis lobe near tip; second forceps segment bowed toward apex; third forceps segment as broad as long.

NYMPH.—Vertex of head roughened, but without distinct tubercles. Prothorax with a pair of small, submedian, dorsal tubercles near posterior margin; each tarsal claw with three or four denticles. Abdominal tergites with a double row of submedian, wartlike tubercles; caudal filaments bearing only short setae.

Known from Maryland, Massachusetts, New York, North Carolina, Quebec, and West Virginia.

9. *Ephemerella serratoides* McDunnough

Ephemerella serratoides McDunnough (1931*b*: 83; 1931*d*: 207).

MALE.—Length of body and of fore wing 5–6 mm. Thorax yellow-brown, with dark brown shading; abdominal tergites red-brown, with darker brown markings; abdominal sternites lighter in color than tergites, each sternite bearing an arcuate, transverse row of four black dots; wings hyaline, with veins faintly shaded. Genitalia, fig. 126, differ only slightly from those of *serrata*.

NYMPH.—Head and thorax smooth, without tubercles or conspicuous hairs; fore femur bearing a few spicules on posterior margin; each tarsal claw with six or seven denticles. Abdominal tergites with a double row of small, submedian, wartlike protuberances; caudal filaments with only short setae.

Known from Maryland, North Carolina, Quebec, and West Virginia.

10. *Ephemerella deficiens* Morgan

Ephemerella deficiens Morgan (1911:111).
Ephemerella atrescens McDunnough (1925*c*:43).

MALE.—Length of body and of fore wing 5–6 mm. Head and body very dark brown, with abdominal sternites uniformly tan. Wings hyaline, with brown staining at wing bases; veins faintly darker than wing membrane. Genitalia, fig. 133: penis lobes fused only two-thirds of the way to tips, and lateral tubercles present on each penis lobe near apex; second forceps segment is relatively straight.

NYMPH.—Head and thorax smooth, without tubercles; maxillary palp entirely wanting, fig. 169; each tarsal claw with eight or nine denticles. Abdominal tergites lacking mid-dorsal tubercles; caudal filaments bearing only short setae.

Known from Georgia, Massachusetts, Michigan, New Brunswick, New Hampshire, New York, North Carolina, Nova Scotia, Ontario, Quebec, and West Virginia.

INVARIA Group

11. *Ephemerella needhami* McDunnough

Ephemerella excrucians Needham (1905:47), not Walsh. Misidentification.
Ephemerella needhami McDunnough (1925*b*:171). New name.

MALE.—Length of body and of fore wing 6–8 mm. Head, thorax, and abdominal tergum dark red-brown to almost black; abdominal venter mostly light red-brown.

Head red-brown, face below ocelli yellow; in life, each eye red-tan in upper portion, yellow in lower portion; antennal scape yellow, pedicel and flagellum brown. Thorax dark red-brown to almost black, with yellow spot on sternum between each pair of coxae; fore leg smoky brown, middle and hind legs yellow, with vague brown shading on outer sides of coxa and near apex of femur; wings hyaline, with brown stain at bases, principal veins light yellow. Abdominal tergum dark red-brown, usually with a pair of yellow, submedian spots at anterior margin of each tergite, occasional specimens with a dorsal, median, longitudinal, yellow stripe; sternites light red-brown, with transverse yellow area near anterior margin of each sternite; four minute, black marks on each sternite; genitalia, fig. 131, yellow-brown, with smoky brown shading toward apexes; caudal filaments uniformly gray-brown, articulations not darkened.

FEMALE.—Length of body 7–8 mm., of fore wing 8–9 mm. Color in general lighter than in male, with dark red-brown areas of male being replaced by yellow-brown. Entire sternum of thorax and abdomen yellow, faintly shaded with brown near apex of mesosternum; fore leg yellow, with brown shading near apex of femur; wings faintly brown at bases; caudal filaments very light yellow, basal articulations red.

NYMPH.—Length of body 6–8 mm., of caudal filaments 3.5–4.5 mm. Color extremely variable, ranging from an almost uniformly dark brown form to a form with a light yellow, or white, longitudinal, mesal stripe that extends from vertex to tenth abdominal tergite; lateral margins of pronotum and abdominal segments usually light yellow or white; caudal filaments usually with narrow, brown crossbands throughout their lengths.

Head and thorax without dorsal tubercles; maxillary palps well developed, fig. 168; each tarsal claw with 8 to 10 denticles; each fore femur with stout, blunt spines along posterior margin and near apex, fig. 161; posterolateral angles of abdominal segments 3–9 produced and spinelike; tergites 2–8 each with a pair of long, submedian tubercles, these forming two almost parallel rows; caudal filaments bearing long setae in apical areas.

Known from Illinois, Indiana, Maine, Michigan, New York, Nova Scotia, and Quebec. Develops in cool, fairly rapid creeks or small rivers.

Illinois Records.—AROMA PARK, Kankakee River: June 11, 1947, B. D. Burks, 4♂, 3♀. EDDYVILLE, Lusk Creek: April 4, 1946, Burks & Sanderson, 4 N; May 24, 1946, Mohr & Burks, 1 N; May 16–17, 1947, B. D. Burks, 1♂, 2♀, 1 N. KANKAKEE, Kankakee River: April 30, 1931, T. H. Frison, 45 N; April 23, 1935, Ross & Mohr, 5 N; May 17, 1935, H. H. Ross, 9 N; July

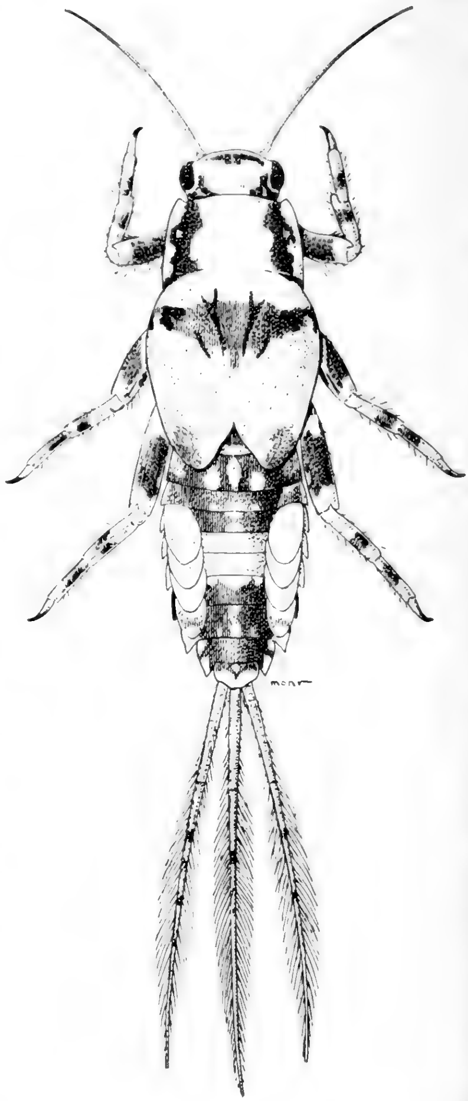


Fig. 173.—*Ephemerella argo*, mature nymph, dorsal aspect.

21, 1935, Ross & Mohr, 1♂. MOMENCE, Kankakee River: June 4, 1932, Frison & Mohr, 7♂; May 26, 1936, H. H. Ross, 4♂; May 17, 1937, Ross & Burks, 24 N; June 1, 1937, B. D. Burks, 1♂; May 15, 1938, Ross & Burks, 8 N; May 21, 1940, Mohr

& Burks, 2 N; June 3–4, 1947, B. D. Burks, 6♂, 1♀.

12. *Ephemerella aurivillii* (Bengtsson)

Chitonophora aurivillii Bengtsson (1908:243; 1909:8).
Ephemerella aronii Eaton (1908:149).
Ephemerella norda McDunnough (1924*d*:223).
Chitonophora aurivilliusi Lestage (1930*a*:204). Emended name.
Ephemerella concinnata Traver (1934:219). New synonymy.

MALE.—Length of body 10–11 mm., of fore wing 11–12 mm. Thorax red-brown, with lateral areas dark brown; wings hyaline, with stigmatic areas milky and veins brown. Abdominal tergites with anterior third of each segment light brown and posterior two-thirds dark brown; abdominal sternites yellow-brown; caudal filaments uniformly dark brown. Genitalia, fig. 130, distinct from those of all other North American species: penis lobes divided almost to bases, inner margins of lobes provided with numerous minute spines; second forceps segment suddenly enlarged at apex.

NYMPH.—Head and thorax entirely lacking dorsal spines or tubercles; maxillary palps well developed; each fore femur bearing spicules at posterior margin and near dorsal apex; each tarsal claw with 8 to 11 denticles; each abdominal tergite with a pair of light-colored, submesal spots at posterior margin, on each spot a cluster of minute spines and a small, acute tubercle; caudal filaments with long setae near apexes.

Known from Alaska, Alberta, Labrador, Michigan, Montana, Ontario, Pennsylvania, Quebec, and northern Europe. This species is distributed throughout the northern part of the Holarctic region.

13. *Ephemerella septentrionalis* McDunnough

Ephemerella septentrionalis McDunnough (1925*b*:171; 1931*d*:201).

MALE.—Length of body 8–9 mm., of fore wing 10–11 mm. Dorsum of thorax and abdomen brown; venter yellow-brown; wings and wing veins hyaline. Genitalia, fig. 134, distinct from those of all other eastern North American species: slender lateral projections of penis lobe are virtually straight and directed posteriorly; mesal area of each lobe with two or three stout spines; second forceps segment relatively straight, but enlarged suddenly at apex.

NYMPH.—Head, thorax, and abdomen without dorsal spines or tubercles; legs conspicuously long, slender, and hairy; each tarsal claw with 10 to 12 denticles; caudal filaments bearing long setae in apical regions.

Known from New York, Ontario, and Quebec.

14. *Ephemerella argo* Burks

Ephemerella argo Burks (1949:232).

MALE.—Length of body 8 mm., of fore wing 9 mm. Thorax light yellowish tan, with vague brown markings; abdomen light yellowish tan, tergites with large areas shaded with brown.

Head deep cream colored, vertex with obscure, light gray markings; each antennal scape and pedicel cream colored, flagellum brown; eyes yellowish tan. Legs deep cream colored, apex of fore tibia and second and third fore tarsal segments darkened; wings hyaline, stigmatic areas milky, anterior veins slightly yellow stained, other veins hyaline. Abdominal tergites light yellowish tan, with brown shading: mid-dorsal area of tergites 1–4 almost completely brown, tergites 5 and 6 shaded only near meson, tergites 7–10 completely brown, shaded on mid-dorsal area; venter of abdomen light yellowish, with vague, longitudinal, brown line near each lateral margin of each sternite; genitalia, fig. 138, light yellowish tan; caudal filaments light yellowish tan, articulations brown.

NYMPH.—Length of body 7–9 mm., of caudal filaments 4–5 mm. Body principally yellowish tan, with a prominent, brown color pattern, fig. 173; caudal filaments each with one to three narrow, brown crossbands in middle and apical areas.

Head, thorax, and abdomen without dorsal spines or tubercles; maxillary palps well developed; each tarsal claw with six to nine denticles; posterolateral angles of abdominal segments 3–9 produced, spinelike; caudal filaments bearing long setae in apical areas.

Known from Illinois and Indiana. Probably a large-river species.

Illinois Record.—MOUNT CARMEL, Wabash River: April 2, 1932, Frison & Ross, 2 N.

15. *Ephemerella ora* Burks

Ephemerella ora Burks (1949:235).

Male.—Length of body 7 mm., of fore wing 8 mm. Head and body yellow, shaded with tan and brown.

Head yellow, shaded with tan between eyes and around ocelli; eyes pinkish tan; each antennal scape and pedicel yellow, flagellum brown. Thorax yellow, with tan shading on dorsomedian area of pronotum, mesonotum mostly tan; legs yellow, with apex of each fore tibia and apex of each of the basal three fore tarsal segments darkened; wings and veins hyaline, with anterior two veins of fore wing stained with faint yellow. Ground color of abdomen yellow, basal tergites with mid-dorsal area of each heavily shaded with brown, apical three tergites pinkish tan; eighth sternite with posterolateral angles pink; genitalia, fig. 127, yellow; caudal filaments light yellow, articulations black.

Female.—Length of body 7.5 mm., of fore wing 9 mm. General color similar to that of male, but lighter; caudal filaments white, articulations black.

Known from Illinois. Apparently a large-river species.

Illinois Record.—Mount Carmel: April 22, 1946, at light, Mohr & Burks, 1 ♂, 1 ♀.

16. *Ephemerella excrucians* Walsh

Ephemerella excrucians Walsh (1862:377).
Ephemerella semiflava McDunnough (1927*b*:300). New synonymy.

McDunnough (1931*d*:192) long ago expressed the opinion that *semiflava* would prove to be a synonym of *excrucians*.

Male.—Length of body 5.5–7.5 mm., of fore wing 7–9 mm. Dorsum of thorax dark red-brown, dorsum of abdomen varying from dark red-brown to almost black; abdominal venter slightly lighter in shade than dorsum.

Head red-brown; eyes yellow in living insect; each antennal pedicel red-brown, flagellum smoky brown. Legs yellow, segments of each fore tarsus darkened at tips. Wings hyaline, veins at costal margin of fore wing slightly yellowish; other veins and all crossveins hyaline; sometimes a faint red-brown staining present at bases of wings. Caudal filaments white, basal articulations light red-brown. Genitalia, fig. 137, with penis lobes only slightly expanded near apexes, each lobe bearing two or three short, stout dorsal spines in basal position, and sometimes one or two lateral spines on either side; second segment of forceps straight and not expanded at apex.

Nymph.—(Described from two specimens reared in Michigan by Dr. J. W. Leonard.) Length of body 5–6 mm., caudal filaments 3 mm. General color dark brown, with relatively large, pale markings; caudal filaments white or pale yellow, with faint, darker crossbands throughout.

Head, thorax, and abdomen entirely without dorsal tubercles; maxillary palps present, segmented; each tarsal claw with seven or eight ventral denticles; posterolateral angles of abdominal segments 4–9 produced as small, relatively blunt spines; caudal filaments bearing long, dense setae in apical areas.

Known from Illinois, Michigan, New Brunswick, Oklahoma, Ontario, and Quebec. The only Illinois specimen of this species I have seen is the lectotype in the Museum of Comparative Zoology. Now known to develop in a cold, rapid river.

Illinois Record.—Rock Island: 12 ♂, 5 ♀, B. D. Walsh (Walsh 1862:377).

17. *Ephemerella dorothea* Needham

Ephemerella dorothea Needham (1908:190).

Male.—Length of body 5–6 mm., of fore wing 7–8 mm. Head and body pale yellow, almost white. Eyes light red, antennae yellow. Thorax pale yellow, without darker shading; wings and veins hyaline; legs entirely yellow, with each fore tarsus faintly darkened. Abdomen entirely light yellow, without darker areas or shading; caudal filaments white, articulations not darkened. Genitalia, fig. 132, light yellow, with each penis lobe bearing six to eight stout spines in basal position; second forceps segment enlarged at apex.

Nymph.—Length of body 6–8 mm., of caudal filaments 4–5 mm. General color pale yellow-brown, with small, light tan, freckle-like spots and larger, pale markings; each caudal filament usually with two or three narrow, brown crossbands near tip.

Head, thorax, and abdomen entirely without dorsal tubercles; maxillary palps well developed; each tarsal claw with six to nine denticles; posterolateral angles of abdominal segments 4–9 slightly produced as relatively blunt spines; caudal filaments bearing long, dense setae in apical areas.

Known from Connecticut, Illinois, Indiana, Michigan, New Brunswick, New Hampshire, New York, North Carolina, Pennsylvania, Quebec, South Carolina, Tennessee, Vermont, Virginia, and West Virginia. Develops in fairly large rivers.

Illinois Records.—GOLCONDA: May 13, 1932, Frison, Mohr, & Ross, 4 N. MOUNT CARMEL: Wabash River, April 2, 1932, Frison & Ross, 19 N.

18. *Ephemerella subvaria* McDunnough

Ephemerella subvaria McDunnough (1931*b*: 84; 1931*d*: 194).

MALE.—Length of body 8–9 mm., of fore wing 9–10 mm. Head, thorax, and abdominal dorsum dark brown; abdominal venter light red-brown; wings hyaline, with veins and crossveins light brown. Genitalia, fig. 136, with penis lobes broad and with five or six stout, basal spines on either side; occasionally one or two apical, ventral spines present also; second forceps segment relatively straight, with apex suddenly expanded.

NYMPH.—Head and thorax entirely without dorsal spines or tubercles, but abdominal tergites with relatively well-developed, submedian spines, fig. 165; each tarsal claw with seven to nine denticles; caudal filaments bearing long setae in apical regions.

Known from Michigan, Ontario, Pennsylvania, Quebec, and Wisconsin.

19. *Ephemerella fratercula* McDunnough

Ephemerella fratercula McDunnough (1925*a*: 213).

MALE.—Length of body 7 mm., of fore wing 8 mm. Thorax and dorsum of terminal abdominal segments light brown, basal abdominal segments dark brown on dorsum; venter yellow; wings and wing veins hyaline. Genitalia, fig. 129: each penis lobe with two or three stout, dorsal spines and seven to nine ventral ones; second forceps segment almost straight, suddenly enlarged at apex.

Known from Quebec.

20. *Ephemerella invaria* (Walker)

Baetis invaria Walker (1853: 568).

MALE.—Length of body and of fore wing 8–9 mm. Head light red-brown, eyes reddish orange. Thorax light red-brown; pronotum red-brown, with faint gray shading; thoracic sternum dark red-brown; legs light yellow, almost white, with apex of each fore femur and fore tibia stained with red-brown; wings hyaline, longitudinal veins stained with light brown. Abdominal tergum smoky brown, becoming slightly lighter on apical tergites; sternum uniformly yellow-brown; caudal filaments white, articulations dark. Genitalia, fig. 135, light yellow; each penis lobe bearing five to eight stout, dorsal spines in basal and lateral positions on either side and, in most specimens, a single pair of ventral spines at apex, in some specimens, as many as four apical spines; second forceps segments sharply expanded at apex.

NYMPH.—Length of body 7–9 mm., of caudal filaments 4–5 mm. Color of body varying from dark brown with yellow markings to yellow with small, brown markings; thorax of light-colored specimens usually with two brown crossbands; abdominal tergites 5 and 6, in area between gills, partly or almost completely light colored.

Head and thorax without dorsal tubercles; maxillary palps well developed; each tarsal claw bearing five to seven denticles; abdominal segments 4–9 with well-developed, stout, spinelike projections at posterolateral angles, segment 3 often with rudimentary posterolateral spines; minute to obsolescent dorsal, submedian spines present on abdominal tergites 3–9; caudal filaments bearing long, dense setae in apical areas.

Known from Illinois, Maryland, Michigan, New York, Ontario, Quebec, and Wisconsin. Develops in fairly rapid, moderate-sized rivers.

Illinois Records.—DIXON: Rock River, May 22, 1925, D. H. Thompson, 3 N. OREGON: Rock River, May 15, 1930, Frison & Ross, 1 N. ROCKFORD: Rock River, May 4, 1926, D. H. Thompson, 13 N. ROCKTON: Rock River, May 15, 1926, D. H. Thompson, 1 N.

21. *Ephemerella rotunda* Morgan

Ephemerella rotunda Morgan (1911: 113).
Ephemerella feminina Needham (1924: 309).

MALE.—Length of body and of fore wing 9–11 mm. Thorax light pinkish yellow, with brown markings; abdominal dorsum yellow, with a broad, brown crossband on each segment; venter light yellow or white with, occasionally, faint tan crossbands; wings hyaline, with veins faintly yellow. Genitalia, fig. 145, differ from those of *invaria* in possessing a ventral, subbasal group of two or three spines on each penis lobe.

NYMPH.—Dorsal tubercles on thorax and head absent, but dorsal, submedian abdominal spines present, although small, fig. 166; each tarsal claw with five to eight denticles; caudal filaments with long setae in apical regions.

Known from Michigan, New York, North Carolina, Ontario, Quebec, and Wisconsin.

BICOLOR Group

22. *Ephemerella prudentalis* McDunnough

Ephemerella prudentalis McDunnough (1931*a*:40).

MALE.—Length of body and of fore wing 7–8 mm. Thorax and basal abdominal tergites red-brown, color gradually changing to yellow on apical tergites; sternites yellow, with black markings; wings hyaline, brown stain at bases; veins hyaline, occasionally tinged with tan. Genitalia, figs. 140, 141, differ from those of all other eastern North American species in having a large, ventral, subapical enlargement on each penis lobe.

NYMPH.—Head with a pair of small occipital tubercles; dorsum of abdominal tergites with two rows of submedian spines converging posteriorly; caudal filaments bearing long setae in apical areas.

Known from Quebec.

23. *Ephemerella lutulenta* Clemens

Ephemerella lutulenta Clemens (1913:335).
Ephemerella lineata Clemens (1913:336).

MALE.—Length of body 8–9 mm., of fore wing 9–10 mm. Thorax dark brown, abdomen yellow-brown, peppered with minute, black dots.

Head yellow-brown, with gray streaks on frons around ocelli and on frontal carina; antennae yellow-brown. Pleura and venter of thorax sprinkled with minute, black dots; wings hyaline, often faintly stained with brown at bases; veins brown; legs yellow-brown, partly or completely covered by a sprinkling of black dots. Both dorsum and venter of abdomen sprinkled with black dots; genitalia, fig. 139, yellow-brown, penis lobes with lateral margins straight and inner peri-treme angles blunt; second forceps segment slightly bowed toward apex; caudal filaments light yellow-brown near bases, becoming white at apexes, articulations dark brown.

FEMALE.—Length of body and of fore wing same as in male; thorax and abdomen lighter colored than in male, causing sprinkling of black dots to show more clearly; brown on wing veins lighter than in male.

NYMPH.—Length of body 9–12 mm., of caudal filaments 6–8 mm. Uniformly dark yellow-brown, sometimes with small, vague, brown markings on dorsum of thorax; caudal filaments usually uniformly tan, sometimes with faint, brown crossbands.

Occipital tubercles of female minute, those of male obsolete, as in figs. 151, 152; maxillary palps completely absent, as in fig. 169; each tarsal claw with 8 to 10 denticles. Posterolateral angles of abdominal segments 2–9 produced as slender spines, those on segment 2 minute, those on segments 3–8 long and slightly curved inward at apexes; tergites 1–7 each with a pair of long, submedian tubercles, fig. 158, these forming two rows diverging posteriorly; platelike gill of segment 4 operculate, almost or quite covering three posterior pairs of gills; caudal filaments with dense, long setae near apexes.

Known from Illinois, Indiana, Maine, Massachusetts, New Brunswick, New York, North Carolina, Ontario, Quebec, Tennessee, and Wisconsin. Develops in relatively small, shallow lakes.

Illinois Records.—ANTIOCH, Channel Lake: May 16, 1936, Ross & Mohr, 1 N; May 27, 1936, H. H. Ross, 1 ♂; May 16, 1938, B. D. Burks, 1 ♀, 1 N.

24. *Ephemerella temporalis* McDunnough

Ephemerella temporalis McDunnough (1924*c*:74; 1931*a*:35).

MALE.—Length of body 7–8 mm., of fore wing 8–10 mm. Thorax bright yellow-brown; abdominal dorsum mostly dark brown; sternum light yellow or tan.

Head yellowish tan, eyes light reddish yellow; each antennal scape and pedicel yellowish tan, flagellum gray-brown. Wings hyaline, veins in costal region faintly stained with tan; legs bright yellow, apex of each fore femur and fore tibia shaded with tan. Abdominal tergites 2–7 dark brown, often with a vague, transverse, black mark at posterior margin of each, tergites 8–10 yellow- or red-brown; sternites light yellow or tan, each sternite usually with an arcuate, transverse row of four black dots. Genitalia, fig. 143, bright yellow, penis lobes vase shaped, greatly enlarged at bases, second forceps segment slightly enlarged at apex; caudal filaments yellow to almost white, articulations light reddish brown.

NYMPH.—Length of body 8–10 mm., of caudal filaments 5–7 mm. Body dark brown, flecked with tan dots; abdomen often with a longitudinal, dorsal tan stripe; caudal filaments usually with alternating, broad crossbands of brown and tan.

Head with well-developed occipital tubercles, fig. 153; maxillary palps wanting. Thorax lacking dorsal tubercles; each tarsal claw bearing 9 to 12 denticles. Posterolateral angles of abdominal segments 2–9 produced, spinelike, those borne by segments 2 and 3 minute, fig. 164; abdominal tergites 1–4 each with a pair of finger-like, submedian tubercles, tergites 5–7 each with a pair of narrow, acute, submedian spines, and segments 8 and 9 each with a pair of rudimentary spines, these spines and tubercles forming two parallel rows; platelike gills borne by abdominal segment 4 not entirely covering more posterior gills; caudal filaments bearing long, dense setae in apical areas.

Known from Georgia, Illinois, Michigan, New Brunswick, New York, North Carolina, Ontario, Quebec, and Wisconsin. Develops in rather small, shallow lakes.

Illinois Records.—FREEPORT: at light, June 11, 1948, Burks, Stannard, Smith, 3 ♂. GRAYSLAKE: May 26, 1936, H. H. Ross, 1 N. HAVANA, Illinois River: May 21, 1895, C. A. Hart, 1 N; shore of Cook's Island, May 17, 1894, C. A. Hart, 1 N; Quiver Lake, June 1–2, 1894, Smith, 1 N; outlet Quiver Lake, June 1, 1895, C. A. Hart, 1 N. LAKE COUNTY: Cedar Lake, June 19, 1892, Hart & Shiga, 8 N; Fourth Lake, June 16–20, 1892, Hart & Shiga, 14 N; Sand Lake, June 15, 1892, Hart & Shiga, 2 N. WICHERT: June 9, 1948, Burks, Stannard, & Smith, 1 ♂.

25. *Ephemerella coxalis* McDunnough

Ephemerella coxalis McDunnough (1926:186; 1931*a*:37).

MALE.—Length of body and of fore wing 7–8 mm. Thorax and abdomen brown, with large, yellow markings; venter light yellow; wings and wing veins hyaline. Genitalia, fig. 144, quite similar to those of *lutulenta*, with minor differences in details of structure of peritreme opening.

NYMPH.—Head with small occipital tubercles. Thorax without dorsal tubercles; each tarsal claw with six to nine denticles. Abdominal tergites 1–7 bearing two rows of relatively large, submedian tubercles, fig. 159, these two rows diverging posteriorly, caudal filaments with long setae in apical regions.

Known from Georgia, Indiana, North Carolina, Ontario, and Quebec.

26. *Ephemerella simplex* McDunnough

? *Ephemerella unicornis* Needham (1905:45).
Ephemerella simplex McDunnough (1925*c*:41; 1931*d*:208).

MALE.—Length of body and of fore wing 6–7 mm. Head dark brown to black, base of each antennal scape surrounded by a yellowish ring; antennae dark brown; eyes deep red-brown. Thoracic dorsum dark brown to black, with minute, light red-brown markings at sutures; thoracic venter vaguely marked with light brown; fore leg black, fading to gray-yellow toward apex of tarsus; middle and hind legs yellow, coxae brown, apexes of tibiae and tarsal segments shaded with faint brown; all wings hyaline, veins stained with brown, those near costal margin of fore wing darker. Abdominal tergites very dark brown, apical tergites vaguely marked with yellow-brown spots; sternum chiefly dark yellow-brown, slightly lighter on sternites 7 and 8; sternite 9 dark brown to black; genitalia, fig. 146, dark smoky brown; caudal filaments uniformly gray-tan, articulations not darker.

FEMALE.—Length of body 5–7 mm., of fore wing 7–8 mm. In general, same color as male, but with vertex of head and areas of thoracic pleura at wing bases stained with deep yellow or red and thoracic venter with large, dark yellow areas; all legs dusky yellow, with coxae mostly dark brown; wings hyaline, veins near costal margin of each fore wing stained faintly yellow, other veins hyaline; caudal filaments very light yellow, with basal articulations red-brown.

NYMPH.—Length of body 6–8 mm., of caudal filaments 4–6 mm. Body and appendages extremely broad, flat, and hairy.

General color tan to brown, often with vague, dark brown marks on abdominal dorsum. Caudal filaments with two or three narrow, brown crossbands near base.

Head, thorax, and abdomen without dorsal tubercles or spines; maxillary palps well developed; tarsal claws without denticles; posterolateral angles of abdominal segments 4–9 produced, spinelike, fig. 162; platelike gills borne by abdominal segment 4 only partly covering more caudal pairs of gills; caudal filaments bearing short, sparse setae throughout.

Known from Illinois, New Brunswick, New York, North Carolina, Ontario, Quebec, and Tennessee. Develops in fairly rapid, moderate-sized rivers.

Illinois Record.—ROCKTON: Rock River, June 25, 1947, B. D. Burks, 5♂, 7♀.

27. *Ephemerella lita* Burks

Ephemerella lita Burks (1949:235).

Adult unknown.

NYMPH.—Length of body 8 mm., of caudal filaments 5.5 mm. General color light tan, with a few small, brown markings; caudal filaments each with a single, narrow, brown crossband near base.

Head and body flat, conspicuously hairy, without dorsal spines or tubercles; head semiquadrate, with clypeo-genal margin beneath each antennal base slightly incised; maxillary palps well developed; tarsal claws without denticles; posterolateral angles of abdominal segments 2–9 produced, spinelike; platelike gills of abdominal segment 4 semioperculate, only partly covering more caudal pairs of gills, fig. 163; caudal filaments bearing relatively few short setae at each articulation, these setae slightly longer in apical area than in basal area of filaments.

Known from Illinois. Taken in small or moderate-sized, fairly rapid rivers.

Illinois Records.—DIXON: Rock River, May 21–22, 1925, D. H. Thompson, 5 N. OAKWOOD: Salt Fork River, May 22, 1928, T. H. Frison, 1 N. ROCKFORD: Rock River, June 2, 1927, D. H. Thompson, 1 N.

28. *Ephemerella bicolor* Clemens

Ephemerella bicolor Clemens (1913:336).

MALE.—Length of body and of fore wing 5–6 mm. Thorax red-brown, abdominal tergites a lighter red-brown, and venter yellow; wings and veins hyaline. Genitalia, fig. 142, with penis lobes enlarged near apexes.

NYMPH.—Head in male lacking occipital tubercles, fig. 151, but in female having very small ones, fig. 152. Each tarsal claw with 8 to 12 denticles. Abdomen with two rows of dorsal, submedian tubercles diverging toward rear, with pair on tergite 5 conspicuously more widely spaced than on anterior tergites; caudal filaments each with long setae in apical area.

Known from Indiana, New Brunswick, New York, Nova Scotia, Ontario, and Quebec.

29. *Ephemerella verisimilis* McDunnough

Ephemerella virisimilis McDunnough (1930:57; 1931*a*:65).

MALE.—Length of body and of fore wing 7–8 mm. Thorax and abdominal tergum dark brown; abdominal venter dark yellow-brown. Wings and veins hyaline. Genitalia, fig. 147, with penis lobes slightly enlarged near apexes.

NYMPH.—Head with well-developed occipital tubercles. Tarsal claws each bearing 9 to 12 denticles. Abdomen with two rows of dorsal, submedian tubercles which diverge gradually toward rear; caudal filaments with long, dense setae in apical areas.

Known from Maine, New Brunswick, Ontario, and Quebec.

30. *Ephemerella minimella* McDunnough

Ephemerella minimella McDunnough (1931*a*:63).

MALE.—Length of body and of fore wing 6 mm. Thorax and basal abdominal tergites mostly very dark brown, with apical two abdominal tergites lighter brown; sternum tan, gradually fading to white on apical two abdominal sternites. Genitalia, fig. 150: penis lobes with a rounded, preapical enlargement on either side, inner peritreme angles acute, and second forceps segment relatively straight.

NYMPH.—Occipital tubercles wanting in male and vestigial in female; dorsal, submedian abdominal spines forming two rows evenly diverging posteriorly; caudal filaments each with long setae in apical region.

Known from Quebec.

31. *Ephemerella funeralis* McDunnough

Ephemerella funeralis McDunnough (1925*a*: 210; 1931*a*: 39).

MALE.—Length of body and of fore wing 6–8 mm. Thorax and abdominal tergites generally red-brown, with sternites lighter red-brown. Wings hyaline, with all veins faintly yellow, and those veins near costal margin of deeper hue. Genitalia, fig. 148: lateral margins of penis lobes nearly straight and parallel near tips, inner peritreme angles acute; second forceps segment almost straight.

NYMPH.—Small occipital tubercles present. Each tarsal claw with 7 to 10 denticles. Abdomen with two rows of dorsal, submedian tubercles diverging posteriorly; caudal filaments with long, dense setae in apical areas.

Known from Georgia, Indiana, New York, Ohio, Ontario, Quebec, South Carolina, Virginia, and West Virginia.

32. *Ephemerella aestiva* McDunnough

Ephemerella aestiva McDunnough (1931*a*: 64).

MALE.—Length of body and of fore wing 6–7 mm. Thorax and abdominal tergites generally very dark brown; basal and apical abdominal sternites shaded with light brown, with median ones white. Genitalia, fig. 149: penis lobes each with lateral margin near apex nearly straight and parallel, inner peritreme angle blunt; second forceps segment relatively straight.

NYMPH.—Head with occipital tubercles. Abdomen with two almost parallel rows of dorsal, submedian spines; caudal filaments bearing long setae in apical regions.

Known from Quebec.

33. *Ephemerella attenuata* McDunnough

Ephemerella attenuata McDunnough (1925*c*: 42; 1931*d*: 209).

MALE.—Length of body and of fore wing 6 mm. Thorax and basal abdominal tergites very dark brown, apical tergites lighter brown; basal sternites light brown, apical three sternites almost white; wings and veins hyaline. Genitalia, fig. 125, distinct from those of all other North American species: penis lobes fused almost to tips and with a subapical, angulate projection on either side; second forceps segment slightly bowed, and third six times as long as broad.

NYMPH.—Occipital, thoracic, and dorsal abdominal tubercles present; each tarsal claw with 8 to 10 denticles; first pair of platelike gills semioperculate, as in fig. 162; caudal filaments bearing long setae in apical regions.

Known from Maryland, Ontario, and Quebec.

BAETISCIDAE

This family includes only the genus *Baetisca*, which was placed in the subfamily Baetiscinae of the family Baetidae by Traver (1935*a*: 555) and in the family Baetiscidae of the superfamily Heptagenioidea by Ulmer (1933: 209). Whereas I agree with Ulmer that *Baetisca* represents a group sufficiently distinct to be properly considered a family rather than a subfamily, I do not agree that it has heptageniid affinities. The wing venation and the number of clearly differentiated segments in the hind tarsus in the adults plainly show that this group has no near affinities with the heptageniid type. It is one of the mayflies, such as *Prosopistoma*, which has no known, closely related forms in the Recent fauna.

14. *BAETISCA* Walsh

Baetisca Walsh (1862: 378).

The compound eyes in the adult males of *Baetisca* are large, almost contiguous on the meson. The eyes project posteriorly so as almost completely to cover the pronotum. Each of these eyes is composed of a ventral portion made up of small facets and a much larger dorsal portion of large facets. The division between these two portions is not clearly marked, although in life the lower portion is slightly darker than the upper. The compound eyes in the females are widely separated, and each eye, in life, has a vertical, anterior, colored stripe near the mesal margin. In the males, the fore leg is about as long as the body; the five-segmented fore tarsus is more than twice as long as the fore tibia, and the fore tibia and fore femur are nearly equal in length. In adults of both sexes, a pair of slender and acutely pointed prosternal projections arise between the fore coxae. Each of the middle and hind tarsi in the males and each tarsus in the females has four clearly differentiated segments. The thorax is quite thickset.

The wings of some adults are washed with red or orange, but those of most are hyaline. In the fore wing, there are quite numerous, weak crossveins, fig. 30, numerous, short marginal intercalaries, and the outer wing margin is always slightly scalloped. The median intercalary vein and M_2 extend almost to the wing base. There are no cubital intercalaries. Vein 1A extends to the outer wing margin, and a series of irregular, weak intercalary veins extends from 1A to the anal wing margin. The hind wing is almost circular in outline, fig. 176, has a broad costal projection near the wing base, and numerous weak crossveins and numerous marginal intercalaries; vein M is forked near the center of the wing.

The abdomen is stocky in the basal half, but the segments are markedly more slender and elongate from the sixth segment posteriorly. The male genitalia, fig. 174, very similar throughout the genus, are composed of a pair of three-segmented forceps and a pair of subconical penis lobes which are fused on the median line almost to the tips. The apical margin of the terminal abdominal segment in the females has a pair of submedian, triangular projections with a V-shaped notch on the meson between them. The median caudal filament is vestigial in both the male and female adults.

In the subimagoes, the wings are heavily shaded with dark brown or black; white spots surround the crossveins and often two vague, white bands extend obliquely across each wing.

The nymphs, the first one of which was described by Walsh (1864), are among the most unique and distinct of all mayfly naiads, fig. 181. In these nymphs, the integument is more heavily armored than in any other Nearctic species. The head is small and hypognathous; a pair of small frontal horns is usually present between the bases of the antennae; and the genae are produced above the bases of the mandibles as a pair of spines or small, flat ledges. These projections of the head vary in size and shape among the different species. The distal margins of the labium and labrum meet to close completely the mouth opening anteriorly; the buccal cavity is closed laterally by the mandibles. The labial and maxillary palps each have three segments; the second segment of the labial palp has an apicolateral projection which forms, with the third seg-

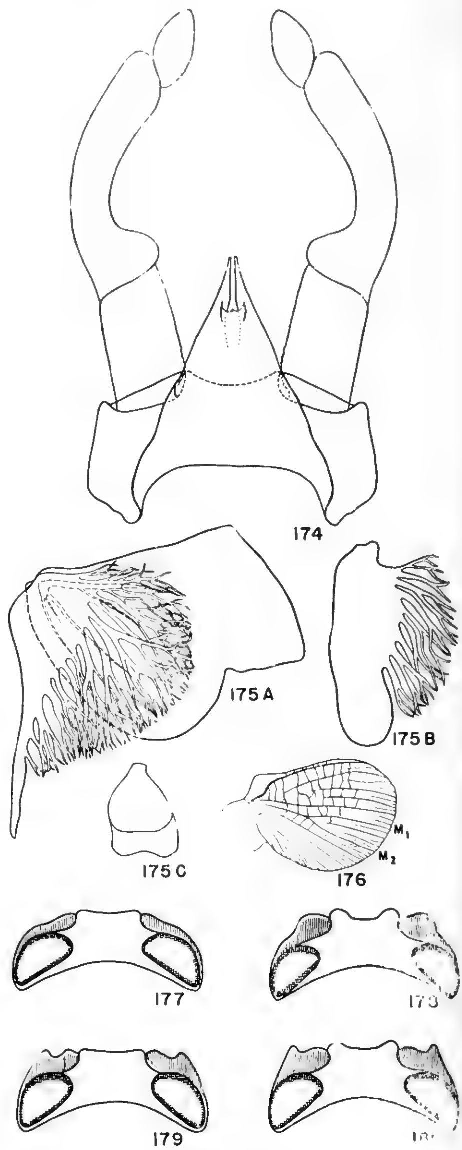


Fig. 174.—*Baetisca obesa,* male genitalia.
Fig. 175*A*.—*Baetisca bajkovi,* gill of first abdominal segment.
Fig. 175*B*.—*Baetisca bajkovi,* gill of fourth abdominal segment.
Fig. 175*C*.—*Baetisca bajkovi,* gill of sixth abdominal segment.
Fig. 176.—*Baetisca obesa,* hind wing.
Fig. 177.—*Baetisca lacustris,* head of mature nymph, dorsal aspect.
Fig. 178.—*Baetisca bajkovi,* head of mature nymph, dorsal aspect.
Fig. 179.—*Baetisca laurentina,* head of mature nymph, dorsal aspect.
Fig. 180.—*Baetisca obesa,* head of mature nymph, dorsal aspect.

ment, a forceps. Each mandible bears, at the apex, two long incisors, a large, tufted lacinia, and a broad, molar surface provided with numerous, lamellate teeth. The hypopharynx is large—about one-half as wide as the labrum—and has a pair of broad, thin parapsides.

The entire thoracic notum is fused and modified to form a carapace, which covers the thorax and the first five abdominal tergites, as well as the anterior part of the sixth abdominal tergite. The legs are relatively short and stout, with long, slender, edentate claws which are almost as long as the tibiae. Each of the abdominal segments 1–6 bears a pair of platelike, fissured gills, fig. 175. These gills normally are completely concealed by the thoracic carapace. Abdominal tergite 6 has a median, truncated, pyramidal lamina against which the apex of the carapace fits. Each of abdominal segments 6–9 has a pair of blunt, posterolateral projections. Tergite 9 has also a median dorsal spine on the posterior margin. Tergite 10 has a median notch on the posterior margin; this tergite is completely surrounded posteriorly and laterally by the incised ninth tergite. Sternite 9 is produced posteriorly and has a median notch on the posterior margin in both males and females. There are three relatively short caudal filaments, each of which bears a dense fringe of setae on both the inner and outer margins.

Baetisca was revised by Traver (1931*c*: 45), and the nymphs were keyed out by McDunnough (1932*b*: 213). Both nymphs and adults were again treated by Traver (1935*a*: 558), and, since the appearance of Traver's and McDunnough's comprehensive papers, three additional Nearctic species have been described, viz., *bajkovi* Neave, *rogersi* Berner, and *thomsenae* Traver.

Specific characters for the females of this genus have not yet been found.

KEY TO SPECIES

Adult Males

1. Wings partly or almost entirely washed with pink . . . . **1. rubescens**
   Wings hyaline 2
2. All longitudinal veins of fore wing brown; caudal filaments white, with articulations brown . . . . **2. laurentina**
   Longitudinal veins of fore wing posterior to R_1 hyaline; veins C, Sc, and R_1 lightly shaded with yellow, and bases stained with brown; caudal filaments usually entirely white, basal articulations sometimes brown 3
3. Abdominal venter almost completely shaded with brown . . . . **3. obesa**
   Abdominal venter white or very pale yellow 4
4. Middle abdominal tergites light brown; fore tibia white, shaded brown at apex; fore wing 10 mm. long . . . . . . **4. bajkovi**
   Middle abdominal tergites dark red-brown; entire fore tibia tan; fore wing 8 mm. long . . . . **5. lacustris**

Nymphs

1. Mesonotum with both lateral and dorsal spines 2
   Mesonotum with lateral spines only, as in fig. 181 3
2. Frontal tubercles of head reduced, virtually wanting, fig. 179 . . . . **2. laurentina**
   Frontal tubercles of head relatively well developed, fig. 180 . . . . **3. obesa**
3. Frontal projections of head reduced; genal shelf small, fig. 177 . . . . **5. lacustris**
   Frontal projections of head relatively well developed; genal shelf well developed, fig. 178 . . . . **4. bajkovi**

1. *Baetisca rubescens* (Provancher)

Cloe unicolor Provancher (1876: 267), not Hagen. Misidentification.
Cloe rubescens Provancher (1878: 127, 144). New name.

MALE.—Length of fore wing 8–9 mm. Base and costal area of fore wing and most of hind wing flushed with a pink stain; thoracic notum dark red-brown, abdominal tergites red-brown, and abdominal sternites lighter reddish or yellowish brown; genital forceps and caudal filaments white or pale yellow.

The nymph is unknown.

The species is known from Quebec.

2. *Baetisca laurentina* McDunnough

Baetisca laurentina McDunnough (1932*b*: 214).

MALE.—Length of fore wing 9–10 mm. Compound eyes in life yellow in upper portion, darker yellow, with brown flecks, in lower portion; head and antennae yellow-brown. Mesonotum dark chestnut brown, darker brown at apex of scutellum; mesopleura light brown, sternum dark brown. All legs yellow-brown, with each fore leg slightly darker than others; wings hyaline, with all longitudinal veins of fore wing light brown and crossveins hyaline. Abdominal tergites dark brown; sternites light brown to almost white; genital forceps tan or red-brown; caudal filaments light yellow or tan, articulations dark brown.

Nymph.—Length of body 8–10 mm. Frontal tubercles of head virtually wanting, only faintly indicated; each gena slightly produced above base of mandible as a small, subtriangular shelf, fig. 179; dorsal and lateral spines of mesonotal shield long and relatively slender; mesonotal shield relatively long and slender, with a maximum width, not including lateral spines, two-thirds as great as maximum length.

Known from Illinois, Michigan, New Brunswick, Ontario, and Quebec. Develops in cool, fairly rapid streams.

Illinois Record.—Aroma Park: Kankakee River, June 4, 1947, B. D. Burks, 1 ♂.

3. *Baetisca obesa* (Say)

Baetis obesa Say (1839:43).

Male.—Length of fore wing 9–11 mm. Compound eyes tan, lower portion slightly darker; head and antennae yellow-brown. Mesonotum red-brown, darker at apex of scutellum; thoracic pleura yellow-brown; sternum yellow-brown, becoming lighter toward posterior margin. Each fore leg light yellow, apex of femur, of tibia, and of each tarsal segment darkened with yellow-brown; middle and hind legs almost white, brown shading at apex of each tarsal segment; wings hyaline, veins C, Sc, and R_1 of fore wing brown-shaded at bases, light yellow distad. Abdominal tergites dark brown, becoming chestnut brown on posterior tergites; sternum light brown, slightly darker on apical three sternites; genital forceps, fig. 174, and caudal filaments usually white or very faintly stained with tan; basal articulations of caudal filaments sometimes brown.

Nymph.—Length of body 8–10 mm. Frontal tubercles of head well developed, projecting as a pair of rounded protuberances; each gena produced above base of mandible as a triangular ledge, fig. 180; dorsal and lateral spines on mesonotal shield relatively short and stout; mesonotal shield relatively long and slender, with a maximum width, not including lateral spines, two-thirds as great as maximum length.

Known from Illinois, Indiana, Manitoba, Michigan, New Hampshire, New York, and Wisconsin. Develops in cool, fairly rapid streams.

Illinois Records.—Havana: Illinois River, April 18, 1894, C. A. Hart, 1 N. Momence: Kankakee River, June 1, 1937, B. D. Burks, 1 ♂. Richmond: at light, June 4, 1938, Ross & Burks, 1 ♂. Rock Island: 20 ♂, 14 ♀ (Walsh, 1862:378).

4. *Baetisca bajkovi* Neave

Baetisca bajkovi Neave (1934:166). Description of nymph.
Baetisca bajkovi Neave. Daggy (1945:388). Description of adult ♂.

This species differs from *lacustris* only by minor and possibly intergrading characters both in the nymph and the adult. It may, thus, eventually be necessary to place *bajkovi* as a synonym of *lacustris*. Until actual intergrades have been found, it is best, however, to continue to separate the two. All specimens referred at present to *bajkovi* came from streams, while *lacustris* has been reported as having come only from lakes.

Male.—Length of fore wing 10 mm. Compound eyes yellowish tan, with lower portion of each slightly darker; head and

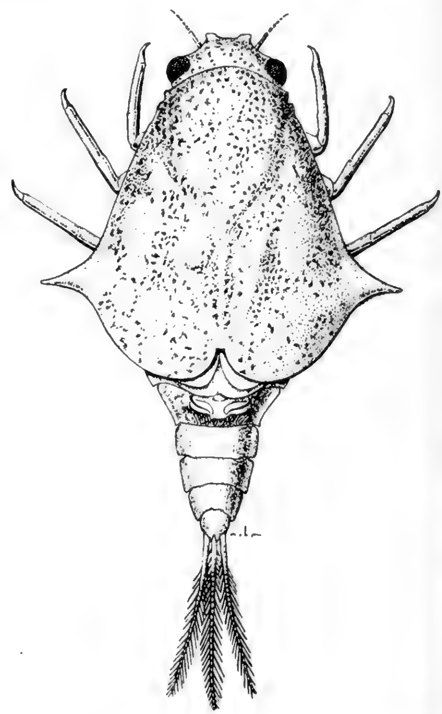


Fig. 181.—*Baetisca bajkovi*, mature nymph, dorsal aspect.

antennae tan. Mesonotum brown, shaded with darker brown at apex of scutellum; thoracic pleura light brown; sternum tan, becoming white on metasternum. Each fore leg white, with faint brown shading at apexes of femur, tibia, and tarsal segments; middle and hind legs white, each with faint brown shading at apexes of tarsal segments; wings hyaline, veins C, Sc, and R_1 brown at bases, light yellow distad. Abdominal tergum chestnut brown, the sternum white; the genital forceps and the caudal filaments white.

NYMPH.—Length of body 7–9 mm. Frontal tubercles of head projecting as a pair of rounded protuberances; each gena produced above base of mandible as a broad, somewhat rounded ledge, fig. 178; long, relatively stout, lateral spines present on mesonotal shield, fig. 181; dorsal mesonotal spines wanting; maximum width of mesonotal shield, not including lateral spines, three-fourths to four-fifths as great as maximum length of shield.

Known from Illinois, Indiana, Manitoba, and Minnesota. Develops in fairly rapid creeks and moderate-sized rivers. The early instar nymphs occur in the swift current, while the late instar nymphs migrate to the comparatively still eddies along the banks.

Illinois Records.—BYRON: Rock River, May 20, 1927, 1 N. DIXON: Rock River, May 22, 1925, D. H. Thompson, 6 N. EAST DUBUQUE: Mississippi River, May 9, 1941, Mohr & Burks, 1 N. GOLCONDA: Big Grand Pierre Creek, May 13, 1932, Frison & Ross, 3 N. HAVANA: Spoon River, April 22, 1898, C. A. Hart, 1 N; White Oak Creek, June 8, 1940, Ross, Riegel, & Burks, 4 N. KANKAKEE: Kankakee River, May 22, 1912, 1 N. MOMENCE: Kankakee River, May 16, 1940, B. D. Burks, 2 N; May 21, 1940, Mohr & Burks, 2 N; June 1, 1940, B. D. Burks, 1 ♂, 1 N. OAKWOOD: Salt Fork River, April 18, 1948, Burks & Stannard, 2 N. OREGON: Rock River, May 25, 1927, D. H. Thompson, 2 N. PECATONICA: Pecatonica River, June 3, 1926, D. H. Thompson, 1 N; May 31, 1927, D. H. Thompson, 2 N. PROPHETSTOWN: Rock River, May 4, 1940, B. D. Burks, 1 N. QUINCY: May 17, 1940, Mohr & Burks, 1 N. ROCK ISLAND: Rock River, April 18, 1931, T. H. Frison, 1 N. ST. JOSEPH: Salt Fork River, June 11, 1940, Thompson & Burks, 19 N.

5. *Baetisca lacustris* McDunnough

Baetisca lacustris McDunnough (1932*b*: 214).

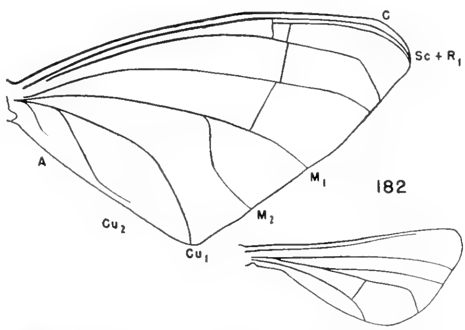
MALE.—Length of fore wing 8 mm. Wings entirely hyaline, with veins C, Sc, and R_1 of fore wing only very faintly tinged with yellow; thoracic notum chestnut brown; abdominal tergites red-brown; sternites white or very pale yellow; genital forceps pale yellow; caudal filaments white.

NYMPH.—Frontal tubercles of head greatly reduced and genae with small, shelf-like projections, fig. 177; mesonotal shield with long and sharp lateral spines; dorsal mesonotal spines wanting.

Known from Manitoba, Ohio, and Ontario.

OLIGONEURIIDAE

The inclusion here of this family is necessitated by the occurrence in Illinois and Indiana of a curious nymph, fig. 184, which is certainly referable to the Oligoneuriidae. A remarkable adult, also belonging to this family, but not congeneric with our nymph, has been taken in Saskatchewan and Utah.



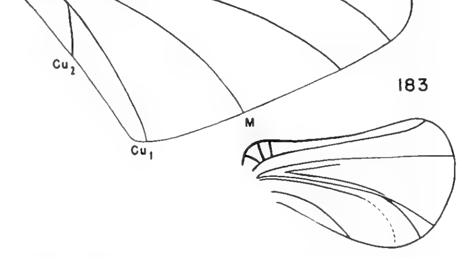


Fig. 182. — *Lachlania saskatchewanensis*, wings. (After Ide.)
Fig. 183. — *Oligoneuria anomala*, wings. (After Eaton.)

In Ulmer's classification (1933: 207), the family Oligoneuriidae includes seven genera, all, up to quite recently, considered to be Palearctic, Neotropical, or Ethiopian in distribution. The members of this family, in the imago stage, are characterized by having the fore wing with vein Sc absent or fused with R, the number of longitudinal veins ranging from four to seven, and the few remaining crossveins restricted to the anterior two to five interspaces; the hind wing has no crossveins, or, at most, very few crossveins, all restricted to the anterior part of the wing. The median caudal filament may be well developed or vestigial. In the nymphs of the Oligoneuriidae, the fore femur and fore tibia have each a dense fringe of long setae on the inner side; the gills of the first abdominal segment are large and situated on the venter, the gills of the following six segments are small, flat, and slender, and are dorsal in position. Each cercus bears a fringe of long setae on the mesal side only; the median caudal filament is either well developed or vestigial.

15. *OLIGONEURIA* Pictet

Oligoneuria Pictet (1845:290, pl. 47).

In the fore wing of the known adults of this genus, vein M is unbranched, veins Cu_1 and Cu_2 diverge near the center, and Rs diverges from R near the base of the wing, fig. 183. The median caudal filament is well developed.

Oligoneuria ammophila Spieth

Oligoneuria ammophila Spieth (1937: 139; 1938*a*: 1).

This species is known only from the nymph. It may be that, when the adult is found, the generic assignment will have to be changed. A complete description of the nymph is given by Spieth (1937:139).

Length of mature specimens 10–12 mm. This nymph, fig. 184, bears gill tufts on the maxillae. All the abdominal gills are single: each gill of pair on segment 1, fig. 184, large, finely dissected, and located on the ventral side in such a position as to project anteriorly between the hind coxae; gills of segments 2–7 small, simple, obovate, with acute apexes, and dorsal in position.

The nymph of *ammophila* holds its legs in a most unusual position: normally, the fore legs are held close to the mouth opening, beneath the head; the middle legs extend almost straight posteriorly, beneath the thorax and basal abdominal segments; the hind legs extend laterally from the metathorax, at right angles to the longitudinal axis of the body. In this position, the middle legs extend much farther posteriorly than do the hind legs. Such an arrangement of the legs probably fits the nymph to maintain its footing in the rather loose sands in which it has been found to live. As is shown in fig. 184, only parts of the coxae and trochanters of the middle legs are visible from the dorsal aspect.

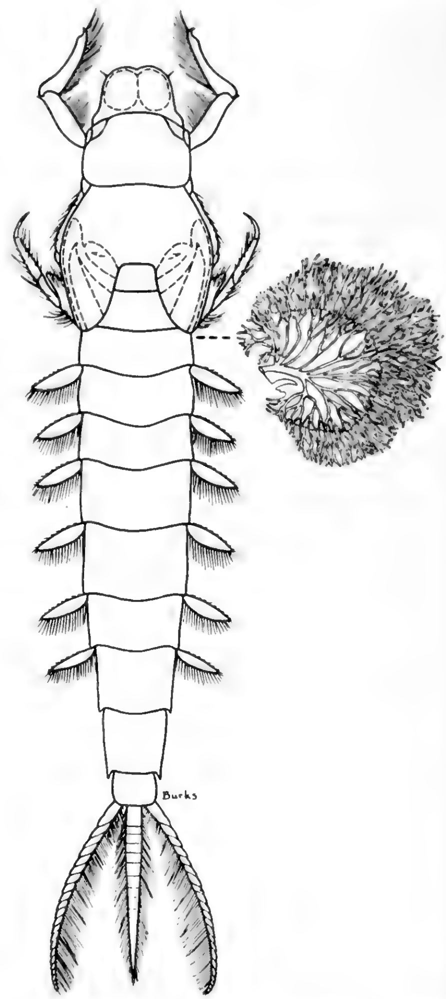


Fig. 184.—*Oligoneuria ammophila*, nymph, dorsal aspect. Small figure at right shows detail of gill of first abdominal segment, borne on venter.

Known from Illinois and Indiana. Lives in shallow, rapid streams with sandy bottoms.

Illinois Records. — HILLSDALE: Rock River at mouth of Canoe Creek, dredging sandy bottom 15 yards from bank, July 30, 1925, R. E. Richardson, 1 ♂ N; Rock River at foot of Lephardt's Island, dredging clean sandy bottom 15 yards from bank, July 30, 1925, R. E. Richardson, 1 ♂ N.

16. *LACHLANIA* Hagen

Lachlania Hagen (1868:372).

This genus is represented in North America only by *saskatchewanensis* Ide (1941: 154), described from a single adult female. Nymphs and adults of *Lachlania* sp. are recorded by Edmunds (1948*b*:43) as occurring in Utah.

In *Lachlania* adults, the fore wing, fig. 182, has only three or four crossveins; vein M branches a little beyond mid-length, and veins Cu_1 and Cu_2 fork close to the wing base. The legs are greatly atrophied and probably nonfunctional. The median caudal filament is vestigial.

LEPTOPHLEBIIDAE

This family corresponds exactly to the subfamily Leptophlebiinae of the family Baetidae in Traver's classification (1935*a*: 504), and to the family Leptophlebiidae of Ulmer's classification (1933:201).

In this family, each compound eye in the adult males is composed of a large upper portion of comparatively large facets, and a small lower portion of smaller and darker-colored facets. These two portions of the eye are distinctly separated, but the upper portion is not set on a well-developed stalk, as in the Baetinae, figs. 255–257. The compound eye in the females is of the same size as the lower portion of the eye in the males. The fore tarsus in the males has five segments; all tarsi in the females and the middle and hind tarsi in the males have four clearly differentiated segments. In all Nearctic genera, the two claws borne by each tarsus are dissimilar, with one claw hooked and one claw lobed.

In all Nearctic genera of Leptophlebiidae, the adults have two pairs of wings; in some exotic leptophlebiids, the adults lack hind wings. The fore wings in Nearctic forms have numerous crossveins, figs. 185–192, and all the principal longitudinal veins are preserved complete, except that the basal part of vein M_2 is obsolete in some genera. Vein R_5 often is sharply bent posteriorly near its base, that is, close to its point of divergence from R_4, as in figs. 185–187. Veins Cu_1 and Cu_2 are separated at their bases; Cu_1 is straight, but Cu_2 at about mid-length is sharply bent toward the anal wing margin. There are two or four cubital intercalary veins. The hind wing may or may not have a costal projection. There is considerable variation within this family in the venation of the hind wing.

The male genitalia are composed of a pair of elongate penis lobes, which are partly or completely fused on the mesal margins, and a pair of four-segmented forceps. The basal segment of each arm of the forceps is often almost completely fused with the second segment; the second segment is elongate and straight; the third and fourth segments are small and semiquadrate or triangular. The terminal abdominal sternite in the females usually has a median cleft or indentation on the posterior margin. There are always three well-developed caudal filaments; the median one may be somewhat shorter and more slender than the cerci.

The nymphs, figs. 199, 212, are typically slender and somewhat flattened forms. They commonly inhabit still water or water with reduced current, such as that in eddies along banks of streams or rivers. The tarsal claws have minute, ventral denticles. Abdominal segments 1–7 bear gills; these gills are slender-lamelliform to filamentous, figs. 193–196. The nymphs always have three long caudal filaments, all of which have relatively inconspicuous setae uniformly distributed over the filaments.

KEY TO GENERA

ADULTS

1. Hind wing without a costal angulation, and with costal margin slightly concave near mid-length, figs. 185–187 2
   Hind wing with a well-marked costal angulation, figs. 188–192 3
2. Fore wing with Cu_1 and Cu_2 closer together than Cu_1 and M in subbasal region where these veins are subparallel, figs. 185, 186 .... **17. Leptophlebia**
   Fore wing with Cu_1 and Cu_2 separated in subbasal region by a space equal to that separating Cu_1 and M, fig. 187 ... . **18. Paraleptophlebia**

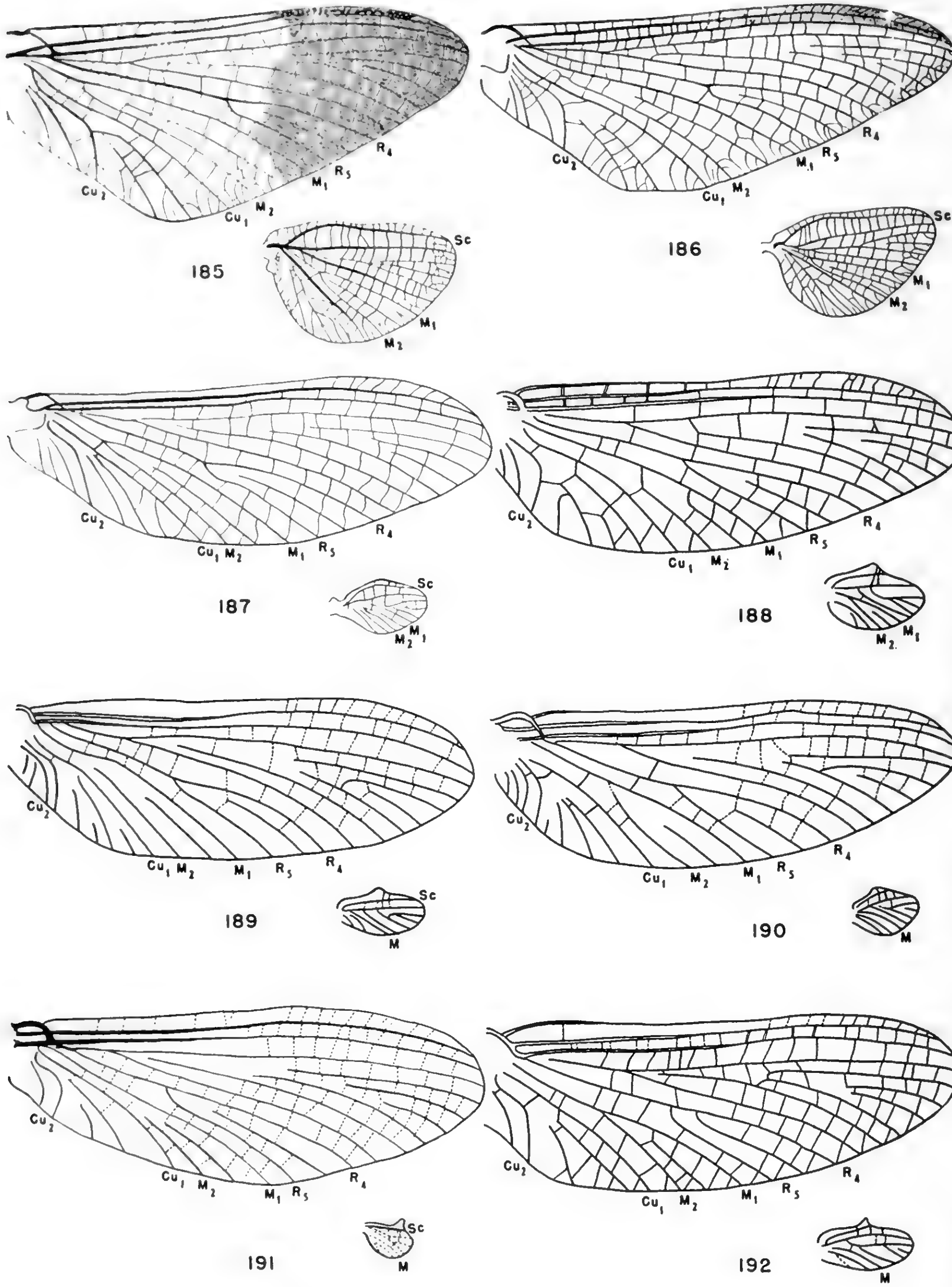
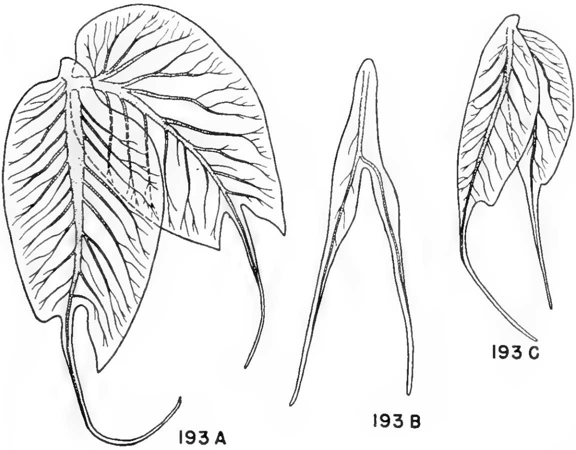


Fig. 185.—*Leptophlebia nebulosa,* wings.
Fig. 186.—*Leptophlebia cupida,* wings.
Fig. 187.—*Paraleptophlebia praepedita,* wings.
Fig. 188.—*Thraulodes speciosus,* wings. (After Traver.)
Fig. 189.—*Habrophlebia vibrans,* wings. (After Traver.)
Fig. 190.—*Choroterpes basalis,* wings. (After Traver.)
Fig. 191.—*Habrophlebiodes americana,* wings. (After Traver.)
Fig. 192.—*Traverella presidiana,* wings. (After Traver.)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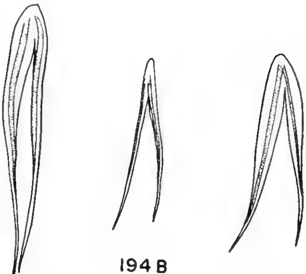
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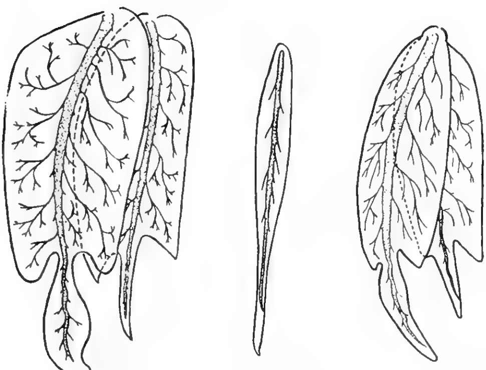
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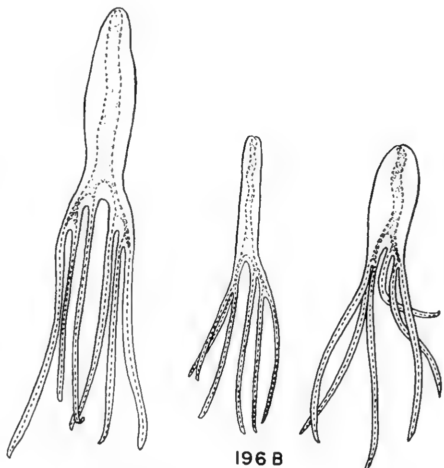
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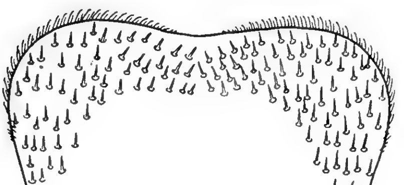
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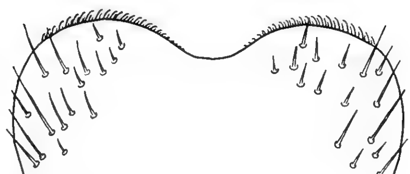
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Fig. 193*A*.—*Leptophlebia* sp., gill of fifth abdominal segment.
Fig. 193*B*.—*Leptophlebia* sp., gill of first abdominal segment.
Fig. 193*C*.—*Leptophlebia* sp., gill of seventh abdominal segment.
Fig. 194*A*.—*Paraleptophlebia praepedita*, gill of fifth abdominal segment.
Fig. 194*B*.—*Paraleptophlebia praepedita*, gill of first abdominal segment.
Fig. 194*C*.—*Paraleptophlebia praepedita*, gill of seventh abdominal segment.
Fig. 195*A*.—*Choroterpes basalis*, gill of fifth abdominal segment.
Fig. 195*B*.—*Choroterpes basalis*, gill of first abdominal segment.
Fig. 195*C*.—*Choroterpes basalis*, gill of seventh abdominal segment.
Fig. 196*A*.—*Habrophlebia vibrans*, gill of fifth abdominal segment.
Fig. 196*B*.—*Habrophlebia vibrans*, gill of first abdominal segment.
Fig. 196*C*.—*Habrophlebia vibrans*, gill of seventh abdominal segment.
Fig. 197.—*Paraleptophlebia praepedita*, nymphal labrum, dorsal aspect.
Fig. 198.—*Habrophlebiodes americana*, nymphal labrum, dorsal aspect.

3. Vein M of hind wing forked, fig. 188. . . . . **19. Thraulodes**
Vein M of hind wing simple, figs. 189–192 4
4. Vein Sc of hind wing extending nearly or quite to apex of wing, fig. 189. . . . . **20. Habrophlebia**
Vein Sc of hind wing ending near costal angulation, figs. 190–192. 5
5. Costal angulation of hind wing small, rounded at apex, fig. 190; penis lobes simple, without appendages, fig. 214. . . . . **21. Choroterpes**
Costal angulation of hind wing prominent, almost or quite acute at apex, figs. 191, 192; penis lobes bearing decurrent appendages, figs. 215, 216. 6
6. Male forceps base divided into two triangular lobes; decurrent appendages of penis lobes projecting anterolaterally, fig. 215; costal projection of hind wing finger-like, stubby at apex, fig. 191. . . . . **22. Habrophlebiodes**
Male forceps base entire, not divided into triangular lobes; decurrent appendages of penis lobes projecting toward meson, and a pair of slender appendages arising from forceps base, fig. 216; costal angulation of hind wing acutely pointed at apex, fig. 192. . . . . . . **23. Traverella**

Mature Nymphs

1. Gills of first abdominal segment similar in type to gills borne by more posterior segments, as in figs. 194, 196. 2
Gills of first abdominal segment of a different type from gills borne by more posterior segments, as in figs. 193, 195; each gill of first pair filamentous, each gill of following pairs double and lamellate. 6
2. Abdominal segments 2–9 with posterolateral spines. . . . . **19. Thraulodes**
Abdominal segments 8 and 9 only bearing posterolateral spines. 3
3. Each abdominal gill lamelliform, the margins of each finely dissected to form numerous, long filaments; gills on segments 1–5 bilamellate; gills becoming progressively smaller from anterior to posterior abdominal segments. . . . . **23. Traverella**
Each abdominal gill not lamelliform, the margins not finely dissected. 4
4. Gills on abdominal segments 2–7 each consisting of two clusters of slender filaments borne on a single, narrow stalk, fig. 196. . . . . . **20. Habrophlebia**
Gills on abdominal segments 2–7 bifid to bases, each part a very slender lamella, fig. 194. 5
5. Apical margin of labrum only slightly indented on meson, fig. 197. . . . . **18. Paraleptophlebia**
Apical margin of labrum deeply indented on meson, fig. 198. . . . . **22. Habrophlebiodes**
6. Each gill of pair borne by first abdominal segment a single filament; apical extensions of gills on segments 2–7 somewhat spatulate at apexes, fig. 195. . . . . **21. Choroterpes**
Each gill of pair borne by first abdominal segment bifid at apex; apical extensions of gills on segments 2–7 slender, acute at apexes, fig. 193. . . . . **12. Leptophlebia**

17. *LEPTOPHLEBIA* Westwood

Leptophlebia Westwood (1840:31).
Blasturus Eaton (1881:193).
Euphyurus Bengtsson (1917:177).

In accordance with the researches of Ide (1935*a*: 123), the American species formerly placed in *Blasturus* are now placed in *Leptophlebia.* It may be noted that Banks (1900: 245) published this synonymy much earlier.

The members of this genus are medium to large mayflies with predominantly dark yellow-brown bodies. The fore tarsus in the males varies from one to one and two-thirds times as long as the fore tibia. The wings, figs. 185, 196, are clear or partly stained with brown, and all veins and most crossveins are brown. In the fore wing, the posterior branch of the outer fork (vein R_5) is sharply bent posteriorly near the base, vein M_2 diverges from M_1 in the subbasal region, the basal costal crossveins are weak or wanting, and there are two long, cubital intercalary veins. The hind wing has no costal angulation, and vein M is forked near the base of the wing.

The male genitalia, fig. 200, are quite uniform in structure throughout the genus. The genital forceps arise from a medianly fissured base and have four or five segments, of which the apical two are minute. The penis lobes are fused on the meson at the bases only; each penis lobe bears a stout, mesal, decurrent appendage. The position of the apexes of these appendages determines whether they look like a "scarf" or a "hood"; actually the structure of these appendages is very similar throughout the genus. The terminal abdominal sternite in the females has a triangular, median notch on the posterior margin. The three caudal filaments may be equal in length and thickness or the median filament may be slightly shorter and weaker than the cerci.

The stout-bodied nymphs, fig. 199, are vigorous swimmers. The thorax and abdomen are slightly flattened on the dorsum, but the head is held almost in a hypognathous position. Each of the maxillary and labial

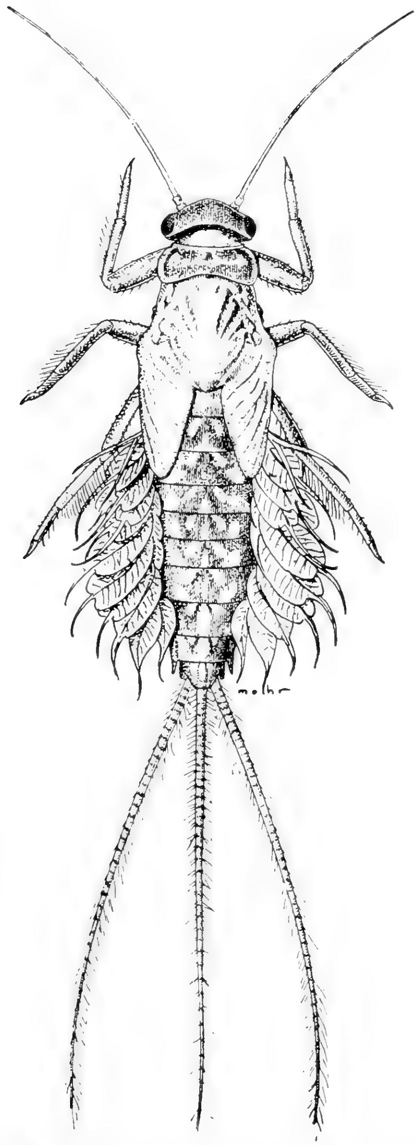


Fig. 199.—*Leptophlebia* sp., mature nymph, dorsal aspect.

palps has three segments. Each antenna is longer than the head and thorax combined. Each tarsal claw has two rows of ventral denticles, a long row from base to near the tip on the outer side, and another, shorter row near the tip on the inner side. Gills of the first abdominal segment are bifid and filamentous, fig. 193*B*; the gills on segments 2–7 are double and lamelliform, figs. 193*A* and *C*, each lamella having a terminal, filamentous extension. Each of the three caudal filaments is slightly longer than the head and body combined.

In this genus, specific characters for the females and nymphs have not yet been found.

KEY TO SPECIES

ADULT MALES

1. Abdominal tergites 2–7 white, with dark spiracular dots . . . . **1. johnsoni**
   Abdominal tergites 2–7 partly or almost completely covered by dark brown shading on a tan background 2
2. Fore wing with apical one-fourth to two-fifths shaded with brown, fig. 185; occasionally a spot at outer apical angle of wing hyaline . . . . **2. nebulosa**
   Fore wing completely hyaline except for faint, brown shading in stigmatic area, fig. 186 . . . . **3. cupida**

1. *Leptophlebia johnsoni* McDunnough

Leptophlebia johnsoni McDunnough (1924*c*: 73).
Blasturus gracilis Traver (1932*a*: 133).

MALE.—Length of body and of fore wing 8–9 mm. Head very dark, glossy brown, with eyes slightly lighter brown. Thorax dark brown to black on dorsum and light brown to tan on pleura and sternum; wings hyaline, with veins and most crossveins dark brown, and each fore wing with a light brown cloud covering stigmatic and outer apical areas. Abdominal segments 2–7 white, with dark brown, or black, spiracular dots and tan ganglionic marks; segments 8–10 dark brown; genital forceps white, penis lobes yellow; caudal filaments tan, with articulations dark brown.

Known from Connecticut, Massachusetts, New Hampshire, New York, North Carolina, Ontario, and Quebec.

2. *Leptophlebia nebulosa* (Walker)

Palingenia nebulosa Walker (1853: 554).
Potamanthus odonatus Walsh (1862: 372).

No authentic Walsh material of *odonatus* is known to be in existence, but the characters given in Walsh's original description of the species certainly indicate that *odonatus* is a synonym of *nebulosa*. When Spieth (1940: 327) examined the type of *nebulosa* in the British Museum, he found no reason to alter the concept of the species as currently identified.

MALE.—Length of body and of fore wing 10–12 mm. Head dark brown, eyes slightly lighter brown. Entire thorax very dark brown, almost black, each fore leg brown, middle and hind coxae brown, rest of middle and hind legs tan; wings hyaline, veins and most crossveins tan or brown, crossveins toward posterior margin in either wing often hyaline, stigmatic crossveins of each fore wing extremely numerous, anastomosed, a brown cloud covering outer, apical one-fourth to two-fifths of fore wing, fig. 185, but sometimes with extreme outer, apical angle hyaline, making wing appear to have a broad subapical, brown crossband. Dorsum of abdomen almost or entirely dark brown, sometimes becoming tan along lateral margins of tergites, and often with a pair of submesal, short, lunate, tan marks present at anterior margin of each tergite; sternites 1 and 2 light brown, sternites 3–8 tan or yellow with, sometimes, vague brown shading, sternites 8 and 9 brown; genitalia, fig. 200, with forceps tan and penes brown; caudal filaments brown, articulations darker brown.

FEMALE.—Length of body 10–12 mm., of fore wing 12–14 mm. Color much as in male, but somewhat lighter. Head with yellow shading on each side, near eyes. Thorax with yellow areas on pleura, with sternum mostly yellow-brown; wings without brown shading. Dorsum of abdomen as in male, sternum entirely tan or yellow-brown, apical two sternites always a little lighter than others; caudal filaments tan or light brown, articulations darker brown.

Known from northeastern and midwestern states and southeastern Canada. Develops in ponds or in the still eddies along the banks of streams.

Illinois Records.—CHESTERVILLE: April 15–May 1, 1936, Ross & Mohr, 9♂. DANVILLE: May 9, 1926, T. H. Frison, 1♂. GEORGETOWN: April 14, 1930, Frison & Ross, 4♂, 2♀. HAVANA: April 15, 1898, Hart, 1♂; April 18, 1894, Hart, 1♂; April 21, 1898, Hart, 1♂; April 22, 1898, Hart, 11♂, 7♀; April 24 & 25, 1898, Hart, 16♂, 10♀; April 28 & 29, 1898, Hart, 1♂, 2♀. HOMER: April 27, 1907, 1♂. MAHOMET: April 16, 1925, T. H. Frison, 4♂, 1♀; April 23, 1925, T. H. Frison, 12♂, 3♀. ST. JOSEPH: Salt Fork River, May 3, 1914, 1♂, 2♀. URBANA: April 25, 1949, J. E. Porter, 1♂. WATSON: April 15–May 5, 1936, Ross & Mohr, 10♂. WAUCONDA: April 30, 1942, Ross & Burks, 2♂, 1♀. WHITE HEATH: April 16, 1932, Ross & Riegel, 1♂; April 22, 1917, 1♂, 1♀; April 28, 1916, 1♂; Sangamon River, May 5, 1940, H. H. Ross, 2♂, 4♀; May 10, 1938, H. H. Ross, 1♂.

3. *Leptophlebia cupida* (Say)

Ephemera cupida Say (1823:163).
Ephemera hebes Walker (1853:538).
Palingenia concinna Walker (1853:553).
Palingenia pallipes Walker (1853:553).
Baetis ignava Hagen (1861:47).

MALE.—Length of body 9–11 mm., of fore wing 10–12 mm. Head very dark brown, almost black, eyes slightly lighter brown. Thorax uniformly very dark brown to black. Each fore leg dark brown, middle and hind legs slightly lighter brown; wings hyaline, with brown staining at bases and light brown shading in stigmatic area of each fore wing, fig. 186; stigmatic crossveins numerous, only slightly or not at all anastomosed. Dorsum of abdomen dark brown, with tan crossline at posterior margin and tan stripe along either lateral margin of each tergite, often a large, irregular, median, tan mark on each tergite; sternites 2–7 tan or very light brown, sternites 1, 8, and 9 washed with brown; genital forceps at base tan or yellow, becoming brown at apexes, penes brown; caudal filaments gray-brown, articulations darker brown.

FEMALE.—Length of body 9–11 mm., of fore wing 10–12 mm. Generally slightly lighter in color than the male. Head dark brown only between and posterior to ocelli, otherwise tan. Thorax dorsally dark brown, pleura marked with tan, sternum tan on meson; wings usually not darkened at bases, sometimes faintly so; each fore leg dark brown, middle and hind legs yellow-brown or tan. Dorsum of abdomen dark brown, each tergite yellow or tan at posterior and lateral margins, entire sternum yellow or tan; caudal filaments as in male.

Known from the northeastern and midwestern states and southeastern Canada. Develops in ponds or in the still eddies along the banks of streams.

Illinois Records.—HEROD: March 24, 1939, Ross & Burks, 1♂; April 4, 1948, 3♂; April 8–9, 1947, B. D. Burks, 2♂, 3♀. KICKAPOO STATE PARK: May 4, 1947, Ross & Stannard, 1♂. ROCK ISLAND: 11♂, 3♀ (Walsh 1862:372). RUDEMENT: Blackman Creek, April 7, 1947, B. D. Burks, 1♀.

URBANA: University Grounds, April 8, 1889, Marten, 5♂; April 15, 1898, Hart, 10♂. WATSON: April 9–24, 1936, Ross & Mohr, 19♂; April 11, 1932, Ross & Mohr, 2♂.

18. *PARALEPTOPHLEBIA* Lestage

Paraleptophlebia Lestage (1917:340); Ulmer (1920*a*:113, 116).

The genus *Paraleptophlebia* was originally distinguished from *Leptophlebia* in the nymphs only. Lestage's description of the genus appeared in a study of the nymphs of Palearctic mayflies. Ulmer (1920*c*:113; 1933:202), however, gave characteristics for the separation of the adults of the two genera. Traver (1934:189; 1935*a*:510) transferred most of the American species of *Leptophlebia* to *Paraleptophlebia*.

The adults of *Paraleptophlebia* are small, extremely frail mayflies. They have clear or faintly tinted wings and most of them have predominantly dark brown bodies; the males of some species have the middle abdominal segments mostly white. The fore wing, fig. 187, has the posterior branch of the outer fork (vein R_5) sharply bent posteriorly near the base, vein M_2 diverges from M_1 near the wing base, and the cubital intercalary veins are detached at their bases. The hind wing is broad and lacks a costal angulation, and vein M is forked near the base of the wing. The fore leg in the males has the tarsus one and one-half to two times as long as the fore tibia. The terminal abdominal sternite in the females is deeply cleft on the meson. The three caudal filaments are equal in length.

The male genitalia in *Paraleptophlebia*, figs. 201–211, consist of a pair of slender penis lobes, which are more or less fused on the meson, and a pair of four-segmented forceps arising from a medianly cleft base. Each penis lobe bears one or two appendages. The shape and arrangement of these appendages, as well as the shape of the penis lobes themselves, provide excellent characters for the recognition of species. Some species also show striking differences in the form of the forceps. The male genitalia may be cleared, stained, and mounted on microscope slides for study, but the operation must be done with great care, as the minute, fragile genital structures of the males of this genus are easily broken or distorted. The genitalia on many dry specimens are suitable for study without special preparation, and the same is true for specimens in alcohol.

The agile nymphs, fig. 212, are small and rather flat dorsoventrally. In life, they hold their heads in a semihypognathous position. They are not strong swimmers, and are most often to be seen crawling among debris and gravel on the bottoms of shallow pools or eddies. They move with a characteristic, snakelike motion.

In most species, the mouth-parts are similar to those to be found in most heptageniid nymphs. There are three segments in each labial palp and three in each maxillary palp. Also, in most species, each mandible is short and terminates in two or three toothed incisors. In a few western species, however, the body of the mandible is greatly elongated and tusklike, projecting anteriorly far past the labrum. In the species with tusked mandibles, the left mandible retains two incisors while the right has but one. Each antenna is as long as the head and thorax combined. The tarsal claws are single, slender, and long, with numerous ventral denticles. Each of abdominal segments 1–7 bears a pair of bifid, filamentous gills, all of which are of the same type, fig. 194. The posterolateral angles of abdominal segments 8 and 9, or 9 only, are produced as slender spines. The three caudal filaments are of about equal length.

Nymphs of this genus develop principally in shallow, fairly rapid streams of small or moderate size. These streams usually have bottoms of coarse gravel.

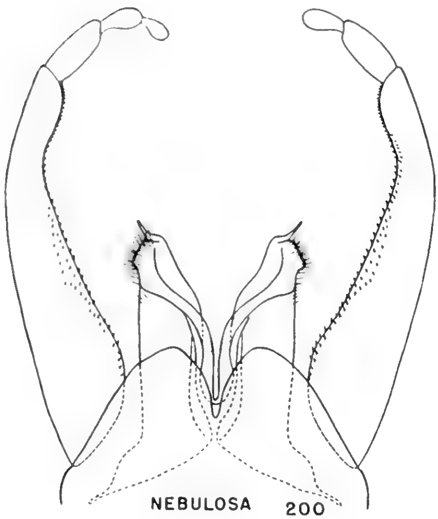
The key to nymphs given below is based on a study of nymphal material in the Cornell University collection and the material reared in Illinois. Gordon (1933:116) and Traver (1935*a*:514) have published keys for the nymphs of *Paraleptophlebia*, and Ide (1930*b*:207) has published descriptions and figures of the nymphs of several northeastern species.

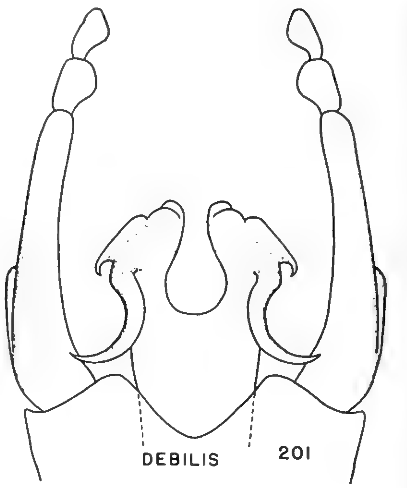
Specific characters for the separation of females of this genus have not yet been found.

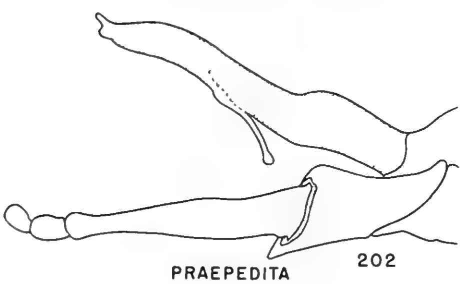
KEY TO SPECIES

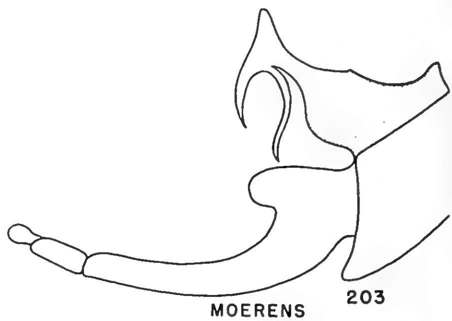
ADULT MALES

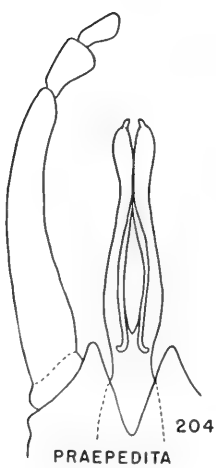
1. Forceps with a large, dorsal enlargement near base, visible in lateral aspect, figs. 201, 203 2
   Forceps without a large, dorsal enlargement near base 3

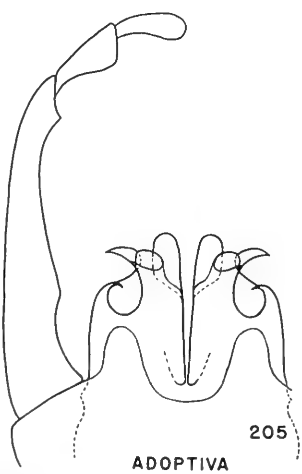












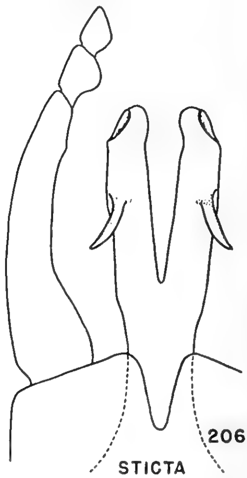


Fig. 200.—*Leptophlebia nebulosa*, male genitalia.
Fig. 201.—*Paraleptophlebia debilis*, male genitalia.
Fig. 202.—*Paraleptophlebia praepedita*, male genitalia, lateral aspect.
Fig. 203.—*Paraleptophlebia moerens*, male genitalia, lateral aspect. (After McDunnough.)
Fig. 204.—*Paraleptophlebia praepedita*, male genitalia.
Fig. 205.—*Paraleptophlebia adoptiva*, male genitalia. (After McDunnough.)
Fig. 206.—*Paraleptophlebia sticta*, male genitalia.

2. All longitudinal veins of fore wing tan, with C, Sc, and R slightly darker; abdominal tergites 2–7 each with a pair of posterolateral, dark brown spots and a dark brown crossband at posterior margin . . . . **1. debilis**
   Veins C, Sc, and R of fore wing a faint tan, other longitudinal veins hyaline; abdominal tergites 2–7 each with a dark brown crossband at posterior margin, but lacking posterolateral spots . . . . **2. moerens**
3. Penis lobes long, straight, and slender, figs. 202, 204, 206 4
   Penis lobes relatively short and broad, figs. 205, 207–211 5
4. Each penis lobe with a terminal papilla, figs. 202, 204 . . . . **3. praepedita**
   Each penis lobe with a lateral depression at tip; papilla wanting, fig. 206 . . . . **4. sticta**
5. Abdominal tergites 2–6 almost entirely dark brown 6
   Abdominal tergites 2–6 almost or completely white 7
6. Penis lobes without decurrent appendages, each lobe with a beaklike, lateral projection, fig. 205 . . . . . . **5. adoptiva**

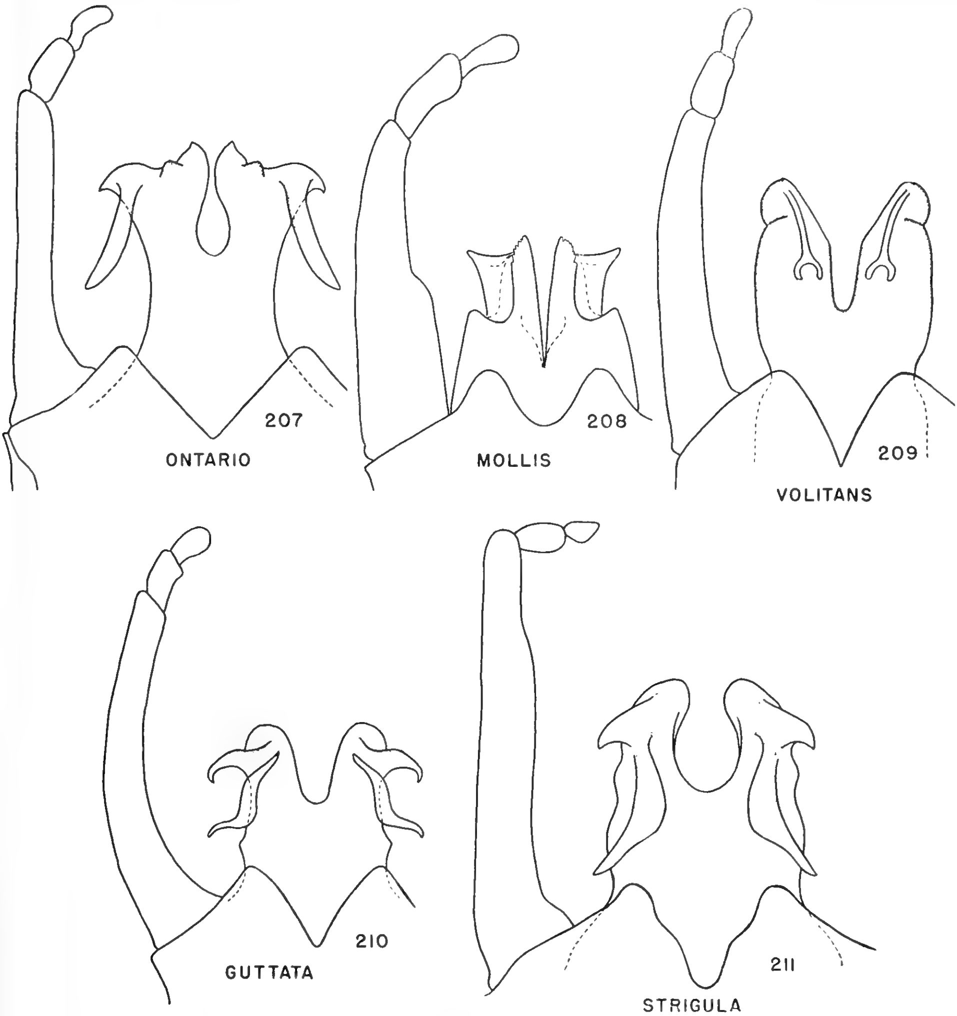


Fig. 207.—*Paraleptophlebia ontario,* male genitalia.
Fig. 208.—*Paraleptophlebia mollis,* male genitalia. (After McDunnough.)
Fig. 209.—*Paraleptophlebia volitans,* male genitalia.
Fig. 210.—*Paraleptophlebia guttata,* male genitalia.
Fig. 211.—*Paraleptophlebia strigula,* male genitalia.

Penis lobes each with a large, decurrent appendage, fig. 207........**6. ontario**

7. Penis lobes without decurrent appendages, fig. 208....................**7. mollis**

Penis lobes with decurrent appendages, figs. 209–211............................8

8. Penis lobes without apicolateral projections; decurrent appendages slender, bifid at apexes, fig. 209.....**8. volitans**

Penis lobes with apicolateral projections; decurrent appendages not bifid at apexes...............................9

9. Abdominal tergites 2–7 white, with spiracular dots; mesal apical angles of penis lobes divergent, fig. 210........ ....**9. guttata**

Abdominal tergites 2–7 white, with spiracular dots and a large, brown spot near each posterolateral angle; mesal apical angles of penis lobes convergent, fig. 211................**10. strigula**

MATURE NYMPHS

1. Gills borne by abdominal segments 3–5 dividing into two branches at a point at least one-third the distance from base to apex of gill; tracheae of these gills with numerous, prominent, lateral branches.........................2

Gills borne by abdominal segments 3–5 divided into two branches at a point not more than one-sixth the distance from base to apex of gill; tracheae of these gills with only a few, minute, lateral branches...................3

2. Anterior margin of labrum slightly indented on meson; each gill of abdominal segments 3–5 divided at a point about one-third distance from base to apex of gill.....................**7. mollis**

Anterior margin of labrum not indented on meson; each gill of abdominal segments 3–5 divided at a point about one-half distance from base to apex of gill ....**5. adoptiva**

3. Abdominal venter with a pair of longitudinal, sublateral brown bands...... ....**3. praepedita**

Abdominal venter without sublateral bands.............................4

4. Only abdominal segment 9 with posterolateral angles produced as spines....5

Both abdominal segments 8 and 9 with posterolateral angles produced as spines 6

5. Abdominal segments 2–6 each with a black streak along either lateral margin ....**10. strigula**

Abdominal segments 2–6 with only a small, black spot near base of each gill ....**9. guttata**

6. Gills borne by abdominal segments 3–5 with long, sparse, marginal hair...... ....**8. volitans**

Gills without marginal hair...........7

7. Tibiae light yellow, with brown band in middle and at base of each.......... ....**1. debilis**

Tibiae light yellow or tan, with brown shading at bases only..............8

8. Combined length of second and third segments of maxillary palp one and one-half times as great as length of first segment..................**6. ontario**

Combined length of second and third segments of maxillary palp equal to length of first segment....**2. moerens**

1. *Paraleptophlebia debilis* (Walker)

Baetis debilis Walker (1853:569).
Leptophlebia mollis Needham (1908:189), not Eaton. Misidentification.
Leptophlebia separata Ulmer (1920*a*:27; 1921:255).

MALE.—Length of body and of fore wing 8–9 mm. Head, thorax, and apex of abdomen dark brown, abdominal segments 2–7 white, with transverse, brown lines at posterior margins of tergites; wings hyaline, with tan longitudinal veins and colorless crossveins; genital forceps, fig. 201, a faint tan, with penis lobes slightly darker; caudal filaments white.

Known from the northern states and the southern part of Canada.

2. *Paraleptophlebia moerens* (McDunnough)

Leptophlebia moerens McDunnough (1924*b*:94).

MALE.—Length of body and of fore wing 5.5–6.5 mm. Head dark brown, almost black; eyes in life brown; antennae dark brown, each becoming hyaline at apex of flagellum. Thorax dark brown; fore leg light brown, with femur and tibia shaded with dark brown; middle and hind legs light brown, with coxae dark brown, femora and tibiae shaded with dark brown, and tarsi white; wings hyaline, with faint brown staining at base of fore wing, veins and crossveins colorless. First abdominal segment dark brown; second tergite shaded with light brown, with dark brown crossband at posterior margin; tergites 3–6 white, with dark brown crossband at posterior margin of each; apical three segments chestnut brown; sternites 2–6 white, with large, median, orange-tan spot on each; forceps base brown, forceps, fig. 203, tan, penis lobes yellow-brown; caudal filaments white.

FEMALE.—Length of body and of fore wing 7 mm. Head and thorax red-brown, lighter than in male; legs light brown, with dark brown shading at base of each tibia; wings very faintly stained with tan, and longitudinal veins of fore wing stained a faint yellow-brown. Abdomen uniformly red-brown, each segment with posterior margin slightly darkened; terminal abdominal sternite with a relatively shallow, broad, rounded, median excavation on posterior margin; caudal filaments a faint yellowish tan.

NYMPH.—Length of body 7–8 mm. Head light yellow-brown, with lateral areas near eyes shaded with red-brown. Thorax light brown, yellowish laterally; legs light yellow-brown, with brown shading near apexes of femora. Abdomen light brown, each tergite with two pairs of vaguely defined, light yellowish spots; gills hyaline, tracheae gray, with only a few, minute, lateral branches; posterolateral angles of tergites 8 and 9 produced as spines; caudal filaments light yellow-brown.

Known from the northeastern and midwestern states and eastern Canadian provinces.

Illinois Record.—HEROD: Branch Big Grand Pierre Creek, May 2, 1946, Burks & Sanderson, 1♂.

3. *Paraleptophlebia praepedita* (Eaton)

Leptophlebia praepedita Eaton (1884:99).

MALE.—Length of body and of fore wing each 4.0–5.5 mm. Head very dark brown, almost black; eyes in life dark red-brown; antennae brown, each becoming hyaline at tip of flagellum. Thorax very dark brown, with yellow-brown markings on pleura; legs usually uniformly light brown, femora sometimes slightly darkened; wings hyaline, each fore wing slightly brown-stained at base, longitudinal veins tan, crossveins colorless. Abdomen usually uniformly brown, middle segments sometimes slightly lighter brown on dorsal meson and at anterior margins; genitalia, figs. 202, 204, light brown; caudal filaments uniformly tan.

FEMALE.—Length of body 5–6 mm., of fore wing 5.5–6.5 mm. Coloration similar to that of male, except that red-brown replaces dark brown, and tan replaces light brown; all crossveins of fore wing, except those in anal and cubital areas, tan; cubital and anal crossveins of fore wing, and all crossveins in hind wing, hyaline; posterior margin of seventh abdominal sternite produced posteriorly to form a long, pointed ovipositor; posterolateral angles of terminal sternite acuminate, median emargination of posterior margin deep and triangular; caudal filaments tan.

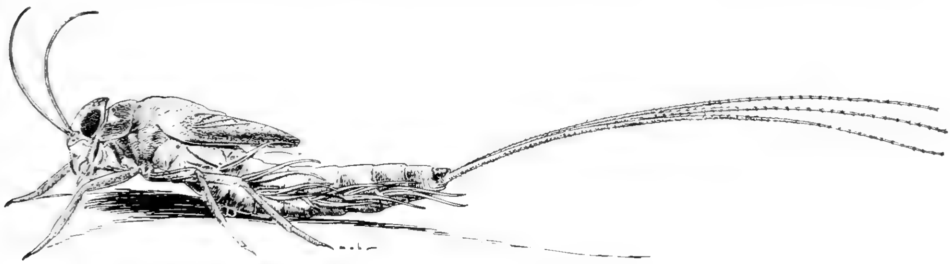


Fig. 212.—*Paraleptophlebia praepedita*, mature nymph, lateral aspect.

NYMPH.—Fig. 212. Length of body 5–7 mm. Head and body tan, vaguely marked with light yellow on dorsum of thorax; legs yellow, shaded with tan near apexes of femora, in middle of tibiae, and near bases of tarsi; abdominal tergum tan, marked with light yellow on meson and near posterolateral angles of each tergite; abdominal venter yellow, with longitudinal, tan bar parallel with and near to each lateral margin; gills hyaline, central tracheal stripes purplish gray; posterolateral angles of abdominal tergites 8 and 9 produced as spines; caudal filaments uniformly tan.

Known from the northeastern and midwestern states and eastern Canada. This is the commonest species of *Paraleptophlebia* in Illinois.

Illinois Records.—DIONA: June 7, 1941, Ross & Mohr, 1♂. EDDYVILLE: Lusk Creek, May 16–17, 1947, B. D. Burks, 1♂. FOX RIDGE STATE PARK: May 13–17, 1938, Ross & Burks, 6♂, 1♀, 1 N; May 25, 1942, Ross & Riegel, 1♂, 2 N. HEROD: May 2–9, 1942, Burks & Mohr, 4♂, 7♀, 16 N; May 13, 1939, Burks & Riegel, 2♂; May 27, 1942, B. D. Burks, 71♂, 8♀; May 2, 1946, Mohr

& Burks, 1 ♂. Monticello: June 6, 1947, Jack Warner, 3 ♂. Muncie: May 24, 1914, 1 ♂. Oakwood: May 22, 1942, Ross & Burks, 6 ♂; May 28, 1948, Burks & Evers, 1 ♂; May 29, 1936, Ross & Mohr, 2 ♂. Richmond: June 14, 1938, Mohr & Burks, 1 ♂. Rosecrans: Des Plaines River, June 8, 1938, B. D. Burks, 2 ♂; May 22–27, 1938, Ross & Burks, 10 ♂, 7 ♀, 8 N. Urbana: May 20, 1914, 1 ♂. Wadsworth: June 3, 1943, Ross & Sanderson, 32 ♂, 13 ♀.

4. *Paraleptophlebia sticta* new species

This species is most closely related, in type of genitalia, to *praepedita,* but differs in that the penis lobes are much shorter and thicker, and lack terminal papillae; the decurrent appendages of the penis lobes also are shorter and stouter in *sticta* than they are in *praepedita.* The two species differ in color, as abdominal tergites 2–6 in *praepedita* usually are uniformly brown, but sometimes have lighter brown areas on dorsal meson and at anterior margins; these tergites in *sticta* are white, faintly tinged with tan, and have dark brown, posterolateral markings.

Male.—Length of body 5 mm., of fore wing 6 mm. Head dark chestnut brown, antennae yellow-brown, each becoming hyaline toward apex of flagellum. Thorax dark chestnut-brown; wings hyaline, longitudinal veins near costal margin of each fore wing tinged with tan, other veins and all crossveins hyaline, stigmatic crossveins not anastomosed, 9 to 11 in number, slanted; legs pale tan, with coxae brown. First abdominal segment brown; tergites 2–6 white, with faint tan tinge, a dark brown spot near posterolateral angle of each tergite and a transverse line on posterior margin, a longitudinal, dark brown line in spiracular region, and a dark brown circle at each spiracle; posterior two-thirds of tergite 7 and all of tergites 8–10 brown of a lighter shade than thorax; sternites 2–7 white, tinged with tan, unmarked, sternite 8 light tan, with transverse, brown line at anterior margin; sternite 9 tan, with dark brown shading at lateral and anterior margins; forceps base, fig. 206, light tan, with deep, median fissure, forceps white, faintly tinged with tan, penis lobes tan; caudal filaments white, articulations not darkened.

Holotype, male.—Watson, Illinois, April 21, 1932, Ross & Mohr. Specimen in alcohol, genitalia on a microscope slide.

Paratype. — Indiana. — Spencer: McCormick's Creek, April 28, 1941, W. E. Ricker, 1 ♂. Specimen in alcohol.

5. *Paraleptophlebia adoptiva* (McDunnough)

Leptophlebia adoptiva McDunnough (1929:169).

Male.—Length of body and of fore wing 7–8 mm. Head and thorax very dark brown, abdomen a lighter brown; wings hyaline, longitudinal veins brown; genital forceps, fig. 205, yellow-brown and penis lobes brown; caudal filaments uniformly light brown.

Known from Michigan, New York, Ontario, and Quebec.

6. *Paraletophlebia ontario* (McDunnough)

Leptophlebia ontario McDunnough (1927*b*:299).

Male.—Length of body and of fore wing 5–6 mm. Head dark brown; eyes in life red-brown; antennae tan, each with flagellum yellow. Thorax dark brown; legs light yellow-brown, with coxae darkened, each fore femur and fore tibia stained with brown, and all tarsi quite light, almost white; wings hyaline, with faint, brown staining at base of fore wing, veins C, Sc, and R_1 of fore wing pale brown, all other veins and all crossveins hyaline. Abdominal tergum dark brown, tergites 2–7 paler brown on meson and across anterior margin of each; first abdominal sternite brown, other sternites pale brown, almost white; genital forceps, fig. 207, tan, penis lobes yellow-brown; caudal filaments mostly white, faintly brown-stained at bases.

Female.—Length of body 5–6 mm., of fore wing 5.5–6.5 mm. Head and body a uniform dark yellow-brown, with posterior margins of abdominal segments shaded darker; legs light yellow; all longitudinal veins of fore wing tan; ovipositor only very slightly produced; terminal abdominal sternite with a deep, triangular, median notch on posterior margin; caudal filaments white.

Nymph.—Length of body 4.5–6.0 mm. Head and body a rich tan, with vague, darker shading on abdominal tergites; abdominal sternites a faint tan; antennae white; legs white, with light brown shading at apexes of femora and bases of tibiae; abdominal gills hyaline, with tracheae purple and showing a few minute, lateral branches; posterolateral angles of abdominal tergites 8 and 9 produced as spines; caudal filaments tan.

Known from Illinois, New York, Ohio, and Ontario.

Illinois Records.—ALTO PASS: branch of Clear Creek, May 23, 1946, Mohr & Burks, 1 ♂. EDDYVILLE: Belle Smith Spring, June 7, 1946, Mohr & Burks, 1 ♂. MUNCIE: June 26, 1948, L. J. Stannard, 1 ♂. WOLF LAKE, Hutchins Creek: May 14–25, 1940, Mohr & Burks, 16 ♂, 19 ♀, 22 N; May 31, 1940, B. D. Burks, 7 ♂, 12 ♀; May 14–29, 1946, Mohr & Burks, 4 ♂, 1 ♀, 4 N.

7. *Paraleptophlebia mollis* (Eaton)

Cloe mollis Hagen (1861:53). Nomen nudum.
Leptophlebia mollis Eaton (1871:88).

MALE.—Length of body and of fore wing 8 mm. Head, thorax, and apex of abdomen dark brown; abdominal segments 2–7 entirely white, without markings; wings hyaline, with veins and crossveins colorless; genital forceps, fig. 208, white, penis lobes tan; caudal filaments white.

Known from the northeastern states and southeastern Canadian provinces.

8. *Paraleptophlebia volitans* (McDunnough)

Leptophlebia volitans McDunnough (1924*b*:95).

MALE.—Length of body and of fore wing 5–6 mm. Head, thorax, and apex of abdomen dark brown; abdominal segment 2 shaded with brown, segments 3–7 white, with brown markings at posterior margins of tergites and in spiracular areas; wings hyaline, with veins and crossveins colorless; genital forceps, fig. 209, white, and penis lobes tan; caudal filaments white.

Known from the Appalachian region and southeastern Canada.

9. *Paraleptophlebia guttata* (McDunnough)

Leptophlebia guttata McDunnough (1924*b*:95).

MALE.—Length of body and of fore wing 5–6 mm. Head, thorax, and apex of abdomen very dark brown; abdominal segments 2–7 white, with a pair of brown spiracular dots on each tergite; wings hyaline, with veins and crossveins colorless; genital forceps, fig. 210, white, penis lobes light yellow-brown; caudal filaments white.

Known from the northeastern states and eastern Canadian provinces.

10. *Paraleptophlebia strigula* (McDunnough)

Leptophlebia strigula McDunnough (1932*b*:209).

MALE.—Length of body and of fore wing 7 mm. Head, thorax, and apex of abdomen brown; abdominal segments 2–7 white, with fairly extensive, brown shading near posterolateral angles of each tergite, a longitudinal, dark brown line present in each spiracular area; wings hyaline, with crossveins colorless and longitudinal veins stained with tan; genital forceps, fig. 211, white, penis lobes tan; caudal filaments white.

Known from Ontario and Pennsylvania.

19. *THRAULODES* Ulmer

Thraulodes Ulmer (1920*a*:33).

This genus includes but two Nearctic species, although Ulmer (1920*c*:116) assigned nine Neotropical and Mexican species to it.

The adults of *Thraulodes* are of medium size, with mostly tan or yellow-brown bodies and clear wings. The wing veins are strong and usually brown; the crossveins, as well as the longitudinal veins, fig. 188, are quite well developed. In the fore wing, the posterior branch of the outer fork (R_5) is not strongly bent posteriorly near its origin, and vein M is branched at about mid-length. There are two long, cubital intercalary veins which are joined to the veins Cu_1 and Cu_2 by strong crossveins. The hind wing has a costal projection, and vein Sc ends just distad of the costal angulation. The crossveins of the hind wing are restricted to the area near the costal angulation.

The fore tarsus in the males is slightly shorter than the fore tibia. The male genital forceps arise from an undivided base and have the two apical segments of each arm relatively minute; the penis lobes are divided to the bases and bear apical appendages.

The nymphs have three-segmented labial and maxillary palps, with the maxillary palp forceps-like at the apex; the head is flattened; all the gills are double and lanceolate, diminishing in size from abdominal segment 1 to 7; the posterolateral angles of abdominal segments 2–9 are produced as slender spines; the three caudal filaments are of the same length. These characters are drawn from Peruvian specimens in the Cornell University collection determined as of this genus by Needham & Murphy.

Thraulodes speciosus Traver (1934:201), described from Texas, and *arizonicus* McDunnough (1942:117), from Arizona, are the only known Nearctic species.

20. *HABROPHLEBIA* Eaton

Habrophlebia Eaton (1881:195).

The Nearctic species of *Habrophlebia* consist of small, slender mayflies with clear wings. The fore tarsus in the males is only two-thirds as long as the fore tibia; the tibiae of all legs in both sexes are conspicuously long and slender, always much longer than the femora. All longitudinal veins of both wings, fig. 189, are hyaline or faintly tinted at the bases only; the cross-veins are all but invisible. Each fore wing has two long and two alternating, short cubital intercalaries, which are free at the bases; vein R_5 is slightly bent posteriorly near the base; vein M_2 diverges from M_1 near the base of the wing, but the basal part of M_2 is obsolete. The hind wing has a costal angulation, and vein Sc ends at or near the apex of the wing. The genital forceps arise from a medianly, deeply fissured base; the length of the apical two forceps segments combined is almost as great as the length of the long basal segment. The penis lobes are divided nearly to the base, fig. 213; each lobe bears a long, bladelike, apical appendage. The terminal abdominal sternite in the females is deeply cleft on the meson of the posterior margin. The median caudal filament is longer than the cerci.

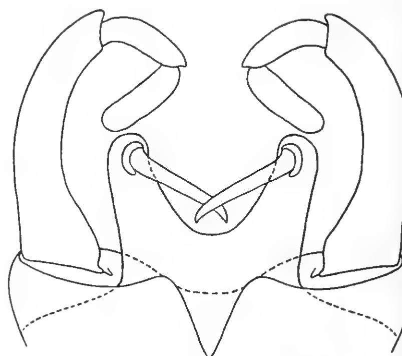
In the nymphs, the body is slender and only slightly flattened; the head is subtriangular and is held in a somewhat prognathous position. The antennae are slender and each about as long as the head and thorax combined. The maxillary palp has three segments, and the labial has three. The tarsal claws are single and relatively short, and bear a single ventral row of denticles. Each of the gills, fig. 196, is single at the base, then quickly branches into two rami, each of which is then subdivided into three or more slender terminal filaments. The median caudal filament is longer than the cerci.

This genus includes two Nearctic species, neither of which has yet been taken in Illinois. One of the two is, however, widely distributed and might eventually be found to occur here.

Habrophlebia vibrans Needham

Habrophlebia vibrans Needham (1908:192).
Habrophlebia jocosa Banks (1914:614).

Male.—Head and thorax dark brown; legs predominantly white; wings hyaline,



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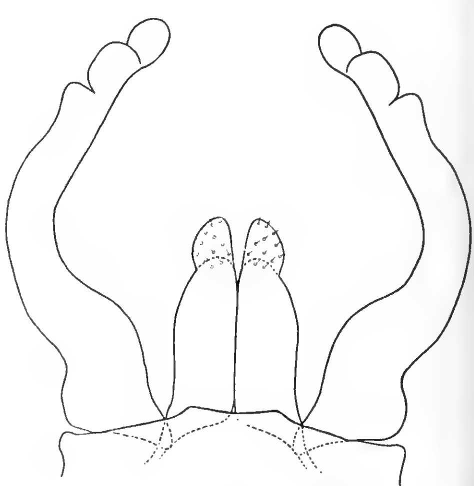

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Fig. 213.—*Habrophlebia vibrans*, male genitalia.
Fig. 214.—*Choroterpes basalis*, male genitalia.

with a small, brown-stained area at base of each fore wing. Basal and apical abdominal tergites dark brown, with middle tergites brown at posterolateral areas only, the central and anterior areas white; anterior and posterior abdominal sternites tan, and middle sternites white; genitalia, fig. 213, tan; caudal filaments predominantly white.

Known from the eastern states and southeastern Canadian provinces.

21. *CHOROTERPES* Eaton

Choroterpes Eaton (1881: 194).

The members of the genus *Choroterpes* are small, extremely delicate mayflies. The males have predominantly dark brown or black bodies, with the abdominal venter of each considerably lighter in color. The females are rather uniformly light brown. The compound eyes of the males are semiturbinate, as there is in each eye a very slight development of a stalk to set off the upper portion from the lower. The wings in both sexes are stained with brown or red-brown at the bases; otherwise, the wings are clear, with the crossveins and posterior longitudinal veins hyaline. The veins near the costal margin of each fore wing are faintly stained with brown. The posterior branch of the outer fork (vein R_5) in the fore wing is not bent posteriorly near the base, fig. 190; vein M_2 diverges from M_1 near the center of the wing, but the basal part of M_2 is obsolescent; there are four cubital intercalary veins, the anterior pair long and the posterior pair short. Each hind wing has a small costal angulation, vein Sc ends just distad of this angulation, and vein M is unbranched.

In the male genitalia, fig. 214, there is a pair of long penis lobes which are fused on the meson only at the bases; these penis lobes lack appendages. Each arm of the forceps, arising from an undivided base, is four segmented, with the suture setting off the basal segment from the second segment extremely obscure. In the females, the terminal abdominal sternite is only slightly or not at all indented on the meson of the posterior margin.

In the nymphs, the head and body are flattened dorsoventrally. The antennae are relatively short—only about as long as the head is wide. There are three segments in each of the labial and maxillary palps. The head itself is quadrate and strongly prognathous. Each tarsal claw is single, relatively short, thick at the base, and provided with a single row of ventral denticles near the tip. The first abdominal segment bears a pair of single, filamentous gills, fig. 195*B*; segments 2–7 have each a pair of bifid, lamelliform gills, each lamina having a spatulate terminal extension, figs. 195*A*, 195*C*, which varies in shape among the different species. The median caudal filament is longer than the cerci.

Choroterpes basalis (Banks)

Leptophlebia basalis Banks (1900: 248).

MALE.—Head and thorax very dark brown; wing bases heavily stained with brown. Abdominal dorsum dark brown, variegated with white, and abdominal venter white; penis lobes, fig. 214, brown; genital forceps and caudal filaments white.

Widely distributed throughout the eastern states and southeastern Canada, it should be taken in Illinois eventually.

22. *HABROPHLEBIODES* Ulmer

Habrophlebiodes Ulmer (1920*a*: 39).

The members of the genus *Habrophlebiodes* are small, extremely delicate, brown mayflies. In the males, the fore tarsus is as long as the fore tibia. The wings are clear or faintly stained with yellow; the longitudinal veins are well marked, but the crossveins are all but invisible. The posterior branch of the outer fork (vein R_5) in the fore wing is bent posteriorly near the base, fig. 191; vein M_2 is obsolete at the base, but apparently diverges from M_1 near the center of the wing; there are two cubital intercalary veins. Each hind wing has a finger-like costal projection, and vein Sc ends just distad of the projection.

The male genital forceps arms arise from a deeply cleft base, fig. 215; the apical two segments are minute and subtriangular. The penis lobes are fused to the tips; each lobe bears a decurrent, lateral appendage. In the females, the well-developed ovipositor is formed by a prolongation of the seventh sternite and underlies the eighth. The ninth sternite is deeply cleft on the meson of the apical margin. The median caudal filament is longer than the cerci.

The nymphs are very similar to those of

Paraleptophlebia, but differ in the shape of the labrum, figs. 197, 198; in *Habrophlebiodes,* the anterior margin has a deeper median cleft. The body is depressed; the head is semiflattened and held in a nearly hypognathous position. Each maxillary palp has three segments, and the labial three. Each antenna is as long as the head and thorax combined. The claws are long and slender and each bears a single ventral row of denticles. The abdominal gills are all of the same type. Each gill has a slender stem which subdivides to produce two long, slender, lanceolate filaments. The caudal filaments are longer than the body.

This genus includes three species, one of which occurs in Illinois.

Habrophlebiodes americana (Banks)

Habrophlebia americana Banks (1903:235).
Choroterpes betteni Needham (1908:194).

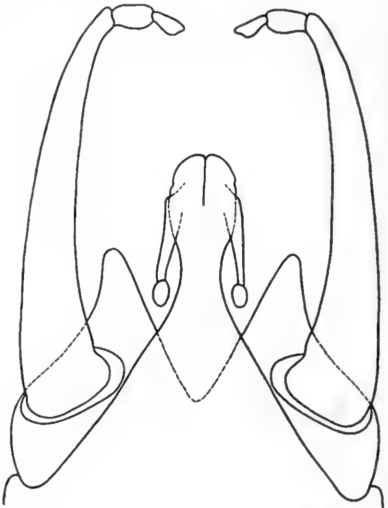
After a study of Banks' types in the Museum of Comparative Zoology and the remains of Needham's types at Cornell University, I agree with McDunnough (1925*a*: 210) that *betteni* is a synonym of *americana.* It has two closely related species: *brunneipennis* Berner (1946:61), a southern species with amber-tinted wings, and *annulata* Traver (1934:199), a species described from Oklahoma that has the posterior margins of the abdominal segments edged with black.

Male.—Length of body and of fore wing 4.5–5.5 mm. Head dark red-brown, antennae tan. Thorax dark brown; fore coxa and femur brown, the latter darker at apex, fore tibia tan, brown at apex, fore tarsus light tan; middle and hind legs mostly light tan or yellowish, with coxae brown, and femur of hind leg darkened with brown in middle and at apex; wings hyaline, longitudinal veins faintly brown-stained, crossveins hyaline. Abdomen mostly dark brown, with pale yellowish markings of variable extent at anterior margins of middle sternites and tergites; genital forceps, fig. 215, light tan to brown, penis lobes light yellow-brown; caudal filaments white or light tan, articulations darkened.

Female.—Length of body and of fore wing 5.5–6.5 mm. Head, thorax, and abdomen uniformly rich red-brown, but considerably lighter than in male; legs and wings marked as in male. Ovipositor projecting slightly past base of ninth sternite. Caudal filaments tan, darkened at articulations.

Nymph.—Length of body 5–6 mm. Head and dorsum of body chestnut brown, venter of thorax and basal abdominal sternites white or light yellow, shading to tan on posterior abdominal sternites; abdominal gills hyaline, tracheae black; caudal filaments uniformly light brown.

Known from the eastern and midwestern states and eastern Canadian provinces. Occurs in the shallow, comparatively still eddies along the banks of streams.



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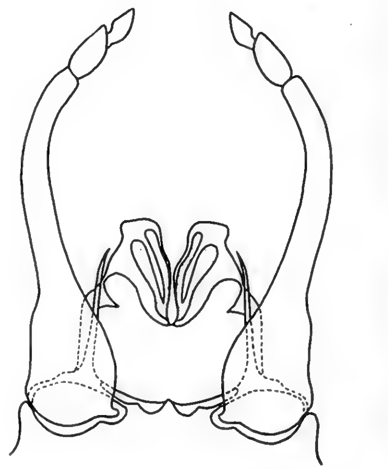

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Fig. 215.—*Habrophlebiodes americana,* male genitalia.
Fig. 216.—*Traverella albertana,* male genitalia.

Illinois Records.—HEROD: May 23, 1946, Ross & Mohr, 1 ♂, 1 ♀; June 20, 1940, Mohr & Riegel, 1 ♂, 2 N; July 16, 1947, L. J. Stannard, 1 ♂.

23. *TRAVERELLA* Edmunds

Traverella Edmunds (1948*c*: 141).

Mayflies of this genus are medium sized and rather heavy bodied. They are strikingly marked with contrasting snow-white and very dark brown areas. The upper portion of each compound eye in the males is extremely broad and is set off from the lower portion by a rudimentary stalk. Two prominently projecting lobes beneath the frontal shelf of the adult head probably are the rudimentary maxillae. The fore tarsus in the males is shorter than the fore tibia. The wings in adults of both sexes are slightly cloudy and tinged with gray-brown so that they look somewhat like subimago wings. The veins and crossveins, fig. 192, are well marked and usually dark brown. The posterior branch of the outer fork (vein R_5) in the fore wing is bent rearward near the base; vein M_2 diverges from M_1 near the center of the wing; there are two long, cubital intercalary veins; vein Cu_2, near the middle, is obliquely bent toward the anal wing margin. The hind wing has a long, acute costal angulation, and vein Sc ends at the distal angle of this projection.

In the male genitalia, the base of the forceps is undivided but bears a median tooth, fig. 216, and a pair of slender lateral processes which lie beside the penis lobes. The penultimate segment of each arm of the forceps is small and semiquadrate; the apical segment is minute and subtriangular. Each penis lobe has one long, slender appendage. In the females, the terminal abdominal sternite projects rearward past the bases of the caudal filaments, and its posterior margin has a deep, median indentation; the eighth sternite has a median, membranous structure which is eversible and undoubtedly serves as an ovipositor. The three caudal filaments are subequal in length in both sexes.

In the nymphs, the body is flattened and the head is quadrate and hypognathous. The labrum is flat and greatly developed, being fully one-third as long as the head. Each of the three-segmented maxillary palps is held in such a position that it projects laterally from beneath the head, the second segment resting parallel to the lateral margin of the head. The apical palpal segment bears a dense brush of long setae. Each labial palp has three segments. Each antenna is almost twice as long as the head. The tarsal claws are relatively short, with a single row of denticles on the ventral side of each. The gills on abdominal segments 1–7 are all of the same type, decreasing in size from the first segment to the seventh. Each gill is bifid, and each element is lamelliform, with the margins finely dissected. Each of the three caudal filaments is as long as the body.

This genus includes only two known Nearctic species: *albertana* (McDunnough) (1931*b*: 82), occurring in Utah, Saskatchewan, and Alberta, and *presidiana* (Traver) (1934: 199), described from Texas.

BAETIDAE

The family Baetidae, as here defined, corresponds to a combination of the Baetidae of the Baetoidea and the Siphlonuridae of the Heptagenioidea in Ulmer's classification (1933), and the name is used in a considerably more restricted sense than by Traver (1935*a*: 427).

The eyes in the males are large, figs. 241, 255–257, and, in many species, each eye is divided into two distinct sections: a lower portion composed of relatively small facets and an upper portion composed of larger facets. In eyes that are divided, the upper portion of each eye is set on a platform which completely separates it from the lower portion, fig. 257. The wing venation in the various members of this family varies from a type approaching that of the fossil Permian mayfly, *Protereisma*, to a much reduced type in which many longitudinal veins and crossveins have been eliminated. Parts of veins may also be atrophied in the wings with reduced venation. This partial atrophy of veins is usually evident toward the bases of the wings. The hind wing in the various genera may be either well developed, or reduced in size and venation, or wanting entirely. The hind tarsus in the adults of both sexes have three or four clearly differentiated segments.

The male penis lobes vary from a well-developed type with relatively complex structure, as in figs. 242–246, to a greatly reduced, almost structureless type, as in figs. 267–269, in the most simplified genera, such as *Cloeon* and *Baetis*. The median caudal filament is vestigial.

All the nymphs are streamlined, rather fishlike forms, and typically vigorous swimmers. The head is not flattened dorsoventrally, as in the Heptageniidae, and the compound eyes are lateral. Usually, the abdominal gills are single and more or less platelike, but, when they are double, the lower element of the pair is not composed of a mass of fibrillae, except in the genus *Isonychia*. In various genera, the median caudal filament may be either well developed or vestigial.

KEY TO SUBFAMILIES

Adults

1. Vein M_2 of fore wing detached at base from stem of M, figs. 31, 220–222; hind wing greatly reduced or wanting entirely; hind tarsus with only three clearly defined segments, fig. 15 .... **Baetinae,** p. 113
   Vein M_2 of fore wing not detached at base from stem of M, figs. 217–219; hind wing well developed; hind tarsus with four clearly defined segments, figs. 18, 20 2
2. Gill remnants present at base of rudimentary maxilla and at base of forecoxa .... **Isonychiinae,** p. 108
   Gill remnants absent .... **Siphlonurinae,** p. 98

Mature Nymphs

1. Each abdominal gill composed of a platelike dorsal element and a ventral fibrillar tuft, fig. 225; fore coxa and maxilla with gill tufts... **Isonychiinae,** p. 108
   All abdominal gills platelike; gills usually single, but, when double, both elements of each gill platelike, figs. 223, 224, 226–228; fore coxa and maxilla without gills 2
2. Posterolateral angles of each apical abdominal tergite prolonged as thin, flat spines, figs. 240*B*, 247, 254; labrum with anterior margin entire or with a broad, median, V-shaped notch, fig. 229 .... **Siphlonurinae,** p. 98
   Posterolateral angles of apical abdominal tergites not prolonged as spines, figs. 266, 298; labrum with a median, square notch, fig. 231 ...... **Baetinae,** p. 113

SIPHLONURINAE

The subfamily Siphlonurinae, as here defined, corresponds very closely to Ulmer's family Siphlonuridae (1933: 209).

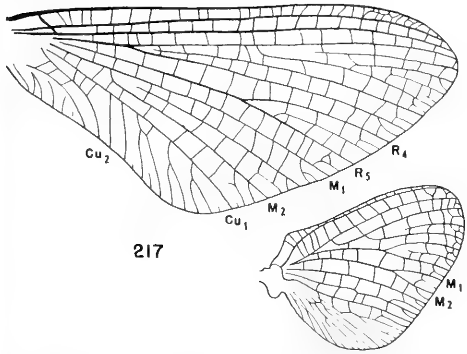
In the Siphlonurinae, each compound eye in the adult males is made up of an upper portion composed of large facets and a lower portion of smaller facets, but the two portions of the eye are not distinctly separated, fig. 241. The fore tarsus in adult males is always much longer than the fore tibia. Gill remnants are wanting on the head and thorax of adults of both sexes. The fore wing in this subfamily is readily distinguished from the fore wing in all other mayflies, in that the cubital intercalary veins form a series of parallel, often sinuate but usually not branched veins extending from vein Cu_1 to the anal margin of the wing, and in that vein Cu_1 is straight throughout its length, fig. 219. In the hind wing, vein M is either not forked or forked in the basal half of its length. In many species, the wings are wholly or partly shaded with brown, yellow, or tan, with prominently colored veins and crossveins. In the adults, the median caudal filament is always vestigial.

The vigorous, fishlike nymphs, figs. 240*B*, 247, of the members of this subfamily are strong and rapid swimmers, almost always living in rapidly flowing water. The tarsal claws of the nymphs are long and slender, but are always shorter than the tibiae, fig. 26. Gills are borne only by the abdomen, and these gills are platelike and usually single, but when they are double both parts of the individual gill are platelike. There are always three well-developed caudal filaments. Each cercus has long setae on the inner side only. The nymphs of *Siphlonurus* have been shown to be at least in part predaceous (Morgan 1913: 386). The structure of the mouth-parts of the nymphs of another genus, *Parameletus*, indicates that it also may be predaceous.

KEY TO GENERA

Adults

1. Abdominal segments 5–9 with broad, flat, lateral expansions, fig. 233; median ventral spine present on mesosternum and metasternum ... **24. Siphlonisca**
   Abdominal segments without broad, lateral expansions; no median ventral spines present on thorax 2
2. Hind wing with an acute costal angulation, and vein M forked near base, fig. 237. .... **25. Ameletus**
   Hind wing with a blunt, or with no, costal angulation, and vein M either not forked or forked well distad of the base, figs. 218, 219 3
3. Vein M of hind wing simple, not forked, fig. 218 .... **26. Parameletus**
   Vein M of hind wing forked, fig. 219 .... **27. Siphlonurus**



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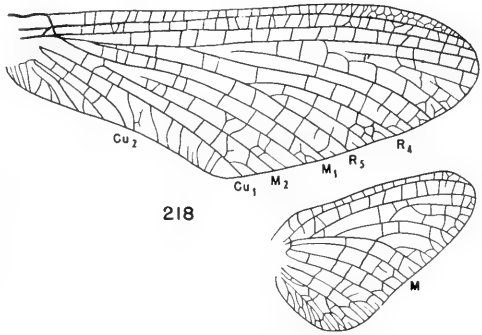

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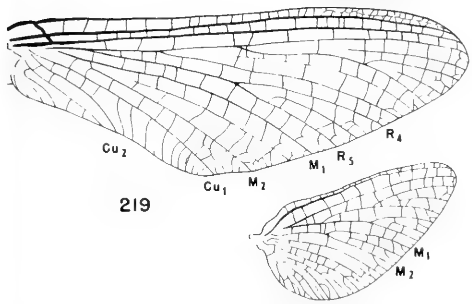

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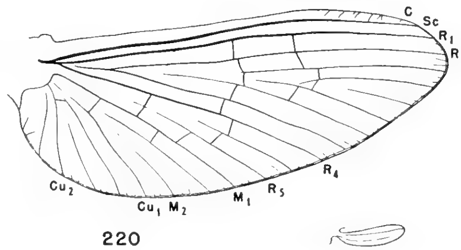

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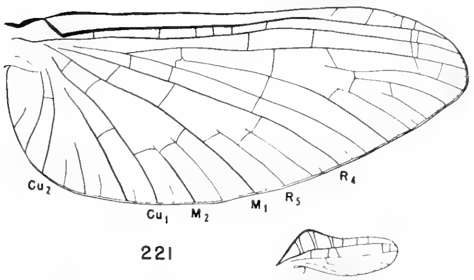

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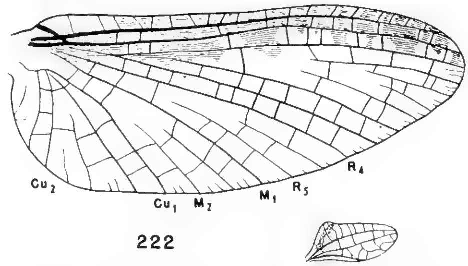

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Fig. 217.—*Isonychia rufa,* wings.
Fig. 218.—*Parameletus midas,* wings. (After Traver.)
Fig. 219.—*Siphlonurus quebecensis,* wings.
Fig. 220.—*Baetis propinquus,* wings.
Fig. 221.—*Callibaetis fluctuans,* wings.
Fig. 222.—*Callibaetis ferrugineus,* wings.

MATURE NYMPHS

1. A stout, median, ventral spine on meso- and metasternum.....**24. Siphlonisca**
   No median ventral spines on thorax...2
2. A conspicuous, transverse pecten of spines present on margin of each maxilla, fig. 240*A*..........**25. Ameletus**
   No pecten of spines present on maxilla..3
3. Apical segment of labial palp and an apposed, thumblike projection of penultimate palp segment forming a forceps, fig. 230............**26. Parameletus**
   Labial palp not forceps-like at apex.........................**27. Siphlonurus**

24. *SIPHLONISCA* Needham

Siphlonisca Needham (1909:71).

This strikingly distinct genus is at once recognizable because of the wide, flat lateral extensions on the margins of abdominal segments 5–9 of the adults, fig. 233, and on all abdominal segments of the nymphs, fig. 234. A midventral spine is present on the mesosternum and metasternum in both the nymphs and the adults. The abdominal gills of the nymphs are single and platelike, with the margins slightly irregular. The median caudal filament is well developed in the nymphs, but is vestigial in the adults.

Siphlonisca most closely resembles *Oniscigaster* McLachlan (1873:108; 1874:139), described from New Zealand.

Siphlonisca aerodromia Needham (1909:71), known from New York, is the only described species. The male genitalia of this species are shown in fig. 232.

25. *AMELETUS* Eaton

Ameletus Eaton (1885:210).

In the members of this genus, each compound eye, in both the males and females, has a slightly oblique, contrastingly colored band extending across the outer surface, fig. 235. This band is visible only in freshly killed or living specimens, as the color pattern of the eyes quickly disappears after

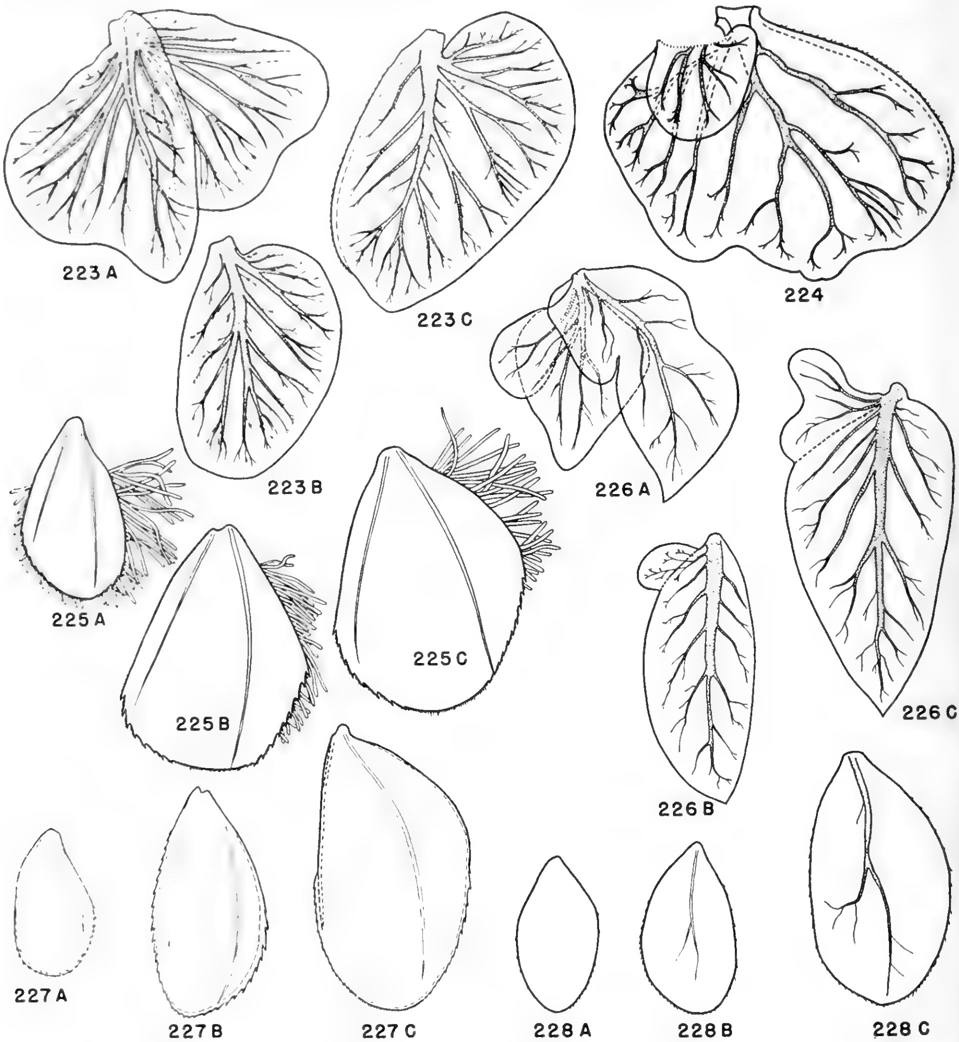
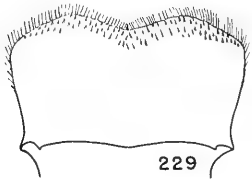


Fig. 223*A*.—*Siphlonurus marshalli*, gill of first abdominal segment.
Fig. 223*B*.—*Siphlonurus marshalli*, gill of seventh abdominal segment.
Fig. 223*C*.—*Siphlonurus marshalli*, gill of fifth abdominal segment.
Fig. 224.—*Siphlonurus alternatus*, gill of fifth abdominal segment.
Fig. 225*A*.—*Isonychia* sp., gill of first abdominal segment.
Fig. 225*B*.—*Isonychia* sp., gill of seventh abdominal segment.
Fig. 225*C*.—*Isonychia* sp., gill of fifth abdominal segment.
Fig. 226*A*.—*Callibaetis skokianus*, gill of first abdominal segment.
Fig. 226*B*.—*Callibaetis skokianus*, gill of seventh abdominal segment.
Fig. 226*C*.—*Callibaetis skokianus*, gill of fifth abdominal segment.
Fig. 227*A*.—*Ameletus lineatus*, gill of first abdominal segment.
Fig. 227*B*.—*Ameletus lineatus*, gill of seventh abdominal segment.
Fig. 227*C*.—*Ameletus lineatus*, gill of fourth abdominal segment.
Fig. 228*A*.—*Baetis brunneicolor*, gill of first abdominal segment.
Fig. 228*B*.—*Baetis brunneicolor*, gill of seventh abdominal segment.
Fig. 228*C*.—*Baetis brunneicolor*, gill of fourth abdominal segment.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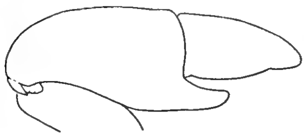
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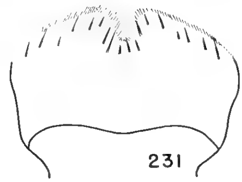
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Fig. 229.—*Siphlonurus marshalli,* labrum of mature nymph, dorsal aspect.
Fig. 230.—*Parameletus columbiae,* libial palp of mature nymph.
Fig. 231.—*Baetis vagans,* labrum of mature nymph, dorsal aspect.

death, regardless of the method of preservation of specimens. The fore wing is typical for the subfamily; the hind wing has an acute costal projection, and vein M is forked near the base of the wing, fig. 237. The male penis lobes are always separated to the base, and the forceps base is deeply excavated on the meson, as in fig. 236. The apical abdominal sternite of the females has a median notch on the posterior margin, figs. 238, 239. There are two well-developed caudal filaments.

The streamlined, vigorously swimming nymphs, fig. 240*B*, are distinguished from all other known mayfly nymphs by the pecten of spines borne by each maxilla, fig. 240*A*. The legs are relatively short, and the tarsal claws are uniformly single, nondenticulate, slender, and much shorter than the tibiae. The gills are single and platelike, each gill having a single, stout, rodlike stiffener near each dorsal margin and a weaker but otherwise similar rod near each ventral margin, fig. 227. There are three well-developed caudal filaments; the cerci bear long, dense setae on the inner sides only.

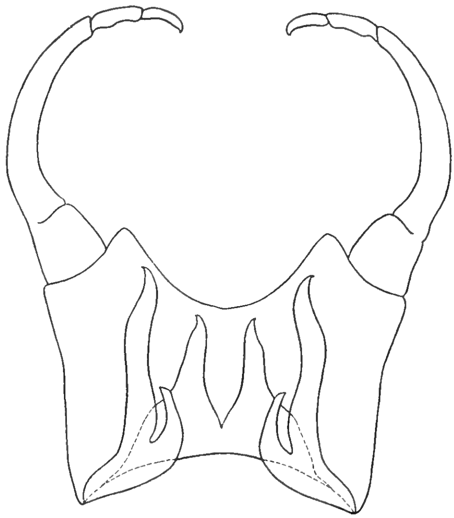
The genus *Ameletus* includes 26 Nearctic species, 22 of which occur in the western states. Two of the remaining four species have been taken only in Quebec and Nova Scotia. The other two species occur in the Midwest and both normally are parthenogenetic. Males are unknown for one species and only two male specimens of the other species are known to have been collected.

KEY TO SPECIES

ADULT FEMALES

Venter of abdomen without ganglionic markings; terminal abdominal sternite as in fig. 239; lateral margins of apical sternite slightly incised................**1. lineatus**

Venter of abdomen with brown ganglionic markings; terminal abdominal sternite as in fig. 238; lateral margins of apical sternite straight........................**2. ludens**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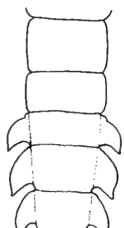
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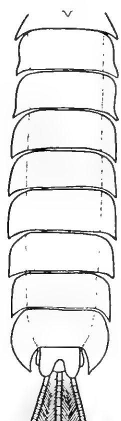
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Fig. 232.—*Siphlonisca aerodromia,* male genitalia.

Fig. 233.—*Siphlonisca aerodromia,* abdomen of adult male, ventral aspect.

Fig. 234.—*Siphlonisca aerodromia,* abdomen of mature male nymph, ventral aspect.

Mature Nymphs

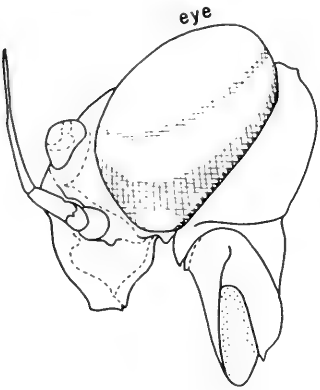
Brown crossbar at posterior margin of terminal abdominal sternite joining three longitudinal, brown stripes on abdominal venter.... 1. **lineatus**

Entire terminal abdominal sternite of abdomen shaded with brown, this shading sometimes also extending over one or two sternites anterior to terminal one........... 2. **ludens**

1. *Ameletus lineatus* Traver

Ameletus lineatus Traver (1932*a*: 194).

Female.—Length of body 11 mm., of fore wing 12 mm. Head yellow-brown, vertex with a longitudinal, median, dark brown line; eyes light brown, with a yellow, dark brown-bordered stripe on outer surface, fig. 235; antennae smoky brown. Thorax dark yellow-brown, with yellow markings at sutures and on pleura around coxal bases; wings hyaline, veins and crossveins brown; legs yellow-brown, with tarsi somewhat darkened. Abdomen yellow-brown, without well-marked color pattern, although slightly darkened at posterior margins of each tergite; sternite 6 with a median, dark brown mark; lateral margins of terminal abdominal sternite slightly incised near apex; caudal filaments light, articulations dark, brown.



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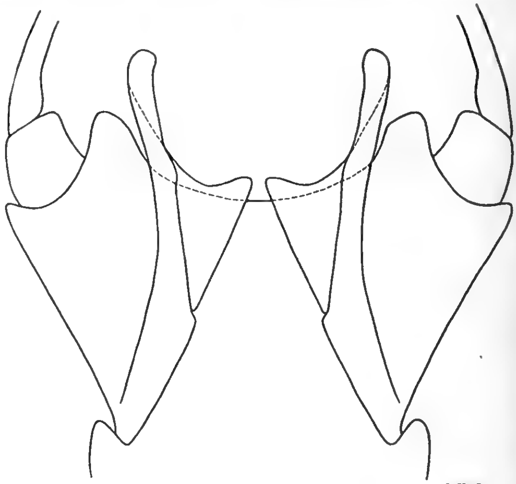

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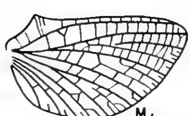

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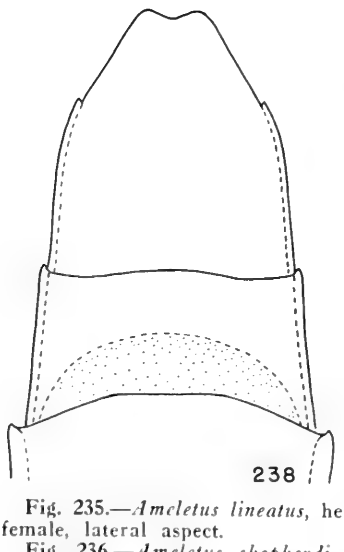

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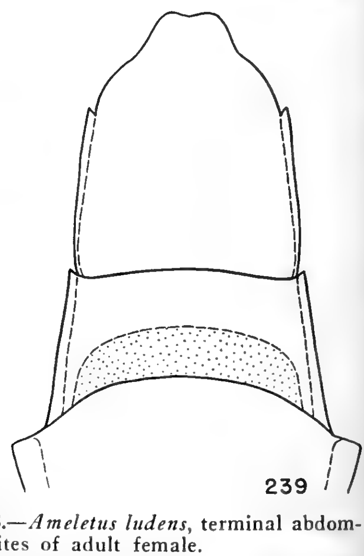

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Fig. 235.—*Ameletus lineatus*, head of adult female, lateral aspect.

Fig. 236.—*Ameletus shepherdi*, male genitalia.

Fig. 237.—*Ameletus lineatus*, hind wing.

Fig. 238.—*Ameletus ludens*, terminal abdominal sternites of adult female.

Fig. 239.—*Ameletus lineatus*, terminal abdominal sternites of adult female.

NYMPH.—Length of body 11–13 mm., of caudal filaments 5–6 mm. Head and body cream colored, with vague, light brown markings. Tarsi ordinarily with a light brown band at base and a dark brown band at apex of each. Abdominal venter with three longitudinal, brown stripes, one median, another near each lateral margin; a brown crossband at posterior margin of sternite 9 joining the three longitudinal stripes; caudal filaments with an extremely broad, brown crossband in middle and a narrow, brown crossband at apex of each filament.

This species, reported from North Carolina and Illinois, is known only from female adults and female nymphs. The nymphs are found among debris and emergent vegetation along the banks of swift, cool streams.

Illinois Records.—CORA: April 24, 1939, Burks & Riegel, 1 ♀ N. HEROD: Gibbons Creek, March 14, 1946, Ross & Burks, 1 ♀ N; Herod Spring, March 14, 1946, Ross & Burks, 1 ♀ N; April 4, 1946, Burks & Sanderson, 2 ♀ N; Gibbons Creek, April 7–10, 1947, B. D. Burks, 2 ♀, numerous ♀ N; May 15, 1941, Mohr & Burks, 4 ♀ N. RUDEMENT, Blackman Creek: April 2, 1932, Frison & Ross, 4 ♀ N; April 4, 1946, Burks & Sanderson, 3 ♀ N; April 4–8, 1947, B. D. Burks, numerous ♀ N.

2. *Ameletus ludens* Needham

Ameletus ludens Needham (1905:36).

This species differs from *lineatus* only in having brown ganglionic markings on the abdominal sternites of the adult female and in having a differently shaped apical abdominal sternite, fig. 238. The nymph of *ludens*, fig. 240, differs from that of *lineatus* in having the entire ninth abdominal sternite brown, and the longitudinal, brown stripes on the abdominal venter relatively wider. The only two adult male specimens of *ludens* known to have been collected were described by Needham (1924:308).

Although *ludens* has been taken in the neighboring state of Indiana as well as in New York and West Virginia, it has not yet been collected in Illinois.

26. *PARAMELETUS* Bengtsson

Parameletus Bengtsson (1908:242).
Potameis Bengtsson (1909:13).
Sparrea Petersen (1909:554).
Siphlonuroides McDunnough (1923:48).
Palmenia Aro *in* Lestage (1924*a*:35).

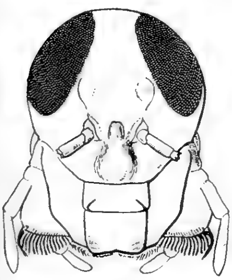
In *Parameletus*, the fore wing, fig. 218, is rather narrow and elongate, the stigmatic crossveins are anastomosed, and the outer wing margin has fairly numerous, short and irregular intercalary veins. The hind wing usually has a low, broadly rounded costal projection, and vein M is always simple and unbranched. In the nymphs, the labial palps are forceps-like, fig. 230; the abdomen is somewhat flattened dorsoventrally, as in *Leptophlebia*, and the gills are broad and single, with the tracheation dense and pinnately branched.

There are no Illinois species of *Parameletus*; *croesus* (McDunnough) and *midas* (McDunnough) (1923:48–9) were described from Ontario; *columbiae* McDunnough (1938:31) occurs in the western states and British Columbia.

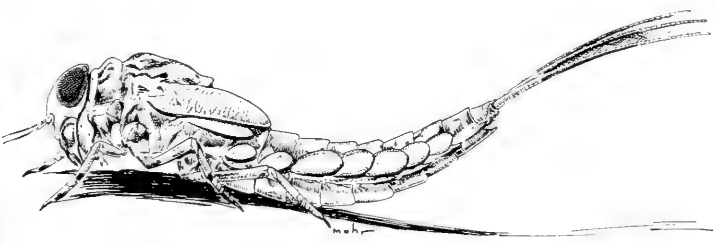
27. *SIPHLONURUS* Eaton

Siphlonurus Eaton (1868:89).
Siphlurus Eaton (1871:37, 125).
Emendation, unnecessarily proposed.
Siphlurella Bengtsson (1909:11).

The genus *Siphlonurus* includes a fairly large number of species of large, strikingly



240 A



240 B

Fig. 240*A*.—*Ameletus ludens*, head of mature nymph, anterior aspect.
Fig. 240*B*.—*Ameletus ludens*, mature nymph, lateral aspect.

marked mayflies. Each compound eye in living males and females has contrastingly colored stripes extending across the outer surface. The head and thorax usually are mostly dark brown, while the abdomen always has a conspicuous color pattern of contrasting light and dark areas which are somewhat annular in arrangement. The fore wing, fig. 219, is long and relatively narrow, with membrane usually hyaline and veins dark. There are numerous, irregular, marginal intercalary veins, and the stigmatic crossveins are usually anastomosed. The cubital intercalary veins are typical for this subfamily. The hind wing has a broadly rounded, inconspicuous costal angulation, and vein M is forked at a point midway between the base and the outer margin of the wing.

The male genitalia in the various species show the most strikingly distinct structural differences to be found in any Nearctic mayfly genus, figs. 242–246. The median caudal filament is represented by a minute vestige in the adults of either sex.

The vigorous, streamlined nymphs, fig. 247, typically inhabit quiet pools along the edges of streams. They also occur commonly in shallow pools filled by seepage water on rock ledges, as well as in small, shallow pools fed only intermittently with fresh water. They are not rheophilus, except in the early instars of some species. The mature nymphs are found invariably in quiet water. As Morgan (1913:386) has shown, *Siphlonurus* nymphs are in part predaceous.

In the *Siphlonurus* nymphs, the compound eyes are lateral, and the head is hypognathous. The tarsal claws are slender and pointed, and considerably shorter than the tibiae. Abdominal segments 1–7 bear platelike gills, the first two pairs of which invariably are double, while the more posterior pairs are single, except in *alternatus*. The posterolateral angles of the abdominal tergites are produced and spinelike. There are three well-developed caudal filaments; each cercus bears a fringe of long setae on the mesal side only.

This genus includes 18 Nearctic species, 4 of which are known to occur in Illinois; 1 other species may be taken here eventually.

Reliable characteristics for the separation of the females of these species have not yet been found.

KEY TO SPECIES

ADULT MALES

1. Membrane of hind wing completely shaded with brown; male genitalia relatively simple, fig. 245 .... **5. marshalli**
   Membrane of hind wing hyaline; male genitalia relatively complex, figs. 242–244, 246 2
2. Each abdominal sternite with a pair of dark brown, lateral, triangular marks, these spots connected on meson by a large V-shaped mark with its apex at median point of anterior margin of sternite; male genitalia with a prominent, serrated bulge on median margin of each inner process, fig. 242 .... **3. quebecensis**
   Abdominal sternites not with lateral, triangular spots connected on meson by V-shaped marks; male genitalia with no serrated bulge on mesal margin of each inner process 3
3. Each abdominal sternite with a median, anterior, brown spot, a pair of oblique, lateral marks, and a pair of submedian dots; male genitalia with a pair of broad, dorsal flaps, fig. 246 .... **2. alternatus**
   Abdominal sternites not with such markings; male genitalia without broad, dorsal flaps 4
4. Abdominal venter with an interrupted, longitudinal, median stripe; inner processes of male genitalia finger-like at apexes, fig. 243 .... **1. rapidus**
   Abdominal venter unmarked or with only faint, lateral, triangular marks on anterior sternites; inner processes of male genitalia nipple-like at apexes, fig. 244 .... **4. typicus**

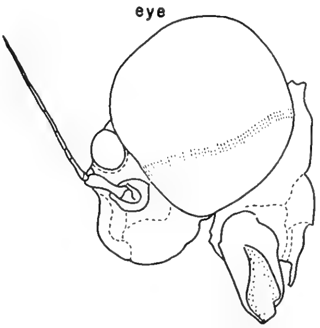
MATURE NYMPHS

1. Each gill borne by abdominal segments 3–6 with a dorsal, recurved flap, fig. 224 .... **2. alternatus**
   Each gill borne by abdominal segments 3–6 simple, without a dorsal, recurved flap, fig. 223*C* 2
2. Abdominal sternites 4–8 each with a pair of broad, longitudinal, lateral, brown bands and four submedian dots .... **5. marshalli**
   Abdominal sternites almost entirely brown, light yellow only on median, triangular area at posterior margin and on small area at anterolateral angles of each sternite .... **3. quebecensis**

1. *Siphlonurus rapidus* McDunnough

Siphlonurus rapidus McDunnough (1924*c*:75).

MALE.—Membrane of fore wing faintly stained with tan, almost hyaline, costal and subcostal crossveins well developed, and



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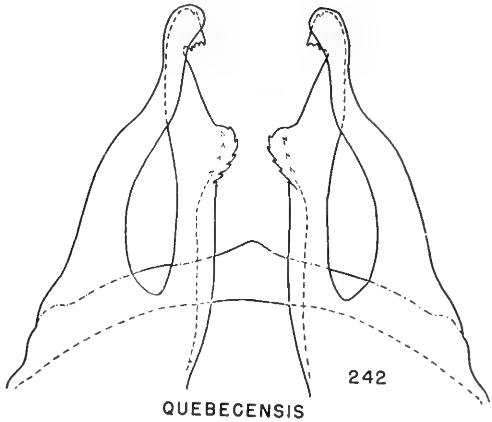

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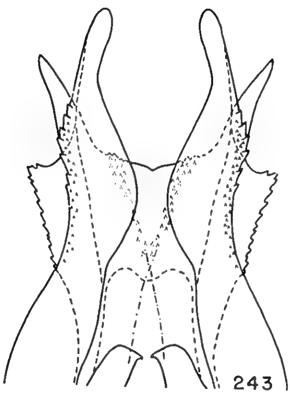
QUEBECENSIS



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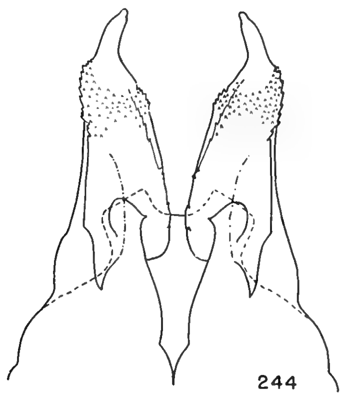
RAPIDUS



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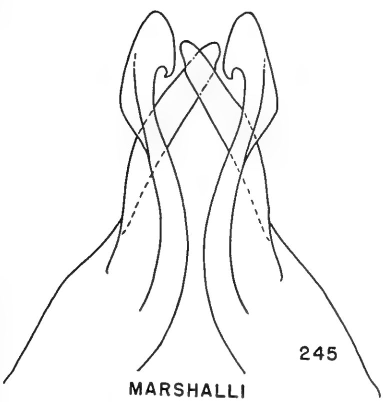
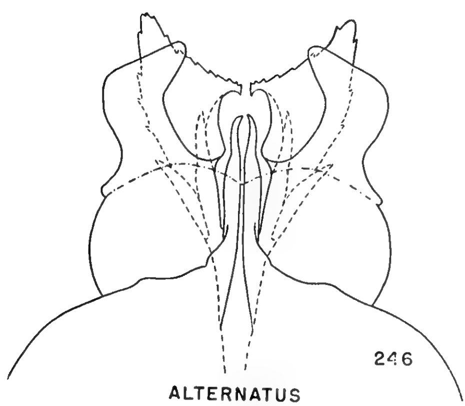
TYPICUS



245

MARSHALLI



246

ALTERNATUS

Fig. 241.—*Siphlonurus alternatus*, head of adult male, lateral aspect.

Fig. 242. — *Siphlonurus quebecensis*, male genitalia.

Fig. 243.—*Siphlonurus rapidus*, male genitalia.

Fig. 244.—*Siphlonurus typicus*, male genitalia.

Fig. 245.—*Siphlonurus marshalli*, male genitalia.

Fig. 246.—*Siphlonurus alternatus*, male genitalia.

stigmal crossveins anastomosed; dorsum of body brown, with yellow markings, abdominal venter almost entirely light yellow or white, with a discontinuous, longitudinal, brown stripe on meson. Male genitalia, fig. 243, with inner processes elongate, finger-like at apexes, and grossly serrate on outer margins; outer processes acute at apexes, with lateral margins flaring and finely serrate; both inner and outer processes with numerous, minute spines.

The nymph is unknown.

This species is known from Connecticut, Massachusetts, Michigan, New Hampshire, New York, and Quebec.

Fig. 247.—*Siphlonurus alternatus*, mature nymph, lateral aspect.

2. *Siphlonurus alternatus* (Say)

Baetis alternata Say (1824:304).
Baetis annulata Walker (1853:567).
Baetis femorata Provancher (1876:267), not Say. Misidentification.
Siphlurus alternans Provancher (1878:127). Misspelling.

MALE.—Length of body 11–13 mm., of fore wing 10–12 mm. Head light yellow, with brown shading at bases of ocelli, on vertex along mesal margin of each compound eye and on meson, and across frontal shelf below antennae; compound eye gray, with two light and two alternating, dark stripes on outer surface of lower portion; antennae tan, each scape slightly darkened at base and apex. Thorax tan, with light yellow to almost white markings on pleura and sternum. Legs light yellow, each with brown annulations at base and near apex of femur, at base and apex of tibia, and at apex of each tarsal segment, all annulations narrow except one near apex of femur; wings hyaline, veins and crossveins dark brown, costal and subcostal crossveins weak, stigmal crossveins anastomosed and stigmal area milky. Ground color of abdomen light tan to almost white, with brown shading; each tergite with a broad, transverse, shaded area at posterior margin, a large, triangular spot near each posterolateral angle, and a broad, longitudinal stripe on meson; each sternite with a pair of oblique, lateral marks, a median spot on anterior margin, and a pair of submesal dots in center; genitalia, fig. 246, light tan; caudal filaments tan at bases, becoming white at apexes, articulations dark brown.

FEMALE.—Length of body 11–13 mm., of fore wing 12–14 mm. Color pattern as in male, but background slightly lighter and brown shading less intense; caudal filaments almost entirely white, only faintly tan-shaded near bases, with articulations chocolate brown. Apical margin of terminal abdominal sternite produced, nipple-like on meson.

NYMPH.—Fig. 247. Length of body 11–13 mm., of caudal filaments 6–7 mm. Color patterns of thorax, legs, and abdomen very similar to those of the adult, but markings of abdominal venter somewhat broader than in the adult; each gill on abdominal segments 1 and 2 composed of two equal-sized plates, gills on the following segments composed of a large plate with a much smaller, recurved, dorsal plate, fig. 224; posterolateral, spine-like prolongations of tergites darkened at tips; each caudal filament with a broad, brown crossband near middle and a narrower crossband at tip.

Known from Illinois, Indiana, Michigan, New York, Nova Scotia, Ontario, Quebec, and Wisconsin.

Illinois Records.—FREEPORT: at light, June 10–11, 1948, Burks, Stannard, & Smith, 1 ♂, 3 ♀. ROCKFORD: Long slough of Rock River, May 13, 1927, D. H. Thompson, 1 N. (Walsh 1862:369 records this species from near Chicago on the Des Plaines River; Coal Valley Creek, Rock Island County; and Rock Island.)

3. *Siphlonurus quebecensis* (Provancher)

Baetis canadensis Provancher (1876:267), not Walker. Misidentification.
Siphlurus quebecensis Provancher (1878:127). New name.
Siphlurus annulatus Provancher (1878:144), not Walker. Erroneous citation.
Siphlurus triangularis Clemens (1915*a*:250).

MALE.—Length of body 9–12 mm., of fore wing 10–14 mm. Head yellow, with dark brown to black shading at bases of ocelli, on vertex at mesal margins of compound eyes, and across frontal shelf below antennae; compound eyes gray, the lower portion with two light bands alternated with two dark bands extending across outer surface; antennae light brown. Thorax brown, with light yellow or white marks on pleura and sternum; wings hyaline, veins and crossveins dark brown, costal and subcostal crossveins weak, stigmatic crossveins anastomosed and stigmatic areas milky; legs light brown, with dark brown marks at apexes of femora, tibiae, and tarsal segments. Ground color of abdomen light yellow-tan, dark brown shading covering all but anterior quarter of each tergite; triangular, shaded area at lateral margin of each sternite, these triangles connected on meson by a V-shaped mark with its apex on median point of anterior margin of each sternite; genitalia, fig. 242, brown; cerci light tan at bases, becoming almost white at apexes, articulations dark brown.

FEMALE.—Length of body 10–12 mm., of fore wing 12–14 mm. Coloration identical with that of male, except that caudal filaments are slightly lighter in color; apical margin of terminal abdominal sternite with a small, rounded, median notch.

NYMPH.—Length of body 10–12 mm., of caudal filaments 5–6 mm. Body light tan, with brown shading; legs tan, each with brown annulation near apex of femur, at base of tibia, and at base and apex of tarsus, these annulations not always completely encircling leg. Gills on abdominal segments 1 and 2 double, others single; spinelike, posterolateral angles of abdominal tergites dark brown at apexes; abdominal sternites with dark markings broad, abdominal color pattern otherwise identical with that of adult; caudal filaments each with a broad, brown crossband near apex.

Known from Connecticut, Illinois, Maine, Michigan, New York, North Carolina, Ontario, Quebec, South Carolina, and Wisconsin.

Illinois Record.—SOUTH BELOIT: Rock River, May 31, 1927, D. H. Thompson, 3 N.

4. *Siphlonurus typicus* (Eaton)

Siphlurus typicus Eaton (1885:222).
Siphlonurus berenice McDunnough (1923:49).
Siphlonurus novangliae McDunnough (1924*c*:75).

Spieth (1941*a*:93) studied Eaton's type and established the above synonymy.

MALE.—Length of body 9–10 mm., of fore wing 10–11 mm. Head chiefly yellowish tan, light yellow on face below ocelli and shaded with dark brown at bases of ocelli; antennae very light tan, almost white; eyes gray. Thorax light yellow-brown, with white spots on pleura and on sternum; membrane of wings faintly stained with tan, veins and crossveins rich red-brown, costal and subcostal crossveins well developed, stigmatic crossveins very little anastomosed; legs yellow, darkened with brown at apexes of tibiae and tarsal segments. Abdominal ground color pale yellow to white, with light red-brown shading: each tergite with transverse, broad, shaded area at posterior margin, triangular, shaded area at each posterolateral angle, and broad, median, longitudinal spot; sternum virtually or quite unmarked, at most with faint, transverse, sinuate brown markings on anterior sternites; genitalia, fig. 244, yellow-tan; caudal filaments tan at bases, fading to white at apexes, articulations red-brown.

Nymph unknown.

Siphlonurus typicus is known from Connecticut, Illinois, Maine, Massachusetts, New Hampshire, New York, Pennsylvania, and Quebec.

Illinois Record.—ALTO PASS: April 30, 1942, Mohr & Burks, 1 ♂.

5. *Siphlonurus marshalli* Traver

Siphlonurus marshalli Traver (1934:236).

MALE.—Length of body and of fore wing 10–13 mm. Head chiefly dark brown, light yellow on face below ocelli and on frontal shelf, dark brown shading present around bases of ocelli; antennae tan, base of each flagellum shaded with dark brown; eyes tan. The thorax dark brown, with light yellow markings on pleura and sternum. Membrane of each fore wing hyaline, with dark brown shading around crossveins, this shading most extensive in discal area of wing; membrane of hind wing almost or quite completely stained dark brown; veins and crossveins of fore wing strong, stigmal crossveins anastomosed; each fore leg dark yellow-brown, with tarsus slightly lighter, middle and hind legs yellow, faintly shaded with red-brown on coxae, near apexes of femora, and at apexes of tarsal segments. Abdominal dorsum dark brown at base and on apical tergites, intervening tergites lighter brown; basal and apical sternites brown, intermediate sternites almost white, with vague tan mark near lateral margin of each sternite; genitalia, fig. 245, yellowish tan; caudal filaments uniformly gray-brown near bases, fading to almost white at apexes, articulations in apical part of each filament faintly stained with brown.

FEMALE.—Length of body 11–14 mm., of fore wing 13–15 mm. Color pattern much as in male, except generally slightly lighter. Each fore leg faintly darker than middle and hind legs; fore wing as in male, hind wing with membrane not quite entirely shaded with brown, small hyaline areas present in center of most cells. Middle abdominal segments only slightly lighter than anterior and posterior ones; apical margin of terminal abdominal sternite produced posteriorly, evenly rounded from side to side, or margin very slightly irregular on meson; caudal filaments uniformly tan throughout, or occasionally becoming a little lighter in shade toward apexes.

NYMPH.—Length of body 11–16 mm., of caudal filaments 6–8 mm. Color pattern of thorax much as in adult, with coloration of adult wings distinctly visible; legs showing only a faint indication of darker shaded areas present in adult legs. Dorsum of abdomen light, with a pair of submedian dots at anterior margin of each tergite; posterolateral, spinelike projections of tergites usually not darkened at tips; each sternite with a pair of broad, longitudinal, brown bands near lateral margins and four submedian, brown dots; gills borne by abdominal segments 1 and 2 double, others single, fig. 223, caudal filaments each with a broad, dark brown crossband at mid-length.

Known from Arkansas and Illinois.

Illinois Records.—ALTO PASS: April 30, 1942, Mohr & Burks, 1 ♂, 4 N; Jan. 25, 1947, Burks, Stannard, & Riegel, 1 N. DIXON SPRINGS: March 13, 1946, Ross & Burks, 7 N; April 4–6, 1946, Burks & Sanderson, 2 ♂, 1 ♀, 5 N. FOUNTAIN BLUFF: May 15, 1932, Ross & Mohr, 1 N. GIANT CITY STATE PARK: April 2–21, 1942, Ross & Burks, 5 ♂, 4 ♀, 23 N; May 16–29, 1946, Burks & Sanderson, 3 ♂, 1 ♀, 9 N. GOREVILLE, Fern Cliff: March 24, 1939, Ross & Burks, 1 N; April 4–23, 1942, Ross & Burks, 2 ♂, 1 ♀, 5 N. HEROD: June 1–3, 1939, Burks & Riegel, 2 ♀, 2 N.

ISONYCHIINAE new subfamily

The subfamily Isonychiinae is here erected for the reception of a single North American genus, *Isonychia,* which has long been the cause of radical disagreement among mayfly workers. This genus has been considered to have both heptageniid and baetid relationships. Ide (1930*b*:227) and Spieth (1933:329) included it in the family Heptageniidae; Ulmer (1933:210) placed it in his superfamily Heptagenioidea; and Traver (1935*a*:477) placed it in the Baetidae. *Isonychia* is, in my opinion, clearly baetid in its family relationships and shows some similarity to *Siphlonurus.* However, both nymphal and adult characteristics are too greatly at variance with those of *Siphlonurus* to permit the two genera to be placed in the same subfamily.

The adults of *Isonychia* have gill remnants persisting at the base of each vestigial maxilla and at the base of each fore coxa. The fore tarsus in the males is approximately as long as the fore tibia. In the fore wing, fig. 217, the cubital intercalaries are a series of short, sinuate, and forked veins which extend from Cu_1 to the anal margin of the wing, much as in *Hexagenia* and *Potamanthus.* In the hind wing, vein M is forked very near the outer margin of the wing. The male genitalia, figs. 248–253, are of a type quite different from those of all other baetid mayflies. The nymphs bear tufted, filamentous maxillary and fore coxal gills, and unique abdominal gills, each of which is composed of an upper, platelike member and a lower, filamentous tuft, fig. 225. These characteristics may be contrasted with those of the members of the Siphlonurinae, as given on page 98 above.

28. *ISONYCHIA* Eaton

Isonychia Eaton (1871: 134).
Chirotonetes Eaton (1881:21). New name, unnecessarily proposed.
Jolia Eaton (1881:192).
Chirotenetes Needham (1905:25). Misspelling.

In *Isonychia,* the adult males have large compound eyes that are contiguous on the dorsal meson; each of these eyes is composed of an upper portion of large facets and an indistinctly separated lower portion of smaller facets. The outer surface of each eye is crossed by a pair of oblique, contrastingly colored stripes. Each compound eye in the adult females is approximately one-half the size of that of the males, and usually it has a single, broad, light-colored stripe extending across the outer surface.

In both sexes of all the species of *Isonychia* occurring in eastern North America, the fore leg is mostly or entirely red-brown, and the middle and hind legs are light yellow or white. The fore tarsus in the males is approximately equal in length to the fore tibia, and is only one and one-third to one and one-half times as long as the fore tarsus in the females. The hind tarsus in both sexes has four clearly differentiated segments. The wings, fig. 217, are relatively broader and shorter than in the members of the subfamily Siphlonurinae. The fore wing has the stigmal crossveins sometimes anastomosed, and the cubital intercalaries extend from vein Cu_1 to the anal wing margin as a series of sinuate, branched veins. The hind wing lacks an angulate or acute, basal costal projection, and vein M is forked very near the outer wing margin. Rudimentary gills persist on the fore coxa in the adults of both sexes. There is a large, blunt, median projection on the mesosternum, between the mid-coxae.

The male genitalia are composed of a pair of short penis lobes and a pair of four-segmented forceps, the first segment of each arm being very obscurely set off. The forceps base is medianly excavated to form a more or less U-shaped cavity, and the characteristically short, stubby penes lie over or within this cavity, figs. 248–253. In this genus, there are four types of penis lobes: the *sicca,* fig. 252, the *bicolor,* fig. 253, the *diversa,* fig. 249, and the *sayi,* fig. 248. The terminal abdominal sternite in the adult females is usually emarginate on the meson of the posterior margin. The median caudal filament in both sexes is represented by a minute vestige.

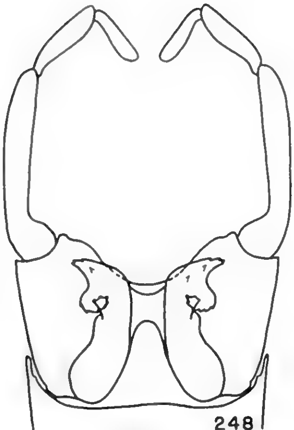
The nymphs, fig. 254, are streamlined, vigorously swimming forms which invariably develop in the rapidly flowing water of creeks and smaller rivers. They are known to be in part predaceous (Morgan 1913:386; Clemens 1917:23); their food is principally vegetable detritus and algae, especially diatoms. Each maxilla and fore coxa bears tufts of filamentous gills. Each tarsal claw is single, acutely pointed, and short, being only one-fourth to one-third as long as the tibia. Each fore leg has a dense comb of long, stout setae on the inner margin, fig. 254. This comb of setae is used in gathering food. Each fore tibia bears an apical spur which is nearly one-half as long as the fore tarsus. Each abdominal segment has small, flat, lateral expansions at the lateral margins; the posterolateral angles of these expansions are produced as large, spinelike projections on segments 8 and 9. Abdominal segments 1–7 bear each a pair of gills, the individual gill being composed of a dorsal, platelike member and a ventral, filamentous tuft, fig. 225. There are three well-developed caudal filaments, and each cercus has a dense fringe of setae on the inner side only.

Reliable characteristics for the separation to species of nymphs and females of this genus have not yet been found.

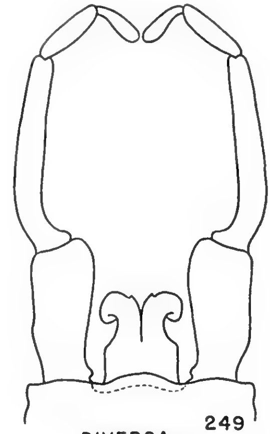
KEY TO SPECIES

ADULT MALES

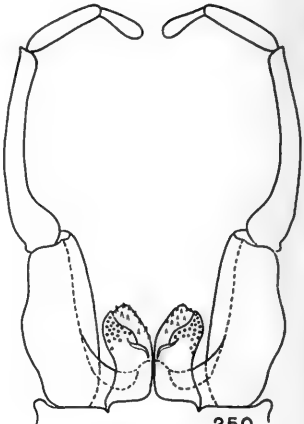
1. Forceps base with only a shallow, median excavation so that penis lobes are almost completely hidden when viewed from ventral side; penis lobes with acute lateral teeth, fig. 248........**1. sayi**
   Forceps base with a deep caudal excavation so that penis lobes are exposed when viewed from ventral side; penis lobes without lateral teeth, figs. 249–253..............................2
2. Penis lobes relatively long, mushroom shaped at apexes, fig. 249...**2. diversa**
   Penis lobes not mushroom shaped at apexes, figs. 250–253...............3
3. Fore tibia white, shaded with brown at base and at apex............**3. arida**



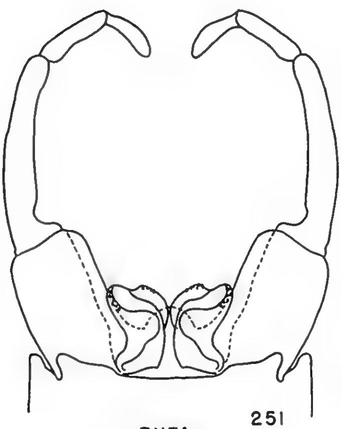
SAYI 248



DIVERSA 249



ARIDA 250



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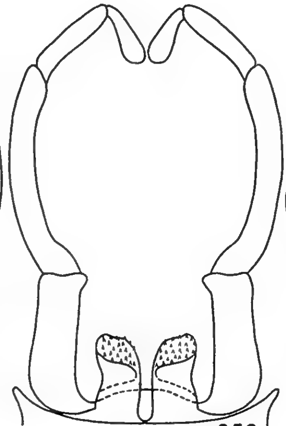
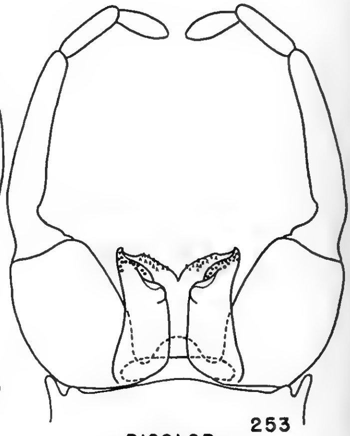


SICCA 252



BICOLOR 253

Fig. 248.—*Isonychia sayi,* male genitalia.
Fig. 249.—*Isonychia diversa,* male genitalia.
Fig. 250.—*Isonychia arida,* male genitalia.
Fig. 251.—*Isonychia rufa,* male genitalia.
Fig. 252.—*Isonychia sicca,* male genitalia.
Fig. 253.—*Isonychia bicolor,* male genitalia.

Fore tibia entirely red-brown, sometimes shaded with darker brown at apex..4

4. Crossveins of disc of fore wing brown; penis lobes relatively short and narrow, fig. 252......................**4. sicca**
Crossveins of disc of fore wing hyaline; penis lobes relatively longer and broader, figs. 251–253....................5

5. Fore wing with stigmatic crossveins relatively numerous and anastomosed, fig. 217......................**5. rufa**
Fore wing with stigmatic crossveins relatively few, not anastomosed...................................**6. bicolor**

1. *Isonychia sayi* new species

Baetis arida? Say. Walsh (1862:370).
Baetis arida Walsh, not Say. Hagen (1863:170); Walsh (1863:191).
Siphlurus aridus Walsh, not Say. Eaton (1871:129).
Chirotonetes aridus Walsh, not Say. Eaton (1885:206).
Isonychia arida Walsh, not Say. McDunnough (1931*c*:159); Traver (1935*a*:485).

The name *sayi* is proposed for the species Walsh identified as *Baetis arida* Say. As is explained on page 111 below, Say's species is another form, long unrecognized. I have seen some of Walsh's original material, as well as McDunnough's and Traver's, and have found that the concept of *arida* Walsh, not Say, has not changed since Walsh's time.

MALE.—Length of body 9–12 mm., of fore wing 10–13 mm. Head light red-brown, antennae white, tinged with brown. Thorax dark red-brown, lighter on pleura; each fore leg brown, with apex of femur darker; wings hyaline, veins faintly tinged with tan, crossveins hyaline. Abdomen dark brown, each tergite and sternite with a large, light yellow-brown spot at either anterolateral angle; each tergite also with a smaller, median, light spot on anterior margin; minute, longitudinal, black lines in spiracular region; genitalia, fig. 248, yellow-brown; caudal filaments light yellow or white.

FEMALE.—Length of body 10–13 mm., of fore wing 12–15 mm. Head yellow-brown. Thorax light red-brown; wings hyaline, veins and crossveins brown. Abdomen dark red-brown, with large, conspicuous, light tan markings: light spot at either anterolateral angle of each tergite, tenth tergite usually entirely light, and entire lateral third of each sternite light; black spot near each spiracle; posterior margin of apical abdominal sternite entire.

Holotype, male.—Rock Island, Illinois, Walsh, 1863. Specimen dry, on pin; genitalia on a microscope slide.

Allotype, female.—Same data as for holotype. Specimen dry, on pin.

The holotype and allotype are in the collection of the Museum of Comparative Zoology and the paratypes listed below are in the collection of the Illinois Natural History Survey.

Known from Indiana, Illinois, and Kansas.

Paratypes.—ILLINOIS.—DIXON: June 27, 1935, DeLong & Ross, 1♂. GULFPORT: Crystal Lake, June 10, 1939, J. S. Ayars, 1♂. OQUAWKA: June 13, 1932, H. L. Dozier, 2♀. PROPHETSTOWN: Rock River, July 24–25, 1947, Burks & Sanderson, 2♀. ROCKFORD: at light, June 29, 1938, B. D. Burks, 1♀. ROCK ISLAND: B. D. Walsh, 1♂, 2♀.

2. *Isonychia diversa* Traver

Isonychia diversa Traver (1934: 244).

This species is included here because it represents one of the four types of male genitalia to be found in the genus. Head and body dark red-brown; wings hyaline, with hyaline veins and crossveins; genitalia, fig. 249, and caudal filaments white.

Known from Tennessee.

3. *Isonychia arida* (Say)

Baetis arida Say (1839:42).

The original description of this species mentions only one character that is specific rather than generic. This is "anterior tibiae whitish, obscure at base and tip." Unfortunately, the species identified as *arida* by Walsh (1862:370) has the anterior tibiae completely brown. Hagen (1863:191) noticed this discrepancy, but concluded that the normal range of variation in the species would include forms with brown and with white tibiae. All workers since Walsh's time have followed his determination of *arida,* although to my knowledge a form of it with white tibiae has never been found. McDunnough (1931*c*:159) stated that there was considerable doubt in his mind that Walsh's determination of *arida* was correct, but that "there seems nothing to be gained by altering his determination and changing the generally accepted idea of the species." I certainly would have followed the same course were it not for the fact that we have an Illinois specimen with white fore tibiae that matches Say's description of *arida* in all particulars. This specimen is quite different from the species determined by Walsh as *arida* and must either be determined as *arida* Say or be described as a new species of extremely doubtful validity. After full consideration of the problem, I have decided that the former course is preferable. Accordingly, the species identified as *arida* by Walsh is renamed *sayi* on page 110 and the name *arida* is here applied to this Illinois specimen, which fully agrees with Say's description.

MALE.—Length of body 9 mm., of fore wing 11 mm. Head light tan, antennae tan, becoming white at apexes of flagella. Thorax red-brown; wings hyaline, veins and crossveins hyaline, stigmal crossveins relatively few, not anastomosed. In fore leg, femur brown, lighter at base; tibia white, darkened with brown at base and tip; tarsus white, segments slightly shaded with brown at apexes. Abdomen red-brown, a transverse stripe of black shading at posterior margin of each tergite; genitalia, fig. 250, white; caudal filaments white.

This species is known from Illinois and Indiana.

Illinois Record.—MOMENCE: at light, August 16, 1938, Ross & Burks, 1♂.

4. *Isonychia sicca* (Walsh)

Baetis sicca Walsh (1862:371).

The lectotype male of this species is in the Museum of Comparative Zoology.

MALE.—Length of body 9–11 mm., of fore wing 10–12 mm. Head dark red-brown, antennae brown, fading to light yellow at tips of flagella. Thorax dark red-brown; wings hyaline, veins and crossveins brown; each fore leg with femur and tibia red-brown, tarsus yellow, with apex of each tarsal segment darkened. Abdomen dark red-brown or very dark purplish red, venter slightly lighter than dorsum; genitalia, fig. 252, light brown or yellow-brown; caudal filaments light yellow to white, with articulations near bases darkened.

FEMALE.—Length of body 10–12 mm., of fore wing 12–14 mm. Head tan, shaded with red-brown. Thorax yellow-brown, with sternum darker brown; wings as in male. Abdomen dull, dark red-brown or purplish red, becoming lighter, yellow brown on apical three segments; caudal filaments light yellow, articulations not darkened.

Known from Illinois, Iowa, Nebraska, and Ontario.

Illinois Records.—EAST DUBUQUE: at light, July 21, 1927, 5♀. FOSTER: Mississippi River, July 4, 1939, B. G. Berger, 1♂. FULTON: July 20, 1927, Frison & Glasgow, 1♂, 11♀. HARRISBURG: at light, Aug. 16, 1937, Ross & Ritcher, 1♂, 1♀. HAVANA: 1♀; June 23, 1894, F. Smith, 1♀; June 24, 1894, 1♀; June 25, 1894, 1♀. HOMER: June 30, 1925, T. H. Frison, 1♀. MOUNT CARMEL: June 30, 1906, 3♀. OREGON: July 9, 1925, T. H. Frison, 1♂. QUINCY: Mississippi River, July 6, 1939, Mohr & Riegel, 1♂; Aug. 13, 1889, C. A. Hart, 1♀. ROCK ISLAND: 3♂, 2♀ (Walsh 1862:371). SAVANNA: July 19, 1892, Forbes, Shiga, Hart, & McElfresh, 3♂, 8♀; July 22, 1892, Hart & Forbes, 4♂; July 27, 1892, McElfresh, Shiga, Forbes, & Hart, 1♀; July 29, 1892, Forbes & Shiga, 1♀. WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 1♂.

5. *Isonychia rufa* McDunnough

Isonychia rufa McDunnough (1931*c*:162).

MALE.—Length of body and of fore wing 10–12 mm. Head light brown, antennae brown, shading to white at apexes of flagella. Thorax bright red-brown, sternum dull red-brown or beige; wings hyaline, veins faintly yellow, crossveins hyaline, stigmatic crossveins anastomosed; fore femur and tibia red-brown, and tarsus yellow, with brown shading at apexes of segments. Abdomen bright red-brown on dorsum, venter lighter, chestnut brown; transverse, black line at posterior margin of each abdominal tergite, this black line often interrupted on meson; genitalia, fig. 251, yellow-brown; caudal filaments light yellow or tan, articulations at base darker.

FEMALE.—Length of body 10–12 mm., of fore wing 12–14 mm. Head and thorax yellow-brown, the latter often also with reddish tinge; veins and crossveins of wings tan or light yellow, stigmatic crossveins anastomosed. Abdomen red-brown on dorsum, pinkish yellow on venter; apical abdominal segment yellow; caudal filaments yellow to white.

Known from Illinois, Iowa, Kansas, Nebraska, and Ohio.

Illinois Records.—APPLE RIVER CANYON STATE PARK: July 3, 1946, Burks & Sanderson, 1♂. AURORA: July 9, 1925, T. H. Frison, 2♀; July 17, 1927, Frison & Glasgow, 7♀. DIXON: May 31, 1914, 1♂. FREEPORT: at light, Aug. 4, 1948, 3♀. KANKAKEE: July 9, 1948, Ross & Burks, 1♀; Aug. 2, 1938, Burks & Boesel, 1♂. MONMOUTH: at light, June 23, 1948, L. J. Stannard, 1♂. OAKWOOD: July 14, 1939, Burks & Riegel, 1♂. ONARGA: at light, July 9, 1948, Ross & Burks, 1♀. OREGON: July 4, 1946, Burks

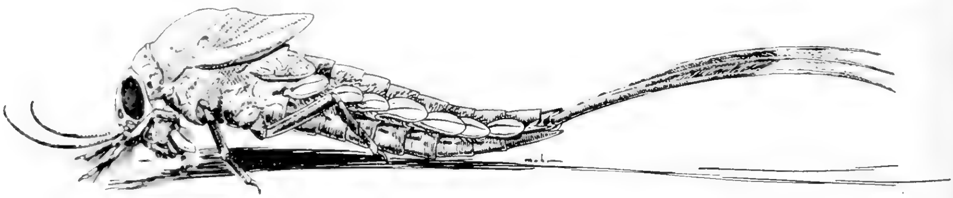


Fig. 254.—*Isonychia sicca*, mature nymph, lateral aspect.

& Sanderson, 5♂, 2♀. PEORIA: July 13, 1940, F. F. Hasbrouck, 1♂. QUINCY: June 2, 1939, Burks & Riegel, 1♂; June 25, 1940, Mohr & Riegel, 1♂. ST. CHARLES: at light, July 8, 1948, Ross & Burks, 2♂. SAVANNA: July 22, 1892, Hart & Forbes, 1♂; July 20, 1927, T. H. Frison, 1♀. WEST CHICAGO: July 9, 1948, Ross & Burks, 1♀. WHITE HEATH: Sangamon River, Aug. 2, 1939, Ross & Riegel, 2♂. WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 7♂, 4♀.

6. *Isonychia bicolor* (Walker)

Palingenia bicolor Walker (1853:552).
Chirotenetes albomanicata Needham (1905:31).

MALE.—Length of body and of fore wing 10–12 mm. Head brown; scape and pedicel of each antenna light brown, flagellum tan at base, becoming yellow toward apex. Thorax dark red-brown, almost black; fore leg same color, with tarsus white, segments shaded with brown at apexes; wings hyaline, veins and crossveins colorless except at costal margin, where they are tan. Abdomen very dark red-brown, the apical segment lighter brown, a narrow, transverse, black band at posterior margin of each tergite; genitalia, fig. 253, tan; caudal filaments light yellow or white, a few basal articulations brown.

FEMALE.—Length of body and of fore wing 12–16 mm. Head yellow or tan, shaded with brown. Thorax yellow-brown, darker on venter; wings with veins and crossveins light brown. Abdomen bright red-brown, with transverse, black-shaded stripe at posterior margin of each tergite; black, longitudinal line and spot at each spiracle; caudal filaments white.

Known from the northeastern and midwestern states and the eastern Canadian provinces.

Illinois Records.—EDDYVILLE: Lusk Creek, May 15–23, 1946, Mohr & Burks, 3♂. KANKAKEE: May 31, 1938, Burks & Mohr, 1♂; June 5, 1932, Frison & Mohr, 1♂; June 15, 1938, Ross & Burks, 2♂; June 17, 1939, B. D. Burks, 1♂, 1♀; July 10, 1925, T. H. Frison, 5♂; July 18, 1925, T. H. Frison, 1♂; Aug. 1, 1933, Ross & Mohr, 1♂; Aug. 2–4, 1938, Burks & Boesel, 9♂, 7♀; Aug. 16, 1938, Ross & Burks, 1♂, 3♀. MOMENCE: June 15, 1938, Ross & Burks, 1♂, 2♀. OAKWOOD: June 6, 1925, T. H. Frison, 1♂; June 9, 1926, Frison & Auden, 1♂; July 24, 1939, B. D. Burks, 3♂, 2♀. POPLAR BLUFF: June 20, 1943, T. H. Frison, 1♂. ROCKFORD: June 13, 1931, Frison & Mohr, 1♂. ROCK ISLAND: June 7, 1937, Burks & Riegel, 1♂; June, 1933, C. O. Mohr, 2♂. WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 2♂, 3♀.

BAETINAE

The most simplified of North American mayflies belong to the subfamily Baetinae. The wing venation is always reduced, both through complete loss of some veins and through partial atrophy of the veins that persist. The basal part of the outer branches of vein Rs and the base of vein M_2 of the fore wing are always atrophied, as in figs. 31, 220–222. The hind wing, figs. 220–222, 270–284, is greatly reduced in size and venation, or wanting entirely. The homologies of the longitudinal veins that persist in the hind wing have not been conclusively determined. When three longitudinal veins persist, however, they perhaps represent the remnants of Sc, R, and M. The middle and hind tarsi, in both sexes, have only three clearly differentiated segments, fig. 15. The male genitalia, figs. 260, 267–269, 289–297, are greatly reduced, the penis lobes being virtually amorphous, membranous, internal structures. There is, between the bases of the forceps, a flaplike penis cover which, in some species of the genus *Baetis*, is obscure. Each arm of the forceps has four segments; the separation between the second and third segments often is so obscure that each arm appears to have only three segments. The adults uniformly have the median caudal filament vestigial in both sexes.

In the members of this subfamily, antigeny is more pronounced than in other mayflies. The compound eyes in the male adults are greatly enlarged and divided, each eye consisting of two distinctly separated portions, figs. 255–257. The eyes in the females are relatively small and simple. This hypertrophy of the eyes in the males has led to the development of a marked difference between the two sexes in the shape of the head. This difference in head shape can be seen in the nymphs as well as in the adults. The nymphs in even the early instars show this difference in head shape. Because of this, the male nymphs in all stages of development may appear quite unlike the female nymphs.

The nymphs, figs. 266, 298, are streamlined and fishlike in body form, each with a labrum having a square notch on the meson of the anterior margin, fig. 231, one or two pairs of wingpads, slender, denticulate, and single tarsal claws, figs. 264, 265, usually single and platelike gills, and two or three well-delevoped caudal filaments.

This entire subfamily is very difficult to treat taxonomically, as really good structural characters for the separation of species have not yet been found. The various species are at present distinguished almost entirely on differences in the color patterns which, unfortunately, in most species are subject to considerable variation. The differentiation of species throughout this subfamily is, thus, made on a rather insecure basis. It often is not possible to separate the females of this subfamily to genus.

KEY TO GENERA

Adult Males

1. Fore wing and hind wing with relatively numerous crossveins, figs. 221, 222. . . . . **29. Callibaetis**
   Fore wing with relatively few crossveins, fig. 220; hind wing with very few crossveins or with none, figs. 270–284, or hind wing wanting entirely 2
2. Hind wing present, although often greatly reduced 3
   Hind wing absent 5
3. Marginal intercalary veins of fore wing single, as in fig. 221 . **30. Centroptilum**
   Marginal intercalary veins of fore wing in pairs, figs. 31, 220, 222 4
4. Hind wing greatly reduced and either without venation or with traces only of a single longitudinal vein . . . . **31. Heterocloeon**
   Hind wing relatively well developed, with two or three longitudinal veins, figs. 270–284 . . . . **32. Baetis**
5. Marginal intercalary veins of fore wing in pairs, as in fig. 220 . . . . **33. Pseudocloeon**
   Marginal intercalary veins of fore wing single, as in fig. 221 6
6. Second forceps segment of male with a prominent, angular projection on mesal margin, fig. 299 . . . . **34. Neocloeon**
   Second forceps segment of male simple, without a mesal projection, fig. 300. . . . . **35. Cloeon**

Mature Nymphs

1. Gills single, platelike on all abdominal segments, fig. 228 2
   Gills double on at least some abdominal segments, or each gill a thin, somewhat irregular sheet with a recurved, dorsal or ventral flap, as in fig. 226 6
2. Hind wingpad absent 3
   Hind wingpad present 4
3. Maxillary palp with two segments; median caudal filament usually vestigial . . . . **33. Pseudocloeon**
   Maxillary palp with three segments; median caudal filament well developed . . . . **34. Neocloeon**
4. Median caudal filament as well developed as the cerci . . . . **30. Centroptilum**
   Median caudal filament reduced or vestigial 5
5. Suture between second and third segments of labial palp partly or completely obliterated; second segment without an apicomesal projection, fig. 261, median caudal filament vestigial . . . . **31. Heterocloeon**
   Suture between second and third segments of labial palp well marked; second segment with an apicomesal projection, figs. 258, 259, 262, 263, median caudal filament reduced or vestigial . . . . **32. Baetis**
6. Hind wingpad absent . . . . **35. Cloeon**
   Hind wingpad present 7
7. Maxillary palp with three segments; each abdominal gill with an inconspicuous dorsal flap . . . . **30. Centroptilum**
   Maxillary palp with two segments; each gill borne by abdominal segments 1 and 2 with two well-developed laminae, each gill borne by more posterior segments with only a relatively small, recurved ventral flap, fig. 226 . . . . **29. Callibaetis**

29. *CALLIBAETIS* Eaton

Callibaetis Eaton (1881:196).

In *Callibaetis*, the upper portion of each compound eye in the males is stalked, but this stalk is relatively low, fig. 257. The width of the vertex separating the compound eyes in the females is about twice as great as the length of one eye. In the fore wing in the males, the basal costal crossveins are weak or wanting, but these crossveins are well developed in the fore wing in the females. The fore wing in the males usually is not pigmented, but in the females it is, at least in the costal and subcostal interspaces in Nearctic species. Two general types of arrangements of the crossveins of the fore wing are to be found in this genus: in one type, there are relatively few crossveins, with none very near the posterior wing margin, and the crossveins form a single irregular row across the wing, fig. 221; in the other type, there are relatively numerous crossveins, some of them located near the posterior wing margin, and the

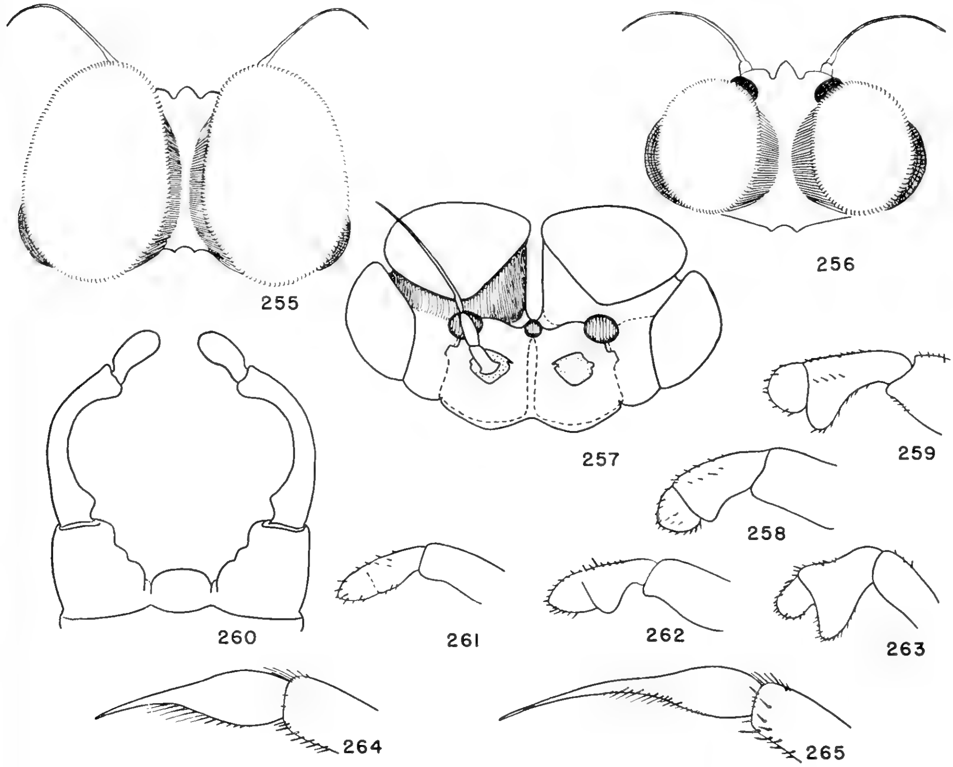


Fig. 255.—*Baetis intercalaris*, head of adult male, dorsal aspect.
Fig. 256.—*Baetis flavistriga*, head of adult male, dorsal aspect.
Fig. 257.—*Callibaetis fluctuans*, head of adult male, anterior aspect.
Fig. 258.—*Baetis intercalaris*, labial palp of mature nymph.
Fig. 259.—*Baetis brunneicolor*, labial palp of mature nymph.
Fig. 260.—*Callibaetis skokianus*, male genitalia.
Fig. 261.—*Heterocloeon curiosum*, labial palp of mature nymph. (After Ide.)
Fig. 262.—*Baetis vagans*, labial palp of mature nymph.
Fig. 263.—*Baetis frondalis*, labial palp of mature nymph. (After Ide.)
Fig. 264.—*Callibaetis fluctuans*, claw of middle leg of mature male nymph.
Fig. 265.—*Callibaetis ferrugineus*, claw of middle leg of mature male nymph.

crossveins form two or more quite irregular rows across the wing, fig. 222. The hind wing is well developed, with abundant crossveins.

The bodies in most species of this genus are thickly sprinkled with minute, brown dots set in small depressions. Similar punctate dots also are often found on the legs. The male genitalia consist of a pair of four-segmented forceps, with a rounded or conic penis cover located between the bases of the forceps. Each basal forceps segment is short and wide, the second segment is narrow, tapering, and indistinctly separated from the third segment, the latter is long, slender, and bowed, while the fourth segment is short, being only about twice as long as wide.

In *Callibaetis* subimagoes, the wings are dark gray, with the paths of the veins and crossveins white.

The nymphs, fig. 226, are streamlined forms which swim with a rapid, darting motion. They live in still water, usually in permanent ponds. The nymphal maxillary palps have two and the labial palps have three segments. The tarsal claws are long and slender, and provided with a row of minute ventral denticles, figs. 264, 265. The abdominal gills are sheetlike and slightly undulated, with a dense net of pinnately branching tracheae. The first and second pairs of gills are always double, with the ventral member often bearing a secondary, recurved flap. The gills on segments 3–6 are single, each having a well-developed, recurved ventral flap. These ventral gill flaps decrease in size from front to rear, so that the recurved flap borne by each gill of segment 3 is almost as large as the gill itself, while the recurved flap of each gill of segment 7 is so small as to be easily overlooked, fig. 226. There are three equally long caudal filaments; the cerci are fringed with long setae on the mesal side only.

Many of the species of this genus are said to be ovoviviparous.

This genus includes about 20 Nearctic species, 3 of which occur in Illinois.

Characteristics for the separation to species of the females of this genus in both adult and nymphal stages have not yet been found.

KEY TO SPECIES

ADULT MALES

1. Crossveins in fore wing in area posterior to vein R_1 relatively few in number, forming a single row across disc of wing, and with none located very near outer wing margin, fig. 221 . . . . **1. fluctuans**
   Crossveins in fore wing in area posterior to vein R_1 relatively abundant, forming two irregular rows across disc of wing, and with many located close to outer wing margin, fig. 222 2
2. Costal margin of fore wing hyaline . . . . **2. ferrugineus**
   Costal margin of fore wing partly or completely shaded with brown or tan 3
3. Fore wing shaded with brown at base only . . . . **3. brevicostatus**
   Fore wing shaded with light tan in costal area from base to apex of wing . . . . **4. skokianus**

MATURE MALE NYMPHS

1. Length of body 12–13 mm. . **4. skokianus**
   Length of body not over 10 mm. 2
2. Claw of fore leg relatively long and slender, the length more than five times greatest thickness, fig. 265; abdominal gills of seventh pair double . . . . **2. ferrugineus**
   Claw of fore leg relatively short and stout, the length less than four times greatest thickness, fig. 264; abdominal gills of seventh pair single . . . . **1. fluctuans**

1. *Callibaetis fluctuans* (Walsh)

Cloe fluctuans Walsh (1862:379).

This species was described from the female only, and the types are lost.

MALE.—Length of body 5.5–7.0 mm., of fore wing 6–8 mm., of caudal filaments 10–12 mm. Head, fig. 257, brown, light yellow around bases of antennae and on lateral areas of frontal shelf; eyes brown when insect is alive; each antennal scape and pedicel brown, flagellum light yellow. Dorsum of thorax brown, venter almost entirely light yellow, with only a few brown, punctate dots on mesosternum; wings hyaline, fig. 221, without any coloration, all veins and crossveins hyaline; costal crossveins of fore wing wanting entirely or vestigial, stigmatic crossveins not anastomosed, slanting, 5–7 in number; crossveins in disc of wing relatively few, fig. 221, marginal intercalaries on outer margin usually single, sometimes double; legs light yellow, fore leg faintly stained with brown near apex of femur and at base and apex of tibia; middle and hind legs each with faint brown staining near apex of femur and with a minute, brown dot at apex of each tarsal segment. Abdomen light yellow, with brown shading: tergite 1 dark brown on meson; tergites 2–9 each completely shaded with light brown except for a narrow, longitudinal, pale streak on meson, a fairly large spot at anterior margin near each anterolateral angle, and a narrow line crossing tergite at posterior margin; a pair of dark brown, submedian dots at anterior margins of tergites 4–10, a pair of short, curved, dark brown dots near anterolateral angles of each abdominal tergite, and a pair of longitudinal, dark brown marks at lateral margins of tergites 1–7; abdominal sternum light yellow, with a pair of short, curved, submedian, dark brown marks near anterior margin of each sternite, and usually a minute, dark brown dot at anterolateral angles of each sternite. Genitalia light yellow; caudal filaments white, articulations not darkened.

FEMALE.—Length of body 6–8 mm., of fore wing 7–9 mm., of each caudal filament 9–10 mm. Coloration much as in male, but brown shading of dorsum of thorax more restricted. When insect is alive, pink staining visible on vertex, on dorsal area of pronotum, and on mesonotum anterior to wing bases; wings hyaline, brown stained in costal, subcostal, and first radial interspaces, this staining often extending on membrane slightly posterior to vein R_2 at apex and in basal area of wing, and on veins as far back as M_1; brown staining interrupted around crossveins; in living insect, pink staining present in wing on basal two-thirds of veins Sc and R_1 and on crossveins in this area, costal crossveins present but irregular and often broken, stigmatic crossveins slanting, irregular, sometimes partly anastomosed, 8 to 12 in number; femur of each leg usually with faint brown shading extending from base to apex, on outer side. Abdomen with dark brown spots as in male, but dorsal, light brown shading faint or wanting; dorsum usually with many minute, punctate, brown dots scattered over surface; sternum punctate, but brown dots few; caudal filaments as in male.

NYMPH.—Length of body 8–9 mm. Head brown, with a white spot just dorsal to each antennal socket and on meson between sockets; each antenna as long as fore leg. Thorax brown, with minute, white mottling on mesonotum; legs uniformly light brown. Abdominal dorsum mostly brown, with small area at base and apex of lateral projection of each segment white, a single median spot or two submedian, coalescing spots on each tergite, and a longitudinal, white stripe on either side of median spot on each of tergites 2–8; gills semihyaline, tracheae lavender-brown; each gill borne by segments 1 and 2 triple, gills of segments 3–6 double, seventh gill single; caudal filaments each with a subapical, dark brown crossband.

Known from Illinois, Iowa, New York, and Wisconsin.

Illinois Records.—Specimens, collected April 23 to November 3, are from Belleville, Brussels, Cairo, Chambersburg, Collinsville, Grand Tower, Greenville, Havana, Herod (pool near Gibbons Creek), Jonesboro, Morris, Mount Carmel, Muncie, Oakwood, Peoria, Pingree Grove, Quincy, Rantoul, Rock Island, Rosiclare, Springfield, St. Jacob, St. Joseph, Sterling, Urbana, Waukegan, and Western Springs.

2. *Callibaetis ferrugineus* (Walsh)

Cloe ferruginea Walsh (1862:379).

There is at present in the Museum of Comparative Zoology a single male specimen, determined as of this species by Walsh, which was collected at Rock Island, Illinois, a year after the original description was published. Unfortunately, it is badly broken but, insofar as the characters can be seen on this fragmentary specimen, it is in agreement with the current concept of the species. The female was unknown to Walsh, but the association of the correct female to be placed with the male has been arrived at through the rearing of adults of both sexes from lots of nymphs that almost certainly represented pure cultures of the species.

MALE.—Length of body 7.0–8.5 mm., of fore wing 8.0–9.5 mm. Color extremely variable, ranging from almost completely light yellow, with a few minute, brown spots, to almost completely brown, with darker brown or black markings. Head brown, with face below antennae white; each antennal scape and pedicel white, with apexes brown, flagellum white at base, gray or tan distad; upper eyes tan, lower gray, each with a brown, longitudinal stripe. Thorax brown to yellow, with dark, punctate spots on pleura and venter; wings hyaline, three costal veins faintly yellow; marginal intercalaries of outer margin of each fore wing usually double; legs white to yellow, femora often with dark red, punctate spots, all femora vaguely darkened at apexes, each fore tibia red-brown at apex. Abdomen varying from yellow to almost black; dark, punctate spots present over most of surface, a dark, longitudinal, median, dorsal stripe often present; genitalia and caudal filaments white.

FEMALE.—Length of body 8–9 mm., of fore wing 9–10 mm. Body invariably darker than that of male, varying from tan to almost black. Head usually grayish tan or brown, face below antennal sockets white to tan, eyes gray, with brown band. Thorax usually dull gray-brown on dorsum; wings hyaline, each typically with dark brown shading occupying entire anterior three interspaces and usually extending posteriorly onto R, sometimes reaching almost to vein M, fig. 222; veins often alternately brown and white and outer margin of wing often spotted with brown; hind wing usually brown at base; legs yellow to tan or light brown; all femora always with broad, darkened areas at apexes. Abdomen usually dark brown to almost black; caudal filaments white, occasionally with some basal articulations darkened.

NYMPH.—Fig. 266. Length of body 8–9 mm. Head brown, with a white spot just dorsal to each antennal socket, on either gena just ventral to each compound eye, and on meson between antennal sockets; each antenna slightly longer than fore leg. Thorax brown, slightly mottled with darker brown

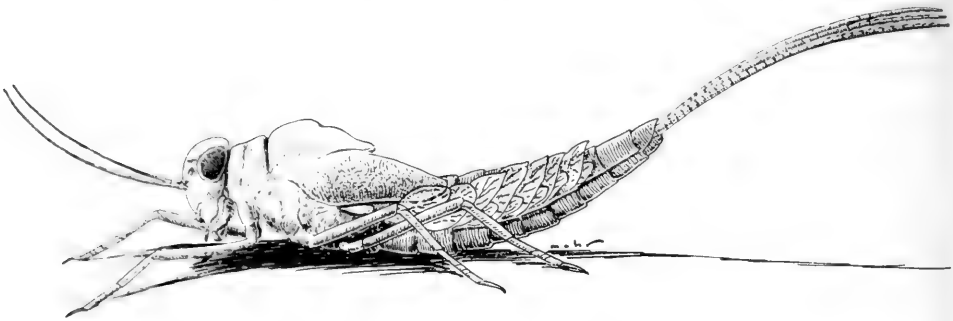


Fig. 266.—*Callibaetis ferrugineus,* mature nymph, lateral aspect.

and white on notum; legs tan, each femur with a subapical, dark brown ring. Abdominal dorsum usually mostly tan or white, with a median, dark brown spot at either lateral margin and a pair of large, sublateral, dark brown spots on each tergite 2–7; median area of tergites 2 and 3 dark brown; tergites 8–9 mostly light brown; gills white, tracheae purple-brown, those on segments 1 and 2 triple, and on segments 3–7 double; caudal filaments each with a dark brown, subapical crossband.

Known from Illinois, Iowa, Maine, Maryland, Michigan, New York, and Wisconsin.

Illinois Records.—Specimens, collected April 18 to September 23, are from Antioch, Channel Lake, East Dubuque, Elgin, Fox Lake, Freeport, Giant City State Park, Havana, Kickapoo State Park, Lake Bluff, McHenry, Richmond, Rockford, Rock Island, Rosecrans, Spring Grove, St. Charles, Waukegan, Wolf Lake, and Zion.

3. *Callibaetis brevicostatus* Daggy

Callibaetis brevicostatus Daggy (1945:388).

This species may prove to be a synonym of *semicostatus* Banks (1914:614), which was described from Manitoba.

MALE.—Length of body and of fore wing 8 mm. Fore wing stained with brown at bases of veins Rs to M, but otherwise hyaline; longitudinal veins brown, crossveins hyaline; costal crossveins weak but present, stagmatic crossveins slanted and partly anastomosed; fore wing with numerous crossveins and paired marginal intercalary veins. Abdomen brown, and densely covered with dark brown, punctate dots; genitalia and caudal filaments white.

Known from Minnesota and Saskatchewan.

4. *Callibaetis skokianus* Needham

Callibaetis skokianus Needham (1903:215).

This species might eventually prove to be a synonym of *ferrugineus*, as the two are separated principally on the color of the wings, a character that is known to vary in other species of the genus. Long series of specimens of both *skokianus* and *ferrugineus* have, however, been studied and no intergrades between the two have as yet been found.

Our recent collecting in Illinois has failed to produce the nymph of this species. The only specimens of the nymph of *skokianus* I have seen are those in the Cornell University collection, and they are in very poor condition.

MALE.—Length of body and of fore wing 9–10 mm. General color bright yellow-brown or tan, shaded with dark red-brown. Head yellow-brown, face tan below antennal sockets; each antennal scape yellow, brown at apex, pedicel usually entirely brown, flagellum yellow at base, shaded with brown in middle, white at apex; upper portion of each eye yellow, lower tan, with a brown band across middle. Thorax yellow or tan; a broad, median, longitudinal, dark brown stripe present on mesonotum; pleura and sternum usually with brown, punctate dots; legs yellow or white, with apexes of all femora lightly shaded with tan, and each fore tibia and tarsus entirely tan to brown; wings hyaline, three costal interspaces of each fore wing washed with tan or light yellow-brown, stigmatic crossveins anastomosed, marginal intercalaries of outer wing margin usually double. Abdomen chestnut brown, with numerous dark brown, punctate dots, a dark brown, longitudinal, median band usually extending the length of the abdominal tergum, this band often interrupted at each suture, a large, dark brown spot present near either anterolateral angle of each tergite; abdominal sternum lighter yellow-brown than dorsum, each sternite with a pair of submedian, parenthesis-shaped, brown marks; genitalia, fig. 260, yellow to white; caudal filaments white.

FEMALE.—Length of body 9–10 mm., of fore wing 10–11 mm. Head and body generally lighter in color than those of male. Head yellow to almost white, with tan shading, face below antennal sockets always white. Thorax yellow to tan, dorsal, longitudinal, median stripe light brown, legs white; all femora usually vaguely washed with tan, brown shading at apexes of all tarsal segments; wings hyaline, longitudinal veins of each fore wing anterior to M tan, first three interspaces of fore wing shaded with chestnut brown, this shading interrupted at crossveins, brown shading also extending over small part of basal area of posterior radial, median, and cubital interspaces; hind wing not shaded. Dorsum of abdomen light brown, thickly sprinkled with dark brown, punctate dots; venter tan to almost white; caudal filaments white.

NYMPH.—Length of body 12–13 mm. Head light yellow to white, with brown shading on frons, between eyes, and ventral to ocelli between antennal sockets. Thorax light yellow, with brown shading on mesonotum and on wingpads; legs white, tarsi tinged with brown. Abdomen mostly light yellow on dorsum, a median, interrupted, longitudinal, brown stripe usually present, this brown area spreading on tergites 2 and 3 to cover most of exposed dorsal area; gills hyaline, tracheae brown; gills on segments 1 and 2 triple, those on 3–7 double, ventral lobe on seventh gill greatly reduced; caudal filaments darkened near apexes.

Callibaetis skokianus is known from Illinois, Minnesota, Missouri, New York, North Dakota, and Ontario. It was originally described from a very long series of specimens collected over a 4-year period at the turn of the century from a pond on the campus of Lake Forest College located on the shore of Lake Michigan north of Chicago. This pond has now disappeared, and intensive, recent collecting and rearing in that area has failed to yield additional specimens, but a few scattered ones have been taken elsewhere in the state.

Illinois Records.—AURORA: July 17, 1927, Frison & Glasgow, 1 ♀. EAST DUBUQUE: at light, July 21, 1927, Frison & Glasgow, 1 ♀. FREEPORT: at light, June 10–11, 1948, Burks, Stannard, & Smith, 1 ♀; Aug. 4, 1948, Burks & Stannard, 1 ♀. HAVANA: April 14, 1894, Hart & Hempel, 1 ♂; April 17, 1894, Hart & Hempel, 1 ♂; April 18–19, 1894, C. A. Hart, 2 ♂. LAKE FOREST: in pond on college campus, April–May, 1899, J. G. Needham, 29 ♂; May, 1902, J. G. Needham, ♂ ♂, ♀ ♀, nymphs. PINGREE GROVE: May 9, 1939, Ross & Burks, 4 ♂.

30. *CENTROPTILUM* Eaton

Centroptilum Eaton (1869:132).

In this genus, the stalk of each turbinate eye in the males is quite low, so that the lower portion of the eye is almost in contact with the faceted upper portion. The width of the vertex separating the compound eyes in the females is only slightly greater than the length of one eye. Typically, the head and thorax in the males are dark brown, with the abdomen light, but often strikingly marked on the dorsum with red or red-brown; the females are generally light in color, the abdominal tergites heavily marked with black tracheal lines. Each fore wing has relatively few crossveins and the marginal intercalary veins are single. The hind wing is long and slender, with a hooked, costal, subbasal projection; with two longitudinal veins and sometimes with vestigial third vein; the crossveins are wanting or vestigial. The male genital forceps are four segmented, the first segment being short and broad, the second also short and broad with, typically, a prominent tubercle on the mesal margin, the third segment is slender and usually not strongly bowed, and the fourth segment is often three or four times as long as broad; occasionally, the fourth segment is only as long as broad. There is a large, variously shaped penis cover between the bases of the forceps arms.

The nymphs are streamlined, vigorously swimming forms, typically developing in the shallow, rapidly flowing water of brooks and creeks. The nymphal labial and maxillary palps have each three segments. The claws are long and slender, and lack ventral denticles. The abdominal gills are platelike and usually single on all segments; in some species each gill borne by the basal segments has a recurved, dorsal flap. There are three well-developed caudal filaments.

Centroptilum includes 22 Nearctic species, only 3 of which occur in Illinois.

Characteristics for the separation to species of the females and nymphs in this genus have not yet been found.

KEY TO SPECIES

Adult Males

1. Entire mid-dorsal area of the abdomen shaded with dark red .... **3. quaesitum**
   Dorsal area of abdomen not entirely shaded with red; tergites 2–6 white or faintly yellow, with small spots or lines of red or black 2
2. Posterior margin of each of middle abdominal tergites with a pair of transverse, sublateral, red lines; longitudinal, black spiracular lines present at lateral margins of tergites 2–6 .... **2. rufostrigatum**
   Abdominal tergites without transverse, red lines; only black spiracular lines present .... **1. walshi**

1. *Centroptilum walshi* McDunnough

Centroptilum walshi McDunnough (1929: 173).

Male.—Length of body and of fore wing 6 mm. Head pale yellow, upper portion of each turbinate eye yellow in life, each antenna yellow, flagellum faintly tinted with tan in basal third. Thorax pale yellow, shaded with light brown on median dorsal area; legs light yellow to white, a minute, longitudinal, black line present on ventral side of each posterior femur; wings completely hyaline, hind wing five times as long as broad, with two longitudinal veins. Abdomen pale yellow, almost white, with irregular, longitudinal, black spiracular line at each lateral margin of tergites 1–7, and tergites 8–10 entirely but lightly shaded with tan; forceps pale yellow, second forceps segment with a prominent tubercle on mesal margin, and apical margin of forceps baseplate evenly rounded from side to side, fig. 267; caudal filaments white.

Female.—Length of body and of fore wing each 5.5–6.5 mm. Entire body pale green when insect is alive, quickly fading to light yellow; thorax lacking brown shading, but abdominal tergites heavily blotched laterally with black and apical abdominal tergite shaded with brown.

Known from Illinois, Iowa, and Kansas.

Illinois Records.—Beardstown: at light, June 13, 1946, Mohr & Burks, 2 ♀. Homer: June 30, 1925, T. H. Frison, 1 ♂, 3 ♀. Oakwood: June 8–9, 1926, Frison & Auden, 1 ♂, 3 ♀. Sterling: at light, June 22, 1948, L. J. Stannard, 1 ♂. Urbana: June 1, 1941, T. H. Frison, 2 ♀.

2. *Centroptilum rufostrigatum* McDunnough

Centroptilum rufostrigatum McDunnough (1924*b*: 95).
Centroptilum bistrigatum Daggy (1945: 389). New synonymy.

I have studied types of both *rufostrigatum* and *bistrigatum* and find them unquestionably of the same species.

Male.—Length of body and of fore wing 4.5–5.0 mm. Head very dark brown, antennae light brown; upper portion of each compound eye bright yellow in life. Thorax dark brown, lighter brown on venter; wings hyaline, hind wing four and one-half times as long as broad, with two longitudinal veins, three or four faint crossveins, and with the costal projection long and hooked; legs yellowish white, coxae light brown. First abdominal segment tan, segments 2–6 white, segments 7–10 dark brown above, white below, a pair of transverse, sublateral, red lines present at posterior margin of each of tergites 2–8, usually these red marks on tergites 7 and 8 visible only on living specimens or specimens preserved in alcohol; longitudinal, black spiracular lines usually present at lateral margins of tergites 2–6; genitalia, fig. 268, white, apical forceps segment minute; caudal filaments white.

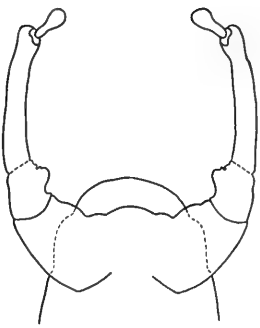
Female.—Length of body 4.5–5.0 mm., of fore wing 5–6 mm. Head and thorax light brown, dorsum of abdomen uniformly light brown, with transverse, red lines at posterior margins of tergites as in male; longitudinal, black spiracular lines of male replaced by heavy, black spiracular blotches at lateral margins; legs and caudal filaments white.

Known from Illinois, Manitoba, Minnesota, New Brunswick, and Wisconsin.

Illinois Records.—Kankakee: July 10, 1925, T. H. Frison, 1 ♂. Oakwood: July 30, 1939, B. D. Burks, 1 ♂.

3. *Centroptilum quaesitum* McDunnough

Centroptilum quaesitum McDunnough (1931*b*: 87).



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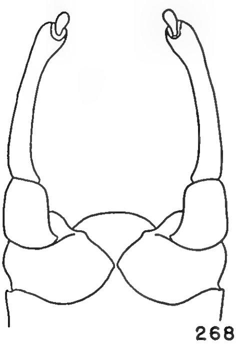

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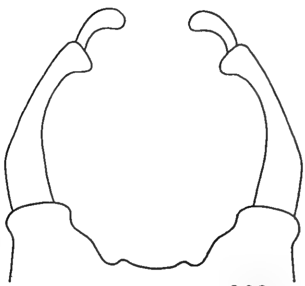


269

Fig. 267.—*Centroptilum walshi*, male genitalia. (After McDunnough.)

Fig. 268.—*Centroptilum rufostrigatum*, male genitalia.

Fig. 269.—*Heterocloeon curiosum*, male genitalia.

MALE.—Length of body and of fore wing 6–7 mm. Head light yellow; scape and pedicel of each antenna yellow, flagellum gray-tan. Thorax tan, pleura faintly stained with red, sternum mostly yellow; legs light yellow, almost white, with each fore femur faintly stained with tan, and each fore tibia and tarsus slightly darkened with gray; wings hyaline, hind wing three and one-half times as long as broad. Entire abdominal tergum, except for narrow area at lateral margins, uniformly shaded with dark red; abdominal venter faint yellow, almost white; genitalia and caudal filaments white.

Known from Alberta and Illinois.

Illinois Record.—CAIRO: at light, July 17, 1947, L. J. Stannard, 1 ♂.

31. *HETEROCLOEON* McDunnough

Heterocloeon McDunnough (1925*b*:175).

In this genus, each fore wing has the marginal intercalary veins arranged in pairs. Each hind wing is reduced to a narrow, almost threadlike vestige which is either entirely without venation or with faint traces of a single longitudinal vein, and is also without a costal projection. The fore tarsus in the males is from one-half to two-thirds as long as the fore tibia. Each arm of the male genital forceps has four segments: the first segment is short and broad, with a small protuberance near the mediobasal angle; the second segment is narrower and conical; the third is long, slender, and bowed, with the medioapical angle produced; and the fourth segment is small, about two and one-half times as long as broad. The penis cover is emarginate on the meson, with each lateral angle conically produced.

In the nymphs, the labial palp, fig. 261, has the suture between segments 2 and 3 partly or completely obliterated and segment 2 is not expanded at the mesoapical angle; the gills are single and platelike, with well-marked, pinnately branched tracheae; there are but two caudal filaments that are well developed.

Heterocloeon curiosum (McDunnough)

Centroptilum curiosum McDunnough (1923:43).
Heterocloeon curiosum (McDunnough). McDunnough (1925*b*:175).
Baetis (*Acentrella*) *curiosum* (McDunnough). Ide (1937*b*:235).

MALE.—Length of body 4.5–5.0 mm., of fore wing 5.0–5.5 mm. Head and thorax very dark brown to black; legs white, with the fore femur shaded with gray and all coxae dark brown; wings hyaline, stigmatic crossveins of fore wing partly anastomosed; hind wing reduced to a narrow vestige, usually entirely without venation, but sometimes with traces of one longitudinal vein. Abdominal segments 2–6 white, or stained faintly with yellow or brown, apical abdominal segments chestnut brown, genitalia and caudal filaments white; apical forceps segments, fig. 269, each three times as long as wide.

Known from Maryland, New York, Ontario, and Quebec.

32. *BAETIS* Leach

Baetis Leach (1815: 137).
Brachyphlebia Westwood (1840: 25).
Acentrella Bengtsson (1912: 110).

In *Baetis,* the stalk of each turbinate eye of the male is relatively high, so that

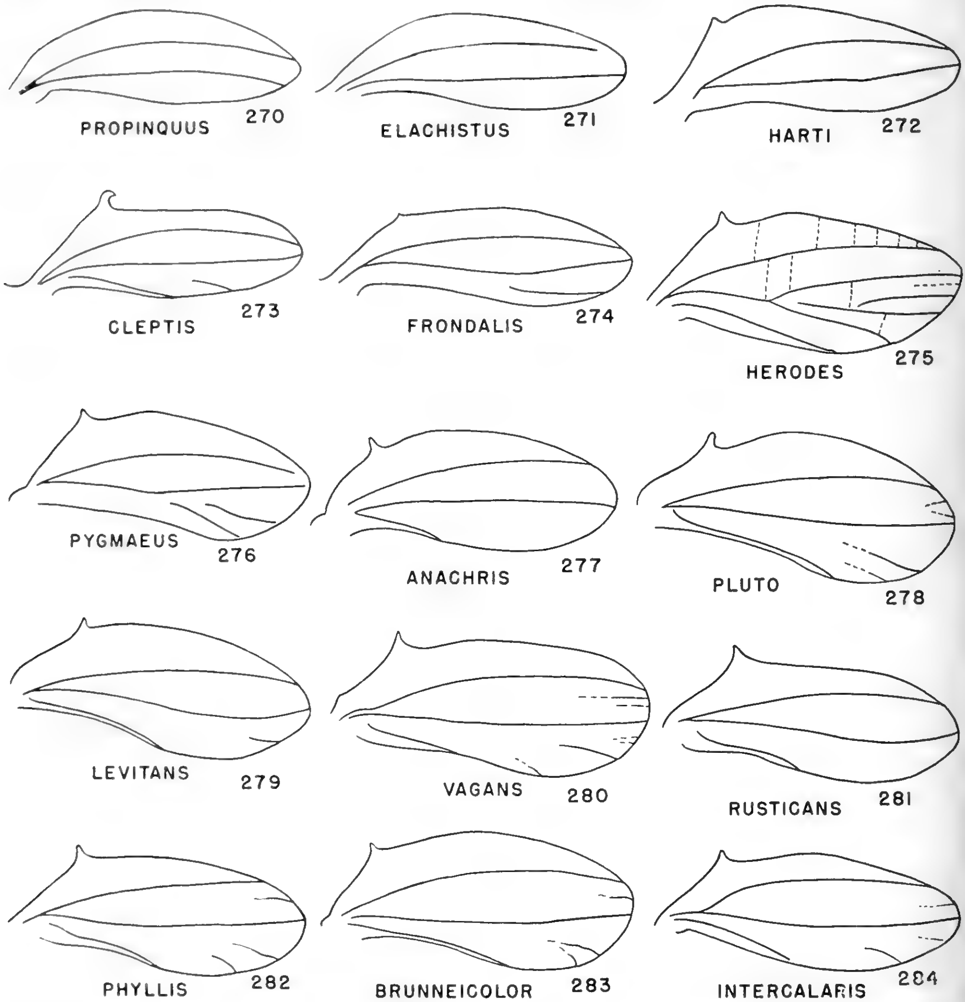


Fig. 270.—*Baetis propinquus,* hind wing of adult male.
Fig. 271.—*Baetis elachistus,* hind wing of adult male.
Fig. 272.—*Baetis harti,* hind wing of adult male.
Fig. 273.—*Baetis cleptis,* hind wing of adult male.
Fig. 274.—*Baetis frondalis,* hind wing of adult male.
Fig. 275.—*Baetis herodes,* hind wing of adult male.
Fig. 276.—*Baetis pygmaeus,* hind wing of adult male.
Fig. 277.—*Baetis anachris,* hind wing of adult male.
Fig. 278.—*Baetis pluto,* hind wing of adult male. (After McDunnough.)
Fig. 279.—*Baetis levitans,* hind wing of adult male.
Fig. 280.—*Baetis vagans,* hind wing of adult male.
Fig. 281.—*Baetis rusticans,* hind wing of adult male. (After McDunnough.)
Fig. 282.—*Baetis phyllis,* hind wing of adult male.
Fig. 283.—*Baetis brunneicolor,* hind wing of adult male.
Fig. 284.—*Baetis intercalaris,* hind wing of adult male.

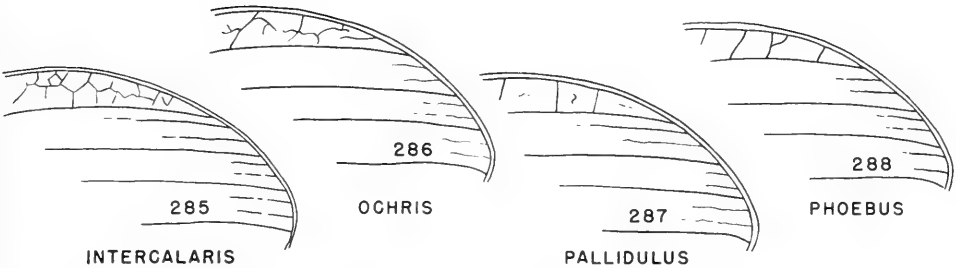


Fig. 285.—*Baetis intercalaris,* anteroapical area of fore wing of male.
Fig. 286.—*Baetis ochris,* anteroapical area of fore wing of male.
Fig. 287.—*Baetis pallidulus,* anteroapical area of fore wing of male.
Fig. 288.—*Baetis phoebus,* anteroapical area of fore wing of male.

the upper faceted portion of the eye is widely separated from the lower portion, figs. 255, 256. The width of the vertex separating the compound eyes in the females is usually three times as great as the width of one eye. Each fore tarsus in the males varies from slightly shorter to slightly longer than each fore tibia. Each fore wing has relatively few crossveins, and the marginal intercalaries are paired, figs. 31, 220. Each hind wing is relatively long and narrow, with or without an acute costal projection, sometimes with two but usually with three longitudinal veins, of which the third is always shortest, virtually or quite without crossveins, and with intercalary veins commonly present, figs. 270–284. The male genitalia, figs. 289–297, consist of a pair of four-segmented forceps and a penis cover. This cover varies from a well-developed, flaplike lobe to a small, extremely inconspicuous, membranous papilla. In some specimens, it is quite difficult to demonstrate the penis cover. The saclike and amorphous penis is membranous and internal, but can be seen extruded on an occasional specimen. The cerci are longer than the body.

The nymphs, fig. 298, are streamlined, and live in shallow running water. They are most commonly found under stones and among debris or emergent vegetation along the banks of brooks or creeks. The maxillary palp has two or three segments; the labial palp has three. The legs are relatively long and slender, with long, narrow claws, each of which bears minute denticles on the inner ventral surface. In all known species, the gills are single and platelike, fig. 228. The median caudal filament is either shorter than the cerci or vestigial.

In order to study the species in this genus, it is necessary to make dry mounts of the wings, especially the hind wings, and to clear, stain, and make slide mounts of the male genitalia. The latter operation must be done with extreme care, as these genitalia are quite fragile and, also, easily distorted while being manipulated.

The genus *Baetis* is one of the largest and most difficult genera of the mayflies. It includes about 50 Nearctic species, of which 17 are at present known to occur in Illinois; 25 species are treated in this report.

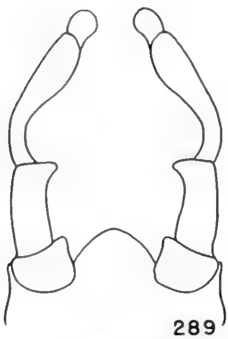
Ide (1937*b*:219) has published complete descriptions and figures of the nymphs of a large number of species of *Baetis.*

Reliable characteristics for the separation to species of adult females and female nymphs of this genus have not yet been found.

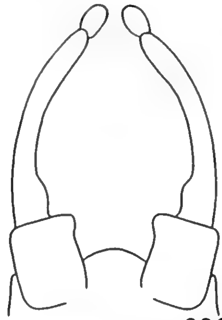
KEY TO SPECIES

ADULT MALES

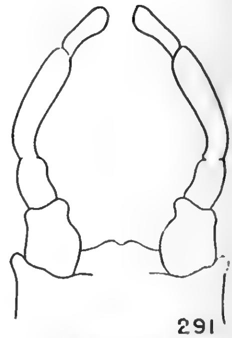
1. A prominent, pointed, mesal projection at apex of second segment of genital forceps arm, fig. 289 . . . . . **1. spinosus**
   No apicomesal projection on second segment of genital forceps arm, figs. 290–297 2
2. Hind wing without a costal projection, figs. 270, 271 3
   Hind wing with a costal projection, figs. 272–284 5
3. Abdominal tergites 2–6 white, or very faintly stained with yellow . . . . . **2. propinquus**
   Abdominal tergites 2–6 mostly or entirely dark brown 4
4. Fourth segment of genital forceps arm as long as wide, fig. 290 . . . . **3. elachistus**
   Fourth segment of genital forceps arm three times as long as wide, fig. 291 . . . . . **4. frivolus**
5. Hind wing entirely without a third longitudinal vein, figs. 272, 274, 276 6
   Hind wing with a third longitudinal vein, figs. 273, 275, 277–284 9
6. Hind wing relatively narrow and lacking marginal intercalary veins posterior to



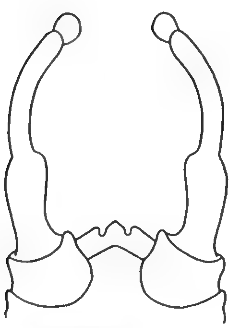
289 SPINOSUS



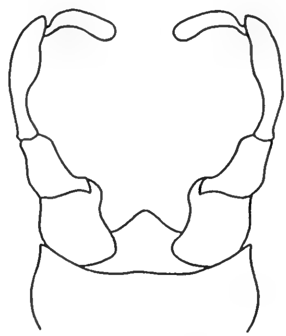
290 ELACHISTUS



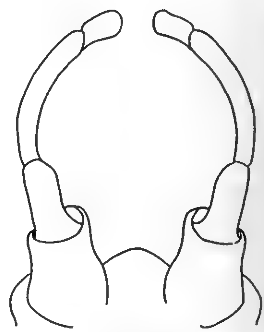
291 FRIVOLUS



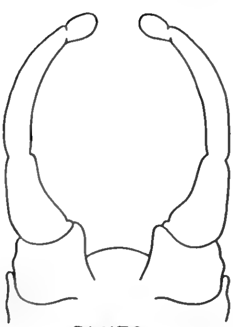
FRONDALIS 292



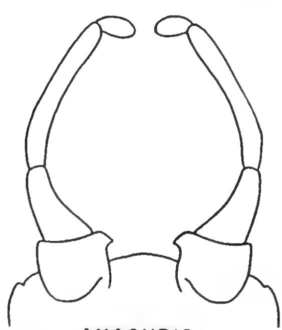
CLEPTIS 293



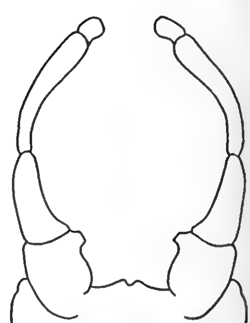
VAGANS 294



PLUTO 295



ANACHRIS 296



INTERCALARIS 297

Fig. 289.—*Baetis spinosus,* male genitalia.
Fig. 290.—*Baetis elachistus,* male genitalia.
Fig. 291.—*Baetis frivolus,* male genitalia.
Fig. 292.—*Baetis frondalis,* male genitalia.
Fig. 293.—*Baetis cleptis,* male genitalia.
Fig. 294.—*Baetis vagans,* male genitalia.
Fig. 295.—*Baetis pluto,* male genitalia. (After McDunnough.)
Fig. 296.—*Baetis anachris,* male genitalia.
Fig. 297.—*Baetis intercalaris,* male genitalia.

second longitudinal vein, fig. 272 .... **5. harti**

Hind wing relatively broad and with one or two long, marginal intercalary veins posterior to second longitudinal vein, figs. 274, 276 7

7\. Abdominal tergites 2–6 entirely white .... **6. pygmaeus**

Abdominal tergites 2–6 almost entirely dark brown, or faintly stained with brown, and with a red crossband at posterior margin of each tergite ... 8

8\. Abdominal tergites 2–6 uniformly dark brown except for anterolateral angles of each tergite .... **7. frondalis**

Abdominal tergite 2 mostly covered by brown staining, tergites 3–6 faintly stained with brown at posterolateral angles and with a medianly interrupted, red crossband at posterior margin of each tergite .... **8. baeticatus**

9\. Second longitudinal vein of hind wing forked, fig. 275 .... **9. herodes**

Second longitudinal vein of hind wing not forked, figs. 273, 277–284 10

10\. Hind wing with an unusually long costal hook, fig. 273 .... **10. cleptis**

Hind wing with a relatively short costal projection, figs. 277–284 11

11\. Male genitalia of the *vagans* type; that is, with the second forceps segment cylindrical, fig. 294 12

Male genitalia of the *intercalaris* type; that is, with the second forceps segment frustate, fig. 297 13

12\. Fore wing 6.5–7.5 mm. long; abdominal sternites 2–6 smoky gray, with a tan tinge .... **11. vagans**

Fore wing 4.5–5.0 mm. long; sternites 2–6 white or faintly yellow . **12. incertans**

13\. Head and thorax bright yellow-tan; abdominal segments 2–6 lightly stained with tan or yellow, apical abdominal tergites light orange-brown or tan ... 14

Head and thorax chestnut brown, dark brown, or black, with apical abdominal tergites same color or lighter red-brown; abdominal segments 2–6 white, pale yellow, or partly or completely brown 15

14\. Marginal intercalaries in second interspace of fore wing shorter than those in first or third interspace, fig. 287; abdominal tergites 2–6 yellow .... **13. pallidulus**

Marginal intercalaries in first three interspaces of fore wing equal in length, fig. 286; abdominal tergites 2–6 white .... **14. ochris**

15\. First genital forceps segment without a mesoapical papilla, fig. 295 16

First genital forceps segment with a mesoapical papilla, figs. 296, 297 17

16\. Thorax very dark brown to black; abdominal tergites 2–6 dark red-brown, with narrow, yellow or tan areas at anterior and lateral margins of each .... **15. pluto**

Thorax dark chestnut brown; abdominal tergites 2–6 light yellow, with transverse, narrow, red-brown line at posterior margin of each ... **16. levitans**

17\. Abdominal tergites 2–6 partly or entirely brown or red-brown 18

Abdominal tergites 2–6 entirely white or pale yellow 23

18\. Compound eyes small, fig. 256 .... **17. flavistriga**

Compound eyes larger, fig. 255 19

19\. Abdominal tergites 2–6 white, with a red-brown band at posterior margin of each .... **18. cingulatus**

Abdominal tergites 2–6 mostly or entirely dark brown 20

20\. Hind wing without marginal intercalary veins, figs. 277, 281 21

Hind wing with marginal intercalary veins, figs. 282, 283 22

21\. Fore wing 5 mm. long, with numerous anastomosed crossveins in stigmatic area; abdominal sternites 2–6 white .... **19. anachris**

Fore wing 4 mm. long, stigmatic area with only two to six nonanastomosed crossveins; abdominal sternites 2–6 a faint smoky gray .... **20. rusticans**

22\. Longitudinal veins of fore wing brown .... **21. phyllis**

Longitudinal veins of fore wing hyaline or only veins Sc and R_1 stained a faint yellow .... **22. brunneicolor**

23\. Fore wing with marginal intercalaries of subcostal interspace two or three times as long as those in first and second R_1 interspaces, fig. 285 ... **23. intercalaris**

Fore wing either with marginal intercalaries absent in subcostal interspace, or, if present, almost as long as those in first and second R_1 interspaces, fig. 288 24

24\. Compound eyes small, as in fig. 256; forewing 4 mm. long .... **24. nanus**

Compound eyes large, as in fig. 255; forewing 5 mm. long .... **25. phoebus**

MATURE MALE NYMPHS

1\. Caudal filaments either entirely dark or entirely light, or basal half to two-thirds of each filament uniformly dark and with apical half or third of filament light, but never with a dark brown crossband at middle and at apex in addition to this shading 2

Caudal filaments relatively light in color, with dark brown crossband at or near the middle and at apex of each 5

2\. Abdominal tergites 2–10 each uniformly brown on disc, with lateral margins white or light tan 3

Abdominal tergites 5, 9, and 10 mostly or completely white, others brown, with lateral margins largely white 4

3\. Each cercus having its basal two-thirds shaded with brown; median caudal filament five-sixths as long as cercus .... **22. brunneicolor**

Each cercus uniformly shaded with brown from base to apex; median caudal filament two-thirds to three-fourths as long as cercus .... **21. phyllis**

4. Median caudal filament two-fifths as long as each cercus .... **20. rusticans**
   Median caudal filament three-fifths as long as each cercus ...... **11. vagans**
5. Gills with prominently darkened, pinnately branching tracheae 6
   Gills either without visible tracheae or with at most a single, median trachea in each gill, these tracheae never conspicuous 10
6. Each gill of seventh pair relatively slender, with apex pointed 7
   Each gill of seventh pair oval, with apex rounded 8
7. Abdominal tergites 2–10 each brown on disc, lateral margins of tergites 2–7 white; a median, light tan or cream-colored, longitudinal stripe extending the length of the abdominal dorsum... .... **6. pygmaeus**
   Abdominal tergites 2–4 and 6–7 mostly dark brown, tergites 5 and 8–10 mostly white; no longitudinal, pale, median stripe present on abdominal dorsum... .... **9. herodes**
8. Abdominal tergites 2–10 each uniformly dark brown on disc, lateral margins white .... **7. frondalis**
   Abdominal tergites 2–10 each variegated with brown and white on disc; tergites 5 and 8–10 usually largely or entirely white 9
9. Each caudal filament with brown shading at base, in addition to dark brown crossbands at middle and at apex......... .... **23. intercalaris**
   Each caudal filament white at base, darkened only at middle and at apex.. .... **16. levitans**
10. Abdominal tergites 2–9 each uniformly brown on disc, with lateral margins white, but tergite 5 usually somewhat lighter in color than others; each caudal filament shaded with brown in basal half, in addition to dark brown crossbands at middle and at apex.......... .... **15. pluto**
    Abdominal tergites 2–9 more or less variegated with brown and white, tergites 5 and 9 mostly or entirely white; each caudal filament white or pale cream colored in basal half................ 11
11. Median caudal filament almost as long as cerci, at least five-sixths as long.... .... **17. flavistriga**
    Median caudal filament not more than three-fourths as long as cerci 12
12. Tenth abdominal tergite entirely white.. .... **18. cingulatus**
    Tenth abdominal tergite mostly brown, white only along anterior margin..... .... **25. phoebus**

1. *Baetis spinosus* McDunnough

Baetis spinosus McDunnough (1925*b*: 174).

MALE.—Length of body 4.0–4.5 mm., of fore wing 5.0–5.5 mm. Head very dark brown to black, yellow-brown at lateral angles of frontal shelf; each antenna light gray-brown, shading to yellow at apex of flagellum; eyes in life dark red-brown. Thoracic notum black, yellow-brown along anterolateral margins of mesoscutum, pleura and sternum dark brown, light red-brown or yellow-brown at wing bases and bordering sutures; all coxae brown, each fore leg faintly yellow, middle and hind leg white; wings hyaline, veins Sc and R_1 of fore wing faintly stained with yellow-brown, stigmatic crossveins 7–9 in number, uniformly slanting, not anastomosed; hind wing with only two longitudinal veins, costal projection either absent or vestigial. Abdominal segments 2–6 white or stained with tan, black spiracular markings present; apical tergites chocolate brown, sternites white. Genitalia, fig. 289, distinctive, second segment of each forceps arm with a prominent, apicomesal tubercle, fourth segment as long as wide; genitalia and caudal filaments white or, occasionally, faintly tinged with yellow.

Known from Illinois, Indiana, Manitoba, New York, Ontario, and Quebec.

Illinois Records.—AROMA PARK: Kankakee River, July 8, 1948, Ross & Burks, 1♂. MUNCIE, Stony Creek: May 24, 1914, 1♂; July 3, 1929, Frison & Park, 1♂. OAKWOOD, Salt Fork River: May 29, 1948, B. D. Burks, 1♂; June 5, 1948, Burks & Sanderson, 3♂. PRINCETON: Big Bureau Creek, May 23, 1941, Ross & Burks, 1♂. PROPHETSTOWN: July 7, 1925, T. H. Frison, 1♂.

2. *Baetis propinquus* (Walsh)

Cloe vicina Walsh (1862: 380), not Hagen. Misidentification.
Cloe propinqua Walsh (1863: 207). New name.
Baetis propinquus (Walsh). Eaton (1871: 121).
Acentrella propinqua (Walsh). Traver (1937: 83).
Baetis dardanus McDunnough (1923: 41).

I have studied the lectotype of *propinquus* and a paratype of *dardanus* and I can find no specific differences between them; McDunnough (1925*b*: 172) long ago concluded that the two species were probably synonymous.

MALE.—Length of body 4–5 mm., of fore wing 4.5–5.5 mm. Head dark brown to black; antennae yellow-brown to tan; eyes dark brown. Thorax dark brown to black, yellow-brown at anterolateral margins of mesoscutum, at apex of scutellum, on pleural sutures and at wing bases, and usually on mesosternum; wings hyaline, veins Sc and R_1 of fore wing faintly tinged with tan near wing base; hind wing, fig. 270, narrow, costal projection absent, only two longitudinal veins present; all coxae yellow-brown, legs otherwise usually white, femora sometimes faintly shaded with gray-brown. Abdominal segments 2–6 white or very faintly stained with tan, black spiracular marks present; apical tergites yellow-brown, sternites white; genitalia and caudal filaments white or faintly stained with yellow.

FEMALE.—Length of body 4.5–5.5 mm., of fore wing 5.5–6.5 mm. Head, thorax, and abdominal tergites chestnut brown, legs light yellow, wings hyaline, longitudinal veins yellow; hind wing as in male; abdominal sternites white, often with a faint pinkish tinge; caudal filaments light yellow.

Known from Illinois, Manitoba, and Ontario.

Illinois Records.—AROMA PARK: July 8, 1948, Ross & Burks, 1♂; Aug. 6, 1947, Burks & Sanderson, 2♂. EAST DUBUQUE: at light, July 21, 1927, Frison & Glasgow, 18♂, 6♀. ELIZABETHTOWN: at light, July 14, 1948, Mills & Ross, 1♂. ERIE: Rock River, June 26, 1947, B. D. Burks, 1♂. MILAN: Rock River, June 4, 1940, Mohr & Burks, 7♂. MOMENCE: Aug. 5, 1938, Burks & Boesel, 2♂; Aug. 16, 1938, Ross & Burks, 1♂. MUNCIE: June 8, 1927, Frison & Glasgow, 1♀. OAKWOOD: May 29, 1948, B. D. Burks, 1♂. ROCK ISLAND: 7♂, 16♀ (Walsh 1862:380). ROCKTON: Rock River, Aug. 4, 1948, Burks & Stannard, 1♂, 1♀. SHAWNEETOWN: 1♂ (Traver 1935*a*:699). URBANA: July 11, 1898, C. A. Hart, 1♀.

3. *Baetis elachistus* new species

This species agrees with *amplus* (Traver), described from North Carolina, in having the wing veins yellow-brown, the hind wing without a costal angulation, and abdominal tergites 2–6 brown. The two differ in that the fourth genital forceps segment in *amplus* is three times as long as wide, while this structure in *elachistus* is only as long as wide; the genitalia of *elachistus* likewise are distinct in that the basal forceps segment is more prominently produced at the mesoapical angle than it is in *amplus*.

MALE.—Length of body and of fore wing each 5.0–5.5 mm. Head dark brown, with a white spot at each lateral margin of frontal shelf; each antennal scape and pedicel white, shaded with tan at apexes, flagellum tan. Thorax very dark brown, almost black; legs white, coxae shaded with brown, fore femur stained with tan, which becomes slightly darker toward apex, middle and hind femora shaded with tan at apexes, all tibiae brown shaded at bases; wings hyaline, veins yellow-brown, fore wing with 10 to 12 highly anastomosed, stigmatic crossveins, no marginal intercalaries in subcostal interspace, usually none also in first R_1 interspace, although one short intercalary sometimes present here; hind wing, fig. 271, narrow, only two longitudinal veins present, costal angulation absent. First abdominal segment dark brown, segments 2–6 uniformly dark yellow-brown, tergites 7–10 brown, sternite 7 yellow-brown, 8 and 9 brown, lateral margins of 9 dark brown; first genital forceps segment brown, mesoapical angle slightly produced, fig. 290, second segment tan, third segment tan, slightly bowed, one and one-half times as long as second segment, fourth segment tan, globose, as long as wide; each caudal filament tan in basal fifth, gradually merging into white distad.

Holotype, male.—Duncans Mills, Illinois, Spoon River, October 20, 1941, B. D. Burks. Specimen in alcohol.

Paratypes.—Same data as for holotype, 5♂. Specimens in alcohol, wings and genitalia on microscope slides.

4. *Baetis frivolus* McDunnough

Baetis frivolus McDunnough (1925*b*:174).

MALE.—Length of body 4–5 mm., of fore wing 5–6 mm. Head very dark brown, lighter at lateral angles of frontal shelf; antennae brown; eyes brown, each stalk shorter than in most species of genus. Thorax very dark brown dorsally, slightly lighter laterally and ventrally; anterolateral margins of mesoscutum, area along outer parapsides, and margins of mesosternum yellow-brown; wings hyaline, anterior longitudinal veins of fore wing shaded with tan, base of fore wing brown, stigmatic crossveins anastomosed, hind wing long, narrow, costal projection and third longitudinal vein lacking; legs with all coxae brown, fore leg faintly shaded with gray-brown, middle and hind legs white or faintly yellow. Abdominal tergites uniformly brown, black tracheal markings at spiracles, sternites 1–6 deep yellow; apical sternites tan; genitalia and caudal filaments white; genitalia, fig. 271, with fourth forceps segment three times as long as wide.

Known from Illinois, Ontario, Quebec.

Illinois Record.—GOLCONDA: April 30, 1940, Mohr & Burks, 1♂.

5. *Baetis harti* McDunnough

Baetis harti McDunnough (1924*a*:7).

MALE.—Length of body 2.5–3.5 mm., of fore wing 3–4 mm. Head very dark brown; each antenna brown, shading to yellow at apex of flagellum; eyes brown. Thorax dark brown, yellow-brown near apex of mesoscutellum; all coxae brown, legs otherwise light yellow to white; wings hyaline, stained with brown at base of vein Sc of fore wing; stigmatic crossveins of fore wing only three or four in number, not anastomosed; hind wing, fig. 272, relatively broad at base, costal projection well developed, third longitudinal vein absent. Abdominal segments 2–6 white to yellow, with black spiracular marks; apical tergites dark brown, sternites tan; genitalia and caudal filaments white.

Known from Illinois.

Illinois Records.—KANKAKEE: Aug. 16, 1938, Ross & Burks, 1♂; May 17, 1938, H. H. Ross, 2♂; July 21, 1935, Ross & Mohr, 1♂. URBANA: West Branch Salt Fork River, July 11, 1898, C. A. Hart, 8♂.

6. *Baetis pygmaeus* (Hagen)

Cloe pygmaea Hagen (1861:54).
Baetis pygmaeus (Hagen). McDunnough (1925*a*:214; 1925*b*:172).

This species was described from a single very small female specimen collected in eastern Canada along the St. Lawrence River. When Eaton examined this type (1885:170), it was fragmentary. When McDunnough saw it (1925*b*:172), it was badly broken, consisting only of one fore wing and part of the mesothorax with the legs attached. At present, the type is but a bare pin, with the label.

McDunnough (1925*b*:172), however, secured male and female specimens of a common species of *Baetis* from Ontario and Quebec, along the St. Lawrence River, and was able to match the female of this species with the few fragments of Hagen's type which were still preserved at that time. McDunnough based his conception, and redescription, of this species on these specimens and the associated males. I have seen some of this topotypic material of *pygmaeus*, as named by McDunnough, and I follow his identification of it.

MALE.—Length of body and of fore wing 3.0–3.5 mm. Head very dark brown to black; each antennal scape and pedicel dark brown, flagellum lighter smoky brown. Thorax very dark brown to black; coxae yellow-brown, fore femur faintly stained with smoky tan, all legs otherwise white; wings hyaline, veins C, Sc, and R_1 stained with tan near bases, stigmatic crossveins six to eight in number, uniformly slanting, not anastomosed and usually none reaching vein Sc; hind wing, fig. 276, relatively narrow, with well-developed costal angulation, one or two long, marginal intercalaries present posterior to second longitudinal vein, and third vein absent. Abdominal segments 2–6 white or faintly yellow, black stigmatic markings present; apical tergites chestnut brown, sternites pale tan to white; genitalia and caudal filaments white.

Known from the midwestern and northeastern states and southern Canada.

Illinois Records.—HEROD: July 16, 1947, sweeping, L. J. Stannard, 1♂. JONESBORO: branch of Clear Creek, May 15, 1946, Mohr & Burks, 1♂. QUINCY: at light, May 18, 1940, Mohr & Burks, 1♂.

7. *Baetis frondalis* McDunnough

Baetis frondalis McDunnough (1925*b*:173).

MALE.—Length of body 4–5 mm., of fore wing 5–6 mm. Head very dark brown, almost black; each antennal scape and pedicel yellow-brown, flagellum tan; eyes in life red-brown. Thorax almost completely very dark brown to black, mesonotum marked with small, vaguely defined, yellow-brown streaks anteriorly on prescutum and laterally on anterior notal wing processes; all coxae brown, front leg faintly shaded with tan, middle and hind legs white to faint yellow-brown, fore tarsus slightly shorter than fore tibia. Wings hyaline, veins C, Sc, and R_1 faintly stained with brown near bases, otherwise all veins hyaline; stigmatic crossveins of each fore wing six to eight in number, obliquely slanting, not anastomosed, and most not reaching vein Sc; hind wing, fig. 274, long and narrow, costal projection minute but always clearly present, third longitudinal vein absent, usually a single long intercalary vein present posterior to second longitudinal vein. Abdominal tergites 2–6 dark brown, with anterolateral angles of each tergite pale yellow, a faint black circle at each spiracle; sternites 2–6 white or faintly yellow, sometimes with a brown, transverse streak at posterior margin of each sternite; apical tergites chocolate brown; sternites opaque white, shaded with brown on median area of basal half of each and laterally on apical sternite; genitalia white, with second segment of forceps semiquadrate, fig. 292; caudal filaments white.

Known from Illinois, Ontario, Quebec.

Illinois Records.—DES PLAINES: Fox River, May 26, 1936, H. H. Ross, 1♂. OAKWOOD, Salt Fork River: May 29, 1948, Burks & Evers, 2♂; June 5, 1948, Burks & Sanderson, 5♂. WEST CHICAGO: July 9, 1948, Ross & Burks, 2♂.

8. *Baetis baeticatus* new species

This species resembles *frondalis* in the structure of the hind wing and the male genitalia; the two differ in that the body of *baeticatus* is strikingly slender and long, being longer than the fore wing, while the body of *frondalis* is shorter than the fore wing. They also differ in color, *baeticatus* having a medianly interrupted, transverse, red stripe at the posterior margin of each of abdominal tergites 2–6, and these tergites are faintly stained with brown; in *frondalis,* abdominal tergites 2–6 are almost completely dark brown, with the red stripes wanting.

MALE.—Length of body 6.0 mm., of fore wing 5.5 mm. Head dark brown, white at lateral angles of frontal shelf; each antennal scape white, with faint brown shading at base and at apex, pedicel tan, flagellum white at base, shading to tan at apex; ocelli white; each compound eye with stalk relatively low, lateral margin of upper faceted portion almost touching upper margin of lower portion, upper portion golden brown, lower black. Thorax dark brown, mesonotum yellow at anterior end of each outer parapsidal furrow, on prescutum, and on scutellum; pleural sutures white, mesosternum light yellow-brown in center, dark brown at margins; all coxae partly shaded with dark brown, legs otherwise white, except that fore tibia is slightly darkened at apex; fore tibia one and one-half times as long as fore femur, fore tarsus four-fifths as long as fore tibia, second fore tarsal segment one and one-half times as long as third, fourth and fifth segments equal in length and each one-half as long as third segment; wings hyaline, base of each fore wing and basal halves of veins Sc and R_1 stained with brown, stigmatic crossveins six in number, all uniformly slanted, not anastomosed and most not quite reaching vein Sc; no marginal intercalaries in subcostal interspace, a single, short intercalary present in first R_1 interspace, two well-developed ones in each of the two following interspaces; hind wing long, narrow, with a minute costal projection, third longitudinal vein absent, a single marginal intercalary vein present posterior to second longitudinal vein. Abdominal segments 2–6 with white ground, tergite 2 suffused with brown stain over all but anterolateral triangles, tergites 3–6 faintly brown stained on posterior third of each, a medianly interrupted, red band at posterior margin of each of tergites 2–7, and a pair of large, black tracheal marks in a cluster covering most of posterolateral area of each of tergites 2–6; a double, longitudinal, black spiracular line extending length of abdomen on either side, and a prominent, black spot at each spiracle on segments 1–6; apical tergites dark yellow-brown, sternite 7 white, 8 brown stained, 9 with lateral margins dark brown; genitalia white, first forceps segment quadrate, second cylindrical, third slender and slightly bowed, fourth as wide as long; a prominent spine present in a median depression between bases of forceps; caudal filaments white.

FEMALE.—Size as in male. Head and thorax dark brown, similar to those of male, legs and wings as in male; abdominal tergites uniformly dark yellow-brown, red crossbands of male absent, but black spiracular and tracheal markings present; sternite 1 faint brown, sternites 2–8 white, with a pair of submedian, brown dots at anterior margin of each; sternite 9 brown at lateral margins; caudal filaments tan at bases.

Holotype, male.—Wichert, Illinois, June 11, 1947, L. J. Stannard. Specimen in alcohol.

Allotype, female.—Same locality as for holotype, June 9, 1948, Burks & Stannard. Specimen in alcohol.

Paratypes.—Oakwood, Illinois, June 4, 1948, B. D. Burks, 1 ♂ adult, 3 ♂ subimagoes. Specimens in alcohol.

9. *Baetis herodes* new species

This species agrees with *parvus* Dodds, described from Colorado, in having the second vein of the hind wing forked, and the first segment of the male genital forceps nontuberculate. The two differ in that the abdominal tergites 2–6 are uniformly white in *parvus,* but are shaded with red-brown at the posterior margins in *herodes;* in *parvus,* the hind wing has a single marginal intercalary vein between the branches of the second vein, while, in *herodes,* the hind wing has one long and two short marginal intercalaries between the branches of the second vein. McDunnough (1925*a*:214-5; 1925*b*: 172) recorded, as the Colorado species *parvus* Dodds, a Quebec species having the venation of the hind wing similar to that of *herodes.* He had female specimens only. As many of the southeastern Canadian species of mayflies also occur in southern Illinois, these Quebec female specimens actually might be the females of *herodes.* Unfortunately, female specimens of *herodes* have not yet been secured here in Illinois.

Male.—Length of body and of fore wing 5.0–5.5 mm. Head very dark brown, almost black; scape and pedicel of each antenna dark brown, flagellum smoky yellow; each eye in life with upper facets dark brown, lower ones black. Thorax black, becoming dark brown after death; wings hyaline, stigmatic crossveins partly anastomosed, 9 to 10 in number; hind wing, fig. 275, with prominent costal projection, second vein branched, two strong and one vestigial marginal intercalaries present between branches, third vein reaching posterior margin of wing at a point three-fifths the distance from base to apex of wing; numerous vestigial crossveins present; fore leg smoky, fore tibia shaded with brown at apex, middle and hind legs faintly yellow, almost white, apexes of femora and bases of tibiae stained with brown. First abdominal segment brown; tergites 2–6 white, with a transverse, brown-shaded area at posterior margin of each tergite, small, black blotch at each spiracle; tergites 7–10 dark red-brown; sternites 2–6 white, 7–10 lightly shaded with red-brown, and 10 also shaded with dark gray-brown at lateral margins; caudal filaments white. Genitalia: first forceps segment nontuberculate, smoky brown, following segments faintly yellow; second and third segments equal in length, second segment frustate, third segment slender, bowed, and slightly enlarged toward apex; fourth segment globose, one and one-half times as long as wide.

Female.—Unknown.

Nymph, male.—Length of body 6–7 mm. Head and thorax mottled brown and white, legs white, with gray-brown shading on coxae, at base, middle, and apex of each femur, and in middle of each tibia and tarsus. Abdominal tergites 1–4 and 6–7 mostly brown, tergites 5 and 8–10 mostly white; abdominal sternites white, with longitudinal, brown streak near each lateral margin of sternites; each gill having a black, median trachea with a few short, lateral branches; each gill of seventh pair slender and pointed at apex; median caudal filament almost as long as cerci, caudal filaments light tan, with a brown crossband near tip of each.

A female nymph associated with these male nymphs, and apparently of the same species, has abdominal tergites 1–9 uniformly brown, tergite 10 white, and each caudal filament uniformly tan, without a brown crossband.

Holotype, male.—Herod, Illinois, Gibbons Creek, April 9, 1947, B. D. Burks. Specimen dry, on a pin.

Paratypes.—Illinois.—Same data as for holotype, 1 ♂; April 10, 1947, 1 ♂ subimago. Nymphs and exuviae also were collected at Herod, Illinois, April 4–10, 1947.

Indiana. — Spencer: McCormick's Creek, April 27, 1948, W. E. Ricker, 3 ♂.

Of these paratypes, one adult male is dry, on a pin; three adult males and subimago male are in alcohol.

10. *Baetis cleptis* new species

This species is similar to *erebus* Traver, described from Arizona, in that the hind wing is long and narrow, and has a prominent, hooklike costal projection, the median abdominal segments are dark brown, and the first male genital forceps segment has a fairly large, rounded anteromedian projection. *B. cleptis* differs from *erebus* in that *cleptis* is smaller, the hind wing is relatively wider, the second forceps segment is semituberculate, and there is a single acute projection between the bases of the genital forceps in *cleptis*, in contrast to two small projections in this position in *erebus*.

MALE.—Length of body 3.5 mm., of fore wing 4 mm. Head dark brown, with white spot at either lateral margin of frontal shelf; each antenna brown, with flagellum becoming white toward the apex. Thorax dark brown, lighter along dorsal sutures and at apex of mesoscutellum; wings hyaline, a brown spot at base of each fore wing, veins light brown; stigmatic crossveins in each of fore wings six or seven in number, slanting, not anastomosed, no marginal intercalaries in Sc interspace; hind wing, fig. 273, narrow, only one-third as wide as long, costal projection hooked, veins 1 and 2 slightly converging at apexes, a single marginal intercalary present between veins 2 and 3, third vein slightly more than half as long as wing; all coxae brown, fore leg entirely tan, middle and hind legs white. Abdominal tergites 1–6 yellow-brown, tergites 7–10 slightly darker brown; sternites yellow-brown, with lateral margins of sternite 9 dark brown; black, longitudinal tracheal lines at spiracles; genital forceps, fig. 293, yellow-brown at bases, graduating to very light tan at apexes; first segment with rounded anteromesal projection, second segment cylindrical, with a suggestion of a mesal tubercle at apex, third segment constricted at base, enlarged toward apex, twice as long as second segment, fourth segment long, slender, four times as long as wide; caudal filaments white, slightly shaded with tan in basal area.

Holotype, male.—Detroit, Illinois, September 15, 1939, Ross & Mohr. Specimen in alcohol.

Paratype.—Same data as for holotype, 1 ♂. Specimen in alcohol, wings and genitalia on microscope slides.

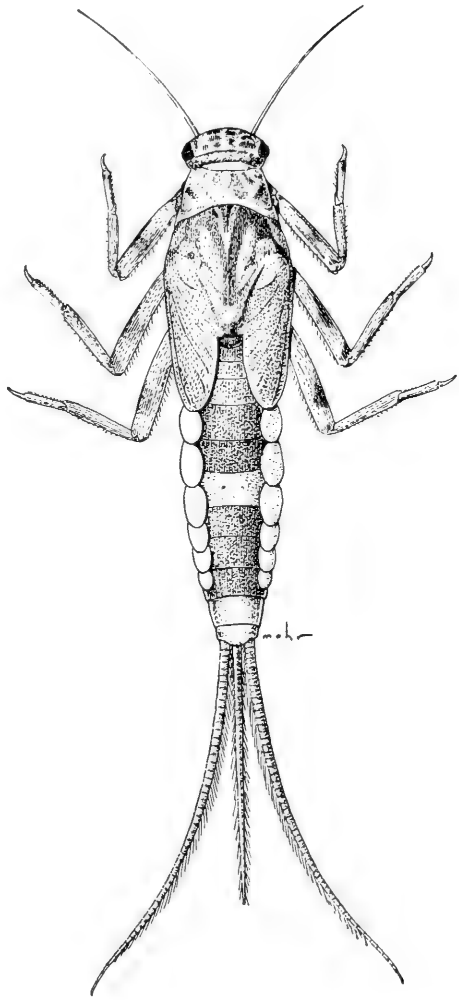


Fig. 298.—*Baetis vagans*, mature nymph.

11. *Baetis vagans* McDunnough

Baetis vagans McDunnough (1925*a*: 219).

MALE.—Length of body 5.5–6.5 mm., of fore wing 6.0–7.5 mm. Head dark brown, yellow-brown at lateral angles of frontal shelf; each antennal scape usually entirely yellow, sometimes partly shaded with brown, pedicel brown, flagellum gray-tan, shading to yellow at apex; eyes red-brown. Thorax dark brown, marked with yellow-brown at anterior and posterior ends of each outer parapsidal furrow, at wing bases, along pleural sutures, on entire prosternum, and on margins of mesosternum; wings hyaline, anterior longitudinal veins stained pale yellow, stigmatic crossveins of fore wing numerous, anastomosed to form a dense network; hind wing, fig. 280, with prominent costal projection, third longitudinal vein well developed, and marginal intercalary veins present between both veins 1 and 2, and 2 and 3; all coxae pale gray-tan, fore leg light gray-brown, fore tibia with a darker gray spot at apex, middle and hind legs pale yellow to white. Abdominal tergites 2–6 brown, with anterior fourth of each tergite yellow, sternites faint gray-brown or smoky tan; apical tergites bright chestnut or chocolate brown, sternites white, sometimes faintly stained with tan; genitalia, fig. 294, white; caudal filaments white.

Known from Illinois, New York, Ontario, Pennsylvania, and Quebec.

Illinois Records. — ELGIN: Botanical Garden, April 25, 1941, Ross & Burks, 1 ♂; April 19, 1939, Burks & Riegel, 8 N; May 9, 1939, Ross & Burks, 5 ♂, 5 ♀, 40 N; May 23, 1939, Burks & Riegel, 16 N.

12. *Baetis incertans* McDunnough

Baetis incertans McDunnough (1925*a*:220).

Ide (1937*b*:223) considers this species to be a synonym of *vagans*. It is quite closely related to *vagans*, differing only in that it is smaller, the length of the body being 4.5 mm. and the length of the fore wing 5 mm.; abdominal tergites 2–6 are uniformly brown, and abdominal sternites 2–6 are white or faintly tinged with yellow.

Known from Quebec.

13. *Baetis pallidulus* McDunnough

Baetis pallidula McDunnough (1924*a*:8).

Live specimens of *pallidulus* can be recognized at once by the brilliant lemon-yellow and tan head and thorax; the bright yellow-orange of the compound eyes also is distinctive. These colors, unfortunately, are quickly lost following death. Regardless of the method of preservation of specimens, all trace of the bright yellow coloration is soon lost. In alcohol, the eyes and thorax fade to a pale tan or deep cream color; dry specimens become light or dark tan.

MALE.—Length of body 4–5 mm., of fore wing 5–6 mm. Head tan and yellow; each antenna with scape and pedicel orange-tan, flagellum yellow; compound eyes orange-yellow. Thorax yellow and tan; legs yellow, with faint, brown shading at apex of each femur; wings hyaline, veins Sc and R_1 yellow at bases, seven to nine stigmatic crossveins, partly anastomosed; marginal intercalaries in second interspace short, fig. 287; hind wing broad, costal angulation well developed, third longitudinal vein only one-fourth as long as wing, usually one marginal intercalary vein posterior to second longitudinal vein. Abdominal segments 2–6 light tan or yellow, black spiracular marks usually present; apical tergites orange-brown or tan, sternites yellow, sometimes stained with tan or orange-brown; genitalia yellow, of the *intercalaris* type, a well-developed apicomesal tubercle on the first forceps segment, the second segment frustate; caudal filaments white.

Known from Illinois, Indiana, and Ontario.

Illinois Records. — ALDRIDGE: May 14, 1940, Mohr & Burks, 1 ♂. APPLE RIVER CANYON STATE PARK: June 6, 1940, Mohr & Burks, 1 ♂; July 12, 1938, Burks & Boesel, 1 ♂. MUNCIE, Stony Creek: May 24, 1914, 3 ♂; June 3, 1917, 1 ♀; June 8, 1927, Frison & Glasgow, 1 ♂. OAKWOOD: May 24, 1926, T. H. Frison, 1 ♂. ROCKFORD: June 13, 1931, Frison & Mohr, 1 ♂. SERENA: Indian Creek, May 12–16, 1938, Ross & Burks, 2 ♂.

14. *Baetis ochris* new species

This species is similar to *pallidulus* in being generally light in color, in having male genitalia of the *intercalaris* type, and in having three well-defined, longitudinal veins and a well-developed costal projection in the hind wing. The two differ in that *ochris* has the marginal intercalaries in the first three interspaces of the fore wing equal in length, while *pallidulus* has them unequal, with those in the second interspace shorter than those in the first and third interspaces; the apical segments of *ochris* are brown, of *pallidulus* yellow or tan; abdominal tergites 2–6 are white in *ochris*, yellow in *pallidulus*.

MALE.—Length of body and of fore wing each 4 mm. Head tan, shaded with light yellow-brown near compound eyes; antennae yellow-brown; eyes yellow-brown. Thorax yellow-brown; wings hyaline, stigmatic crossveins 7 to 10 in number, partly anastomosed, a strong crossvein usually present in second interspace below stigmatic area near margin of wing; marginal intercalaries in first three interspaces nearly equal in length, fig. 286; hind wing broad, with three longitudinal veins and usually no marginal intercalaries, sometimes a very short one present between first and second veins; legs white.

Abdominal segments 2–6 white, extensive black tracheal outlines at each spiracle; apical segments brown; genitalia and caudal filaments white; genitalia of the *intercalaris* type, with a papillate projection at mesoapical angle of first forceps segment, second segment conical, and fourth segment slightly longer than wide.

Holotype, male.—Richmond, Illinois, at light, June 24, 1938, B. D. Burks. Specimen in alcohol.

Paratypes.—Same data as for holotype, 2♂. Specimens in alcohol.

15. *Baetis pluto* McDunnough

Baetis pluto McDunnough (1925*a*: 218).

MALE.—Length of body and of fore wing 4.5 mm. Head and thorax dark brown; legs yellow, with femora somewhat darker yellow; stigmatic crossveins of each fore wing anastomosed; hind wing, fig. 278, with third longitudinal vein relatively long. Abdominal tergites 2–6 dark red-brown, with only anterior and lateral margins lighter in color; genitalia, fig. 295, tinged with brown and of the *intercalaris* type, with mesoapical papilla of first forceps segment wanting; caudal filaments white.

Known from Ontario and Quebec.

16. *Baetis levitans* McDunnough

Baetis laevitans McDunnough (1925*a*: 215).
Baetis levitans McDunnough (1925*a*: 216).

This species differs from *pluto* only in that the thorax is chestnut brown, the hind wing, fig. 279, usually has fewer marginal intercalary veins and a shorter third longitudinal vein, the abdominal tergites 2–6 are yellow, with a brown, transverse streak at the posterior margin of each, and the genitalia are white.

Known from New York, Pennsylvania, and Quebec.

17. *Baetis flavistriga* McDunnough

Baetis flavistriga McDunnough (1921: 120).

MALE.—Length of body 4.5 mm., of fore wing 5.0 mm. Head gray-brown, with face black and antennae dark smoky gray. Thorax dark gray-brown, with a greenish cast and yellow markings; legs white, femora shaded with yellow; each hind wing with third longitudinal vein well developed, one-half as long as wing, and a single marginal intercalary vein usually present between veins 2 and 3. Abdominal tergites 2–6 light yellow-brown, apical tergites dark yellow-brown, faint black spiracular markings present; genitalia and caudal filaments white.

Known from New York, Ontario, and Quebec.

18. *Baetis cingulatus* McDunnough

Baetis cingulatus McDunnough (1925*a*: 216).

MALE.—Length of body 5.0 mm., of fore wing 5.5 mm. Head very dark brown. Thorax dark gray-brown, with small, variable tan or yellow markings; legs light yellow, with all femora shaded with brown; each hind wing with third longitudinal vein well developed, one-half as long as wing, marginal intercalaries absent or extremely faint. Abdominal tergites 2–6 yellow, with a narrow, bright red-brown, transverse stripe at posterior margin of each, apical tergites darker red-brown; genitalia and caudal filaments white.

Known from New York, Pennsylvania, and Quebec.

19. *Baetis anachris* new species

This species is similar to *rusticans* in that the hind wing is relatively broad and has three longitudinal veins, abdominal tergites 2–6 are brown, and the genitalia are of the *intercalaris* type, having the mesoapical papilla of the first forceps segment present. The two differ in that the stigmatic crossveins of the fore wing in *anachris* are numerous and anastomosed, while there are only four to six nonanastomosed stigmatic crossveins in *rusticans;* abdominal sternites 2–6 in *anachris* are white, while they are a light smoky gray in *rusticans*.

MALE.—Length of body 4.5 mm., of fore wing 5.0 mm. Head chestnut brown, each antenna chestnut brown, blending into yellow at apex of flagellum; compound eyes light red-brown, extremely large. Thorax chestnut brown, with yellow areas along anterior lateral margins of mesoscutum, on prescuta, at wing bases, at apex of scutellum, and on anteromedian and dorsolateral areas of metanotum; all legs yellow, except coxae shaded with brown and each fore femur stained with tan; wings hyaline, veins colorless, stigmatic area of each fore wing with numerous partly incomplete and anastomosed crossveins; intercalary veins in first interspace long, obsolescent, those in following interspaces well developed but shorter; hind wing, fig. 277, wide, no marginal intercalaries present, third vein short. Abdominal tergites brown, with white area at anterolateral angle and anteromedian area of each; a darker brown, median spot at posterior margin of each tergite; basal sternites faint yellow, almost white; apical tergites opaque pinkish tan, sternites yellow, apical sternite with longitudinal, brown streak near each lateral margin; genitalia, fig. 296, and bases of caudal filaments tan, filaments white distad of bases.

NYMPH, MALE.—Length of body 6.0–6.5 mm. Head and thorax light brown, with median, longitudinal, dorsal stripe and apex of scutellum white or a faint tan; thoracic venter white; legs white, shaded with brown on coxae, basal three-fourths of femora, apexes of tibiae, and apical one-fourth of each tarsus. Abdominal tergites light brown, with traces of a median, longitudinal, white streak; tergites 5, 9, and 10 mostly white, lateral margins of each tergite white; gills white, with a single, well-marked, brown trachea on each gill of pairs borne by segments 2–6, anterior and posterior margins of these gills also brown; sternite 1 white, all following sternites tan, shading to brown at lateral margins, apical three sternites almost entirely brown; caudal filaments tan, median one three-fourths as long as each cercus.

Holotype, male.—Havana, Illinois, White Oak Creek near Matanzas Lake, June 13, 1946, Mohr & Burks. Specimen dry, on pin; hind wing and genitalia on microscope slides. Specimens of nymphs associated with this adult collected on same date.

20. *Baetis rusticans* McDunnough

Baetis rusticans McDunnough (1925*a*:217).

MALE.—Length of body 3.5 mm., of fore wing 4.0 mm. Head and thorax dark gray-brown, with yellow-brown or red-brown markings on thoracic notum; legs very light yellow-brown, femora shaded with darker brown; stigmatic crossveins of each fore wing only four to six in number and not anastomosed; hind wing, fig. 281, with third longitudinal vein short and marginal intercalary veins absent. Abdominal tergites 2–6 gray-brown, apical tergites dark walnut brown; genitalia and caudal filaments white.

Known from New York and Quebec.

21. *Baetis phyllis* new species

This species is similar to *brunneicolor* in having abdominal tergites 1–10 uniformly brown in color, the hind wing with three longitudinal veins and marginal intercalaries, and the first segment of the male genital forceps tuberculate, the second segment frustate. The two differ in that the wing veins are brown in *phyllis* but hyaline in *brunneicolor;* the third vein of the hind wing is shorter in *phyllis* than in *brunneicolor,* and the tubercle of the first forceps segment is somewhat better developed in *brunneicolor* than it is in *phyllis.*

MALE.—Length of body and of fore wing each 6 mm. Head dark brown; each antennal scape tan, pedicel brown, flagellum smoky tan. Thorax brown, with yellow along anterolateral margins of mesoscutum, along outer parapsides, and on meson at posterior margin of mesoscutum; legs white, except coxae shaded with brown, each fore femur tan, fore tibia with brown spot at apex; wings hyaline, veins of fore wing tan, crossveins hyaline, stigmatic crossveins numerous, anastomosed; hind wing, fig. 282, broad, two and one-third times as long as broad, costal angulation prominent, veins brown at bases, tan distad, first and second veins converging slightly at wing margin, a single marginal intercalary between veins 1 and 2, and two marginal intercalaries between veins 2 and 3, a single, irregular crossvein extending from vein 2 to 3, vein 3 reaching wing margin slightly basad of the middle. All abdominal tergites brown, tenth tergite darker brown; narrow, transverse, yellow stripe at anterior and posterior margins of each tergite; dark brown, almost black, spiracular lines present; entire abdominal sternum white, apical sternite shaded with brown at lateral margins; first forceps segment shaded with brown, bearing a minute tubercle at inner apical angle, second segment frustate, third segment two and one-half times as long as second, fourth segment twice as long as broad; caudal filaments white, basal five or six articulations stained with red-brown.

NYMPH, MALE.—Length of body 6–8 mm. Head and dorsum of thorax dark brown; thoracic sternum white; legs white, all femora almost completely shaded with brown, fore tibia and tarsus brown, middle and hind tibiae shaded with brown at bases, tarsi darkened at apexes; tergum of abdomen uniformly dark brown, sternum also usually uniform brown, but basal sternites sometimes lighter brown toward meson; each gill with median, black trachea only; median caudal filament two-thirds to three-fourths as long as cerci.

Holotype, male. — Vandalia, Illinois, April 16, 1946, Mohr & Burks. Specimen dry, on pin.

Paratypes.—ILLINOIS.—Same data as for holotype, 1 ♂. PORT BYRON: May 15, 1942, Ross & Burks, 8 ♂. Specimens in alcohol. Numerous specimens of nymphs collected at both above localities, along with adults.

22. *Baetis brunneicolor* McDunnough

Baetis brunneicolor McDunnough (1925*b*: 173).

MALE.—Length of body 6.0–6.5 mm., of fore wing 6.5–7.5 mm. Head brown, lighter at lateral angles of frontal shelf; each antennal scape brown, pedicel tan, flagellum tan at base, shading to yellow at apex. Thorax dark brown, marked with yellow or tan at anterior apex of mesoprescutum, at posterior ends of outer parapsidal sutures, on mesoscutellum, on pleural sutures, and on sternal sutures; legs with all coxae yellow-brown, fore leg light yellow-brown, middle and hind legs white, often with femora faintly stained with tan; wings hyaline, veins Sc and R_1 of fore wing usually stained with pale yellow, stigmatic crossveins numerous, anastomosed; hind wing, fig. 283, with third longitudinal vein long, marginal intercalaries present between veins 1 and 2, and 2 and 3. Abdominal tergites 2–6 brown, sternites tan; apical tergites opaque brown, sternites yellow-brown; genitalia pale tan, of the *intercalaris* type, with a well-developed anteromesal tubercle on each first forceps segment; caudal filaments pale tan at bases, white distad.

Known from Illinois and Ontario.

Illinois Records. — DUNDEE: May 23, 1939, Burks & Riegel, 1 ♂. HAVANA: Matanzas Lake, Nov. 5, 1939, Ross & Burks, 2 ♂.

23. *Baetis intercalaris* McDunnough

Baetis intercalaris McDunnough (1921: 118).
Baetis lasallei Banks (1924: 425).

McDunnough (1938:25) stated that *intercalaris* and *lasallei* were so close as scarcely to warrant a separation. I have studied types of both species at the Museum of Comparative Zoology, and find no characters that serve to separate the two.

MALE.—Length of body 4.0–4.5 mm., of fore wing 4.5–5.0 mm. Head very dark brown, antennae brown, each becoming yellow toward tip of flagellum; eyes in life red-tan. Thorax very dark brown to black, with yellow-tan on lateral margins of mesonotum, at wing bases, and lateral margins of mesosternum; all coxae brown, legs otherwise white; wings hyaline, veins Sc and R_1 of fore wing stained with faint yellow near bases, stigmatic crossveins numerous, anastomosed marginal intercalaries in subcostal interspace extremely long, fig. 285; hind wing, fig. 284, with marginal intercalaries present, and with third longitudinal vein short. Abdominal segments 2–6 snow-white, black spiracular dots present; apical tergites dark chestnut brown, sternites creamy white; genitalia, fig. 297, white, mesoapical papilla of first forceps segment well developed; caudal filaments white.

Known from Connecticut, Illinois, Indiana, Maryland, New York, Ontario, and Pennsylvania. This is by far the commonest Illinois *Baetis*.

Illinois Records.—ALTO PASS: May 14, 1940, Mohr & Burks, 1 ♂. AMBOY: Green River, July 7, 1939, Mohr & Riegel, 1 ♂. CEDARVILLE: May 26, 1938, Ross & Burks, 1 ♂. DES PLAINES: Fox River, May 26, 1936, H. H. Ross, 1 ♂. FREEPORT: at light, June 10–11, 1948, Burks, Stannard, & Smith, 2 ♀. KANKAKEE: Kankakee River, June 6, 1935, Ross & Mohr, 1 ♂; June 29, 1939, Burks & Ayars, 1 ♂; July 21, 1935, Ross & Mohr, 1 ♂; Aug. 1, 1933, Ross & Mohr, 1 ♂; Aug. 16, 1938, Ross & Burks, 1 ♂; at light, July 9, 1948, Ross & Burks, 3 ♂. MILAN: Rock River, June 4, 1940, Mohr & Burks, 1 ♂. MOMENCE: June 15, 1938, Ross & Burks, 1 ♂; Aug. 16, 1938, Ross & Burks, 4 ♂. Mount Carroll: July 14, 1944, Frison & Sanderson, 1 ♂. Muncie: June 8, 1927, Frison & Glasgow, 1 ♂. Oakwood: June 2, 1927, T. H. Frison, 1 ♂; June 14, 1935, C. O. Mohr, 4 ♂, 1 ♀; July 4, 1946, Mohr & Burks, 1 ♂; Salt Fork River, June 23, 1948, B. D. Burks, 5 ♂. Oregon: July 4, 1946, Mohr & Burks, 3 ♂; July 9, 1925, T. H. Frison, 1 ♂, 1 ♀. Rock City: May 24, 1938, Ross & Burks, 1 ♂; May 30, 1938, Mohr & Burks, 2 ♂, 1 ♀. St. Charles: Fox River, July 8, 1948, Ross & Burks, 50 ♂. Sterling: at light, May 22, 1941, Ross & Burks, 40 ♂. Wilmington: at light, Aug. 6, 1947, Burks & Sanderson, 5 ♂.

24. *Baetis nanus* McDunnough

Baetis nanus McDunnough (1923:42).

Male.—Length of body 3 mm., of fore wing 4 mm. Head and thorax light gray-tan, with dorsal thoracic sutures shaded with brown; legs white, each fore femur yellow; hind wing with third longitudinal vein long, extending slightly beyond the middle of wing, and with a single marginal intercalary vein usually present posterior to vein 2; abdominal tergites 2–6 light yellow, apical tergites dark grayish yellow-brown; genitalia and caudal filaments white.

Known from Indiana and Ontario.

25. *Baetis phoebus* McDunnough

Baetis phoebus McDunnough (1923:41).

Male.—Length of body 5.0 mm., of fore wing 5.5 mm. Head and thorax brown, with yellow or yellow-brown shading on thoracic notum; legs faintly yellow, almost white; each fore wing with intercalary vein of first three interspaces of approximately equal length, fig. 288; hind wing with third longitudinal vein slightly more than one-half as long as wing, a single marginal intercalary vein present posterior to vein 2; abdominal tergites 2–6 white, apical tergites bright chestnut brown; genitalia and caudal filaments white.

Known from Ontario.

33. *PSEUDOCLOEON* Klapálek

Pseudocloeon Klapálek (1905:105).

In this genus, the upper portion of each compound eye in the adult males is set on a high stalk. In Illinois species, the height of this stalk is at least as great as the diameter of the lower portion of the eye. In some South American species of *Pseudocloeon,* the height of the stalk supporting the upper portion of the eye is several times as great as the diameter of the lower portion. Each compound eye in the females is small, and the two eyes are separated by a space at least three times as great as the width of one eye. In each fore wing, there are relatively few crossveins, the stigmatic area is usually milky, the stigmatic crossveins are slanting and partly anastomosed, and the marginal intercalary veins occur in pairs. The hind wings are wanting. The male in all species known to me has a small, brown, or black, median dorsal dot on the base of the second abdominal segment; the basal 6 or 7 abdominal sternites in both sexes almost always show the blackened outlines of vestigial tracheae decurrent from the spiracles. In the male genitalia, the first forceps segment is about as broad as long, with the inner apical angle usually produced toward the meson, the second segment is narrower than the first, the third is long, slender, and usually bowed, and the fourth is small; there is a small penis cover between the bases of the forceps.

The nymphs are streamlined and typically live in the shallow, fairly rapidly flowing water along the banks of brooks or creeks. The maxillary palps have two segments, and the labial palps three. There is but a single pair of wingpads, the gills are single and platelike, and there usually are but two well-developed caudal filaments. The nymph of one species, *minutum* Daggy (1945:395), is described as having three well-developed caudal filaments.

Pseudocloeon has 19 described Nearctic species, 5 of which occur in Illinois. Reliable characteristics for the separation of the females of these species have not yet been found.

KEY TO SPECIES

Adult Males

1. Abdominal tergites 2–6 entirely white, or white faintly tinged with tan, and without any markings except black spiracular dots or lines....................2
   Abdominal tergites 2–6 light tan or white, with red, tan, or brown spots or dots..3
2. Abdominal sternites with midventral, brown or black dots..**1. punctiventris**

Abdominal sternites without midventral dots.....................**2. dubium**

3. Abdominal tergites 2–6 or –7 with large, bright red spot near either lateral margin of each tergite.......**3. parvulum**
Abdominal tergites 2–6 lacking large, sublateral, bright red spots; sometimes with a brown spot near each spiracle..4

4. Abdominal tergites 2–6 each with a pair of submedian, red-brown dots and a short, median, longitudinal, red line........................**4. myrsum**
Abdominal tergites 2–6 each with a pair of submedian, red or red-brown dots, but longitudinal, median, red line wanting.......................**5. veteris**

MATURE MALE NYMPHS

1. Caudal filaments each with alternating brown and white crossbands from base to apex; each abdominal gill with a subapical, brown spot...**3. parvulum**
Caudal filaments white, each with a brown crossband in middle; apex of each filament may or may not be brown.....2

2. Caudal filaments each with a brown crossband in middle and another at apex........................**4. myrsum**
Caudal filaments each with a brown crossband in middle only................3

3. Abdomen with median, ventral, dark spots on posterior margins of sternites 3– or 4–6 or –7...........**1. punctiventris**
Each abdominal sternite may have a pair of submedian, dark dots or streaks, but middle sternites lack median dots at posterior margins.........**2. dubium**

1. *Pseudocloeon punctiventris* (McDunnough)

Cloeon punctiventris McDunnough (1923:45).

MALE.—Length of body 3.5–4.5 mm., of fore wing 4–5 mm. Head very dark brown, almost black; antennae dark brown, becoming light toward apex of flagellum of each. Thorax dark brown, almost black; legs very light yellow, with coxae and trochanters brown, and each fore femur shaded with smoky brown; wings hyaline. First abdominal segment light brown; tergites 2–6 white, without markings, except that there may be faint, black spiracular dots; sternites 2–6 white, with a black or dark brown, median dot on posterior margin of each; apical abdominal segments red-brown, median black or dark brown dot may be present on posterior margin of each of segments 7 and 8; genital forceps faintly tinted with tan, apical forceps segment twice as long as broad; cerci white.

FEMALE.—Length of body 4.0–4.5 mm., of fore wing 5.0–5.5 mm. Head and thorax light brown. Abdomen tan, heavily shaded with black tracheal markings; median ventral dots large, black, present on posterior margins of sternites 1–6 or –7.

NYMPH.—Length of body 4.5–5.5 mm. Head and thorax brown and tan; legs white or light yellow, with femora vaguely shaded with brown in the middle and at apex of each. Abdomen tan, with brown markings: first and second tergites almost entirely brown, lighter on posterior margins near posterolateral angles; tergites 3 and 4 tan, each with a pair of brown, submedian dots and lateral margins shaded with brown; tergite 5 mostly brown, lighter on meson; tergite 6 entirely brown except for a pair of submedian, tan dots at posterior margin; tergite 7 mostly brown, tan on meson and at posterolateral angles; tergites 8 and 9 tan, with a pair of submedian, brown dots on each, tergite 9 often also vaguely shaded with brown at lateral margins; abdominal sternum tan, a pair of submedian, brown dots present on each sternite, a median, dark brown dot on posterior margin of each of sternites 3–7, apical sternites vaguely shaded with brown; gills with pinnately branched, black or dark brown tracheae; caudal filaments light yellow, with a dark brown crossband in middle of each.

Known from Illinois, Ohio, and Ontario.

Illinois Records.—MOUNT CARMEL: at light, June 18, 1947, Burks & Sanderson, 1 ♂. OAKWOOD, Salt Fork River: May 2, 1943, H. H. Ross, 2 ♂; May 6, 1936, Ross & Mohr, 1 ♂; June 4, 1948, B. D. Burks, 2 ♂. SERENA, Indian Creek: May 12, 1938, Ross & Burks, 1 ♂, 1 ♀; May 16, 1938, B. D. Burks, 3 N. WOLF LAKE: Hutchins Creek, May 12, 1939, Burks & Riegel, 3 N.

2. *Pseudocloeon dubium* (Walsh)

Cloe dubia Walsh (1862:380).

The male lectotype of this species is in the Museum of Comparative Zoology. This specimen is somewhat broken, but agrees quite well with the current concept of the species.

MALE.—Length of body 3–5 mm., of fore wing 4.0–5.5 mm. Head brown; each antennal scape and pedicel brown, flagellum white; each compound eye, in life, with faceted area of upper portion tan, columnar area yellow, and lower portion brown. Thorax dark, rich brown, almost black;

legs white, with coxae shaded with brown, a minute red-orange or red-brown mark at apex of each trochanter, each femur stained with orange-red or tan in middle and at apex, and each tibia stained with same color at apex; wings hyaline, with brown spot at base of each extending from vein Sc to 1A. First abdominal tergite brown, tergites 2–6 white, often very faintly stained with tan, apical tergites brown; black spiracular dots and, usually, longitudinal lines present on tergites 2–6 or –7, each spiracular dot almost always white in center; abdominal venter with first sternite variably stained with tan, sternites 2–6 white, apical ones stained with tan of varying intensity; genitalia with first forceps segment tan, other segments white, apical forceps segment two to two and one-half times as long as broad; the two cerci white.

Nymph.—Length of body 4–5 mm. Head and thorax mottled brown and white; legs white, with brown shading in middle and at apex of each femur. Dorsum of abdomen with strongly contrasting areas of brown and white: first and second tergites mostly brown, with white spot at each posterolateral angle; tergites 3 and 4 white, usually with a pair of submedian dots on each tergite, lateral margins brown; tergite 5 with broad middle area white, the lateral areas brown; tergites 6 and 7 almost entirely brown, usually with a pair of submedian, white dots at the posterior margin of each; tergite 8 marked like tergite 4; tergite 9 with a pair of large, brown, lateral spots; basal abdominal sternites white, apical ones shaded with brown, in some specimens each sternite bearing a pair of submedian dots; gills with tracheae obscure, almost invisible; caudal filaments white, with a broad, brown crossband at middle of each.

Known from Illinois, Ontario, and New York.

Illinois Records.—Aroma Park: Kankakee River, June 4, 1947, B. D. Burks, 1 ♂. Baker: Indian Creek, May 12, 1938, Ross & Burks, 2 N. Eddyville: Lusk Creek, May 28, 1946, Mohr & Burks, 1 ♂. Mazon: Mazon Creek, May 16, 1938, Ross & Burks, 10 N. Muncie: May 13, 1941, H. H. Ross, 1 ♂. Oakwood, Salt Fork River: May 2, 1943, H. H. Ross, 5 ♂; May 6, 1936, Ross & Mohr, 60 N. Rock Island: 18 ♂, 24 ♀ (Walsh 1862:380). Serena, Indian Creek: May 12, 1938, Ross & Burks, 2 N; May 16, 1938, B. D. Burks, 2 N. Watson: April 23, 1932, Ross & Mohr, 1 N. Wolf Lake, Hutchins Creek: May 12, 1939, Burks & Riegel, 2 N; May 15, 1940, Mohr & Burks, 3 N.

3. *Pseudocloeon parvulum* McDunnough

Pseudocloeon parvulum McDunnough (1932*b*:210).

Male.—Length of body 3.0–3.5 mm., of fore wing 3.5–4.0 mm. Head dark brown; antennae brown, apex of each flagellum slightly lighter. Thorax dark brown; legs light yellow, with coxae brown, each fore femur uniformly shaded with smoky tan, and middle and hind femora with red shading near apexes and on ventral margins; wings hyaline, longitudinal veins faintly stained with tan, vein Sc with dark tan spot at base. First abdominal tergite tan, tergites 2–6 white, very faintly suffused with tan, each with a pair of large, red spots and black spiracular lines at lateral margin; apical tergites dark tan; first abdominal sternite suffused with tan, sternites 2–6 lighter, almost white, no ventral markings present, apical sternites same color as basal one; genitalia white, with first segment of forceps suffused with tan, apical forceps segment only slightly longer than broad; cerci white or light yellow.

Female.—Length of body 3–4 mm., of fore wing 3.5–4.5 mm. Head and entire body tan or light brown, with abdominal sternites slightly lighter in color; red shading of abdominal tergites sometimes visible; wings tan at bases, wing veins faintly yellow; cerci white or faintly yellow.

Nymph.—Length of body 4.0–4.5 mm. Head and body brown, without large, contrastingly colored areas on dorsum of abdomen; legs each with femur brown on basal half to two-thirds, tibia brown at apex, tarsus brown in apical half; abdominal tergites typically each with a median anterior, two submedian, and a pair of posterolateral, light colored spots; gills platelike, each with a subapical, brown spot and black tracheae, the latter usually with a single stem and only one lateral branch; caudal filaments with narrow, alternating brown and white crossbands from base to apex of each.

Known from Alberta, Illinois, Quebec, and Ontario.

Illinois Records.—MAZON: Mazon Creek, May 16, 1938, Ross & Burks, 2 N. OAKWOOD: May 24, 1926, T. H. Frison, 2♂, 3♀. SERENA, Indian Creek: May 12, 1938, Ross & Burks, 17 N; May 16, 1938, B. D. Burks, 2 N.

4. *Pseudocloeon myrsum* new species

This species resembles *rubrolaterale* McDunnough (1931*b*:86) in possessing large, lateral, red-brown spots on the abdominal tergites and median, brown dots on the sternites, but differs in that each tergite possesses a pair of submedian, red-brown dots with a median, longitudinal, red mark between each pair of dots. This species likewise resembles *anoka* Daggy (1945:391) in possessing a large, brown mark on abdominal tergites 2 and 6, but differs in possessing the submedian dots and median marks mentioned above, as well as the lateral, red-brown spots.

MALE.—Length of body 3.5–4.0 mm., of fore wing 5.0–5.5 mm. Head dark yellow-brown, bright yellow around bases of antennae and at lateral angles of frontal shelf; ocelli yellow; faceted portion of upper section of each compound eye (in life) tan, columnar portion yellow, lower section of eye brown; scape and pedicel of antenna brown, flagellum yellow. Thorax dark, rich brown dorsally, with bright yellow markings along sutures; pleura and sternum mostly yellow, with dark brown shading only in central areas of scleromes; wings hyaline, each stained with red at base of costa and on anterior wing sclerites, base of subcosta dark brown, this color extending across wing base to vein 1A; veins and crossveins hyaline, stigmatic crossveins slanting, partially anastomosed; legs very light yellow, almost hyaline, with coxae brown and each femur stained with red-brown at base, middle, and apex; fore femur shaded with dull brown in basal three-fourths; each tibia shaded with rose red in middle, fore tibia shaded with dull brown at apex. First abdominal segment dull brown: tergites 2–6 hyaline, faintly stained with tan; tergites 2 and 6 each with a large, median, brown spot, each of tergites 2–6 with a pair of submedian, dark red or red-brown dots and a vague, longitudinal, median, red mark between each pair of dots; a large, vague, red-brown spot near lateral margin of each of these tergites and a pair of longitudinal, black spiracular lines on each tergite; apical four tergites yellow-brown, tergite 7 shaded on all but lateral and apical margins with dark red-brown; abdominal sternum hyaline, with a median, dark red-brown dot at posterior margin of sternites 2–, 3–, or 4–8; sternites 7 and 8 faintly shaded with red or red-brown; genitalia and caudal filaments white.

FEMALE.—Length of body 5 mm., of fore wing 6 mm. Body bright golden-brown; yellow at apex of mesoscutellum, on apical abdominal tergite, and on venter of entire body; lateral, brown shading of tergites 2–6 faintly indicated; legs as in male, except that each fore femur is almost completely brown; costal vein of fore wing red at base, but basal, brown area of male wanting; caudal filaments white, each faintly stained with yellow at base.

NYMPH.—Length of body 5.0–5.5 mm., caudal filaments 3.0–3.5 mm. Head yellow, faintly shaded with brown on face. Thorax white or tan, mottled with brown on dorsum and pleura, venter white; wingpads with pattern of future adult, longitudinal veins shown by brown lines; legs white, each femur with a brown cloud at base and middle and, sometimes, at apex. Abdomen white or tan, with brown shading: tergites 1 and 2 almost completely shaded with brown, a pair of submedian, circular, light spots at posterior margin of each, tergite 2 with a large, median, brown spot; tergites 2–5 mostly light, with a pair of submedian, brown dots on each; tergites 6 and 7 shaded like tergite 1; tergites 8 and 9 light, each with two pairs of submedian, brown dots; tergite 10 light, with a pair of submedian, brown streaks and a pair of dark spots at lateral margins; in dark individuals, these dark areas and spots tend to spread and almost coalesce; gills hyaline, tracheae pinnate, brown; abdominal sternum white or tan, with a pair of submedian, brown dots on each of sternites 2–7; apical sternites usually uniformly shaded with brown; cerci white, except for a brown apex and a brown crossband at middle of each.

Holotype, male. — Eddyville, Illinois, Lusk Creek, May 16–17, 1947, B. D. Burks. Specimen dry, on pin.

Allotype, female.—Wolf Lake, Illinois, Hutchins Creek, April 2–3, 1946, Burks & Sanderson. Specimen dry, on pin.

Paratypes.—Same data as for allotype, 2♂. Specimens dry, on pins.

Nymphs.—Illinois.—Eddyville: Lusk Creek, May 16–17, 1947, B. D. Burks, 2 N. Wolf Lake, Hutchins Creek: April 3, 1946, Burks & Sanderson, 10 N; May 12, 1939, Burks & Riegel, 1 N.

5. *Pseudocloeon veteris* McDunnough

Pseudocloeon veteris McDunnough (1924*a*: 8).

As McDunnough remarked when describing this species, he based his description on old, faded specimens. Recently collected specimens, which could be studied while still alive, necessitate considerable change in the description of the color of this species.

Male.—Length of body 4.5–5.0 mm., of fore wing 5.0–6.0 mm. Head dull brown, frontal shelf hyaline; antennae dull tan, each scape white at apex; eyes orange-yellow. Thorax bright orange-brown; yellow on prescutum, along outer parapsidal furrows, on scutellum, on pleural sutures, and covering the entire thoracic sternum; wings hyaline, faintly stained yellow at bases, stigmatic crossveins numerous, anastomosed; legs pale yellow, apex of each femur shaded with orange. Abdominal segments 2–6 yellow, sometimes faintly suffused with tan, each tergite with a pair of submedian, red or red-brown dots, and usually a short, median, red or red-brown, transverse stripe at posterior margin; segments 1–6 with black spiracular dots and longitudinal spiracular line usually present on either side; sternites 1–6 yellow, with a median, dark brown spot at posterior margin of each and often black tracheal outlines extending ventrad from spiracles on anterior sternites; apical tergites dark orange-brown, sternites suffused with pale pink; genitalia white, apical forceps segment two and one-half times as long as broad; caudal filaments white.

Female.—Length of body 5 mm., of fore wing 6 mm. Head and thorax light brown; legs light yellow, femora shaded toward apexes with pink or tan; abdominal dorsum light brown, with a pair of submedian, red-brown dots faintly visible on each tergite; abdominal sternum light tan, with a fairly large, black dot on meson of posterior margin of thoracic metasternum and abdominal sternites 1–7.

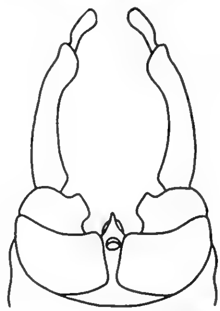
Known from Illinois.

Illinois Records.—Muncie: May 13, 1931, H. H. Ross, 1♂. Oakwood: April 24, 1925, T. H. Frison, 10♂, 4♀; May 18, 1926, T. H. Frison, 2♂; June 5, 1948, Burks & Sanderson, 2♂. Urbana: Salt Fork River, May 13, 1898, 4♂, 3♀.

34. *NEOCLOEON* Traver

Neocloeon Traver (1932*b*: 365).

The genus *Neocloeon* is similar to *Cloeon* in that the fore wings have relatively few



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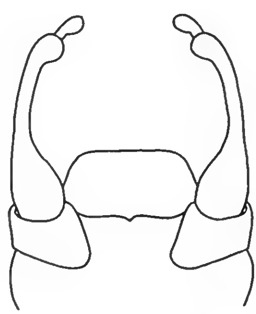

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Fig. 299.—*Neocloeon alamance*, male genitalia.

Fig. 300.—*Cloeon mendax*, male genitalia. (After Traver.)

crossveins and single marginal intercalary veins, and the hind wings are wanting.

In the males of *Neocloeon*, the fore tarsus is approximately as long as the fore tibia, and either one is one and one-third to one and one-half times as long as the fore femur; the partly differentiated first tarsal segment of the hind leg is as long as the three apical, clearly differentiated segments combined. The stalk supporting the upper faceted portion of each compound eye is quite low; its height is only about one-half as great as the diameter of the lower portion. Each arm of the genital forceps, fig. 299, has the basal segment broad and short, the second segment semiquadrate, with a large projection on the median margin, the third segment long, relatively stout, and very little bowed, and the fourth segment two and one-half to three times as long as broad. The penis cover is produced on the meson.

The nymphs have long, three-segmented maxillary palps, the labial palps are broad, truncate, and three-segmented; the tarsal claws are long, slender, and nondenticulate; the abdominal gills are single and platelike, and they bear blackened tracheae which branch on the inner sides only; the three caudal filaments are well developed.

Neocloeon alamance Traver (1932:365), originally described from North Carolina and later recorded from Tennessee, is the only known species in this genus.

35. *CLOEON* Leach

Cloeon Leach (1815:137).
Cloea Billberg (1820:97). Emendation, unnecessarily proposed.
Cloe Burmeister (1839:797). Emendation, unnecessarily proposed.
Chloeon Lubbock (1863:61). Emendation, unnecessarily proposed.
Cloeopsis Eaton (1866:146).
Procloeon Bengtsson (1915:34). New synonymy.

In species of the genus *Cloeon*, the fore wing has relatively few crossveins and only a single marginal intercalary vein in each interspace of the outer wing margin; the hind wings are wanting.

In the males, the fore tarsus is approximately equal in length to the fore tibia, and either one is slightly longer than the fore femur. The hind tarsus has the partly differentiated first segment as long as, or slightly longer than, the two apical tarsal segments combined. Each arm of the genital forceps, fig. 300, has the first segment broad, short, and narrowed at the apex; the second segment is somewhat conic and not clearly separated from the third segment; the third segment is long, slender to fairly stout, and usually slightly bowed; the fourth segment is about as broad as long. The penis cover is usually truncate at its apex.

Both maxillary and labial palps in the nymphs have three segments; each tarsal claw is relatively short, broad at the base, and slender at the tip, and bears a single row of minute ventral denticles; the abdominal gills are sheetlike, undulated, and double, with the tracheae usually branching palmately; the three caudal filaments are well developed. Mayflies of this genus, so far as is known, develop in small ponds or in the still eddies along the banks of streams.

Cloeon includes 10 described Nearctic species, 8 of which are treated here. The species of *Cloeon* all seem to be quite rare in eastern North America.

Reliable characteristics for the specific determination of the females and nymphs in this genus have not yet been found.

KEY TO SPECIES

ADULT MALES

1. Abdominal tergites 2–6 almost entirely dark red-brown or gray-brown......2
   Abdominal tergites 2–6 hyaline, white or faintly yellowish, often with red or dark brown markings..............3
2. Caudal filaments white, stained with red-brown at bases, but articulations not darkened; abdominal tergites 2–6 light gray-brown................**1. ingens**
   Caudal filaments white, with articulations dark brown or black throughout; abdominal tergites 2–6 almost entirely dark red-brown.........**2. dipterum**
3. Abdominal tergites 2–6 uniformly stained with light red, without darker markings ....**3. mendax**
   Abdominal tergites 2–6 hyaline, white, or faintly yellow, often with red or dark brown markings...................4
4. Abdominal tergites 2–6 hyaline, with a pair of large, lateral, dark brown blotches on each, these blotches on segments 3 and 6 so large as to coalesce on meson....................**4. minor**
   Abdominal tergites 2–6 white or light yellowish, without large, lateral, dark brown blotches, but sometimes with small, red marks on some or all of these tergites..........................5
5. At least some of abdominal tergites 2–6 with small, red markings...........6
   Abdominal tergites 2–6 white, without red markings.....................7
6. Abdominal tergites 2 and 3 each with a faint, median, red streak........... ....**5. insignificans**
   Posterior margin of each of abdominal tergites 2–6 with a pair of submedian, red dashes..........**6. rubropictum**
7. Mesonotum light yellow-brown......... ....**7. vicinum**
   Mesonotum dark brown, shading to creamy white at lateral margins and at apex of scutellum.........**8. simplex**

1. *Cloeon ingens* McDunnough

Cloen ingens McDunnough (1923:44).

MALE.—Length of body 8 mm., of fore wing 9 mm. Thoracic notum black, pleura light brown, legs gray-brown, and wings hyaline. Basal abdominal tergites uniformly shaded with gray-brown, with a narrow, transverse, black-shaded area at posterior margin of each tergite; apical abdominal tergites chocolate brown; venter dirty white, apical sternites faintly stained with brown; and genital forceps and caudal filaments white, the latter stained with red-brown at bases.

Known from Alberta, Maine, and Quebec.

2. *Cloeon dipterum* (Linnaeus)

Ephemera diptera Linnaeus (1761:377).

A single female specimen of this Palearctic species has been taken in Illinois. Comparison of this specimen with the description given in Eaton (1885:182) and with reliably determined European material of *dipterum* leaves no doubt of the correctness of the identification. *C. dipterum* is a common and widespread European species which has not heretofore been proved to be present in North America. The description given below of the male was written from specimens collected in Switzerland, which were sent to the Illinois Natural History Survey collection by Dr. F. Schmid of Lausanne.

MALE.—Length of body 6–7 mm., of fore wing 7–8 mm. Thorax very dark brown to black, legs tan or brown, wings hyaline, with longitudinal veins and most crossveins light brown. Basal abdominal tergites heavily shaded with dark red-brown, basal sternites tan, with dark red-brown shading at lateral margins; apical abdominal segments dark chocolate brown, almost black; genital forceps light yellow, almost white; caudal filaments white, articulations throughout dark brown to black.

FEMALE.—Length of body 8 mm., of fore wing 9 mm. Head light yellow, almost white, without darker markings; bases of ocelli and entire compound eyes very dark gray, almost black; antennae light yellow, each with a narrow band of dark brown shading at apex of scape and of pedicel. Thorax uniformly light tan, shaded with brown along posterior margin of mesotergum; small, brown spot on meso- and metasternum near base of each coxa; legs light yellow, with a small, brown spot on ventral side of each middle and hind coxa, at apex on dorsal side of each fore trochanter, and near apex of each femur; minute, brown dot on dorsal side at apex of each of three apical tarsal segments. Wings hyaline, with light brown shading in costal and subcostal interspaces of each fore wing, this shading extending from base to apex of wing, but interrupted at each crossvein in these interspaces; 5 crossveins in costal interspace basad of bulla, 10 crossveins present in this interspace distad of bulla; crossveins partly anastomosed in stigmatic area; all longitudinal veins brown; crossveins in costal, subcostal, first radial, cubital, and anal interspaces hyaline, all other crossveins brown; marginal intercalary veins brown except in anal region. Abdomen light tan, tergites faintly shaded with brown; tergites 2–8 each with small, longitudinal spot on meson at anterior margin, a pair of rather broad, sublateral, curved spots on basal two-thirds, a pair of very small spiracular dots and a pair of narrow, lateral, longitudinal lines; tenth tergite with a pair of large, lateral, triangular marks; abdominal sternum pale yellow, with dark red-brown markings; sternites 2–8 each with a pair of sublateral, longitudinal bars, a minute, transverse line at posterior margin at point where each longitudinal, red-brown bar ends, a transverse bar at anterior margin extending laterally from each longitudinal bar to anterolateral angle of sternite, and a short, narrow, longitudinal mark extending posteriorly from a point near each anterolateral angle of sternite; sternites 2 and 3 also each with a pair of short, longitudinal lines at basolateral angles; sternite 9 with a pair of vague, fairly large, red-brown spots near anterolateral angles; each paraproct with a submedian, longitudinal, brown line. Caudal filaments white, articulations dark red-brown; in basal area of each filament, alternating articulations with broader color band.

In Europe, *Cloeon dipterum* has long been recorded as ovoviviparous and the length of life of an adult female may be as much as 3 weeks. The single female specimen from Illinois is probably an adventive.

Illinois Record.—CHAMPAIGN: at light, Aug. 26, 1939, C. O. Mohr, 1♀.

3. *Cloeon mendax* (Walsh)

Cloe mendax Walsh (1862:381).

The lectotype of this species, now in the Museum of Comparative Zoology, is a female and, as it is a true *Cloeon,* it must be a different specimen from the one McDunnough found labeled as *mendax* in the M.C.Z. about 1928 (McDunnough 1929: 173). The specimen he saw was a *Centroptilum,* with two pairs of wings, while the specimen I saw there in 1942 clearly had only one pair of wings. Walsh's male type, unfortunately, is lost, and additional male specimens from Illinois are yet to be taken. I have seen males of this species from New York.

Male.—Length of body 4 mm., of fore wing 6 mm. Thoracic notum and pleura stained with red; thoracic venter white, with a gray-green cast; legs white, often with a green cast; wings hyaline. Abdominal tergites stained with red; sternites greenish white; apical segments opaque, basal ones translucent; genital forceps, fig. 300, and the three well-developed caudal filaments white.

Female.—Length of body 5 mm., of fore wing 7 mm. General color very light yellowish, lacking red staining of male. Thorax, wings, and legs in fresh specimens variably stained with bright green.

This species is known from Illinois, Massachusetts, Michigan, New York, and Ontario.

Illinois Records.—Barry: sweeping willows near pond, Aug. 12, 1948, Sanderson & Stannard, 2♀. Rock Island: 2♂, 4♀ (Walsh 1862:381).

4. *Cloeon minor* McDunnough

Cloeon minor McDunnough (1926:190).

Male.—Length of body and of fore wing 3 mm. Thoracic notum black; each pleuron very dark brown, with pink staining near wing base; sternum dark brown; legs white, with a faint, red spot near middle of each femur; wings hyaline. Abdominal tergites 2–6 hyaline, with a pair of large, brown, sublateral blotches on each segment, these blotches coalescing on meson of tergites 3 and 6; sternites 2–6 hyaline, each with a pair of lateral, brown triangles and a pair of submedian, black dashes at posterior margin; apical tergites dark brown and sternites light brown; genital forceps and caudal filaments white.

Known from Ontario.

5. *Cloeon insignificans* McDunnough

Cloeon insignificans McDunnough (1925*b*:186).

Male.—Length of body 3 mm., of fore wing 4 mm. Thoracic notum and pleura dark brown, sternum lighter brown, legs white, and wings hyaline, with longitudinal veins faintly yellowish. Basal abdominal tergites white, with a faint red, median streak on tergites 2 and 3, sternites 2 and 3 white; apical tergites light brown, sternites tan; genital forceps and caudal filaments white.

Known from Ontario.

6. *Cloeon rubropictum* McDunnough

Cloeon dubium Clemens (1913:341), not Walsh. Misidentification.
Cloeon rubropicta McDunnough (1923:43).

Male.—Length of body 3–4 mm., of fore wing 4–5 mm. Head dark brown, shading to yellow below ocelli, antennae yellow, flagella slightly dusky. Thorax dark brown on dorsum and pleura, venter yellow; legs light yellow; wings hyaline. Abdominal segments 2–6 white, translucent, each tergite with a pair of submedian, red, transverse marks at posterior margin and a pair of sublateral, red dots; tergites 2, 3, and 6 with vague, median, longitudinal, red marks; a longitudinal, black spiracular hairline present at lateral margins of these segments; sternites 2–6 unmarked, apical tergites red-brown, apical sternites vaguely shaded with brown; genital forceps and caudal filaments white.

Female.—Length of body 4–5 mm., of fore wing 5–6 mm. Head and thorax yellow to dull tan, thoracic venter dirty white to yellow. Abdominal tergites translucent tan, faint, submedian, red marks often present on posterior margins of all tergites, extensive, black tracheal and spiracular marks present; venter pale yellow to white; legs and caudal filaments white or faint yellow.

Known from Illinois, New York, Ontario, Ohio, and Quebec.

Illinois Records. — Eddyville: Lusk Creek, June 19, 1940, Mohr & Riegel, 1♂. Oakwood: June 6, 1925, T. H. Frison, 1♂, 1♀; June 9, 1926, Frison & Auden, 1♂, 3♀.

7. *Cloeon vicinum* (Hagen)

Cloe vicina Hagen (1861:56).

MALE.—Length of body 4 mm., of fore wing 4–5 mm. Thorax almost completely light yellow-brown, only slightly darker on mesoscutum; wings hyaline and in stigmatic area of each wing five or six crossveins which do not quite reach subcostal vein; legs white, with each fore coxa and base of fore femur stained with tan. Abdominal segments 2–6 white, without red or brown markings; apical tergites dull brown; apical sternites very light tan; genital forceps white, basal segment of each bearing a very small, mesoapical projection; caudal filaments white.

Known from the District of Columbia, New York, and West Virginia.

8. *Cloeon simplex* McDunnough

Cloeon simplex McDunnough (1925*b*:185).

MALE.—Length of body 4.5–5.5 mm., of fore wing 5–6 mm. Head brown, scape and pedicel of each antenna yellow, flagellum brown. Thoracic notum brown, with posterior margins of pronotum and mesoscutum and entire mesoscutellum white; pleura white, with vague, tan shading; prosternum white; meso- and metasternum brown, with white markings; wings hyaline; legs white. Abdominal segments 1–6 translucent white, with longitudinal, black spiracular lines; apical tergites yellow-brown, sternites white, opaque; genital forceps and caudal filaments white.

FEMALE.—Length of body 5–6 mm., of fore wing 6–7 mm. Head and thorax yellow or light tan, sometimes tinged with green; abdomen yellow, with extensive, black tracheal and spiracular markings; legs white, wings hyaline, both sometimes with green stain.

Known from Illinois, Indiana, Ontario, Quebec, and Wisconsin.

Illinois Records.—RICHMOND: June 13, 1938, B. D. Burks, 1♂. ROSECRANS: Des Plaines River, June 14–21, 1938, B. D. Burks, 1♂, 3♀, 5 N. SPRING GROVE: June 9, 1938, Mohr & Burks, 1♂.

AMETROPIDAE

This family as treated here includes some of the genera that were placed in the families Ametropodidae and Ecdyonuridae in Ulmer's classification (1933), and represents a combination of the subfamilies Ametropinae and Metretopinae of Traver's classification (1935*a*:429, 433). Lestage (1938: 180) has divided these genera among three families, Ametropodidae, Metretopodidae, and Siphloplectonidae.

The Ametropidae contain forms which are interstitial between the typical heptageniids and the typical baetids. The wing venation is quite similar to, or identical with, that of the Heptageniidae, but the hind tarsus in all ametropid genera has only four clearly differentiated segments. The nymphs resemble either the heptageniid or baetid form, but the tarsal claws of the middle and hind legs are slender (at least six times as long as greatest width) and usually longer than their respective tibiae, figs. 25, 301, 302, 312.

In the male ametropid adults, the fore tarsus is from two and one-half to nearly five times as long as the fore tibia, the first fore tarsal segment varies from three-fourths to one and one-half times as long as the second segment; the compound eyes are almost or quite contiguous on the meson, each eye is obscurely divided into an upper area of larger facets and a lower area of slightly smaller facets, and the living insect often has a faint color band crossing the eye at the boundary line between the two areas of facets in the eye. In both sexes, the cubital intercalaries, fig. 308, consist of two or, more often, four straight veins which are detached at the bases; the hind wing always has a broadly angulate costal projection; and vein M of the hind wing is forked near the wing base, or, farther distad, near the middle of the wing. In both sexes of all members of this family, the abdomen is markedly long and slender, with the apical segments more slender and elongate than are the basal segments. There may be either two or three well-developed caudal filaments.

In the nymphs, which are quite heterogeneous, the head is flattened laterally or dorsoventrally and the eyes are directed anteriorly, dorsally, or laterally. The fore tarsal claw is single, slender, and long in *Pseudiron, Ametropus,* and *Metreturus,* but bifid in *Siphloplecton,* fig. 303, and *Metretopus;* the claws of the middle and hind legs are longer than their respective tibiae, figs. 301, 302. In the nymphs of most genera, the body is elongate and fishlike, but in *Pseudiron,* it is flattened dorsoventrally.

Gills are borne by abdominal segments 1–7, but the structure of these gills varies greatly

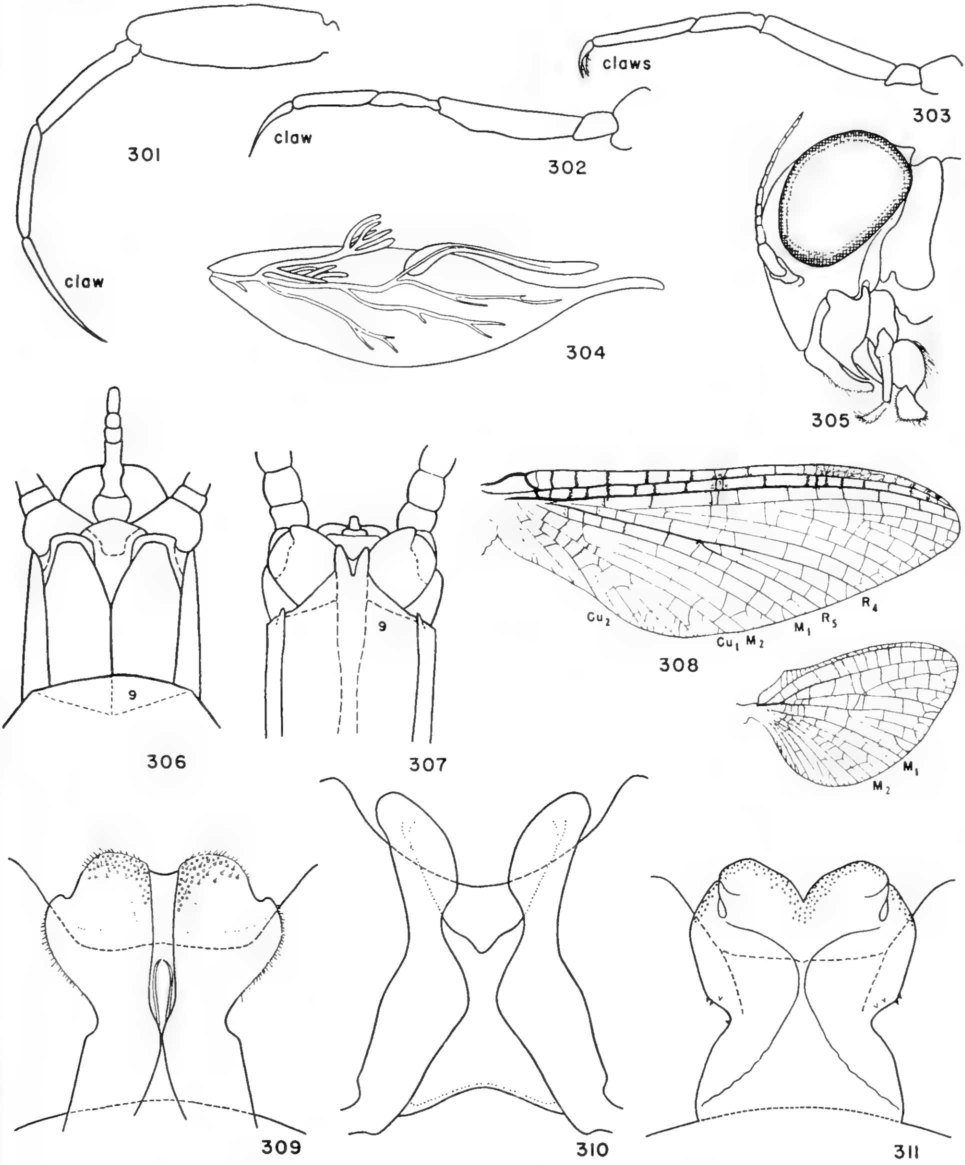


Fig. 301.—*Pseudiron centralis,* hind leg of mature nymph.
Fig. 302.—*Siphloplecton interlineatum,* middle leg of mature nymph.
Fig. 303.—*Siphloplecton interlineatum,* fore leg of mature nymph.
Fig. 304.—*Pseudiron centralis,* gill of third abdominal segment.
Fig. 305.—*Siphloplecton interlineatum,* head of adult male, lateral aspect.
Fig. 306.—*Siphloplecton interlineatum,* terminal abdominal sternites of female.
Fig. 307.—*Pseudiron centralis,* terminal abdominal sternites of female.
Fig. 308.—*Siphloplecton basale,* wings.
Fig. 309.—*Siphloplecton interlineatum,* male genitalia.
Fig. 310.—*Pseudiron centralis,* male genitalia.
Fig. 311.—*Siphloplecton basale,* male genitalia.

among the various genera in this family. All known nymphs have each three relatively short caudal filaments, with each outer filament bearing a dense fringe of setae on the mesal margin only.

KEY TO GENERA

ADULTS

1. Median caudal filament well developed, almost as long as cerci .... **36. Ametropus**
   Median caudal filament vestigial or represented by only a one- to four-segmented stub 2
2. One pair of cubital intercalary veins present in fore wing ..... **38. Metretopus**
   Two pairs of cubital intercalary veins present in each fore wing 3
3. First segment of fore tarsus of male three-fourths as long as second segment; ninth abdominal sternite of female extended caudad and with a pronounced median notch on posterior margin, fig. 307 .... **39. Pseudiron**
   First segment of fore tarsus of male slightly longer than second segment; ninth abdominal sternite of female not produced caudad and without a median notch on posterior margin, fig. 306 .... **40. Siphloplecton**

MATURE NYMPHS

1. Eyes directed anteriorly; each fore coxa with a large, lobelike, median appendage .... **36. Ametropus**
   Eyes directed laterally or dorsally 2
2. A median, ventral, hooklike spur present on each thoracic segment and a median, dorsal, hooklike spur present on each abdominal segment, fig. 312 .... **37. Metreturus**
   Thoracic and abdominal segments without median, dorsal, or ventral, hooklike spurs 3
3. Head flattened dorsally, prognathous; eyes dorsal; claw of fore tarsus single .. .. **39. Pseudiron**
   Head not flattened dorsally, hypognathous; eyes lateral; claw of fore tarsus double, fig. 303 4
4. Maxillary palp two-segmented .... **38. Metretopus**
   Maxillary palp three-segmented .... **40. Siphloplecton**

36. *AMETROPUS* Albarda

Ametropus Albarda (1878:129).

In the genus *Ametropus,* the wing venation differs only slightly from that of the typical heptageniid form, the fore wing having two pairs of cubital intercalary veins. The hind wing has an acute costal angulation, vein M is forked at a point halfway from its base to the apex, and veins R_4 and R_5 are fused throughout their length. The male penis lobes are fused to form a conical structure with a narrow, V-shaped apical cleft, somewhat as in *Baetisca* and some species of *Ephemerella.* The apical abdominal sternite of the female has a median caudal cleft. The median caudal filament is long, nearly as well developed as are the cerci.

The nymphs are fishlike in general body form, with the eyes directed anteriorly. The head is small, with the frontal margin cut away almost to the antennal sockets, nearly completely exposing the mouth-parts. The pronotum is wider than the head, and a projecting, membranous flap is borne by the prosternum. Each fore coxa has a fleshy, lobelike mesal projection. All the tarsal claws are single, slender, and pointed, and are much longer than the tibiae. The abdominal gills are single and platelike.

Only two Nearctic species are known in the genus *Ametropus.* One of these, ***neavei*** McDunnough (1928*a*:9), was described from Alberta. The other, ***albrighti*** Traver (1935*a*:431), described from the nymph only, was first collected in New Mexico and has subsequently been found in Utah.

37. *METRETURUS* new genus

The genus *Metreturus* is here erected for a new species, known only in the nymphal stage, fig. 312, which is radically different from that of all other North American mayflies. It is referred to the family Ametropidae because of the very short tibiae, the long, slender tarsal claws, and the three short caudal filaments, each of the outer ones of which bears a dense fringe of setae on the mesal margin only. The wing venation, visible in the nymphal wingpads, can be seen with sufficient clarity to show that the adult of this form could be referred to the Ametropidae, as there are two pairs of parallel and basally detached cubital intercalary veins.

The nymph of *Metreturus* has the head small and hypognathous, with the eyes lateral; there is a pair of short, submedian horns near the antennal bases, on the face above the clypeus; there is a median, acute projection on the margin of the clypeus, and there is an oblique, laterally projecting lobe arising at the lower margin of each com-

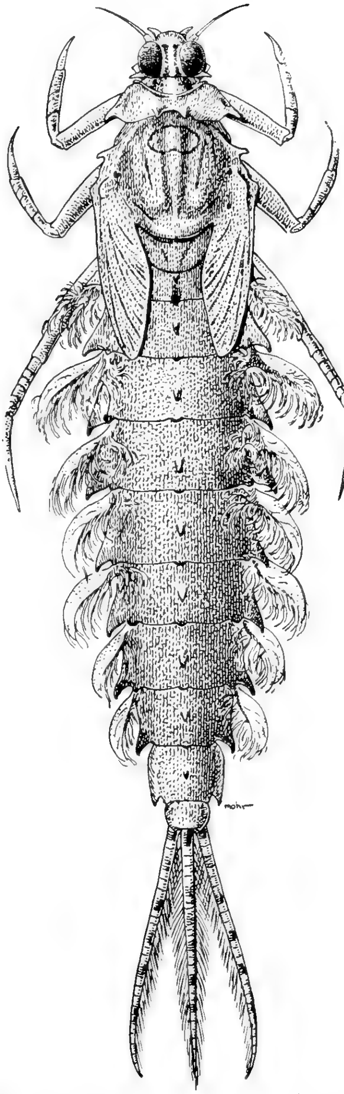


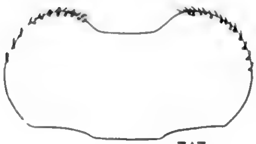
Fig. 312.—*Metreturus pecatonica*, mature nymph, dorsal aspect.

pound eye. The thorax has a pair of finger-like, projecting lobes on the lateral margins of both the pronotum and the mesonotum; a hooklike, median projection is borne on the sternum of each thoracic segment; each fore tarsal claw is single, long, and slender, and each of the middle and hind tarsal claws is single, slender, and much longer than the respective tibia. Abdominal segments 1 to 9 have each a pair of acute projections at the posterolateral angles; a single, hooklike, median projection is present in the center of each tergite 1 to 9, and also a small, acute, median papilla on the posterior margin of each of these tergites; each of segments 1 to 7 bears a pair of deeply fissured gills, each gill consisting of a dorsal member with a recurved, ventral flap and a smaller, ventral member; the three caudal filaments are relatively short, the outer ones bearing a fringe of setae on the mesal margins only. The available material of this genus shows that the adult would have three well-developed caudal filaments.

Genotype: *Metreturus pecatonica* new species.

Metreturus pecatonica new species

FEMALE NYMPH.—Fig. 312. Length of body 20.0 mm., of caudal filaments 5.5 mm. Entire head and body creamy white, virtually without dark markings except for the brown lines on wingpads indicating paths of adult wingveins, vague, brown crossband at base of each front wingpad, and light brown crossbands on caudal filaments. Head with eyes separated on vertex by space three-fourths as great as the width of one eye; a pair of large and hornlike projections arising on face between the antennal sockets; an oblique and finger-like, projecting lobe arising from each gena just ventral to compound eye; antennal scape about three-fifths as long as pedicel, flagellum five times as long as pedicel; clypeus with margin acutely projecting on meson, laterally cut away so as to expose bases of mandibles; labrum, fig. 313, with broad, mesal emargination on outer margin; mandibles, fig. 314, each with apex broad, bearing seven teeth in three groups, molar area wanting; maxilla, fig. 316, with apex broad, mandible-like, bearing five or six slender, acute teeth; palp reduced to a single, small, lobelike segment; hypopharynx bilobed; labium, fig. 315, with glossa large, rounded, each paraglossa with mesal margin straight, lateral margin convex, palp three-segmented, with apical segment relatively minute, apposed to an apicomesal projection of second segment. Pronotum with a finger-like projection at each posterolateral angle and a pair of small, submedian projections at posterior margin; hooklike projection in center of prosternum; fore femur as long as tibia and tarsus (without claw), fore tarsal claw single, slender at apex, enlarged near base, one and one-half times as long as tibia; mesonotum with finger-like, lateral projection at base of each front wingpad, mesosternum with hooklike projection in center of basisternum, middle femur as long as tibia and tarsus without claw, middle tarsal claw long, slender, more than twice as long as middle tibia;



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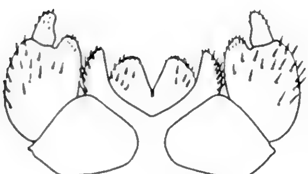

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Fig. 313.—*Metreturus pecatonica*, labrum of nymph.
Fig. 314.—*Metreturus pecatonica*, mandible of nymph.
Fig. 315.—*Metreturus pecatonica*, labium of nymph.
Fig. 316.—*Metreturus pecatonica*, maxilla of nymph.

metasternum with hooklike projection in the center, hind femur one and one-half times as long as tibia and tarsus without claw, hind tarsal claw five times as long as tibia. Abdomen three times as long as thorax, tapering toward posterior end, so that segment 9 is two-fifths as wide as segment 1; prominent, flat flange and projecting, posterolateral angle present at each lateral margin of tergites 1–9; a hooklike projection present in center of each tergite 1–9, with a small, median papilla present at posterior margin of each of these tergites; segments 1–7 each bearing a pair of gills, each gill composed of a dorsal member, with a recurved ventral flap, and a ventral member, each gill member having a stout, median tracheal trunk from which arise numerous, pinnately branching tracheae; lamina of gill partly eroded away between these tracheae, so that ventral member of each gill almost assumes appearance of a cluster of branching filaments; nearly all or smaller part of upper member of each gill having a similar appearance, this atrophy of gill lamina of upper member almost complete in first gill, but becoming progressively less so in more posterior gills, the upper member of seventh gill with lamina eroded only at apex and on mesal side; caudal filaments alternately banded with faint yellow and light brown.

Holotype, female nymph. — Taken by seining in Sugar River, one-fourth mile above mouth, near Harrison, Illinois, July 6, 1926, R. E. Richardson. Specimen mature, taken just as molt to subimaginal stadium was beginning. Specimen in alcohol.

Paratype. — ILLINOIS: Taken with dipnet near water's edge at mouth of Pecatonica River, near Rockton, May 8, 1927, R. E. Richardson, 1 ♀ nymph, about half grown. Specimen in alcohol.

The streams in which these specimens were found have subsequently been dredged and straightened, but the available information indicates that, at the time the collecting was done, they were fairly rapid, shallow, and moderate-sized streams with sand and rock bottoms. Since being dredged, they have been sluggish, heavily silted streams with mud bottoms. Intensive collecting in these rivers in recent years has failed to produce additional specimens; the species probably has disappeared completely from them.

38. *METRETOPUS* Eaton

Metretopus Eaton (1901:253).

In *Metretopus,* the wing venation is similar to that of *Siphlonurus,* fig. 219, but differs principally in that the cubital intercalary veins of the fore wing consist of two long, straight veins instead of a series of short, sinuate veins decurrent from vein Cu_1. The hind wing in *Metretopus* also has a relatively acute costal projection. The median caudal filament is vestigial in the adult. Characters of the nymph, used in the above key to genera, are from Bengtsson (1909:16).

One Holarctic species, *norvegicus* Eaton (1901:254), has been reported from Alberta by McDunnough (1925*b*:187).

39. *PSEUDIRON* McDunnough

Pseudiron McDunnough (1931*b*:91).

Pseudiron is clearly an interstitial genus showing similarity to the members of both the Heptageniidae and Baetidae. The adult wing venation is typical for the Heptageniidae, resembling most closely that of *Rhithrogena,* fig. 320, but the hind tarsus has only four clearly differentiated segments. The abdomen is quite long and slender, and the ninth sternite of the female has a median indentation on the posterior margin, fig. 307. The male genitalia are quite similar in structure to the genitalia of the *jejuna* group of species in the genus *Rhithrogena.* The median caudal filament is vestigial in the adults of *Pseudiron.*

Each of the nymphs has a somewhat flattened, heptageniid-like head, with the eyes dorsal in position; in addition, the head is slightly elevated on the meson between the antennal bases, faintly suggesting the baetine head form. The mouth-parts evidently are fitted for predatism (Spieth 1938*a*:3). The tarsal claws, fig. 301, are longer than the tibiae. The gills, fig. 304, are elongate and slender, with a small fibrillar tuft near the base on the ventral side and a narrow, flagellum-like appendage near the center of the posterior margin, also on the ventral side of the gill. This type of gill occurs in no other known member of the order Ephemeroptera.

Spieth (1938*a*:3) described a nymph which he had collected in southwestern Indiana and thought to be the nymph of *Pseudiron.* A nymph, apparently of the same species, has been collected in Illinois. In my opinion, this nymph can be accepted as that of *Pseudiron* without further question despite the fact that an actual rearing from nymph to adult has not yet been accomplished. The tarsal characters place it in the Ametropidae and the wing venation visible in the nymphal wingpads, as well as the form of the abdomen, are in agreement with the adult *Pseudiron* characteristics. Furthermore, this nymph and the adults of *Pseudiron* have been collected at the same location in Illinois.

Pseudiron centralis McDunnough

Pseudiron centralis McDunnough (1931*b*:91).

MALE.—Length of body and of fore wing 12 mm. Head light yellow, with red-brown shading on face and on vertex between compound eyes; each antennal scape and pedicel red-tan, flagellum light yellow; compound eyes of living insect dark gray. Dorsum of thorax reddish brown, with narrow, yellow stripes on lateral sutures of mesonotum; pleura and sternum yellow. Legs markedly long and slender, yellow-brown, with a dark, red-brown crossband present at middle and at apex of each femur, each tibia and tarsal segment darkened at apex; wings hyaline, each brown stained in stigmatic area, veins and crossveins brown. Abdomen with broad, dorsomedian, longitudinal, brown stripe, edges of this stripe extended to lateral margin at posterior margin of each tergite; abdominal sternum yellow, with ganglionic areas faintly brown-stained; genitalia, fig. 310, yellow-brown; caudal filaments yellow, with basal two or three segments shaded with brown, articulations light brown, becoming colorless toward the apexes of the filaments.

FEMALE.—Length of body 12–13 mm., of fore wing 13–14 mm. Coloration almost identical with that of male except that dorsum of thorax is mostly yellow-brown; stigmatic area of fore wing not brown stained, veins and crossveins of hind wing almost or quite hyaline; ninth abdominal sternite incised on meson of posterior margin, fig. 307; caudal filaments white, basal articulations light brown.

NYMPH.—Length of body 12–13 mm. Head broad, flattened dorsally, but slightly elevated on median area between antennal bases, thus somewhat intermediate in form between typical heptageniid and baetid nymphal heads. Pronotum with lateral margins expanded laterally as thin, platelike projections, reminiscent of the pronotum in some Palaeodictyoptera. Legs long, slender, fig. 301, with each tarsal claw longer than respective tibia; wingpads showing venational pattern typical for this genus. Abdomen long, slender, with lateral margins flaring; platelike, posterolateral angles acute on segments 8 and 9, rounded on more anterior segments; gills, fig. 304, with a small fibrillar tuft near base and a flagellum-like projection near middle of posterior margin; apex of gill lanceolate; cerci each with a fringe of long setae on inner side only, median caudal filament bearing long setae on both sides.

Known from Illinois, Indiana, Iowa, Kansas, Manitoba, and Missouri. Evidently develops in rivers that are fairly rapid and of moderate size.

Illinois Records.—CENTRALIA: at light, June 17, 1947, L. J. Stannard, 2♀. DIXON: at light, June 26, 1947, B. D. Burks, 1♀. KEITHSBURG: at light on Mississippi River, June, 1932, 1♂. MOUNT CARMEL: at light, Burks & Sanderson, 1♀. PROPHETSTOWN: dredging sandy bottom of Rock River 15 yards from bank, May 21, 1925, R. E. Richardson, 1 N; sweeping vegetation on bank of Rock River, June 26, 1947, B. D. Burks, 1♂, 2♀. QUINCY: at light, June 8, 1939, Burks & Riegel, 1♀; July 6, 1939, Mohr & Riegel, 1♀. ROCK FALLS: at light, June 26, 1947, B. D. Burks, 1♀. ROCKFORD: June 2, 1944, H. S. Dybas, 1♀.

40. *SIPHLOPLECTON* Clemens

Siphloplecton Clemens (1915*a*:258).

The adult wing venation in *Siphloplecton* is very similar to that in the heptageniid type, differing principally in that the cubital intercalary veins of the fore wing are partly or completely joined by crossveins to the branches of Cu, fig. 308. In the true heptageniid wing, these intercalary veins are free at the bases, as in fig. 317. In the hind wing of *Siphloplecton,* vein M is forked near the base, fig. 308. The hind tarsus has four clearly differentiated segments. The abdomen is relatively long and slender, and the ninth sternite of the female is entire and not greatly produced posteriorly, fig. 306. There are two long caudal filaments, with the median one represented by a three- to six-segmented stub.

In the nymphs, which are streamlined and fishlike, the eyes are placed laterally on the head, which is typically baetid in form, as in fig. 305. The mouth-parts are evidently not fitted for predatism. Each fore tarsal claw is bifid, fig. 303; all other claws are slender and longer than the tibiae, fig. 302. Gills are present on abdominal segments 1–7; these gills are single and platelike on segments 4–7 and double on segments 1–3, except in *interlineatum,* where the gills of segments 1–3 have merely a small, recurved ventral flap. There are three well-developed caudal filaments; each of the cerci has long, dense setae on the mesal side only.

This genus includes four species, only one of which has been taken in Illinois. Another species occurs in Indiana and it will probably eventually be found to occur in Illinois.

KEY TO SPECIES

ADULTS

Crossveins in entire fore wing brown, hind wing with entire basal third shaded with brown. . . . . **1. basale**

Crossveins in fore wing brown only near costal margin and along stem of R_{4+5}; hind wing with brown shading confined to area around bases of C, Sc, and R . . . **2. interlineatum**

MATURE NYMPHS

Median ventral stripe of abdomen continuous, uninterrupted; claw of middle leg 10 times as long as wide at base. . . . . **1. basale**

Median ventral stripe of abdomen interrupted at each intersegmental suture; claw of middle leg 7 to 8 times as long as wide at base. . . . . **2. interlineatum**

1. *Siphloplecton basale* (Walker)

Baetis basalis Walker (1853:565).
Siphlurus flexus Clemens (1913:338).

MALE.—Thorax dark brown, with white areas on pleura. Each fore wing with a prominent, brown color pattern in anterior basal area; hind wing with an intense, brown cloud at base, fig. 308. Abdominal dorsum dark brown; sternum white, with sternites 1 and 9 dark brown and intermediate sternites each with three brown dots, one median and two lateral; genitalia as shown in fig. 311.

FEMALE.—Similar to the male but color lighter in tone, with brown shading at wing bases faint or absent.

NYMPH.—Three longitudinal, brown bands present on abdominal venter; gills on segments 1–3 double; each caudal filament with a dark, broad, vaguely defined crossband located just distad of middle.

Known from Indiana, Manitoba, Michigan, New York, North Carolina, Ontario, and Quebec.

2. *Siphloplecton interlineatum* (Walsh)

Baetis femorata Walsh (1862:386), not Say. Misidentification.
Baetis interlineata Walsh (1863:190). New name.

MALE.—Length of body and of fore wing 12–14 mm. Head and thorax dark brown to black, with light yellow markings on pleura and sternum. Wings hyaline, small area of brown staining at each wing base, costal crossveins margined with brown; short, longitudinal, brown dash in second interspace below bulla; fore leg gray-tan, femur with broad, brown band at base and near apex, dark brown mark at apex of tibia and each tarsal segment; middle and hind legs yellow, with brown markings as in fore leg. Abdominal tergum white, with faint, brown shading on tergites 2–6, tergites 1 and 7–9 almost completely dark brown; venter white, ganglia and two small, lateral spots on each sternite may be brown stained; sternites 1 and 9 completely dark brown; male genitalia, fig. 309; the two well-developed caudal filaments white, the articulations brown.

FEMALE.—Length of body 12–14 mm., of fore wing 14–15 mm. Color almost identical with that of male, except that wings completely lack brown staining at bases, and brown shading of abdominal tergites is usually more intense; abdominal sternum almost completely white, with sternite 1 largely brown and sternites 7–9 heavily shaded with brown; caudal filaments similar to those of the male.

NYMPH.—Length of body 15–16 mm., of caudal filaments 5–6 mm. Thorax yellow and brown on dorsum, yellow on venter. Abdominal tergum yellow, with varying brown markings and with tergites 1, 6, and 9 almost completely brown; venter yellow, with three longitudinal, brown stripes; gills single on segments 4–7, those on segments 1–3 each with a minute, recurved ventral flap; caudal filaments each with a brown crossband near tip.

Known from Illinois, Indiana, Manitoba, and Minnesota. Develops in fairly rapid, moderate-sized rivers.

Illinois Records.—ILLINOIS: 1♂. HAVANA: Chautauqua Park, April 29, 1914, 1♂. MOMENCE, Kankakee River: May 5, 1938, Ross & Burks, 3♀; May 8, 1940, Mohr & Burks, 2♀, 1 N. ROCK ISLAND: 5♂, 2♀ (Walsh 1862:369).

HEPTAGENIIDAE

This family, as limited here, corresponds to the family Heptageniidae in Traver's classification (1935*a*:293) and is similar to, but not identical with, Ulmer's family Ecdyonuridae (1933:212).

In the family Heptageniidae, the male adults have large compound eyes, but these eyes show no obvious division into upper and lower portions. The upper portion of each eye is, however, composed of facets which are slightly smaller and usually less heavily pigmented than are those in the lower. The line that divides these two portions is quite obscure. The fore tarsus in the males is longer than the fore tibia in all genera except the rare *Anepeorus*. In all genera, the hind tarsus has five clearly defined segments, figs. 17, 19. Each fore wing invariably has four cubital intercalary veins, all of which are free at the bases, figs. 317–321. The hind wing has veins R_4 and R_5 diverging at or near the center of the wing, figs. 317–320, except in *Arthroplea*, in which R_4 and R_5 are fused for their entire length, fig. 321. The male genitalia consist of a pair of four- or five-segmented forceps and a pair of variously modified penis lobes, figs. 331–356, 363–380, 387–389, 391–393. The median caudal filament is invariably vestigial in the adults.

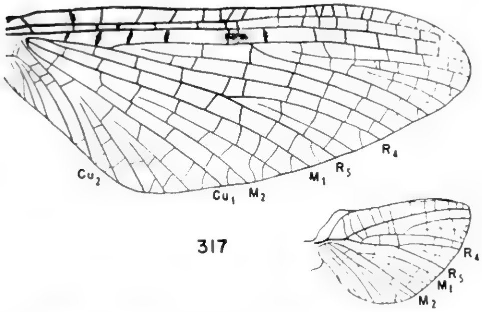
In the nymphs, figs. 360, 383–386, 390, 394, 395, the body is flattened, the head is broad, almost or quite flat, with the eyes located dorsally and the mouth-parts ventrally. The labrum is always much wider than long, each mandible has two canines, and each maxillary and labial palp has two segments. The mouth-parts in all but one genus are fitted for a diet of vegetable matter, such as diatoms, and animal and vegetable detritus. The exception is a nymph, tentatively placed as that of *Anepeorus*, fig. 394, which has mouth-parts clearly fitted for predacity. Almost all heptagenine nymphs have seven pairs of dorsal abdominal gills, each of which is composed of a dorsal, platelike member and a ventral, filamentous tuft. In *Rhithrogena*, however, the filamentous tuft is dorsal and the platelike element ventral, in *Arthroplea* the filamentous portion of each gill is wanting entirely, and in the supposed nymph of *Anepeorus* the gills are ventral and each gill consists of a narrow, elongate, anterior member and a posterior, fimbriate member. All heptagenine nymphs have three well-developed caudal filaments.

The differentiation and separation of the genera in this group can hardly be said to be on a firm and rational basis. The nymphs and the male adults can be segregated generically, but the females usually cannot. Pending the discovery of generic characters which will serve for the segregation of the females, also, I am using the generic characters employed by Traver (1935) and Ulmer (1933).

KEY TO GENERA

ADULT MALES

1. Fore tarsus not more than three-fourths as long as fore tibia....**47. Anepeorus**
   Fore tarsus longer than fore tibia.......2
2. Vein R_{4+5} of hind wing unbranched, fig. 321....................**48. Arthroplea**
   Vein R_{4+5} of hind wing forked at or near center of wing, figs. 317–320........3
3. First segment of fore tarsus as long as or longer than second.......**43. Epeorus**
   First segment of fore tarsus shorter than second...............................4
4. Stigmatic crossveins of fore wing anastomosed, figs. 320–323; penes a pair of relatively undifferentiated, elongate or stubby lobes, fig. 391..................................**46. Rhithrogena**
   Stigmatic crossveins of fore wing not anastomosed, or only partly so, as in fig. 319, or anastomosed and forming two rows of cellules, as in fig. 322; penis lobes variously modified, with lateral or apical expansions, figs. 331–356, 363–380, 389...........................5
5. Penis lobes divided to base or fused on meson at base only, fig. 388.............................**44. Cinygmula**
   Penis lobes fused on meson for at least their basal halves, figs. 331–356, 363–380, 389...........................6



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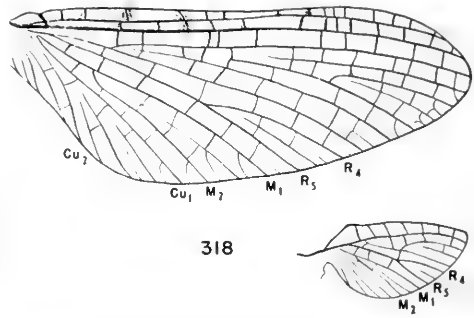

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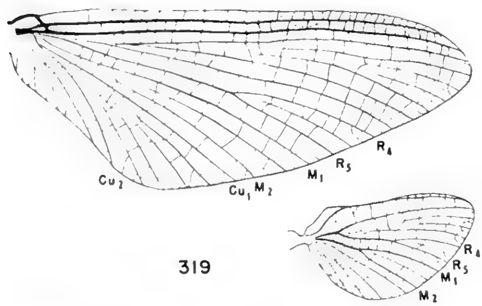

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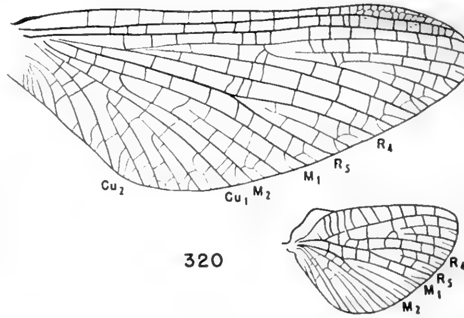

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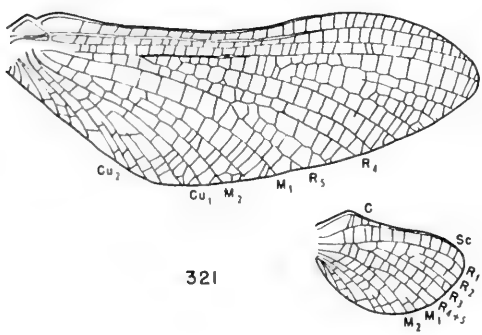

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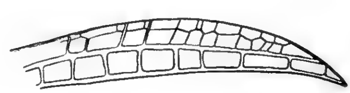

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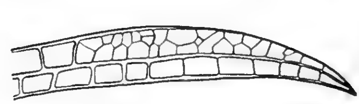

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Fig. 317.—*Stenonema canadense,* wings.
Fig. 318.—*Heptagenia maculipennis,* wings.
Fig. 319.—*Epeorus pleuralis,* wings.
Fig. 320.—*Rhithrogena morrisoni,* wings.
Fig. 321.—*Arthroplea* sp., wings. (After Blair.)
Fig. 322.—*Cinygma integrum,* stigmatic area of fore wing.
Fig. 323.—*Rhithrogena morrisoni,* stigmatic area of fore wing.

6. Stigmatic area of fore wing with an irregular, longitudinal line dividing the stigmatic crossveins into two rows of cellules, fig. 322 .... **45. Cinygma**
   Stigmatic area of fore wing not divided into two rows of cellules, fig. 318, although the crossveins are often partly or greatly anastomosed 7

width of each less than one-third the length .... **41. Stenonema**
   Small subapical spine absent; large mesal spines robust, greatest width of each more than one-third the length, fig. 363 .... **42. Heptagenia**

12. Small, mesal subapical spine present, figs. 348, 350, 352 .... **41. Stenonema**

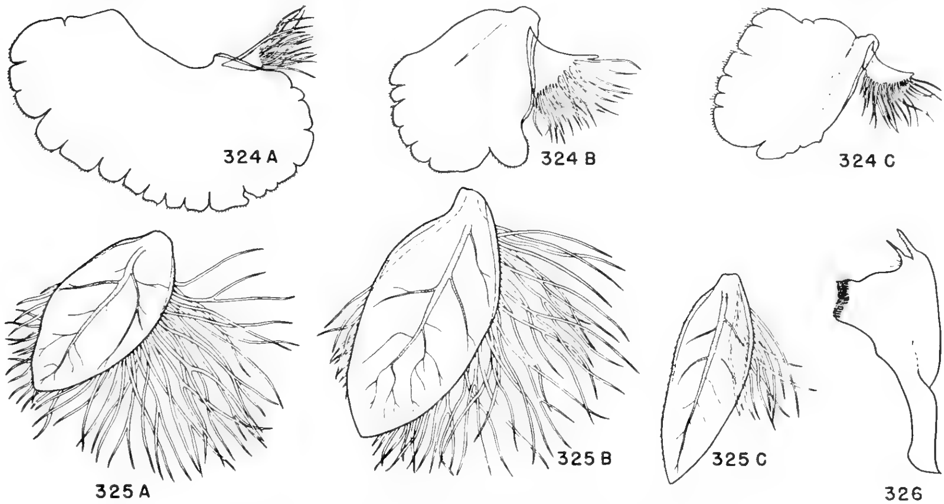


Fig. 324A.—*Rhithrogena* sp., gill of first abdominal segment.
Fig. 324B.—*Rhithrogena* sp., gill of fifth abdominal segment.
Fig. 324C.—*Rhithrogena* sp., gill of seventh abdominal segment.
Fig. 325A.—*Heptagenia diabasia*, gill of first abdominal segment.
Fig. 325B.—*Heptagenia diabasia*, gill of fifth abdominal segment.
Fig. 325C.—*Heptagenia diabasia*, gill of seventh abdominal segment.
Fig. 326.—*Heptagenia maculipennis*, mandible of mature nymph.

7. Outer lateral margin of each penis lobe with a cluster of spines which may be either large, figs. 333–339, or small, fig. 332 .... **41. Stenonema**
   Outer lateral margin of each penis lobe without a cluster of spines 8
8. Apex of each penis lobe transversely or obliquely truncate, with a rounded or angulate, apicomesal corner, figs. 331, 340–347, 349–351, 353–356, 363–366 .. 9
   Apex of each penis lobe not transversely or obliquely truncate 12
9. Apex of each lobe with the mesal angle lower than the apicolateral angle, figs. 331, 364–366 10
   Apex of each lobe with mesal angle nearly on a level with, figs. 340–346, 349, 351, 353–356, 363, or higher than, figs. 347, 350, apicolateral angle 11
10. Apical angle of each penis lobe with a cluster of rather large spines, fig. 331 .. .. **41. Stenonema**
   Apical angle of each penis lobe without a cluster of spines, figs. 364–366 .... **42. Heptagenia**
11. Small subapical spine, fig. 10*b*, present at apicomesal angle of each penis lobe, figs. 340–347, 349–351, 353–356; large mesal spines, fig. 10*g*, slender, greatest

   Small, mesal subapical spine absent, figs. 366–370, 375, or, if present, greatly enlarged as in figs. 374, 376–380 .... **42. Heptagenia**

MATURE NYMPHS

1. Second segment of maxillary palp extremely long, recurved over dorsum of thorax, fig. 395 ...... **48. Arthroplea**
   Second segment of maxillary palp not recurved over dorsum of thorax 2
2. Mouth-parts fitted for predatism, with maxillae and mandibles fanglike .... **47. ?Anepeorus**
   Mouth-parts fitted for a diet of vegetable matter or plant and animal detritus; each mandible with a broad molar area, figs. 326, 330 3
3. Median caudal filament vestigial, fig. 386 .... **43. Epeorus**
   Median caudal filament well developed, figs. 360, 383–385 4
4. Gills on seventh abdominal segment slender and semifilamentous, either entirely without tracheae or with one, two, or three simple tracheae without lateral branches, fig. 360 .... **41. Stenonema**

Gills on seventh abdominal segment platelike and bearing tracheae which possess lateral branches, figs. 325*C*, 328*C*, 329*C* 5

5. Front of head incised on meson, so as to expose a portion of labrum when viewed from dorsal aspect .... **44. Cinygmula**

Front of head not incised on meson, labrum not exposed dorsally 6

6. Gills of first and seventh pairs enlarged, converging beneath abdomen to form, with intermediate gills, an adhesive disc, fig. 390; fibrillar portion of each gill dorsal, fig. 324 ... **46. Rhithrogena**

Gills of first and seventh pairs not converging beneath abdomen, gills not forming an adhesive disc; fibrillar portion of each gill ventral, figs. 325, 329 7

7. Each mandible with a heavily chitinized lobe on mesal margin, basad of molar area, fig. 330; platelike component of first abdominal gill only two-thirds as long as that of seventh gill, fig. 329 ... . **45. Cinygma**

Mandibles without a chitinized lobe basad of molar area, fig. 326; platelike components of first and seventh gills subequal in length, fig. 325 .... **42. Heptagenia**

41. *STENONEMA* Traver

Stenonema Traver (1933*a*: 173).

Most of the American species in the genus *Stenonema* were formerly placed under the

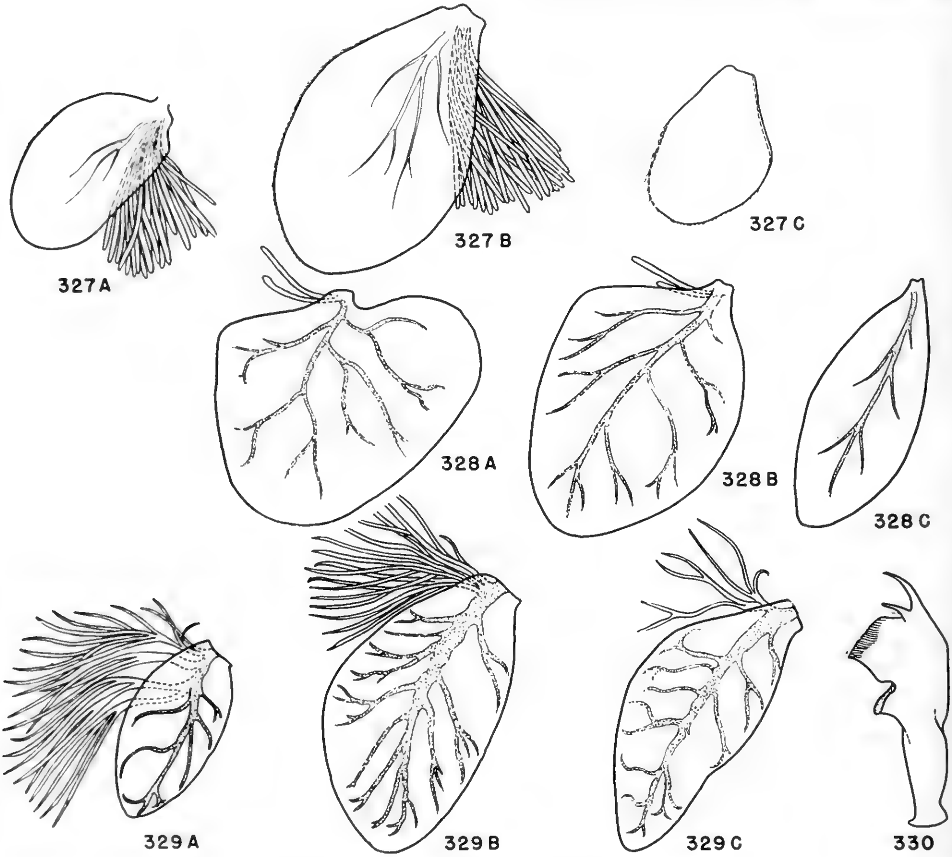


Fig. 327*A*.—*Epeorus* sp., gill of first abdominal segment.
Fig. 327*B*.—*Epeorus* sp., gill of fifth abdominal segment.
Fig. 327*C*.—*Epeorus* sp., gill of seventh abdominal segment.
Fig. 328*A*.—*Cinygmula* sp., gill of first abdominal segment.
Fig. 328*B*.—*Cinygmula* sp., gill of second abdominal segment.
Fig. 328*C*.—*Cinygmula* sp., gill of seventh abdominal segment.
Fig. 329*A*.—*Cinygma integrum*, gill of first abdominal segment. (After McDunnough.)
Fig. 329*B*.—*Cinygma integrum*, gill of second abdominal segment. (After McDunnough.)
Fig. 329*C*.—*Cinygma integrum*, gill of seventh abdominal segment. (After McDunnough.)
Fig. 330—*Cinygma integrum*, mandible of mature nymph. (After McDunnough.)

generic names *Heptagenia* and *Ecdyonurus* (or the emended form *Ecdyurus*). As Traver (1933*a*: 173) pointed out, however, these American species actually represent a discrete generic unit, differing from either *Heptagenia* or *Ecdyonurus* both in type of male genitalia and in nymphal characters.

Stenonema is the most difficult genus in the order Ephemeroptera. This is due to the fact that the male genitalia are quite similar throughout the genus, and the genitalic differences between closely related species are, therefore, obscure. The principal bases for the separation of species are the colors of the males and the relative proportions of the male first and second fore tarsal segments. Unfortunately, both vary considerably. Specimens collected early in the season usually are much darker and larger than specimens of the same species collected in midsummer. In the large male specimens, the first fore tarsal segment tends to be relatively longer than it is in smaller specimens. However, a decision as to the proper limitation of a given species can be made when all available characters of the adult males and the mature nymphs are considered together. Fortunately, most of our species of *Stenonema* have been reared, and good series of nymphs and adult males are available for study. The females are usually separable at best to species groups only.

In the adult males, the large eyes, never contiguous on the meson, are usually separated on the vertex by a space at least one-half as wide as one eye. Each fore leg is, in all species except *integrum,* as long as, or slightly longer than, the body. In *integrum,* the fore leg is slightly shorter than the body. In all species, the fore tarsus is longer than the fore tibia and the first fore tarsal segment varies from one-third to four-fifths as long as the second segment. The wing venation in both sexes, fig. 317, is typical for the family; the species of *Stenonema* and *Heptagenia* cannot, unfortunately, be distinguished generically by the characteristics of the wings. The male genitalia, figs. 331–356, consist of a pair of four-segmented forceps, the second segment being longer than the other three combined, and a pair of Γ-shaped penis lobes.

Use of these generic characters will require the transfer of the species *Epeorus modestus* Banks (1910: 202) to the genus *Stenonema.*

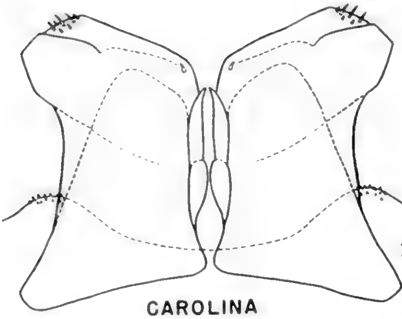
The nymphs, fig. 360, are greatly flattened, the legs sprawling laterally; the anterior margin of the head is entire or only very slightly emarginate on the meson, and the eyes are dorsal and just touching the posterior margin of the head. Each tarsal claw is single, short, slightly hooked at the apex, and has a fairly large ventral tooth near the base; in many species, each claw also has two or three minute ventral denticles near the tip. The abdominal gills are of three types: those on segments 1–6 in the members of the *interpunctatum* group are pointed at the apexes, fig. 358, and each gill of the seventh pair has one longitudinal trachea; in the members of the *tripunctatum* group, the first six pairs of gills are rounded at the apexes, fig. 357, and each gill of the seventh pair has one or two longitudinal tracheae; in the *pulchellum* and *bipunctatum* groups, the gills on segments 1–6 are truncate at the apexes, fig. 359, and the gills of the seventh pair are without tracheae. The three caudal filaments are equally long, uniformly clothed with short setae, and, often, with alternating pairs of segments dark and light in color.

All Illinois species of *Stenonema* develop under stones in the shallower parts of creeks and rivers. Some, such as *tripunctatum,* can tolerate a great deal of silt; in many of the small, sluggish, heavily silted streams in central Illinois, *tripunctatum* is the only mayfly now found. The later instar nymphs of most species of *Stenonema* can be reared through to maturity in stagnant water.

Adult specimens of *Stenonema* should be pinned for preservation and study. Most specimens, if collected and preserved in alcohol, cannot reliably be determined to species, as the necessary color characters, at best impermanent, are quickly lost in alcohol; dry specimens retain their colors for several years if stored out of the light. Correct specific determinations can seldom be made from the male genitalia and fore tarsal characters alone. The color of the eyes in adult males should be recorded at the time of collection, as these eye colors are helpful in placing specimens in the proper species or species group.

My views as to specific limits in this genus most closely coincide with those of Traver (1935*a*:297).

The adult females can be distinguished only to groups.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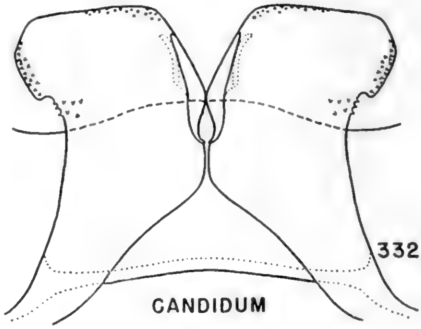
CAROLINA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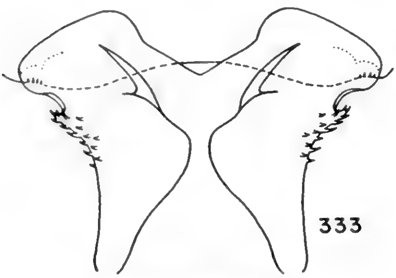
CANDIDUM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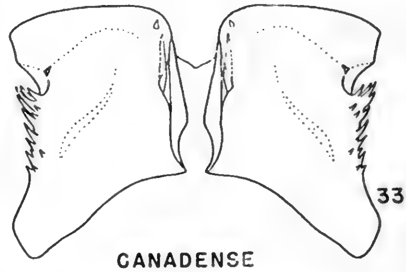
GILDERSLEEVEI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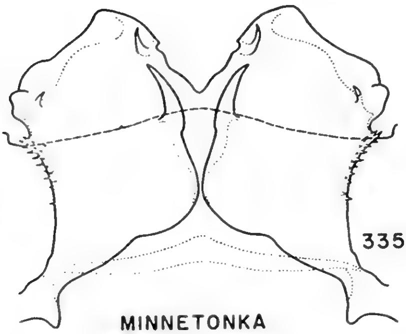
CANADENSE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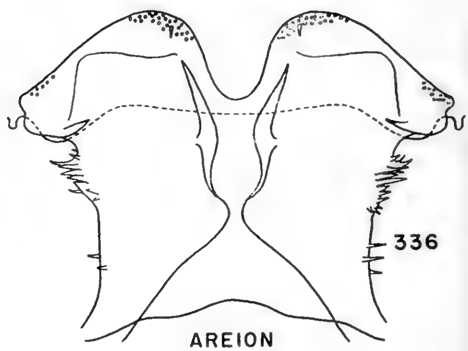
MINNETONKA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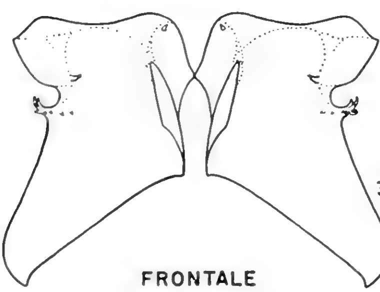
AREION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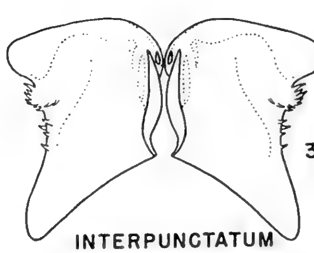
FRONTALE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INTERPUNCTATUM

Fig. 331.—*Stenonema carolina,* male genitalia.
Fig. 332.—*Stenonema candidum,* male genitalia.
Fig. 333.—*Stenonema gildersleevei,* male genitalia.
Fig. 334.—*Stenonema canadense,* male genitalia.
Fig. 335.—*Stenonema minnetonka,* male genitalia.
Fig. 336.—*Stenonema areion,* male genitalia.
Fig. 337.—*Stenonema frontale,* male genitalia.
Fig. 338.—*Stenonema interpunctatum,* male genitalia.

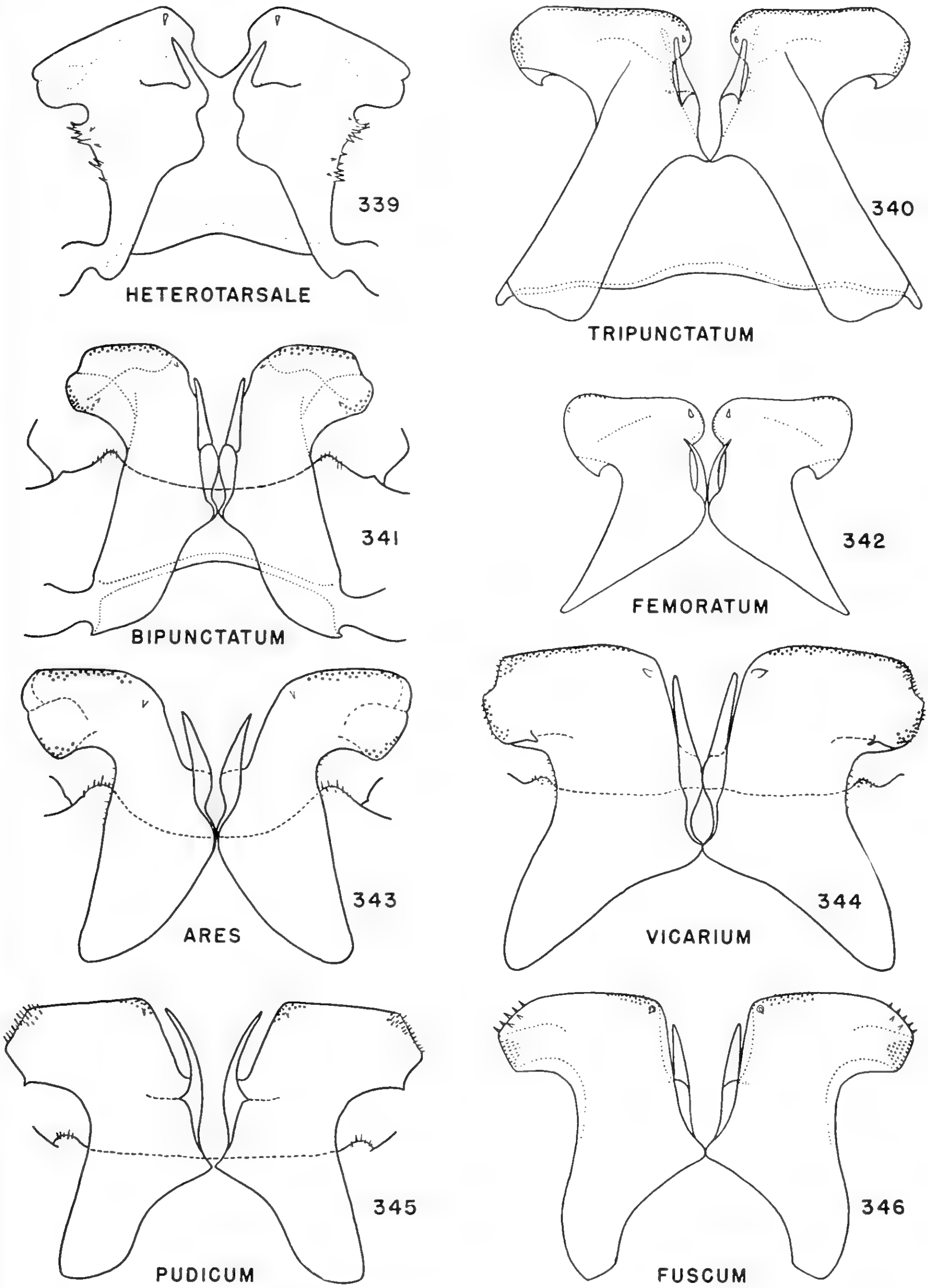
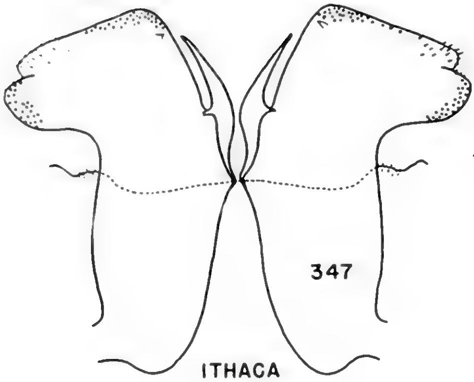
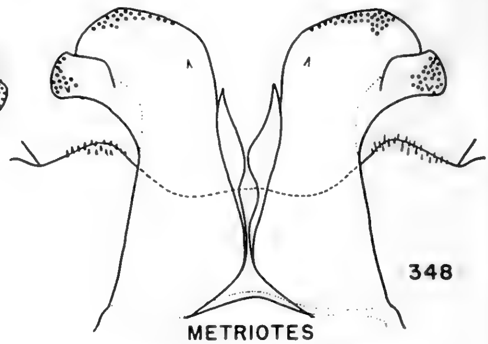
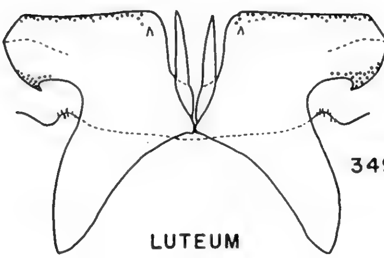
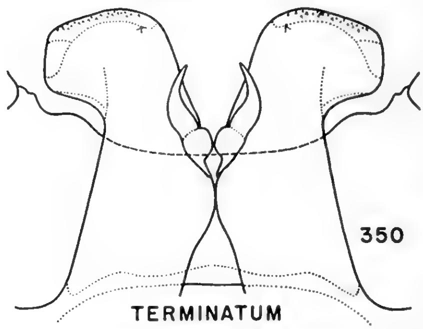


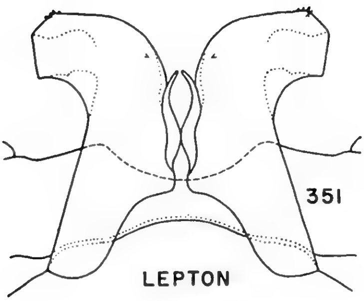
Fig. 339.—*Stenonema heterotarsale*, male genitalia.
Fig. 340.—*Stenonema tripunctatum*, male genitalia.
Fig. 341.—*Stenonema bipunctatum*, male genitalia.
Fig. 342.—*Stenonema femoratum*, male genitalia.
Fig. 343.—*Stenonema ares*, male genitalia.
Fig. 344.—*Stenonema vicarium*, male genitalia.
Fig. 345.—*Stenonema pudicum*, male genitalia.
Fig. 346.—*Stenonema fuscum*, male genitalia.

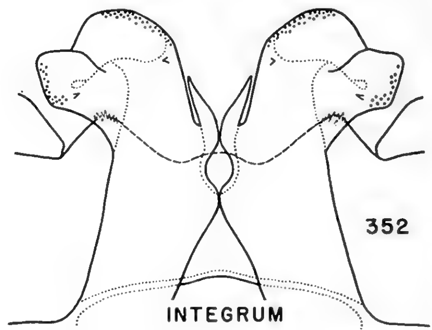


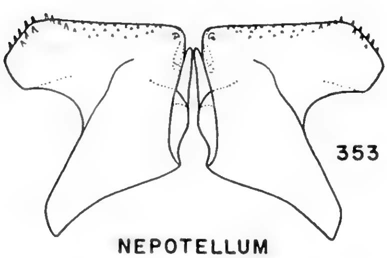












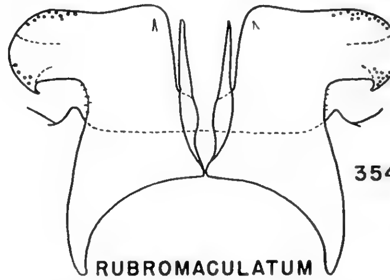


Fig. 347.—*Stenonema ithaca*, male genitalia.

Fig. 348.—*Stenonema metriotes*, male genitalia.

Fig. 349.—*Stenonema luteum*, male genitalia.

Fig. 350.—*Stenonema terminatum*, male genitalia.

Fig. 351.—*Stenonema lepton*, male genitalia.

Fig. 352.—*Stenonema integrum*, male genitalia.

Fig. 353.—*Stenonema nepotellum*, male genitalia.

Fig. 354.—*Stenonema rubromaculatum*, male genitalia.

KEY TO SPECIES

Adult Males

1. Basal crossveins in first radial interspace of fore wing thickened and darkened in the middle, fig. 317; crossveins below bulla often connected by a longitudinal, black mark, always at least a black spot in the middle of one, two, or three crossveins below bulla..............2

   Basal crossveins in first radial interspace of fore wing not thickened and darkened, or thickened uniformly from end to end; longitudinal, black mark never connecting crossveins below bulla, and these crossveins never widened and darkened in the middle only........10

2. Caudal filaments and genital forceps uniformly gray-tan; genitalia as in fig. 331, forceps base with a pair of large, sublateral, setose projections..**1. carolina**

   Caudal filaments not uniformly gray-tan; filaments entirely white, without dark-colored rings at articulations, or these filaments white, yellow, or tan, with darker articulations; genital forceps white or yellow; eyes in life always light green........................3

3. Outer lateral margin of each penis lobe with extremely minute spines, fig. 332 ....**2. candidum**

   Outer lateral margin of each penis lobe with a cluster of large spines, figs. 333–339..........................4

4. Venter of abdomen with a median, longitudinal, dark brown or black line extending from anterior to posterior ends, this line slightly widened and with a narrow interruption at posterior margin of each sternite.......**3. gildersleevei**

   Venter of abdomen usually entirely immaculate, occasionally with a faint mark on meson of posterior margin of some sternites.....................5

5. Abdomen white, with a bright Mars orange crossband at posterior margin of each tergite 1–7........**4. areion**

   Abdomen yellow, with black or very dark brown crossbands at posterior margins of tergites.........................6

6. Spiracular dots present on abdominal segments, in very dark specimens these dots tending to fuse with black crossbands at posterior margins of tergites; each penis lobe with an apicomesal and a mesially directed lateral spine, figs. 334, 335, 337......................7

   Spiracular dots absent from abdominal segments; each penis lobe with only the apicomesal spine, figs. 338, 339.......9

7. Thoracic pleuron uniformly yellow, lacking an oblique, black streak ventral to base of fore wing.....**5. minnetonka**

   Thoracic pleuron with an oblique, black streak ventral to base of fore wing, also a similar streak sometimes present ventral to base of hind wing........8

8. Abdominal tergites with a relatively broad, black crossband at posterior margin of each; a longitudinal, black or dark gray line usually extending almost or quite the entire length of abdominal dorsum; in very dark specimens abdomen almost completely black on dorsum; meso- and metascutellum dark brown to black....**6. canadense**

   Abdominal tergites with a narrow, black line at posterior margin of each; median, dark, longitudinal line absent from abdominal dorsum, or, at most, with this line evident on basal one to three tergites only; meso- and metascutellum yellow...................**7. frontale**

9. Black marks always present on face ventral to antennal sockets; usually a dark brown, oblique streak present on pleuron ventral to base of fore wing; first segment of fore tarsus one-fourth to one-third as long as second segment ....**8. interpunctatum**

   Black marks usually absent from face ventral to antennal sockets; dark streak never present on pleuron; first fore tarsal segment one-half to two-thirds as long as second segment..... ....**9. heterotarsale**

10. Abdominal tergites 1– or 2–8 with three black marks at posterior margin of each: a median dot and a pair of submedian, transverse dashes.........11

    Abdominal tergites with a pair of submesal, transverse, black lines at posterior margin of each; or with a continuous, black or dark brown crossline at each posterior margin; or with dark brown shading covering posterior one-quarter to one-half of each tergite; or with tergites almost or entirely unmarked.........................12

11. Outer margin of hind wing hyaline; compound eyes separated on meson by a space as wide as a lateral ocellus...... ....**10. tripunctatum**

    Outer margin of hind wing shaded with dark brown; compound eyes separated on meson by a space two-thirds as wide as one lateral ocellus..**11. femoratum**

12. Abdominal tergites 3–8 each with a pair of submedian, transverse, short lines at posterior margin.................13

    Abdominal tergites with a continuous, dark brown or black crossline or color band at posterior margin of each or virtually without markings at posterior margin.........................14

13. Mesonotum dull gray-brown, first fore tarsal segment two-thirds as long as second...........**12. bipunctatum**

    Mesonotum bright Mars orange, first fore tarsal segment one-half as long as second....................**13. ares**

14. Ground color of abdomen dark tan or yellow-brown; each abdominal tergite 2–7 with a broad, dark brown, transverse color band occupying posterior one-fourth to one-half of tergite, apical three tergites almost completely shaded with dark brown................15

Ground color of abdomen white or yellow; abdominal tergites 1–7 each with a narrow, black, transverse stripe at posterior margin or this margin virtually without markings 18

15. Eyes of living insect brown; outer margin of hind wing shaded with brown ....**14. pudicum**

Eyes of living insect gray; outer margin of hind wing not shaded 16

16. Stigmatic area of fore wing shaded with dark red, this pigmentation concentrated in basal part of stigmatic area ....**15. vicarium**

Entire stigmatic area of fore wing uniformly stained with yellow-brown..17

17. Abdominal tergites 8 and 9 dark brown, with lateral margins white........... ....**16. fuscum**

Abdominal tergites 8 and 9 uniformly dark brown..............**17. ithaca**

18. Posterior margin of each tergite 2–7 with only minute, black dash on meson...19

Posterior margin of each tergite 2–7 with a black line extending completely across dorsum; occasional specimens entirely lacking marks at these posterior margins..........................20

19. Mesonotum dark brown; abdomen usually with spiracular dots ....**18. mediopunctatum**

Mesonotum chalky white; abdomen always lacking spiracular marks of any kind.....................**19. metriotes**

20. Abdomen lacking spiracular marks of any kind.............................21

Abdomen with spiracular dots or oblique streaks on at least middle segments.. 23

21. Articulations of caudal filaments dark red-brown throughout; middle and hind femora each with a prominent, red-brown crossband in middle and at apex...................**20. luteum**

Caudal filaments white or a faint yellow throughout, articulations not darkened, or sometimes basal 2 or 3 articulations only of each filament darkened; middle and hind femora each with red-brown shading at apex only, occasionally middle femur with faint shading in the middle...........................22

22. First fore tarsal segment two-fifths as long as second segment..**21. terminatum**

First fore tarsal segment two-thirds to five-sixths as long as second segment.. ....**22. lepton**

23. Abdominal spiracular marks a series of short, oblique streaks...**23. integrum**

Abdominal spiracular marks a series of dots..............................24

24. Mesonotum light clay-colored or yellow-brown..........................25

Mesonotum dark red-brown or black-brown...........................26

25. Pink-brown shading almost completely covering abdominal tergite 8; mesonotum yellow-brown....**24. nepotellum**

Pink-brown shading of tergite 8 restricted to a median, longitudinal bar; mesonotum light clay-colored.............. ....**25. rubromaculatum**

26. Mesonotum red-brown; stigmatic area of fore wing stained a faint pink; only apex of mesoscutellum white........ ....**26. rubrum**

Mesonotum dark, blackish-brown; stigmatic area of fore wing stained light brown; entire mesoscutellum white... ....**27. pulchellum**

KEY TO SPECIES GROUPS

Adult Females

1. Fore wing with basal crossveins in first radial interspace thickened and darkened in the middle, as in fig. 317; two or three crossveins below bulla thickened and blackened in the middle, these black spots often fused to form a short, longitudinal dash............. ....**interpunctatum group**

Fore wing with basal crossveins in first radial interspace not thickened and darkened in the middle; two or three crossveins below bulla never thickened and darkened in the middle and never with a short, longitudinal black dash connecting these crossveins 2

2. Abdominal tergites 2–8 with three small, black marks at posterior margin of each: a median, black dot and a pair of submedian, transverse dashes........ ....**tripunctatum group**

Abdominal tergites not with three small, black marks at posterior margin of each...............................3

3. Abdominal tergites 3–8 each with a pair of short, submedian, transverse lines at posterior margin.................... ....**bipunctatum group**

Abdominal tergites 2– or 3–7 or –8 each with a continuous, dark crossline or color band at posterior margin, or each of these tergites virtually or quite without markings at posterior margin....4

4. Ground color of abdomen tan or yellow-brown; tergites 2–7 each with a broad, dark brown, transverse band occupying posterior fourth to half of tergite.. ....**vicarium group**

Ground color of abdomen light yellow or white; tergites entirely unmarked, with spiracular dots only, or with a narrow, black, transverse line at posterior margin of each of some or all tergites..........................5

5. Abdomen lacking spiracular marks of any kind...........**terminatum group**

Abdomen with spiracular dots or oblique streaks....**mediopunctatum group, pulchellum group**

KEY TO SPECIES

Mature Nymphs

1. Gills borne by abdominal segments 1–6 pointed at apexes, fig. 358 2

Gills borne by abdominal segments 1–6

rounded or truncate at apexes, figs. 357, 359 . . . 6

2. Dorsum of abdomen almost entirely brown, each tergite with only a pair of short, submedian streaks at anterior margin . . . **1. carolina**
Dorsum of abdomen marked otherwise . . 3

3. Abdominal dorsal color pattern made up of a series of large, elongate and submedian, pale spots, with a transverse, black, median line at posterior margin of each of tergites 1–9 . . . **3. gildersleevei**
Abdominal dorsum with a pair of submedian, pale, longitudinal stripes, in most specimens these markings almost or quite continuous, but in others confined to tergites 4– or 5–10 and, in that case, stripes suddenly widened on tergites 8 and 9, constricted again on 10 . . . 4

4. Submedian, pale stripes present on tergites 3– or 4–10 only, these stripes suddenly widened on tergites 8 and 9, constricted again on tergite 10 . . . **9. heterotarsale**
Submedian, pale stripes extending length of abdomen and not suddenly widened on tergites 8 and 9 . . . 5

5. Apex of ninth sternite entirely pale or very faintly stained with brown; anterior, dorsal margin of head usually with a pale, median spot . . **7. frontale**
Apex of ninth sternite with a broad, dark brown crossband; anterior, dorsal margin of head without a pale, median spot or with such a spot only very faintly indicated . . . **2. candidum; 6. canadense; 8. interpunctatum**

6. Gills borne by abdominal segments 1–6 rounded at apexes, fig. 357 . . . 7
Gills borne by abdominal segments 1–6 truncate at apexes, fig. 359 . . . 8

7. Median, pale spot usually present on anterior margin of head; sublateral, brown spots present on sternites 2–8 . . . **10. tripunctatum**
Median, pale spot absent from anterior margin of head; sublateral, brown spots present on sternites 5– or 6–8, sometimes these spots entirely absent . . . **11. femoratum**

8. Each tarsal claw with two minute ventral denticles near tip . . . 9
Tarsal claws without ventral denticles . 13

9. Posterolateral angles of abdominal segments 3– or 4–9 spinelike . . . 10
Posterolateral angles of abdominal segments 6– or 7–9 spinelike . . . 11

10. Pale spot on meson of anterior margin of head; abdominal dorsum light brown, with large, median, pale spots on tergites 5, 8, and 9 . . . **12. bipunctatum**
Head without median, pale spot on anterior margin; abdominal dorsum usually dark brown, apical tergites sometimes with small, faint, pale spots at anterior margins . . . **25. rubromaculatum**

11. Each abdominal sternite 2–8 with somewhat irregular, brown shading extending across posterior margin and at each lateral margin . . . **20. luteum**
Each abdominal sternite 1–7 entirely white, sternite 8 either entirely white, or with only a small, median, brown spot at anterior margin . . . 12

12. Normally exposed portions of abdominal tergites 1–10 uniformly brown, sometimes with faint, median, lighter spots on apical tergites . . . **26. rubrum**
Normally exposed portions of abdominal tergites 1–5, 7, and usually 9 mostly white, but with some small, brown markings; tergites 6, 8, and 10 almost entirely brown, tergite 9 sometimes also mostly brown . . . **27. pulchellum**

13. Posterolateral angles of abdominal segments 6– or 7–9 spinelike . . . 14
Posterolateral angles of abdominal segments 3– or 4–9 spinelike . . . 15

14. Abdominal sternites 4– or 5–8 each with a medianly sinuate, transverse, brown cross-stripe located near middle of sternite . . . **17. ithaca**
Abdominal sternites 1–8 white, without markings except for slight, vague darkening along lateral margins of more posterior sternites . . . **13. ares**

15. Abdominal sternites 3– or 4–8 each with a brown crossbar located at posterior margin . . . 16
Abdominal sternites 3– or 4–8 each with transverse, brown shading at anterior margin or in middle of sternite . . . 17

16. Sternite 9 with entire posterior half dark brown . . . **15. vicarium**
Sternite 9 with a pair of large, brown, sublateral spots at posterior margin . . . **16. fuscum**

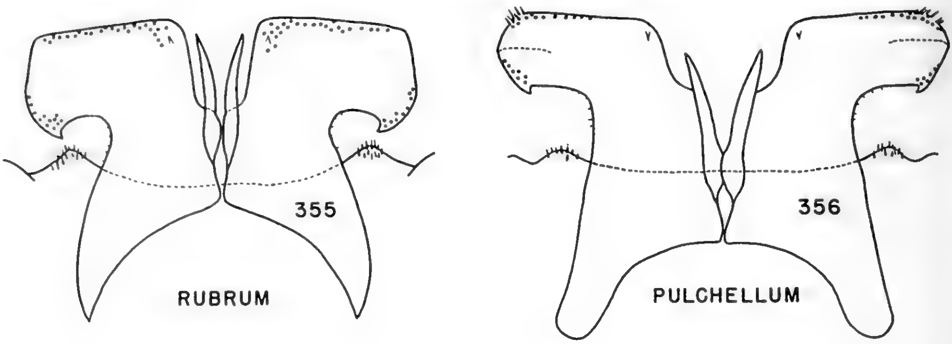
17. Each sternite 3– or 4–8 with a transverse, brown bar occupying median two-thirds of anterior margin . **14. pudicum**
Each sternite 3– or 4–8 with a medianly sinuate, brown crossband extending from side to side near anterior margin . . . **24. nepotellum**

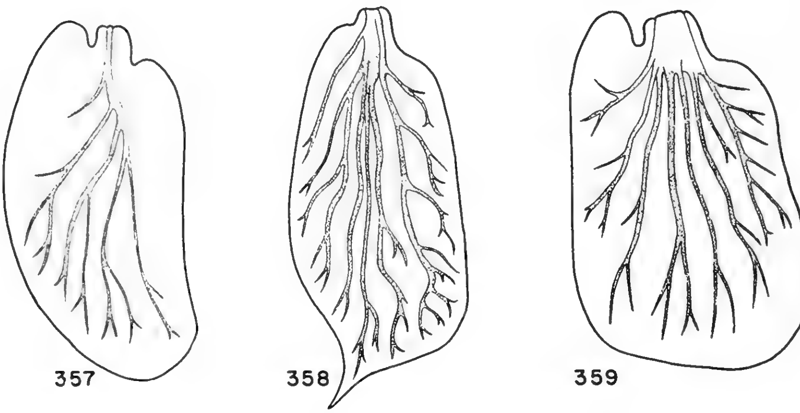
INTERPUNCTATUM Group

1. *Stenonema carolina* (Banks)

Heptagenia carolina Banks (1914:616).

MALE.—Length of body 9–10 mm., of fore wing 11–12 mm. Compound eyes relatively small, separated on vertex by a space as wide as one eye; head and thorax yellow to tan-yellow; first fore tarsal segment one-half to three-fifths as long as second segment; wings hyaline, with veins and crossveins red-brown; basal subcostal and first radial crossveins blackened and widened at their anterior ends, and two crossveins in first radial interspace, below bulla, thickened and blackened in the middle, these marks sometimes fusing to form a longitudinal,





357 358 359

Fig. 355.—*Stenonema rubrum*, male genitalia.
Fig. 356.—*Stenonema pulchellum*, male genitalia.
Fig. 357.—*Stenonema tripunctatum*, fifth gill of nymph.
Fig. 358.—*Stenonema interpunctatum*, fifth gill of nymph.
Fig. 359.—*Stenonema nepotellum*, fifth gill of nymph.

black dash; stigmatic area stained yellow-brown; outer margin of hind wing dark brown. Abdomen white, with a faint gray or green tinge; posterior margin of each tergite bordered with brown or black; spiracular dots absent; penis lobes lacking lateral spines, fig. 331; genital forceps and caudal filaments uniformly gray-tan.

Nymph.—Length of body 10–12 mm. No pale, mesal spot on anterior margin of head. Abdominal dorsum almost uniformly brown, with only a pair of short, narrow, submedian, light-colored marks at anterior margin of each tergite; sternum uniformly light gray-tan, without darker markings; gills on segments 1–6 pointed at apexes, on 7 slender, with a single, longitudinal trachea in each; caudal filaments dark.

Known from New York, North Carolina, Quebec, South Carolina, Tennessee, and West Virginia.

2. *Stenonema candidum* Traver

Stenonema candidum Traver (1935*a*:308).

Spieth (1947:109) considers this to be a synonym of the form he designates *interpunctatum frontale* (Banks). I have seen the types of *candidum* and, as can be seen from fig. 332, the genitalia are quite distinct from those of all other species in the genus.

Male.—Length of body 7–8 mm., of fore wing 9–10 mm. Head deep yellow, a black mark on face below each antennal socket; antennal scape and pedicel dark yellow, flagellum gray-tan at base, fading to white at apex; eyes in life light gray-green. Thorax bright yellow, with mesonotum brown except on lateral margins and at apex of scutellum; legs yellow, with fore leg a little darker yellow, each femur with a median and an apical black band, median band of hind femur sometimes reduced or wanting; the first fore tarsal segment three-fifths to two-thirds as long as second; wings hyaline, veins light yellow-brown, crossveins in anterior two-thirds of fore wing dark brown, those in basal half of first radial interspace thickened and blackened in the middle, a longitudinal, black dash below the bulla usually not present, but occasionally faintly indicated, the stigmatic area faintly stained with brown, outer margin of hind wing slightly darkened. Abdomen bright yellow, with a black, transverse line at posterior margin of each tergite and with a slightly wider, black mark at meson and near either lateral margin, somewhat suggesting the color pattern of *femoratum;* large, black mark at each spiracle; tergites 8 and 9 suffused with red-brown; genitalia, fig. 332, light yellow, penis lobes with minute, lateral spines; caudal filaments entirely white.

NYMPH.—Length of body 8–9 mm. Head light brown, anterior, dorsal margin of head without a median, white spot, or with such a spot only faintly indicated, triangular, white mark in front of anterior ocellus. Pronotum with a pair of large, sublateral, white spots at anterior margin, thoracic notum otherwise light brown except on median line and on sutures anterior to wing bases; legs brown, each femur with a basal, median, and apical, white crossband, each tibia white near base and at apex. Abdomen dorsally light brown, with a pair of narrow, discontinuous, submedian, white lines; gills 1–6 pointed at apexes, seventh gill with a single trachea, venter of body white, lateral margins of sternite 8 and lateral and apical margins of 9 brown; caudal filaments white, alternating articulations faint brown.

Known from Illinois and Ohio.

Illinois Records. — EDDYVILLE: Lusk Creek, June 6, 1946, Mohr & Burks, 3♂; Belle Smith Spring, June 7, 1946, Mohr & Burks, 1♂. GRAYVILLE: Wabash River, April 10, 1946, Mohr & Burks, 1♂, 4 N.

3. *Stenonema gildersleevei* Traver

Stenonema gildersleevei Traver (1935*a*:315).

MALE.—Length of body 9–11 mm., of fore wing 10–12 mm. Head orange-tan, usually a continuous, black line crossing face below antennal bases; each antennal scape and pedicel white, flagellum gray-brown; black markings on vertex between eyes. Thorax largely red-brown, pronotum mostly shaded with dark gray or black, dark shading along dorsal sutures of mesonotum and on mesoscutellum, metanotum black in median dorsal area; thoracic pleura with black shading below wing bases; sternum tan. All coxae light brown, the femora tan, with a median and an apical, dark brown crossband on each, tibiae yellow, tarsi tan, shaded with faint gray, first fore tarsal segment one-half as long as second; wings hyaline, veins and crossveins red-brown, crossveins below bulla usually connected by a black dash, stigmal area faintly stained with yellow, outer margin of hind wing shaded with light brown. Ground color of abdomen tan, overlaid with lavender-black shading: mid-dorsal line, posterior margin of each tergite, large sublateral area near posterior margin, and spiracular spot all dark shaded; on venter, mid-ventral line, anterior margin of each sternite, and, usually, a semitriangular, sublateral spot at anterior margin of each sternite dark shaded; genitalia, fig. 333, with penis lobes and forceps tan or yellow-brown; caudal filaments light yellow, articulations near apexes slightly darker.

NYMPH.—Length of body 11–13 mm. No pale spot on meson of anterior margin of head; gills borne by abdominal segments 1–6 pointed at apexes, seventh pair slender, with a single, longitudinal trachea in each; abdominal tergites each with a pair of submedian, longitudinal, light-colored streaks and a transverse, black crossband at posterior margin; abdominal venter white, with dark, longitudinal markings faintly indicated at lateral margins of sternites 7–9; caudal filaments yellow.

Known from Illinois, New York, and Ohio.

Illinois Record.—KANKAKEE: at light, June 6, 1935, Ross & Mohr, 2♂.

4. *Stenonema areion* new species

This species resembles *interpunctatum* in lacking spiracular dots on the abdomen and *heterotarsale* in lacking the oblique, black mark below the base of the fore wing on either pleuron; *areion* differs from both those species in having a bright Mars orange crossband at the posterior margin of each abdominal tergite, and in having the ground color of the abdomen white rather than yellow, as in *interpunctatum* and *heterotarsale*.

MALE.—Length of body 7 mm., of fore wing 8 mm. Face below antennal sockets light yellow, a small, black mark on margin of frontal shelf ventral to each antennal socket; each antenna yellow, flagellum slightly grayed near base; area of face between antennal sockets and ocelli deep yellow; vertex Mars orange; eyes in life pale green. Pronotum yellow, black streak on either side; mesonotum amber-brown, with red-brown shading at posterior ends of outer parapsides and on lateral margins anterior to fore wing bases; mesoscutellum yellow in the center, Mars orange at margins, Mars orange shading also present on lateral margins of mesonotum posterior to fore wing bases; pleura bright yellow, minute, a dark brown point on each middle and hind coxal suture; thoracic sternum bright yellow. Wings hyaline, stigmatic areas stained with brown, veins light yellow-brown, crossveins black, two crossveins below bulla connected by black dash; veins and crossveins of each hind wing pale yellow, but crossveins and intercalaries at outer margin black; fore femur deep yellow, median and apical, dark brown crossbands present, tibia pale yellow, apex black, tarsus white, apexes of segments slightly darkened, first segment three-fifths as long as second segment; middle and hind legs white, each femur with a faint, dark brown shading in middle and a well-marked, brown band at apex. Abdomen white, posterior margin of each tergite 1–7 with Mars orange crossband; spiracular dots absent; apical three tergites yellow-orange, with overlying Mars orange shading; genitalia, fig. 336, white; caudal filaments white, articulations not darkened.

Holotype, male. — Oakwood, Illinois, June 25, 1948, B. D. Burks. Specimen dry, on pin.

Paratypes.—Same data as for holotype, 2 ♂. Specimens dry, on pins; genitalia on microscope slide.

5. *Stenonema minnetonka* Daggy

Stenonema minnetonka Daggy (1945:376).

MALE.—Length of body 9–10 mm., of fore wing 10–11 mm. Head yellow, a black mark on face ventral to each antennal base; vertex shaded with orange-brown on meson and at posterior margin; antennal scape and pedicel yellow, flagellum gray-tan at base, hyaline at tip. Mesonotum brown, scutellum yellow; semimembranous area anterior to base of fore wing shaded with light orange-brown, pleuron yellow, sternum yellow; fore leg deep yellow, apex of tibia and apexes of all tarsal segments black, first tarsal segment one-half as long as second; middle and hind legs yellow, tarsi shaded with gray-brown; middle and apex of each femur usually shaded with dark brown, middle band on hind femur sometimes obsolescent; wings hyaline, stigmatic area of fore wing stained with brown, veins yellow-brown, crossveins very dark brown or black; hind wing with all veins and crossveins yellow, outer margin dark brown. Abdomen yellow, black crossband at posterior margin of each tergite 1–8 with a black crossline; spiracular marks present; posterior half of tergite 8 and all of tergites 9 and 10 shaded with orange-brown; genitalia, fig. 335, yellow; caudal filaments gray-yellow, articulations brown.

Known from Illinois and Minnesota.

Illinois Records. — BENTON: at light, June 10, 1946, H. H. Ross, 2 ♂. FREEPORT: June 10–11, 1948, Burks, Stannard, & Smith, 1 ♂. QUINCY: July 6, 1939, Mohr & Riegel, 1 ♂. ROCKFORD: May 22, 1941, Ross & Burks, 1 ♂. SHAWNEETOWN: July 14, 1948, Mills & Ross, 1 ♂.

6. *Stenonema canadense* (Walker)

Baetis canadensis Walker (1853:569).
Stenonema interpunctatum canadense (Walker). Spieth (1947:107).
Stenonema conjunctum Traver (1935*a*:309).
Stenonema ohioense Traver (1935*a*:322).
Stenonema proximum Traver (1935*a*:325).

Spieth (1947:109) considers that *proximum* and *conjunctum* are synonyms of the form that he designates as *interpunctatum frontale* (Banks).

In the Museum of Comparative Zoology, the specimens determined as *interpunctata* (Say) by Walsh are clearly of the species we now are calling *canadense* (Walker). Walsh's redescription (1862:374) of *interpunctata* (Say) also obviously fits the present-day concept of *canadense*, and, as Spieth has shown (1940:333), the current concept of *canadense* is in agreement with Walker's type. The type of *interpunctata* is lost, but the original description of this species more nearly matches the species at present called by that name than it does *canadense*. Walsh's use of the name *interpunctata* thus may safely be considered to have been based on a misidentification.

Stenonema canadense is an extremely variable species, being almost entirely black in northern Ontario and grading to an almost entirely yellow form in southern Illinois.

MALE.—Length of body 8–10 mm., of fore wing 9–11 mm. Face white, with black streak ventral to each antennal base, in darkest specimens entire frontal shelf black; eyes in life light green; vertex red-brown, often with median, black shading. Mesonotum dark red-brown, often with a longitudinal, median, black stripe, scutellum sometimes yellow-brown, usually dark; semimembranous area anterior to base of fore wing yellow to bright red-brown; pleuron yellow, with variable amounts of dark brown and black shading, and an oblique, dark streak always present ventral to base of fore wing; sternum yellow, sometimes shaded with dark brown; fore leg deep yellow to light brown, apex of tibia black, tarsus largely shaded with gray, first tarsal segment from two-fifths to three-fifths as long as second; middle and hind legs yellow to tan; all femora with median and apical, dark brown or black shaded areas; wings hyaline, stigmatic area of fore wing stained with brown, veins yellow-brown, crossveins dark brown or black; veins and crossveins in hind wing yellow to yellow-brown, outer margin of hind wing shaded with brown. Abdomen with ground color yellow; tergites varying widely, in some specimens almost completely black, in others with only a black crossline at posterior margin of each tergite and a median, longitudinal, gray line extending partly or completely the length of dorsum; spiracular marks present in lighter specimens, these marks fusing with dark shading of tergites in darker specimens; apical three tergites shaded with red-brown; genitalia, fig. 334, yellow; caudal filaments gray-yellow to light yellow, articulations dark brown.

NYMPH.—Length of body 8–11 mm. Head anterior to eyes uniform brown, no median, pale spot on meson of anterior margin, but usually pale spot on this margin anterior to each antennal socket; large, pale spots lateral to compound eyes. Thoracic dorsum mostly brown, a pair of large, sublateral, pale spots usually present on pronotum; tarsal claws without ventral denticles. Dorsum of abdomen brown, with a pair of somewhat variable, longitudinal, submedian, pale stripes and a row of pale spots near either lateral margin; gills borne by segments 1–6 pointed at apexes, gills of seventh pair each with one trachea; apical two or three abdominal sternites with longitudinal, brown band at lateral margins, more anterior sternites either unmarked or with vague, brown spots near lateral margins, entire apical fourth of ninth sternite brown; posterolateral angles of segments 7–9 spinelike; caudal filaments light brown, articulations perceptibly darker near apexes of filaments.

Known from Arkansas, Connecticut, Illinois, Indiana, Manitoba, Michigan, Minnesota, New Jersey, New York, North Carolina, Ohio, Oklahoma, Ontario, Tennessee, Quebec, West Virginia, and Wisconsin.

Illinois Records.—Adult specimens, collected April 10 to September 17, are from Alton, Apple River Canyon State Park, Aroma Park, Aurora, Carlinville, Cedarville, Charleston, Chicago, Crescent City, Erie, Fieldon, Freeport, Galena, Golconda, Havana, Kankakee, La Grange, Mahomet, Milan, Momence, Mount Vernon, Oakwood, Oregon, Palisades State Park, Prophetstown, Quincy, Richmond, Rock City, Rockford, Rock Island, Spring Grove, St. Charles, Starved Rock State Park, Sterling, Urbana, Waukegan, White Pines Forest State Park, and Wilmington.

7. *Stenonema frontale* (Banks)

Heptagenia frontalis Banks (1910:199).
Stenonema interpunctatum frontale (Banks). Spieth (1947:109).
Stenonema majus Traver (1935*a*:320).

The type of *frontale* is, unfortunately, in quite poor condition, but the species can be placed with reasonable certainty despite this.

MALE.—Length of body 8–10 mm., of fore wing 9–11 mm. Face below antennae yellow, black marks below each antennal socket; vertex yellow, shaded with brown near posterior margin; compound eyes in life light green; each antennal scape and pedicel yellow, flagellum gray-tan at base, becoming hyaline at apex. Mesonotum dark yellow-brown, shading to yellow at lateral margins and, usually, at ends of outer parapsides; scutellum yellow; semimembranous area anterior to base of fore wing shaded with rose-pink; pleuron yellow, an oblique, black streak ventral to base of fore and hind wings; sternum yellow; fore leg tan or deep yellow, apex of tibia black, first tarsal segment two-fifths to three-fifths as long as second segment; middle and hind legs yellow; each femur of all legs with a median and an apical, dark brown crossband; wings hyaline, stigmatic area of fore wing very slightly stained with brown, veins yellow-brown, crossveins very dark brown or black, veins and crossveins of hind wing yellow, outer wing margin shaded. Abdomen yellow, a black crossline at posterior margin of each tergite 1–8; spiracular marks present; apical three tergites shaded with orange-brown, sometimes with a rosy flush added; genitalia, fig. 337, light yellow; caudal filaments gray-yellow, articulations brown.

NYMPH.—Length of body 9–10 mm. Head anterior to compound eyes uniform brown, with a pale spot on anterior margin at meson and a lateral, pale spot on this margin anterior to each antennal socket; large, pale spots lateral to eyes. Thoracic notum mostly uniform brown, pronotum usually pale at lateral and posterior margins, and mesonotum pale on meson in anterior half; tarsal claws without ventral denticles. Abdomen dorsally mostly dark brown, a row of elongate, pale spots present on either side of the dorsal meson on tergites 4–10, sometimes these pale spots almost continuous; each sternite 1–9 with a pair of sublateral, brown spots, these spots more elongate and extending nearly the length of the segment on posterior two or three sternites, posterior margin of ninth sternite either entirely pale or faintly shaded with brown; caudal filaments light brown.

This species is known from Illinois, Kentucky, Massachusetts, Minnesota, and Ontario.

Illinois Records. — BENTON: at light, June 10, 1946, H. H. Ross, 1♂. KANKAKEE: June 6, 1935, Ross & Mohr, 1♂. MOMENCE: Aug. 16, 1938, Ross & Burks, 2♂. PALISADES STATE PARK: at light, June 16, 1948, Stannard & Smith, 1♂. WAUKEGAN: Aug. 15, 1938, Ross & Burks, 2♂. WHITE HEATH: Aug. 2, 1940, Ross & Riegel, 1♂.

8. *Stenonema interpunctatum* (Say)

Baetis interpunctata Say (1839:41).
Stenonema interpunctatum interpunctatum (Say). Spieth (1947:106).

MALE.—Length of body 7–9 mm., of fore wing 8–10 mm. Head yellow, face with prominent, black marks ventral to antennal sockets, vertex shaded with orange-brown; compound eyes in life light green; each antennal scape and pedicel yellow, flagellum gray-brown at base, becoming hyaline toward apex. Mesonotum dark yellow-brown; yellow at lateral margins, at posterior ends of outer parapsides, and on scutellum; semimembranous area anterior to base of fore wing yellow or flesh colored; each pleuron yellow, a gray-brown oblique streak present ventral to fore wing base, also, sometimes, ventral to hind wing base; sternum yellow; fore leg deep yellow, tibia black at apex, first fore tarsal segment from one-fourth to one-third as long as second segment; middle and hind legs light yellow; front and middle femora each with a median and an apical, dark brown crossband, hind femur with only apical band; wings hyaline, stigmatic area of fore wing faintly stained with brown, veins yellow-brown, crossveins dark brown or black; veins and crossveins of hind wing yellow, outer margin shaded with black. Abdomen yellow, posterior margin of each tergite 1–8 with a narrow, black cross-stripe; spiracular markings absent; apical three tergites shaded with pink- or orange-tan; genitalia, fig. 338, yellow; caudal filaments gray-yellow to almost hyaline, articulations not, or only obscurely, darkened.

NYMPH.—Length of body 8–10 mm. Head anterior to compound eyes uniform brown, anterior margin without light spots; relatively small, pale spots on margins lateral to eyes. Dorsum of thorax mostly uniform brown; pronotum with a pair of sublateral and a pair of anterolateral, pale spots, the latter sometimes extending along part or all of lateral pronotal margin; longitudinal, pale stripe on meson of anterior half of mesonotum; tarsal claws without ventral denticles. Gills borne by first six abdominal segments pointed at apexes, each gill of seventh pair with one trachea; dorsum of abdomen brown, a pair of submedian, longitudinal, pale streaks on each of tergites 1–9, these forming an almost continuous pair of stripes, usually of uniform width from end to end; sternites 7–9 each with a pair of sublateral, longitudinal, brown stripes, usually all anterior segments each with a pair of sublateral, brown spots; apex of ninth sternite with a broad, transverse, brown band, this fusing with sublateral, longitudinal marks; caudal filaments light brown, each filament with alternating articulations dark and light in the area near the tip.

Known from Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Minnesota, Ohio, Ontario, Tennessee, and Wisconsin.

Illinois Records.—Adult specimens, collected May 5 to August 22, are from Aroma Park, Aurora, Batavia, Benton, Carbondale, Carlinville, Cowling, Dixon, East Dubuque, Effingham, Evanston, Freeport, Galesburg, Havana, Henry, Herod, Highland, Homer, Kankakee, Keithsburg, Mahomet, McHenry, Momence, Mount Carmel, Mount Carroll, Muncie, Murphysboro, Oakwood, Oregon, Ottawa, Pontiac, Rockford, Rock Island, Russellville, St. Charles, Savanna, Springfield, Spring Grove, Starved Rock State Park, Urbana, Waukegan, West Chicago, White Heath, and Wilmington.

9. *Stenonema heterotarsale* (McDunnough)

Ecdyonurus heterotarsalis McDunnough (1933*a*:42).
Stenonema affine Traver (1933*a*:184).
Stenonema interpunctatum heterotarsale (McDunnough). Spieth (1947:110).

Male.—Length of body 7–9 mm., of fore wing 9–11 mm. Face light yellow, usually unmarked; each antenna with scape and pedicel yellow, flagellum gray-tan at base, hyaline at apex; eyes in life light green; vertex orange-brown, usually a pair of black dots present, one near margin of each compound eye. Mesonotum light brown, lateral margins and scutellum yellow; semimembranous area anterior to base of fore wing yellow, occasionally edged with pink; pleuron yellow, unmarked; fore leg deep yellow, apex of tibia and apexes of tarsal segments dark brown or black, first tarsal segment two-fifths to three-fifths as long as second segment; middle and hind legs light yellow; fore and middle femora with median and apical, dark brown crossbands, hind femur with only apical dark band; wings hyaline, stigmatic area of fore wing very faintly stained with brown, veins yellow-brown, crossveins black; hind wing with veins and crossveins yellow, outer wing margin darkened with black shading. Abdomen yellow, a narrow, black crossline at posterior margin of each of tergites 1–8; spiracular dots absent; apical three tergites shaded with pinkish brown; genitalia, fig. 339, light yellow; the caudal filaments pale yellow, the articulations not at all or only very faintly darkened.

Nymph.—Length of body 9–10 mm. Head anterior to eyes a uniform brown; anterior margin usually with small, pale spot on meson, fairly large, pale spot on this margin just anterior to each antennal socket, two relatively small, pale spots on head margin lateral to each compound eye. Dorsum of thorax mostly uniform brown; pronotum with a pair of sublateral, round spots and lateral margin pale; anterior half of mesonotum pale on meson; tarsal claws without ventral denticles. Gills borne by abdominal segments 1–6 pointed at apexes, gills of seventh pair each with one trachea; dorsum of abdomen uniform brown, most specimens with a pair of submedian, longitudinal, pale streaks on each of tergites 4– or 5–10, those on 8 and 9 much the wider and those on 10 much reduced; sternites 5– or 6–9 each with a pair of sublateral, brown spots, those on sternite 9 extending almost the length of the segment and fused with a broad, transverse, brown band occupying apical fifth of sternite; caudal filaments light brown, in apical area these filaments with alternating articulations dark and light.

Known from Illinois, North Carolina, Ontario, and Quebec.

Illinois Records. — Chicago: July 3, 1940, J. J. Janacek, 1 ♂; July 8, 1937, Frison & Ross, 1 ♂; at light, July 13, 1931, T. H. Frison, 7 ♂; Sept. 2, 1902, Titus, 1 ♂. Homer: at light, June 26, 1925, R. D. Glasgow, 1 ♂; Aug. 10, 1925, T. H. Frison, 1 ♂. Kankakee: June 6, 1935, Ross & Mohr, 3 ♂; June 15, 1938, Ross & Burks, 4 ♂; June 29, 1939, Burks & Ayars, 1 ♂; July 10, 1925, T. H. Frison, 10 ♂. Mount Vernon: Big Muddy River, April 10, 1946, Mohr & Burks, 1 ♂, 9 N. Muncie: Stony Creek, May 24, 1914, 1 ♂. Oakwood: May 24, 1926, T. H. Frison, 3 ♂; June 6, 1925, T. H. Frison, 1 ♂; June 16, 1925, 1 ♂; June 24, 1948, Mills & Ross, 2 ♂; June 25, 1948, B. D. Burks, 6 ♂. Sterling: at light, May

21, 1925, D. H. Thompson, 1♂. Waukegan: July 16, 1935, Ross & DeLong, 4♂; Aug. 4, 1926, 1♂. Wilmington: May 27, 1935, Ross & Mohr, 1♂.

TRIPUNCTATUM Group

10. *Stenonema tripunctatum* (Banks)

Heptagenia tripunctata Banks (1910:199).
Stenonema femoratum tripunctatum (Banks). Spieth (1947:99).

Male.—Length of body 8–11 mm., of fore wing 10–13 mm. Head tan to pale yellow, a brown line crossing face just ventral to antennal bases, vertex shaded with light brown along inner margins of compound eyes; each antennal scape brown, pedicel completely light brown or light brown only at apex and with basal part yellow, flagellum tan at base, becoming hyaline at apex; each compound eye in life pearl-gray, usually with a brown crossband, the two compound eyes separated on meson by a space as wide as lateral ocellus. Thoracic notum varying from uniform brown to pale yellow, almost white; each pleuron tan to pale yellow, always with darker shading ventral to base of fore wing; sternum tan to yellow; all coxae darkened with gray-tan, fore femur tan to yellow-brown, fore tibia and tarsus yellow to tan, apex of tibia and apexes of tarsal segments dark brown, first tarsal segment from two-fifths to one-half as long as second segment; middle and hind legs yellow to tan; each femur of all legs with median and apical, red-brown crossbands, each of middle and hind tibiae with a red spot near base; wings hyaline, stigmatic area shaded with brown, proximal part also with red suffusion, all veins and crossveins dark brown, outer margin of hind wing hyaline; in fore wing, veins crowded in region of bulla. Ground color of abdomen varying from light brown to light yellow, almost white; darker specimens with two mesal, dark brown stripes extending the length of abdomen and with a broad, dark brown crossband at posterior margin of each tergite; all specimens with a median, black dot and a pair of submedian, black dashes at posterior margin of each tergite 2–9; apical tergites uniformly shaded with dull tan or brown; abdominal sternites tan, with vague, brown shading near either lateral margin of each sternite, or uniform, light yellow; genitalia, fig. 340, tan to yellow; caudal filaments tan or yellow, articulations brown.

Nymph.—Fig. 360. Length of body 9–12 mm. Head brown, freckled with pale dots, with a median and two sublateral, pale spots on anterior margin, a pair of large, pale

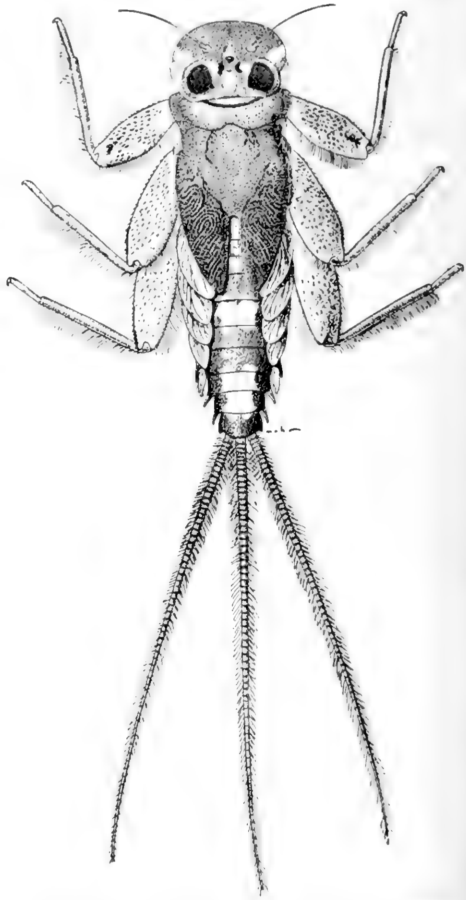


Fig. 360.—*Stenonema tripunctatum*, mature nymph, dorsal aspect.

spots lateral to each compound eye, and posterior margin of vertex mostly pale; pronotum brown, with relatively few pale dots and usually four pale spots near each lateral margin; each tarsal claw with two ventral denticles. Gills borne by abdominal segments 1–6 rounded at apexes, gills of seventh pair each with one or two longitudinal tracheae; abdominal tergites mostly brown, large, white, median spots on tergite 5, a pair of small, submedian, white spots at base and apex of tergites 6 and 7, and large, median, white spots on tergites 8 and 9; posterolateral angles of segments 2–9 produced as large spines, apical angles slightly sinuate; sternites 2–8 each with a pair of sublateral, brown spots, sternite 9 with a pair of sublateral, brown spots near basal margin and a pair of very large, brown spots at apical margin, basal and apical spots sometimes connected and apical spots occasionally fusing on meson; each caudal filament deep yellow at base, alternating pairs of segments dark and light in middle and apical areas.

Known from Alabama, Arkansas, Georgia, Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, New York, Ohio, Oklahoma, Ontario, Pennsylvania, Quebec, Texas, and Wisconsin.

Illinois Records.—Adult specimens, collected April 4 to August 23, are from Alto Pass, Anna, Antioch, Apple River Canyon State Park, Chicago, Cora, Elizabethtown, Evanston, Fox Lake, Golconda, Havana, Herod, Jonesboro, Monticello, Muncie, Oakwood, Parker, Spring Grove, St. Joseph, Wilmington, and Wolf Lake.

11. *Stenonema femoratum* (Say)

Baetis femorata Say (1823:162).
Stenonema femoratum femoratum (Say). Spieth (1947:98).

MALE.—Length of body 8–11 mm., of fore wing 10–13 mm. Differs from *tripunctatum* only in the following particulars: compound eyes separated on meson by a space only two-thirds as wide as lateral ocellus; outer margin of hind wing shaded with light brown; in dark specimens, area between inner and outer parapsides of mesonotum lighter brown than rest of mesonotum; genitalia, fig. 342, with penis lobes relatively more truncate laterally; in most specimens, alternating articulations of caudal filaments darker brown than others.

NYMPH.—Length of body 9–12 mm. Very similar to nymph of *tripunctatum,* but differing in having anterior margin of head slightly flattened on meson, rather than evenly rounded from side to side, median, white spot on anterior margin absent; abdominal sternum with sublateral, brown spots usually present on sternites 5– or 6–8 only, occasionally spots entirely wanting from these sternites; sternite 9 always with sublateral, longitudinal, brown stripe and pair of large, brown spots at posterior margin.

Known from Georgia, Illinois, Indiana, New York, Ohio, Ontario, Quebec, and South Carolina.

Illinois Records. — ASHLEY: Little Muddy River, April 29, 1946, Mohr & Burks, 1 ♂. CARBONDALE: June 13, 1944, Frison & Sanderson, 1 ♂. DIXON SPRINGS: at light, April 3, 1946, Burks and Sanderson, 5 ♂. EDDYVILLE: Lusk Creek, April 4, 1946, Burks & Sanderson, 1 ♂ ; Lusk Creek, May 24, 1940, Ross & Riegel, 1 ♂ ; Lusk Creek, June 1, 1940, B. D. Burks, 2 ♂ ; Belle Smith Springs, June 7, 1946, Mohr & Burks, 9 ♂ ; Belle Smith Springs, July 16, 1946, Mills & Ross, 1 ♂. FOX LAKE: July 1, 1931, Frison, Betten, & Ross, 1 ♂. GIANT CITY STATE PARK: Aug. 22, 1944, Sanderson & Leighton, 12 ♂. GOLCONDA: May 30, 1928, T. H. Frison, 1 ♂. HEROD: May 2, 1946, Burks & Sanderson, 1 ♂ ; May 23, 1946, Ross & Mohr, 1 ♂ ; May 29, 1939, Burks & Riegel, 1 ♂ ; July 8, 1935, DeLong & Ross, 1 ♂. MOMENCE: June 22, 1938, Ross & Burks, 1 ♂. OAKWOOD: May 7, 1936, Ross & Mohr, 1 ♂. PITTSFIELD: at light, Aug. 11, 1948, Sanderson & Stannard, 1 ♂. QUINCY: June 24, 1948, L. J. Stannard, 2 ♂. RUDEMENT: Blackman Creek, May 14, 1946, Mohr & Burks, 2 ♂. WAUKEGAN: Aug. 15, 1938, Ross & Burks, 1 ♂.

BIPUNCTATUM Group

12. *Stenonema bipunctatum* (McDunnough)

Ecdyonurus bipunctatus McDunnough (1926:191).

MALE.—Length of body 6–8 mm., of fore wing 8–10 mm. Face below antennal sockets white, vertex red- or orange-brown; eyes in life pearl-gray; each antenna light yellow, flagellum usually slightly darkened in basal half. Thoracic notum dull gray-tan or gray-brown, with apex of mesoscutellum white; semimembranous area of pleuron anterior to base of fore wing, and dorsal to spiracle, pink, balance of pleuron white except for brown-shaded spot dorsal to each middle coxa; thoracic sternum light yellow; fore leg light tan, with red-brown shading in middle and at apex of fore femur, and with black shading at apex of fore tibia and at apexes of tarsal segments; first tarsal segment two-thirds as long as second segment; middle and hind legs light yellow, each femur usually with a median and an apical red crossband, apical segment of each tarsus shaded with brown; wings hyaline, brown shading always present in humeral cell of fore wing, this brown often extending almost across base of wings; veins and crossveins of fore wing very dark brown, those of hind wing usually hyaline, sometimes light brown; stigmatic area of fore wing not colored, crossveins not crowded in region of bulla. Abdomen mostly white, apical three tergites with pinkish-tan shading, each tergite 3–7 with a pair of black, transverse, submedian dashes, these marks occasionally present also on tergite 2; genitalia, fig. 341, white or light yellow; caudal filaments white, basal articulations usually shaded with orange-tan or brown.

Nymph.—Length of body 7–8 mm. Pale median spot present on anterior margin of head. Each tarsal claw with two minute ventral denticles near apex. Abdominal gills borne by segments 1–6 truncate at apexes, seventh pair of gills without tracheae; abdominal dorsum solid brown, interrupted by light-colored areas on meson of segments 5, 8, and 9, and with a pair of lateral, light-colored spots near anterolateral angles of tergites 2–7, these lateral spots normally covered by gills; venter white, with a pair of brown, sublateral spots on sternites 5–8; posterolateral angles of segments 3–9 spinelike; sternite 9 with a pair of lateral, longitudinal, brown stripes and with two large, brown spots at posterior margin; caudal filaments white, the middle area of each filament with alternating pairs of segments brown and white.

Known from Illinois and Ontario.

Illinois Records.—Aroma Park: June 4, 1947, B. D. Burks, 2♂. Aurora: July 9, 1925, T. H. Frison, 1♂; at light, July 17, 1927, Frison & Glasgow, 2♂. Casey: Catfish Creek, April 29, 1942, H. H. Ross, 1♂. Dixon: June 27, 1935, DeLong & Ross, 3♂. Exline: Kankakee River, June 4, 1947, B. D. Burks, 1♂. Grand Tower: May 30, 1935, Ross & Mohr, 1♂. Harrisburg: at light, Aug. 16, 1937, Ross & Ritcher, 1♂. Havana: June 1, 1938, C. O. Mohr, 1♂. Keithsburg: July 4, 1946, Burks & Sanderson, 1♂. Momence: Aug. 16, 1938, Ross & Burks, 1♂. Monticello: May 7, 1936, Ross & Burks, 1♂. Oakwood: June 5, 1948, Burks & Sanderson, 2♂; June 23, 1948, B. D. Burks, 5♂; Aug. 4, 1939, Burks & Riegel, 1♂. Oregon: at light, July 2, 1946, Burks & Sanderson, 5♂; July 9, 1925, T. H. Frison, 1♂; Rock River, Aug. 5, 1948, Burks & Stannard, 1♂. Pittsfield: at light, Aug. 11, 1948, Sanderson & Stannard, 1♂. Pontiac: Aug. 22, 1938, H. H. Ross, 4♂. Prophetstown: Rock River, July 24–25, 1947, Burks & Sanderson, 1♂. Rockford: May 13, 1942, Ross & Burks, 2♂; May 15, 1946, Ross & Burks, 1♂; at light, June 29, 1938, B. D. Burks, 1♂; July 12, 1938, Burks & Boesel, 2♂. Rock Island: June 7, 1938, Burks & Riegel, 1♂. Rockton: Rock River, June 25, 1947, B. D. Burks, 3♂. Serena: Indian Creek, May 12–16, 1938, Ross & Burks, 2♂. South Beloit: July 2, 1931, Frison, Betten, & Ross, 1♂. Urbana: June 22, 1947, H. H. Ross, 1♂. Wilmington: at light, Aug. 6, 1947, Burks & Sanderson, 1♂.

13. *Stenonema ares* new species

This species is most closely related to *Stenonema bipunctatum* (McDunnough) in having a medianly interrupted, black crossline at the posterior margin of each abdominal tergite 2–7, but differs in having the mesonotum bright Mars orange rather than gray-brown or gray-tan; each of abdominal tergites 1–7 in *ares* has a relatively broad, Mars orange crossband at the posterior margin, and the first fore tarsal segment is one half as long as the second, rather than two-thirds as long, as in *bipunctatum.* Specimens of *ares* and *bipunctatum* which have remained very long in alcohol are quite difficult to separate to species.

The nymph of *ares* differs from that of *bipunctatum* in abdominal color pattern and in having no ventral denticles on the claws.

Male.—Length of body 6–9 mm., of fore wing 8–11 mm. Head below level of antennal sockets white, vertex chrome orange, shaded on meson and laterally with Mars orange; each antenna with scape Mars orange, pedicel yellow, flagellum white, somewhat grayed near base; eyes in life pearl-gray. Thoracic notum Mars orange, apex of meso- and metascutellum white, area on meson of mesonotum extending anteriorly from apex of scutellum to outer parapsides usually chrome orange, occasionally becoming grenadine pink; pleuron mostly pinkish-tan or testaceous, semimembranous area anterior to fore wing base grenadine pink or orange-brown, area of pleuron ventral to fore wing base light yellow; thoracic sternum pale yellow, anterior end of mesobasisternum shaded with testaceous; coxae of all legs shaded with light Mars orange, apical segment of tarsus of each leg gray; fore leg light tan, middle and apex of femur shaded with red-brown, apex of tibia and apexes of tarsal segments dark brown, first tarsal segment one-half as long as second; middle and hind legs light yellow, apex of hind femur and middle and apex of middle femur shaded with red-brown; wings hyaline, humeral cell of fore wing shaded with light brown, proximal part of stigmatic area faintly stained with brown, veins of fore wing yellow-brown, crossveins dark brown, anterior veins and crossveins of hind wing pale yellow, more posterior ones hyaline. Abdomen pale yellow or white, each tergite 2–7 with a medianly interrupted, narrow, black crossline at posterior margin and, in addition, a fairly broad, Mars orange crossband at posterior margin of each tergite 1–7; spiracular markings absent; apical three tergites Mars orange, shading to chrome orange at apex of tergite 10, these tergites sometimes also with a pink suffusion; genitalia, fig. 343, white; caudal filaments white, basal articulations Mars orange, more distal articulations white.

NYMPH.—Length of body 10 mm. Head light brown in area anterior to compound eyes and on vertex, this dark area freckled with numerous, relatively large, white dots; three large, white spots on lateral margin near each compound eye; median, white spot anterior to median ocellus and on vertex near posterior margin; base of each antennal flagellum dark; rest of antenna white. Pronotum light brown, with many irregular, white spots; each tibia with a basal and a median, brown band; each tarsus brown except at base and apex; tarsal claws without ventral denticles. Abdominal tergites 1 and 2 white, 3–5 mostly white, each with a longitudinal, median, brown mark on basal half, a brown spot at posterolateral angle, and a pair of large, submedian, vague, light brown spots at posterior margin; tergites 6–8 mostly brown, a pair of small, anterolateral and submedian, white marks at anterior margin of each; tergite 9 brown on meson and near lateral margins; and 10 brown except for two submedian, basal spots; sternites 1–8 white, 9 with vague, lateral and basal, brown markings; posterolateral angles of segments 7–9 spinelike; gills borne by segments 1–6 truncate at apexes, seventh pair without tracheae; caudal filaments light yellow, apical articulations slightly darkened with tan.

Holotype, male.—Rockford, Illinois, at light, June 11, 1948, Burks, Stannard, & Smith. Specimen dry, on pin.

Paratypes.—ILLINOIS: Same data as for holotype, 18♂. DIXON: at light, June 25, 1947, B. D. Burks, 5♂. ELIZABETHTOWN: at light, July 14, 1948, Mills & Ross, 1♂. FREEPORT: at light, June 10–11, 1948, Burks, Stannard, & Smith, 11♂; Aug. 4, 1948, Burks & Stannard, 2♂. GREENVILLE: Shoal Creek, April 12, 1946, Mohr & Burks, 1♂. OREGON: July 4, 1946, Burks & Sanderson, 8♂; July 9, 1925, T. H. Frison, 1♂; Aug. 5, 1948, Burks & Stannard, 4♂. PITTSFIELD: at light, Aug. 11, 1948, Sanderson & Stannard, 3♂. PROPHETSTOWN: at light, June 25, 1947, B. D. Burks, 1♂; July 24–25, 1947, Burks & Sanderson, 10♂. ROCKTON: June 25, 1947, B. D. Burks, 17♂; Aug. 4, 1948, Burks & Stannard, 6♂. ROSCOE: June 25, 1947, B. D. Burks, 4♂. SHAWNEETOWN: July 14, 1948, Mills & Ross, 2♂. STERLING: at light, June 26, 1947, B. D. Burks, 5♂. URBANA: at light, May 29, 1947, H. H. Ross, 1♂. All specimens dry, on pins; genitalia on microscope slides.

Additional Illinois specimens preserved in alcohol, and not included in the type series, are from the following: ALTON: May 18, 1932, Ross & Mohr, 1♂. BILLETT: Wabash River, May 15, 1942, Mohr & Burks, 4♂. ROCKFORD: May 22, 1941, Ross & Burks, 31♂. STERLING: May 22, 1941, Ross & Burks, 23♂.

VICARIUM Group

14. *Stenonema pudicum* (Hagen)

Ephemera pudica Hagen (1861:39).

Eaton (1885:280) placed this species as a synonym of *vicarium*, but McDunnough (1925*b*:191) studied the type and was able to show that *pudicum* was not synonymous with *vicarium*. The type specimen is a female subimago in poor condition, now in the collection of the Museum of Comparative Zoology. I have studied it and agree with McDunnough.

MALE.—Length of body 10–12 mm., of fore wing 12–14 mm. Head brown, usually a narrow, black line extending across face, from eye to eye, below antennal bases; eyes in life brown, each antenna brown, becoming hyaline toward tip of flagellum. Thoracic notum dark olive-brown, often with a reddish cast toward anterior margin of mesonotum, pleuron anterior to wing bases light yellow or clay color, elsewhere light clay-brown; thoracic sternum chestnut brown; wings hyaline, entire stigmatic area of fore wing shaded with dark red-brown, outer margin of hind wing brown; all veins and crossveins brown, fore wing with 3 or 4 crossveins in each interspace crowded together in region of bulla; usually all coxae brown, the fore leg dark yellow-brown to olive-brown, middle and hind legs light yellow-brown, each femur with a middle and an apical, dark-brown color band, apex of fore tibia black, first fore tarsal segment from one-half to two-thirds as long as second segment. Abdomen dark yellow-brown to medium brown, with a broad, somewhat diffuse, dark brown, transverse band at posterior margin of each tergite 2–8 and, usually, double, longitudinal, dark brown line on meson extending the length of these tergites; apical tergites uniformly very dark brown; sternum gray-brown, lateral and posterior margins of middle sternites usually dark brown; genitalia, fig. 345, yellow-brown; caudal filaments light gray-tan, articulations brown.

NYMPH.—Length of body 12–14 mm. Entire dorsum of head anterior to ocelli and vertex between eyes dark brown, freckled with pale dots, areas lateral to eyes almost completely light. Pronotum variegated with fairly large, light spots near lateral margins, balance of thoracic notum dark brown; pronotum as wide as head; tarsal claws without denticles. Abdominal tergites 6 and 8–10 usually uniformly dark brown, others variegated with light spots; gills borne by segments 1–6 truncate at apexes, gills of seventh pair without tracheae; slender, spinelike projections borne by posterolateral angles of abdominal segments 3– or 4–9; sternum pale yellow, sternites 3– or 4–8 each with a broad, dark brown crossband on median two-thirds of anterior margin; sternite 9 with a broad, longitudinal, dark brown band near each lateral margin, these two bands sometimes almost or quite joined at anterior margin of sternite; caudal filaments usually uniformly yellow or tan.

Known from District of Columbia, Illinois, New York, North Carolina, Tennessee, and Virginia.

Illinois Record. — EDDYVILLE: Lusk Creek, May 16, 1947, B. D. Burks, 1 ♂.

15. *Stenonema vicarium* (Walker)

Baetis vicaria Walker (1853:565).
Baetis tesselata Walker (1853:566).
Ecdyonurus rivulicolus McDunnough (1933*a*:40). New synonymy.

Spieth (1940:336) gives notes made from a study of the type of this species in the British Museum. The identity of the species now is firmly established. McDunnough's *rivulicolus* differs from *vicarium* only in being slightly smaller and in having the tibiae more tan than red-brown; I have found those characters to intergrade.

MALE.—Length of body 10–14 mm., of fore wing 12–16 mm. Head brown, vertex often tinged with red; eyes in life gray; each antenna tan, shaded with brown at apex of pedicel and on basal half of flagellum, dorsum of thorax dark brown, apex of scutellum red-brown; pleuron yellow-brown, dark red-brown to almost black shading present at wing bases and dorsal to mid-coxa; thoracic sternum brown, anterior and posterior margins of mesobasisternum yellow to light brown, wings hyaline, proximal part of stigmatic area of fore wing shaded with dark red; all veins and crossveins dark brown, crossveins in region of bulla in the fore wing usually not greatly crowded, usually only two or three in each interspace; all coxae brown, with black shading on outer side of each, fore femur light brown, tibia gray-yellow, with apex black, fore tarsus brown, with apexes of segments black, first segment from one-fourth to two-fifths as long as second segment; middle and hind legs yellow-brown, with tarsi darkened; each femur with a median and an apical, broad, dark red-brown band; some or all of the tibiae may be faintly stained with red, especially near bases. Abdomen dark yellow-brown, heavily shaded with blackish brown at posterior margins of tergites 1–7 and on median longitudinal line; apical three tergites lighter, red-brown, with lateral margins often salmon-pink; sternites 1–7 yellow-brown or red-brown, in lighter specimens dark brown shading usually visible near posterolateral angles and on meson; genitalia, fig. 344, smoky yellow; caudal filaments gray-brown or tan, articulations brown.

NYMPH.—Length of body 14–18 mm. Head anterior to ocelli brown, freckled with pale dots, area lateral to eyes and at posterior margin of head mostly pale. Pronotum with large pale spots at lateral and anterior margins, disc with pale dots, rest of thoracic notum usually uniform brown; tarsal claws without ventral denticles. Gills borne by abdominal segments 1–6 truncate at apexes, gills of seventh pair without tracheae; abdominal tergites 1–10 with broad, dark brown crossband at posterior margin of each, these bands sometimes obsolescent or wanting entirely on meson of basal three or four tergites; brown, mid-dorsal band extending from base to apex of abdomen, tergites 5 and 6 often almost completely shaded with brown, occasional specimens with almost entire abdominal dorsum brown; venter white, with a broad, dark brown crossband at posterior margin of each sternite, entire apical half to two-thirds of terminal segment dark brown; posterolateral angles of segments 3– or 4–9 produced, spinelike; caudal filaments uniformly tan or yellow-brown in basal and middle areas, alternating pairs of segments usually dark and light in apical areas of filaments.

Known from Illinois, Indiana, Kentucky, Michigan, New Hampshire, New York, Ontario, Pennsylvania, Quebec, and Wisconsin.

Illinois Records. — ALTO PASS: Union Springs, May 15, 1946, Mohr & Burks, 1 ♂. EDDYVILLE: Belle Smith Springs, April 29, 1949, Sanderson & Stannard, 1 ♂.

16. *Stenonema fuscum* (Clemens)

Heptagenia fusca Clemens (1913:254).

MALE.—Length of body 9–11 mm., of fore wing 12–14 mm. Head yellow-brown, face with dark red-brown, transverse stripe below antennal sockets; eyes gray in living insect; each antenna tan, scape and base of flagellum shaded with red-brown. Thoracic notum dark chestnut brown, apex of scutellum white or yellow; area of each pleuron anterior to base of fore wing and dorsal to middle and hind coxae red-brown, pleuron otherwise tan or yellow; thoracic sternum yellow-brown, with mesobasisternum usually entirely yellow; all coxae red-brown, fore leg dark yellow-brown, apex of fore tibia and apexes of all tarsal segments dark red-brown, first tarsal segment one-third to one-half as long as second segment; middle and hind legs light yellow-brown; each femur with a median and an apical, dark red-brown crossband; wings hyaline, entire stigmatic area of fore wing washed with yellow-brown, crossveins in region of bulla often not at all crowded, occasionally two or three crossveins in each interspace at this point; all veins and crossveins of both wings very dark yellow-brown. Abdominal segments with ground color yellow, tergites usually almost entirely shaded with brown, occasionally this darkening confined to posterior margins of tergites and to median dorsal line; apical three tergites always tinged with bright Mars orange, with white or pale yellow on lateral margins; abdominal sternum dull yellow, rarely with vague, brown shading either side of median line; genitalia, fig. 346, grayish yellow; caudal filaments pale gray-yellow, articulations brown.

NYMPH.—Length of body 10–12 mm. Head and thorax mostly brown, pale spots on lateral margins of head lateral to compound eyes and near margins of pronotum; tarsal claws without ventral denticles. Gills borne by abdominal segments 1–6 truncate at apexes, gills of seventh pair without tracheae; abdominal tergites with rather vague, transverse, darkened area at each posterior margin, tergites 6 and 7 often almost completely brown; posterolateral angles of segments 3– or 4–9 produced, spinelike; sternites 1–8 each with a broad, transverse, brown crossband at posterior margin, sternite 9 with a large, brown spot near each posterolateral angle, these spots usually extending almost to anterior margin of sternite; each caudal filament uniformly tan in basal area, alternating pairs of segments dark and light in more distal area.

Known from Michigan, New Brunswick, New York, Ohio, Ontario, Pennsylvania, Quebec, and Tennessee.

17. *Stenonema ithaca* (Clemens & Leonard)

Heptagenia ithaca Clemens & Leonard (1924:17).

MALE.—Length of body 9–10 mm., of fore wing 11–12 mm. Head and thoracic notum dark red-brown, thoracic pleuron mostly yellow-brown, with darker shading at wing bases and dorsal to coxae; thoracic venter red-brown; stigmatic area of fore wing washed with yellow-brown, crossveins usually not crowded in region of bulla; first fore tarsal segment about one-half as long as second segment. Abdominal tergites 1–7 almost entirely dark brown, each tergite slightly lighter only near anterior margin; apical tergites uniformly dark yellow-brown, often with an added reddish suffusion; genitalia, fig. 347, yellow; the three well-developed caudal filaments gray-yellow, with articulations brown.

NYMPH. — Length of body 10–11 mm. Tarsal claws without ventral denticles. Gills borne by abdominal segments 1–6 truncate at apexes, posterolateral angles spinelike on segments 6– or 7–9; tergites 6 and 8–10 mostly brown, the others mostly light; middle and apical sternites each with a medianly sinuate, transverse, brown band crossing middle of sternite; the three caudal filaments usually uniformly yellow, with the apical segments sometimes alternately dark and light.

Known from Georgia, Michigan, New York, North Carolina, Ohio, Quebec, South Carolina, Tennessee, and West Virginia.

MEDIOPUNCTATUM Group

18. *Stenonema mediopunctatum* (McDunnough)

Ecdyonurus mediopunctatus McDunnough (1926:191).

MALE.—Length of body 9 mm., of fore wing 10 mm. Face below antennal bases white, vertex sepia brown. Dorsum of thorax entirely blackish brown, except that apex of mesoscutellum is light brown; thoracic pleura very dark brown, each with small, white areas at wing bases; thoracic sternum dark brown; first fore tarsal segment two-thirds as long as second segment, each femur with a median and an apical, red crossband. Abdominal segments white, with a small, black spot on meson of posterior margin of each of tergites 2–8, black spiracular dots usually present on segments 4–7, apical three tergites shaded with brown; caudal filaments entirely white.

Known from Ontario.

19. *Stenonema metriotes* new species

This species resembles *mediopunctatum* in having the markings at the posterior margins of abdominal tergites 2–7 reduced to very short, median dashes; the two differ in that the mesonotum is dark brown in *mediopunctatum,* while it is white in *metriotes*; in *mediopunctatum,* usually the spiracular dots on the abdomen and the articulations of the caudal filaments are not darkened, but, in *metriotes,* the spiracular dots always are wanting and the articulations of the caudal filaments are red-brown. *S. metriotes* may eventually prove to be only a variant of *integrum,* although the abdominal markings characteristic of *integrum* are wanting in this species.

MALE.—Length of body 5–6 mm., of fore wing 7–8 mm. Face below antennal sockets white; vertex flesh colored, with a pair of short, oblique, submedian, tan streaks between eyes; eyes in life white; each antenna white, flagellum slightly grayed near base. Mesonotum chalky white, a pair of faint, tan marks near posterior ends of outer parapsides; pleuron white, a very faint, tan, oblique streak ventral to each wing base; venter of thorax white; fore coxa shaded with tan, fore femur tan, with middle and apex red-brown, tibia white, with brown or tan shading at base and apex; apexes of tarsal segments tan, first tarsal segment three-fifths to two-thirds as long as second segment; middle and hind legs white, apexes of femora shaded with red-brown; wings hyaline, stigmatic area of fore wing stained with tan, anterior veins yellow-brown, crossveins dark brown, posterior veins of fore wing and all veins and crossveins of hind wing hyaline, outer margin of hind wing shaded with brown. Abdomen white, tergites 2–6 each with a minute, black, median dash at posterior margin, tergites 7 and 8 each with a medianly interrupted, black crossline at posterior margin, tergite 9 with a continuous, black crossline at posterior margin, tergites 8 and 9 shaded with tan on meson; spiracular markings absent on abdomen; genitalia, fig. 348, white; caudal filaments white, articulations red-brown.

Holotype, male. — East Dubuque, Illinois, at light, July 3, 1946, Burks & Sanderson. Specimen dry, on pin.

Paratypes. — ILLINOIS: Data same as for holotype, 3 ♂. OREGON: July 4, 1946, Burks

& Sanderson, 1 ♂. PROPHETSTOWN: July 24–25, 1947, Burks & Sanderson, 3 ♂. QUINCY: June 24, 1948, L. J. Stannard, 2 ♂. SHAWNEETOWN: July 14, 1948, Mills & Ross, 3 ♂. All specimens dry, on pins.

TERMINATUM Group

20. *Stenonema luteum* (Clemens)

Heptagenia lutea Clemens (1913:252).

MALE.—Length of body 9–11 mm., of fore wing 10–12 mm. Face below level of antennae light yellow, vertex yellow, with orange-red shading; eyes in life light green; a red-brown ring surrounding each antennal socket, antenna pale yellow, flagellum darkened in basal half. Thoracic notum light yellow, usually gray-brown shading present on meson of pronotum, mesoscutellum white; pleuron pale yellow, dark shading present around all coxae, area anterior to base of fore wing usually faintly tinged with orange-brown; sternum pale yellow, anterior part of mesobasisternum usually shaded with gray-tan; fore leg dark yellow, middle and hind legs light yellow, each femur with a median and an apical, dark red-brown cross-band, apex of each tibia and apexes of all tarsal segments dark brown or black, first fore tarsal segment slightly less than one-half as long as second segment; wings hyaline, stigmatic area of fore wing stained with red-tan; veins and crossveins of fore wing dark brown or black, those of hind wing hyaline. Abdomen light yellow, posterior margin of each tergite 1–7 with a narrow, black cross-stripe; spiracular markings absent; apical three tergites pinkish tan; genitalia, fig. 349, pale yellow; caudal filaments pale yellow, articulations faintly darkened with gray, sometimes three or four basal articulations of each filament light brown.

NYMPH.—Length of body 10 mm. Head with area anterior to eyes brown, freckled with pale dots, large, pale spots lateral to each compound eye and at posterior margin of vertex. Each lateral margin of pronotum with a large, light spot, disc of pronotum brown, with numerous minute, pale dots; each tarsal claw with two ventral denticles near apex. Abdominal tergites 3, 6, and 7 almost entirely dark brown, others with a contrasting pattern of dark and light markings, tergite 9 almost entirely light; gills borne by segments 1–6 truncate at apexes, gills of segment 7 without tracheae; abdominal venter white, sternites 2–8 each with brown shading near lateral margins and at posterior margin, sternite 9 with two large, dark brown, sublateral spots; each caudal filament uniformly tan in basal half, apically with alternating pairs of segments dark and light.

Known from Illinois, Ontario, and Quebec.

Illinois Records.—KANKAKEE: June 17, 1939, B. D. Burks, 1 ♂. MOMENCE: June 15, 1938, Ross & Burks, 3 ♂; Aug. 5, 1938, Burks & Boesel, 1 ♂; Aug. 22, 1939, B. D. Burks, 1 ♂. MOUNT CARMEL: June 25, 1936, DeLong & Ross, 1 ♂. OAKWOOD: June 5, 1948, Burks & Sanderson, 1 ♂; June 9, 1926, Frison & Auden, 1 ♂. ROCKFORD: May 22, 1941, Ross & Burks, 1 ♂; June 12, 1938, Ross & Burks, 1 ♂. SAVANNA: June 29, 1935, DeLong & Ross, 1 ♂. WHITE HEATH: Sangamon River, Aug. 5, 1939, Ross & Riegel, 2 ♂.

21. *Stenonema terminatum* (Walsh)

Palingenia terminata Walsh (1862:376).
Heptagenia placita Banks (1910:199). New synonymy.

The lectotype of Walsh's species and the type of *placita* Banks are in the Museum of Comparative Zoology.

MALE.—Length of body 6–8 mm., of fore wing 8–11 mm. Head below antennal sockets light yellow, vertex orange-rufous or clay color, with lateral, orange shading; eyes in life light yellow-green; each antenna white or faint yellow, flagellum darkened in basal half. Thoracic notum light clay color to ochraceous-tawny, apex of mesoscutellum white; pleuron light yellow, area anterior to fore wing base often tinged with light buff-brown, a pale orange-rufous spot dorsal to each coxa; fore leg deep yellow, middle and hind legs light yellow, fore femur with a median and an apical red-brown spot, apex of fore tibia and apexes of all tarsal segments dark brown or black; first fore tarsal segment two-fifths as long as second segment; wings hyaline, stigmatic area faintly stained with yellow-brown, veins of fore wing light yellow-brown, crossveins brown, veins and crossveins of hind wing usually entirely hyaline. Abdomen pale yellowish, tergites 1–7 each with a fairly broad, but rather vague, dark brown or black crossband at posterior margin; spiracular markings absent; apical three tergites ochraceous-tawny; genitalia, fig. 350, light yellow; caudal filaments white or pale yellowish, basal two or three articulations of each filament sometimes darkened with brown.

Known from Illinois, Manitoba, New York, Ontario, and Quebec.

Illinois Records. — MONTICELLO: May 24, 1947, B. D. Burks, 1 ♂. OREGON: July 9, 1925, T. H. Frison, 2 ♂. ROCKFORD: May 22, 1941, Ross & Burks, 5 ♂; June 29, 1938, B. D. Burks, 2 ♂; Sept. 4, 1940, Frison & Ross, 2 ♂. ROCK ISLAND: 14 ♂, 7 ♀ (Walsh 1862:376). ROCKTON: Aug. 4, 1948, Burks & Stannard, 3 ♂. SHAWNEETOWN: July 14, 1948, Mills & Ross, 2 ♂.

22. *Stenonema lepton* Burks

Stenonema lepton Burks (1946:614).

In the male of this species, the first fore tarsal segment often is as much as five-sixths as long as the second segment. In previously used keys to the genera of the Heptageniidae, this character would refer the species to the genera *Cinygmula, Cinygma, Epeorus,* or *Iron.* The male genitalia of *lepton* are, however, typical for the genus *Stenonema.* I have, accordingly, placed it here.

Several recent collections of this species have been made, and the specimens have been preserved dry, on pins. Study of these specimens necessitates some change in the color description of the species, which was drawn from alcoholic material.

MALE.—Length of body 7–9 mm., of fore wing 8–10 mm. Face ventral to antennae white; four minute, gray spots on posterior margin of vertex between eyes: a pair at margins of compound eyes and a submedian pair; vertex near ocelli yellow, shaded with orange-brown posteriorly; each antenna white, flagellum slightly darkened in basal half; eyes in life chalky white. Pronotum very pale yellow, mesonotum chalky white, scutellum white, pleuron white, a faintly darkened streak ventral to base of fore wing between middle and hind coxae, and dorsal to hind coxa; thoracic sternum white; fore leg very pale yellow, red-brown shading present in middle and at apex of fore femur, apex of fore tibia and apexes of all fore tarsal segments darkened with brown, first fore tarsal segment from two-thirds to five-sixths as long as second segment; middle and hind legs white, femora not (or very faintly) shaded with red-brown in the middle; wings hyaline, stigmatic area washed with very light red stain, anterior veins and all crossveins of fore wing yellow-brown, those of hind wing hyaline; posterior margin of hind wing slightly darkened with brown. Abdomen white, each of tergites 1–9 with a narrow, black crossline at posterior margin, spiracular markings absent, apical three tergites shaded with faint tan on meson; genitalia, fig. 351, white; caudal filaments entirely white.

Known only from Illinois.

Illinois Records. — AROMA PARK: July 8, 1948, Ross & Burks, 1 ♂; Aug. 6, 1947, Burks & Sanderson, 1 ♂. KANKAKEE: at light, July 9, 1948, Ross & Burks, 3 ♂. MOMENCE: at light, June 22, 1938, Ross & Burks, 6 ♂; June 24, 1939, Burks & Ayars, 23 ♂. WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 10 ♂.

PULCHELLUM Group

23. *Stenonema integrum* (McDunnough)

Heptagenia (Ecdyonurus?) integer McDunnough (1924*a*:9).
Stenonema bellum Traver (1933*a*:202). New synonymy.
Stenonema wabasha Daggy (1945:378). New synonymy.

The concept of *integrum* followed here is derived entirely from a study of the holotype of the species.

MALE.—Length of body 5–7 mm., of fore wing 6–8 mm. Head chalky white, vertex stained with pale yellow, a pair of submedian, light brown dots between compound eyes; each antenna white, flagellum slightly darkened with gray. Pronotum pale yellow, sometimes with a lunate, black streak on either side; meso- and metanotum chalky white, with clay-colored shading along outer parapsides of mesonotum and just dorsal to fore wing bases; pleura and sternum chalky white, occasionally with pale yellow-brown shading on each pleuron near mesocoxa. Fore leg pale yellow, dark brown at apex of tibia and at apexes of tarsal segments, first tarsal segment three-fifths as long as second; middle and hind legs white; each femur of all legs with a prominent, red-brown crossband in middle and at apex, each middle and hind tibia with a subbasal, red-brown spot; wings hyaline, stigmatic area stained with brown, outer margin of hind wing shaded with brown, veins of fore wing a faint yellow-brown, crossveins dark brown, veins and crossveins of hind wing hyaline. Abdomen chalky white, each tergite 1–9 with a narrow, black crossline at posterior margin, those on tergites 8 and 9 often interrupted on the meson; a longitudinal, dark gray line on meson of tergites 3 and 6, sometimes also on tergites 2 and 7; in each spiracular area of segments 3–8 an oblique, dark brown streak present, occasionally these markings becoming obsolete on anterior and posterior segments but always persisting on at least segments 5 and 6; genitalia, fig. 352, white; caudal filaments white, articulations dark red-brown.

Known from Georgia, Illinois, Indiana, Kansas, Kentucky, Michigan, Minnesota, Missouri, and North Carolina.

Illinois Records.—Adult specimens, collected June 7 to August 27, are from Alton, Aroma Park, Dixon, East Dubuque, Elizabethtown, Foster (Mississippi River), Freeport, Fort Kaskaskia State Park, Kankakee, Keithsburg, Momence, Monmouth, Monticello, Oregon, Poplar Bluff, Prophetstown, Quincy, Rockton, Shawneetown, Urbana, and Wilmington.

24. *Stenonema nepotellum* (McDunnough)

Ecdyonurus nepotellus McDunnough (1933*a*:20).

Although the nymphs of this species and those of *rubromaculatum* are, as pointed out by McDunnough (1933*a*:20), quite different, the adults of the two species are very similar. Freshly collected, dry specimens of the adult males can, however, be separated by color characters.

MALE.—Length of body 8–9 mm., of fore wing 8–11 mm. Face below antennal sockets light yellow, vertex yellow, shaded with orange-brown; eyes in life pearl-gray; each antennal scape orange-brown, pedicel tan, flagellum tan at base, hyaline toward apex. Thoracic notum yellow-brown, mesoscutellum and lateral margins of posterior half of mesonotum white; pleuron pale yellow, with brown shading dorsal to coxae, semimembranous area anterior to fore wing base red-brown; sternum pale yellow, mesofurcisternum shaded with tan. Fore leg pale yellow-brown, apex of tibia and apexes of tarsal segments very dark brown or black, first fore tarsal segment one-half as long as second segment; middle and hind legs pale yellow, each femur of all legs with a median and an apical, red-brown crossband; wings hyaline, basal part of stigmatic area red, entire stigmatic area also stained with light brown; all veins and crossveins of fore wing brown, anterior ones of hind wing brown, posterior ones hyaline; crossveins in bullar area of fore wing not crowded. Abdomen yellow, a black crossline at posterior margins of tergites 1– or 2–7; large spiracular dots present; apical tergites shaded with pinkish brown, almost all of tergite 8 suffused with this color, tergite 10 with narrow, white area at posterior margin; abdominal venter yellow; genitalia, fig. 353, white; caudal filaments white, articulations red-brown.

NYMPH.—Length of body 7–9 mm. Anterior border of head rather truncate, lacking a median, pale spot; large, pale spot on lateral margin of head lateral to each compound eye, this pale spot sometimes divided by a brown crossbar. Pronotum with a broad, pale area at either lateral margin; tarsal claws without ventral denticles. Abdominal dorsum with rather vague color pattern of light and dark spots, tergites 5 and 7 predominantly pale, others mostly dark; gills borne by segments 1–6 truncate at apexes, gills of seventh pair without tracheae; abdominal venter white, each of sternites 2– or 3–8 with a curved, brown crossbar borne near anterior margin, these bars wider and more intensely colored on posterior segments; sternite 9 with a U–shaped, brown mark, the open end directed posteriorly, occasional specimens with basal crossbar of this U–shaped mark faint or obsolete; posterolateral angles of abdominal segments 3–9 spinelike, those borne by segment 9 long and slender; caudal filaments light brown near bases, apically alternating pairs of segments dark and light.

Known from Illinois, Indiana, Ohio, Ontario, Quebec, and Wisconsin.

Illinois Records. — OAKWOOD: July 14, 1939, Burks & Riegel, 1♂; July 30, 1939, Burks & Riegel, 1♂; Aug. 4, 1939, Burks & Riegel, 1♂; Aug. 10–14, 1939, B. D. Burks, 3♂, 3♀, 5 N. SPRING GROVE: June

15, 1938, B. D. Burks, 1♂; Nippersink Creek, June 12–29, 1938, B. D. Burks, 3♂, 11♀, 30 N. ST. CHARLES: at light, June 9, 1948, Burks & Stannard, 1♂. STERLING: June 7, 1939, Burks & Riegel, 1♂.

25. *Stenonema rubromaculatum* (Clemens)

Heptagenia rubromaculata Clemens (1913:256).

MALE.—Length of body 8–9 mm., of fore wing 9–10 mm. Face below antennal sockets white, vertex pinkish yellow except at posterior margin, where it is white; eyes in life pearl-gray; each antennal scape and pedicel light brown, flagellum light yellow. Thoracic notum light clay colored, occasionally tinged with olive-gray; each pleuron white or pale yellow, with a brown spot at base of each coxa, semimembranous area of mesopleuron anterior to base of fore wing and dorsal to spiracle pale flesh color; sternum light yellow; all legs yellow, fore coxa shaded with brown, femur with a median and an apical red-brown band, apex of fore tibia and apical segment of each tarsus shaded with brown; wings hyaline, stigmatic area of fore wing shaded with yellow-brown, basal area suffused with red; all veins and crossveins of fore wing brown, anterior ones of hind wing tan, others hyaline; crossveins near bulla, in fore wing, usually not crowded. Abdomen light yellow or white; fine, black, transverse line at posterior margin of each tergite 1–7, black or dark brown spiracular dots present; meson of tergite 8, all of tergite 9, and all but white, posterior margin of tergite 10 pinkish brown; abdominal venter light yellow to white; genitalia, fig. 354, light yellow to white; caudal filaments white, articulations dark brown.

NYMPH.—Length of body 8–10 mm. Head dark brown, freckled with pale dots, a pair of large, pale spots lateral to each compound eye. Pronotum with a broad, pale area at each lateral margin and, usually, a sublateral, pale spot near either margin; each tarsal claw with two ventral denticles near tip. Abdominal dorsum without conspicuous color pattern, nearly uniform dark brown, sometimes with minute, light-colored spots on meson and near lateral margins of middle and apical tergites; venter white, with variable, dark brown color pattern: usually two pairs of submedian dots on each sternite, as well as a third pair near anterolateral angles, the areas between these dots filled in on some darker specimens to produce a mushroom-like figure on each of sternites 3– or 4–8; sternite 9 usually with lateral and basal margins brown, so as to make a somewhat rectangular pattern; posterolateral angles of segments 3–9 spinelike, those on segment 9 small; caudal filaments brown.

Known from Illinois, Massachusetts, New Brunswick, Nova Scotia, Ontario, Quebec.

Illinois Records. — OAKWOOD: June 5, 1948, Burks & Sanderson, 1♂; June 6, 1925, T. H. Frison, 10♂; June 9, 1926, Frison & Auden, 4♂; July 8, 1946, B. D. Burks, 1♂.

26. *Stenonema rubrum* (McDunnough)

Ecdyonurus ruber McDunnough (1926:192).

MALE.—Length of body 7–8 mm., of fore wing 8–9 mm. Face below level of ocelli white, vertex deep orange-brown; antennae pale yellow; eyes in life pearl-gray. Thoracic pro- and mesonotum red-brown, apex of mesoscutellum white, with a red area just anterior to this; metanotum yellow, with a red stain on meson; semimembranous area of each mesopleuron anterior to base of fore wing and dorsal to spiracle orange-brown, sometimes with a pinkish cast; pleuron pale yellow, except for a pinkish brown stain dorsal to each fore and middle coxa; sternum pale yellow; fore leg yellow-tan, with brown shading in middle and at apex of femur, at apex of tibia, and at apexes of tarsal segments; first tarsal segment three-fifths as long as second segment; middle and hind legs yellow, with red-brown shading in middle and at apex of each femur, and dark brown shading at apexes of tibiae and tarsal segments; wings hyaline, faint pink shading in stigmatic area of each fore wing, humeral cell shaded with dark brown, veins and crossveins orange-brown, no crowding of crossveins at bulla. Abdomen light yellow, a rather broad, dark, orange-brown crossband at posterior margin of each tergite 1–7, large spiracular dots present; apical tergites bright orange-brown with, usually, red shading overlying ground color; abdominal venter light yellow; genitalia, fig. 355, pale yellow; caudal filaments pale yellow or white, articulations dark brown.

NYMPH.—Length of body 8–9 mm. Each tarsal claw with two minute denticles on ventral side near apex. Abdominal gills borne by segments 1–6 truncate at apexes, gills of seventh pair without tracheae; abdominal tergites usually uniformly brown, sometimes tergites with median, lighter spots faintly indicated; abdominal sternum white, sternite 8 with a median, dark brown spot at anterior margin and sternite 9 with a median, U–shaped, dark brown mark; caudal filaments uniformly tan in basal and middle areas, but usually with alternating pairs of light and dark segments toward apexes.

Known from Connecticut, Georgia, Illinois, New York, Ontario, and Quebec.

Illinois Records.—MOMENCE: May 26, 1936, H. H. Ross, 1 ♂; June 15, 1938, Ross & Burks, 1 ♂. WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 5 ♂.

27. *Stenonema pulchellum* (Walsh)

Palingenia pulchella Walsh (1862:375).

The male lectotype of this species, now in the Museum of Comparative Zoology, is considerably bleached, due probably to exposure to sunlight sometime in the past, and the genitalia are missing. The remaining parts of this specimen, however, agree well with recently collected material from near the type locality. Also in the M.C.Z. is another male specimen, taken by Walsh at Rock Island in 1863 and identified by him as of this species. This specimen is in good condition and unquestionably agrees with specimens at present being identified as of this species. Specimens collected very early in the season are very large and deep yellow in color; specimens taken in midsummer are smaller and predominately white.

MALE.—Length of body 6–9 mm., of fore wing 8–11 mm. Face below antennal sockets white, vertex yellow, shaded with tan; each antennal scape tan, pedicel white, flagellum faintly gray in basal part; eyes in life pearl-gray. Dorsum of thorax blackish brown, meson of mesoscutellum with a white area, this area usually extending anteriorly to ends of outer parapsides and along lateral scutellar ridge toward wing bases; metanotum with broad, white area on meson; pleuron mostly tan, white, or faint pink on semimembranous area anterior to fore wing base; mesosternum tan, metasternum white; front leg light tan, apexes of tibia and tarsal segments dark brown, first tarsal segment three-fifths as long as second; middle and hind legs white; each femur of all legs with a median and an apical red-brown band; wings hyaline, pale brown stain in stigmatic area; fore wing with dark brown shading

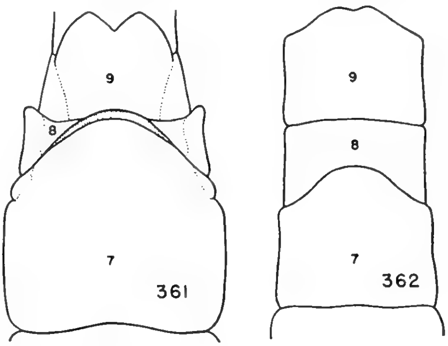


Fig. 361. — *Epeorus namatus*, terminal abdominal sternites of female.

Fig. 362.—*Heptagenia diabasia*, terminal abdominal sternites of female.

at base; longitudinal veins of fore wing yellow-brown, crossveins dark brown; veins and crossveins in costal area of hind wing light yellow, others hyaline. Abdominal segments white, a narrow, black or dark red-brown crossline at posterior margin of each tergite 1–7; dark spiracular dots present; terminal three abdominal tergites bright orange-brown, sometimes with pink suffusion also; genitalia, fig. 356, white; caudal filaments white, articulations dark red-brown.

NYMPH.—Length of body 7–9 mm. Head anterior to eyes, and on vertex between eyes, dark brown, with numerous pale, freckle-like dots, large, pale spot lateral to each compound eye and, on posterior margin of head, at inner eye margins. Pronotum with two or three large, pale spots near either lateral margin; each tarsal claw with two minute denticles; gills borne by abdominal segments 1–6 truncate at apexes, gills of seventh pair without tracheae; abdominal tergites 6, 8, and 10 almost entirely dark brown, tergites 1–5 white, with brown markings, tergite 7 brown near lateral margins and on meson, white elsewhere, and tergite 9 brown with large, submedian white areas; abdominal sternites 1–8 entirely white, sternite 9 white, with longitudinal, brown mark near either lateral margin, also sometimes with median, brown spot at anterior margin; posterolateral angles of segments 7 and 8 produced as spines, these angles of segment 9 slightly produced, spines obsolescent; caudal filaments brown in basal half, apically alternating pairs of segments dark and light.

Known from Illinois, Indiana, Iowa, New York, Ontario, and Wisconsin.

Illinois Records.—Adult specimens, collected April 24 to August 13, are from Aroma Park, Aurora, Dixon, Elizabethtown, Erie, Havana, Kankakee, Keithsburg, Milan, Momence, Mount Carmel, New Boston, Oakwood, Oregon, Prophetstown, Rockford, Rock Island, St. Charles, Savanna, Shawneetown, Sterling, White Heath, Wichert, and Wilmington.

42. *HEPTAGENIA* Walsh

Heptagenia Walsh (1863:197).

In the males of this important and widely distributed genus, the compound eyes are large, but are not contiguous on the meson, except in the *lucidipennis* group of species; each fore leg is slightly longer than the body, the fore tarsus is from one and one-quarter to one and one-half times as long as the fore tibia, and the first tarsal segment varies from one-fifth to nearly one-half as long as the second tarsal segment. In both sexes, the wing venation is typical for the family, fig. 318, with the costal crossveins in the basal area usually well developed and the stigmatic crossveins not, or sometimes very slightly, anastomosed; in the hind wing, vein M_2 diverges from M_1 slightly basad of the center of the wing. In the male genitalia, the forceps are four-segmented, the second segment being as long as or longer than the two apical segments combined; the penis lobes, figs. 363–380, are fused on the meson two-thirds the distance from the base to the apex, each lobe typically bears spines or teeth, and a single posterolateral spine often is present on each penis lobe. The posterior margin of the terminal abdominal sternite in the females, fig. 362, is either evenly rounded from side to side or has a small median indentation.

In the nymphs, figs. 383–385, the frontal margin of the head is entire; the apical segment of the maxillary palp is relatively slender, with the apex acute, bears a dense row of hair along the outer margin, and lacks pectinate spines; the crown of each galea-lacinia of the maxilla bears a row of small, hooklike teeth; the apical segment of each labial palp is extremely broad, with the apex truncate; the outer margin bears a dense row of hair, below which is a bank of pectinate spines. In the legs, the femora are only moderately flattened, and the posterior margin of each bears a dense row of hair and a sparse row of short, stout spines; the tarsal claws are long, slightly enlarged at the bases, and are either edentate or have a short row of ventral denticles; there may be a prominent ventral tooth in the basal area of each claw. Gills are borne by abdominal segments 1–7, with all gills of the same form but not same size. Each gill, fig. 325, is composed of a dorsal, platelike element and a ventral, filamentous tuft; in some species this tuft of filaments is greatly reduced or wanting on the gills of segment 7. None of the gills is extended beneath the abdominal venter. The three caudal filaments are equal in length or the median one is slightly the longer. Each of the cerci bears fairly prominent setae on the mesal side in the basal area; otherwise the cerci are virtually bare.

The nymphs of this genus occur under stones and among debris in shallow water near the banks of brooks, creeks, and rivers. They cannot be reared through to maturity in stagnant water.

The species *Heptagenia quebecensis* (Provancher) (1876:267; 1878:127) is shown by an examination of the lectotype, now in the Provincial Museum in Quebec, to have been based on a female specimen of the genus *Ephemerella*. This female specimen cannot be identified specifically.

The species *Heptagenia manifesta* (Eaton) remains unknown. It was originally the species identified as *Baetis debilis* Walker by Walsh (1862:371), using specimens collected at Rock Island, Illinois. Eaton (1871:130) transferred this species to the genus *Siphlurus* without seeing specimens of Walsh's material. Later, Eaton (1885:253) transferred it to *Rhithrogena* and renamed it *manifesta* (as he considered it to have been originally misidentified as Walker's species). There is no evidence that Eaton ever saw Walsh's material. I have been unable to locate specimens determined as *debilis* by Walsh; there is none in the Hagen collection at the Museum of Comparative Zoology.

Reliable characteristics for the specific separation of the females of this genus have not yet been found.

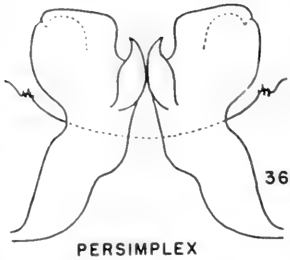
KEY TO SPECIES

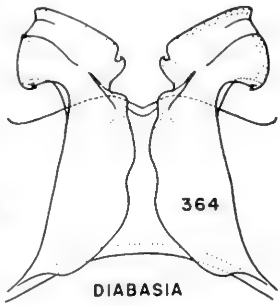
ADULT MALES

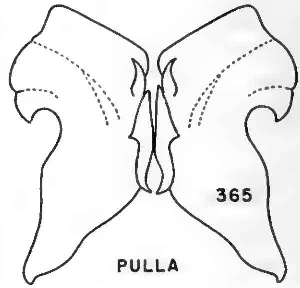
1. Genitalia of the *persimplex* type, fig. 363: penis lobes short, somewhat rounded at apexes; discal, posterolateral, and subapical spines absent....**1. persimplex**
   Genitalia not of the *persimplex* type, but of the types shown in figs. 364, 365, 368, 372, or 374..............2
2. Genitalia of the *elegantula* type, fig. 364: each penis lobe semiquadrate, and with a prominent, medioapical, hooked spine ....**2. diabasia**
   Genitalia not of the *elegantula* type, but of the types shown in figs. 365, 368, 372, or 374........................3
3. Genitalia of the *pulla* type, fig. 365: penis lobes stout, divergent; each lobe bearing two stout, median spines and a minute, posterolateral spine..**3. pulla**
   Genitalia not of the *pulla* type, but of the types shown in figs. 368, 372, or 374..4
4. Genitalia of the *flavescens* type, figs. 366–369: penis lobes relatively long and slender, with apexes strongly diverged 5
   Genitalia not of the *flavescens* type, but of the types shown in figs. 372 or 374.. 8
5. Abdominal segments white or faintly smoky, each tergite with a narrow, black, transverse line at posterior margin and a pair of oblique, sublateral, black lines...........**4. marginalis**
   Abdominal segments light yellow or golden tan, tergites shaded on broad, median area with red-brown or orange-brown............................6
6. Median spines of penis lobes slender throughout, fig. 367.......**5. patoka**
   Median spines of penis lobes broadened at apexes, figs. 368, 369.............7
7. Basal costal crossveins extremely weak or entirely wanting......**6. flavescens**
   Basal costal crossveins well developed, black.................**7. cruentata**
8. Genitalia of the *lucidipennis* type, figs. 370–373: each penis lobe short and broad, with a heavy, usually recurved lobe at both apical and lateral margins and bearing a large, spinulose, mesal spine; discal spines sometimes present 9
   Genitalia of the *maculipennis* type, figs. 374–380: each penis lobe relatively elongate and narrow, and bearing one subapical, one posterolateral, one mesal, and always at least one discal spine..12
9. Penis lobes without discal spines, fig. 370 ....**8. rusticalis**
   Each penis lobe with at least one discal spine, figs. 371–373...............10
10. Abdominal tergites uniformly shaded with light orange-brown; fore wing not over 6 mm. long..........**9. inconspicua**
    Abdominal tergites shaded with tan, red-brown, or dark orange, but with prominent, light yellow spots or stripes on meson of basal and middle tergites; fore wing at least 7 mm. long......11
11. Apex of each penis lobe with a large, rounded, projecting lobule, and apical margin of forceps base with a pair of obscure, sublateral projections, fig. 372 ....**10. lucidipennis**
    Apex of each penis lobe with a broad, recurved lobule, and apical margin of forceps base with a pair of conspicuous, sublateral projections, fig. 373....... ....**11. perfida**
12. Costal and subcostal crossveins stained with brown, but this dark staining not extending to membrane surrounding these crossveins......**12. umbratica**
    Costal and subcostal crossveins dark, and with this shading extending to membrane surrounding these crossveins, fig. 318.........................13
13. Discal spines of penis lobes extremely long, fig. 375; abdominal tergites usually entirely dark brown...........**13. hebe**
    Discal spines of penis lobes shorter, figs. 376–380; basal and middle abdominal tergites partly or almost entirely white 14
14. Basal and middle abdominal tergites entirely white, without darker markings ....**14. maculipennis**
    Basal and middle abdominal tergites white, with posterior margins marked with black, or these tergites white or yellow, with dark red-brown spots near lateral margins...................15
15. Basal and middle abdominal tergites white, with a narrow, black, transverse line at posterior margin of each tergite 16
    Basal and middle abdominal tergites white or yellow, with a pair of large, dark brown, triangular marks on each tergite at posterolateral angles......17
16. Thorax dark brown dorsally and on each pleuron..................**15. walshi**
    Thorax entirely light yellow or white.... ....**16. juno**
17. Fore femur with a median, reddish streak and a black mark at apex; mesonotum shaded with dark brown on meson only near anterior margin....**17. minerva**
    Fore femur with a black mark at apex only; mesonotum with a broad, dark brown-shaded area on meson which extends from anterior to posterior margin.... ....**18. aphrodite**

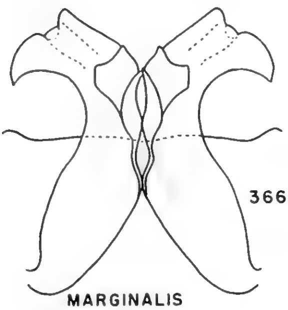
MATURE NYMPHS

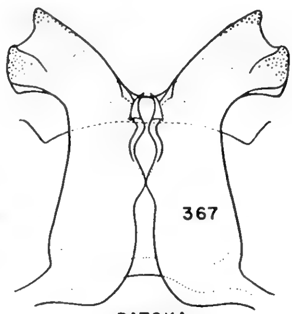
1. Each gill borne by seventh abdominal segment with a well-developed ventral, filamentous tuft; each tarsal claw with a large basal tooth, but with ventral denticles absent, fig. 382...........2
   Each gill borne by seventh abdominal

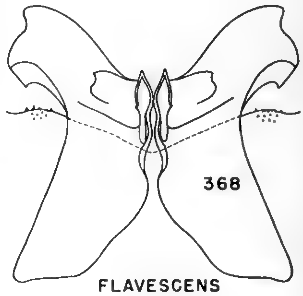


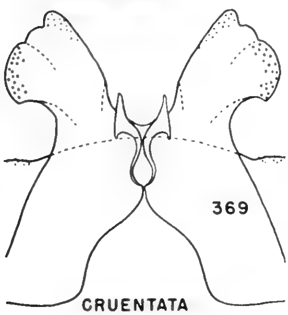


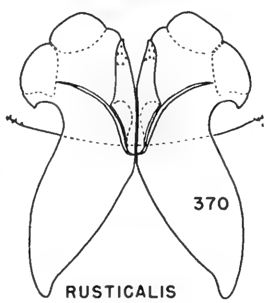


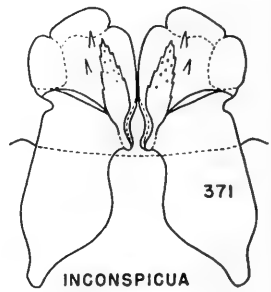


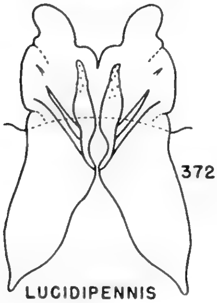


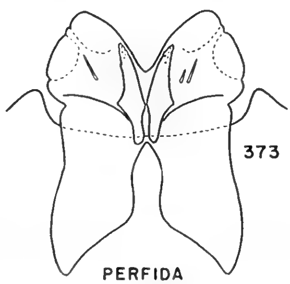












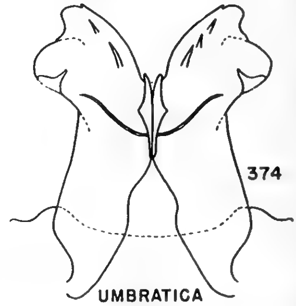
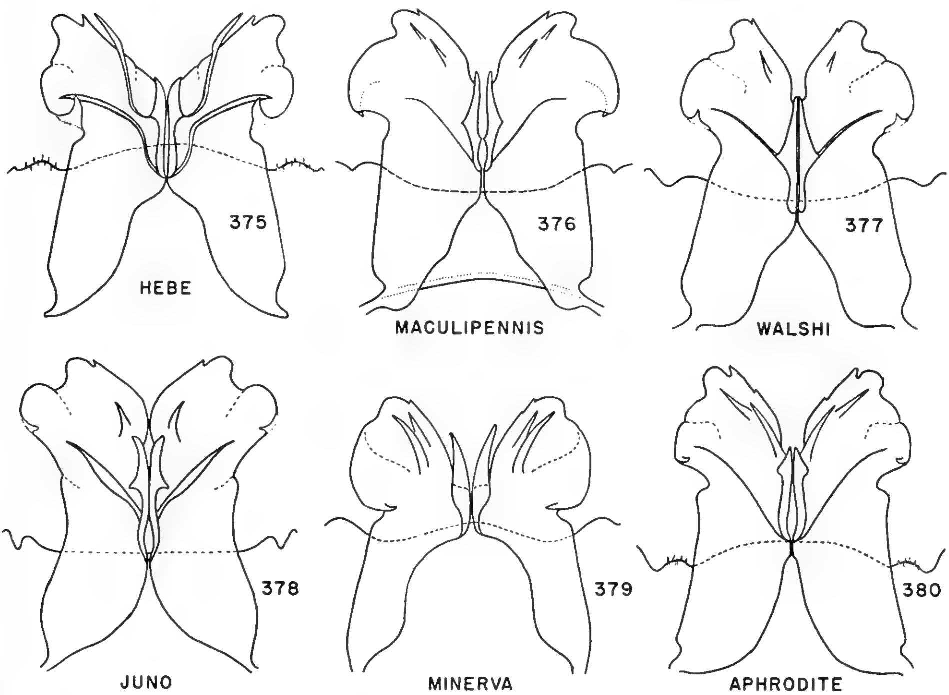


Fig. 363.—*Heptagenia persimplex,* male genitalia.
Fig. 364.—*Heptagenia diabasia,* male genitalia.
Fig. 365.—*Heptagenia pulla,* male genitalia.
Fig. 366.—*Heptagenia marginalis,* male genitalia.
Fig. 367.—*Heptagenia patoka,* male genitalia.
Fig. 368.—*Heptagenia flavescens,* male genitalia.
Fig. 369.—*Heptagenia cruentata,* male genitalia.
Fig. 370.—*Heptagenia rusticalis,* male genitalia.
Fig. 371.—*Heptagenia inconspicua,* male genitalia.
Fig. 372.—*Heptagenia lucidipennis,* male genitalia.
Fig. 373.—*Heptagenia perfida,* male genitalia.
Fig. 374.—*Heptagenia umbratica,* male genitalia.

segment lacking ventral, filamentous tuft; each tarsal claw with a prominent basal tooth and a row of minute ventral denticles, fig. 381 5

2. Venter of abdomen light yellow to white, and with a longitudinal, dark brown bar extending the length of the abdomen near either lateral margin 3
   Venter of abdomen light yellow to white, and entirely without darker markings, or with dark shading present only at posterior margin of ninth sternite . . 4
3. Abdominal tergites almost entirely dark brown, with only a pair of submedian and a pair of anterolateral, small, white marks on each tergite, fig. 383 . . . . **2. diabasia**
   Abdominal tergites with dark brown shading more restricted: submedian and lateral marks relatively large and round, first tergite almost entirely white, fourth and eighth each with a large, median, white mark . . . **3. pulla**
4. Venter of abdomen entirely white or light yellow, without darker markings . . . . **4. marginalis**
   Posterior margin of ninth sternite with a broad, dark brown border . . . . **6. flavescens**
5. Caudal filaments entirely white, articulations not darkened . . . **10. lucidipennis**
   Caudal filaments white, with articulations brown, or these filaments tan, gray, or brown 6
6. Caudal filaments white, with articulations brown 7
   Caudal filaments tan, brown, or gray . . . 8
7. Abdominal sternites 8 and 9 each with a short, transverse, brown mark on meson of anterior margin . . . . **16. juno**



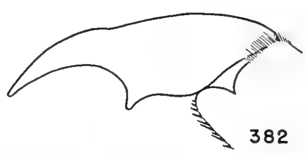


Fig. 375.—*Heptagenia hebe*, male genitalia.
Fig. 376. — *Heptagenia maculipennis*, male genitalia.
Fig. 377.—*Heptagenia walshi*, male genitalia.
Fig. 378.—*Heptagenia juno*, male genitalia.
Fig. 379.—*Heptagenia minerva*, male genitalia.
Fig. 380.—*Heptagenia aphrodite*, male genitalia.
Fig. 381.—*Heptagenia maculipennis*, middle tarsal claw of mature nymph.
Fig. 382.—*Heptagenia diabasia*, middle tarsal claw of mature nymph.

Abdominal sternites 8 and 9 usually entirely without brown, median marks at anterior margins, occasionally a small, median, brown dot at anterior margin of sternite 9 .... **14. maculipennis**

8. Dorsum of abdomen uniformly dark brown, entirely or virtually without light markings; caudal filaments gray .... **12. umbratica**

Dorsum of abdomen brown, with well-marked pattern of fairly large, white spots; caudal filaments tan or brown . . 9

9. Abdominal sternites 1–8 uniformly light tan, sternite 9 with lateral and posterior margins shaded with dark brown .... **18. aphrodite**

Abdominal sternum white, with brown markings on sternites 2–9 10

10. Abdominal sternites 2–8 each with an irregular, brown crossband at anterior margin .... **11. perfida**

Abdominal sternites 2–8 each with a pair of fairly large, sublateral, brown spots .... **13. hebe**

PERSIMPLEX Group

1. *Heptagenia persimplex* McDunnough

Heptagenia persimplex McDunnough (1929:179).

This species often has been confused with *Anepeorus simplex*. As McDunnough has pointed out (1929:179), even Walsh's type material of *simplex* included specimens of *persimplex*. I have seen specimens of *persimplex* in several collections identified as *simplex*.

MALE.—Length of body 6–7 mm., of fore wing 7–8 mm. Compound eyes separated on meson by a space as wide as one compound eye; head very light yellow-brown; eyes in life light gray. Thorax very light cream color, almost white; legs light yellow, with apexes of tibiae and tarsi darkened with dirty tan; fore tibia as long as fore femur, fore tarsus one and one-third times as long as tibia, first tarsal segment one-third to almost one-half as long as second segment; wings hyaline, with veins and crossveins in costal half of fore wing light brown. Abdomen light cream colored, without darker markings; genitalia, fig. 363, light cream colored, forceps segments 3 and 4 of the same length, and their combined lengths slightly less than one-half as great as length of second segment; caudal filaments almost white.

NYMPH.—Unknown.

This species is known from Illinois, Iowa, Missouri, Nebraska, and Ohio.

Illinois Records. — HAVANA: Matanzas Beach, June 20, 1947, Ross & Stannard, 1 ♂; at light, June 25, 1898, C. A. Hart, 1 ♂. MOUNT CARMEL: June 18, 1947, B. D. Burks, 1 ♂. QUINCY: Mississippi River, June 7, 1939, Burks & Riegel, 1 ♂; July 6, 1939, Mohr & Riegel, 2 ♂. SHAWNEETOWN: at light, June 21, 1927, Frison & Glasgow, 3 ♂.

ELEGANTULA Group

2. *Heptagenia diabasia* Burks

Heptagenia diabasia Burks (1946:610).

MALE.—Length of body 9–13 mm., of fore wing 8–12 mm. Compound eyes pearl-gray, with a faint, yellow-green tint, the two eyes separated on meson by a space almost as wide as median ocellus; head yellow, shaded with light red on vertex and with a minute, black dot at base of frontal shelf at either eye margin. Thorax yellow, with tan shading on dorsal meson; legs yellow, with red-brown shading at apexes of middle and hind femora and at middle and apex of fore femur; all tibiae shaded at bases and apexes with brown; fore tibia slightly longer than fore femur, fore tarsus one and one-fifth times as long as tibia, first tarsal segment one-fourth as long as second; wings hyaline, with veins and crossveins brown, and crossveins in costal and subcostal interspaces slightly thickened; stigmatic crossveins of fore wing occasionally partly anastomosed. Abdomen yellow, with a longitudinal, black spiracular line on either side, a narrow, black, transverse line at posterior margin of each tergite, and apical three tergites shaded with golden- or carmine-brown; genital forceps light yellow, penis lobes, fig. 364, tan; third forceps segment one-third longer than fourth, second segment four times as long as third; caudal filaments white, with brown articulations.

FEMALE.—Length of body 9–14 mm., of fore wing 10–15 mm. Color lighter than in male, almost white; black markings of head and abdomen as in male; apical abdominal tergites without brown shading; apical abdominal sternites shaped as shown in fig. 362; caudal filaments white, articulations brown.

NYMPH.—Fig. 383. Length of body 8–15 mm. Each tarsal claw with large basal tooth, apical denticles wanting. Dorsum of

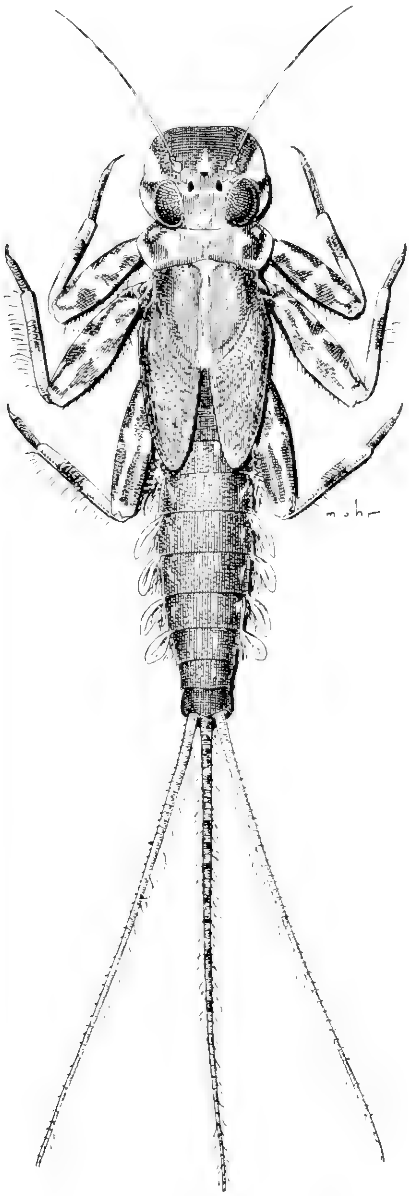


Fig. 383. — *Heptagenia diabasia*, mature nymph, dorsal aspect.

abdomen uniformly dark brown, with minute, submedian and anterolateral, light spots on tergites; abdominal sternites white, with a wide, brown, sublateral, longitudinal band near either lateral margin; gills, fig. 325, relatively slender, with filamentous tuft prominent and bushy, gills borne by seventh segment with well-developed, filamentous tuft; caudal filaments rather vaguely marked with alternating, narrow, dark and light color bands.

Known from Illinois, Iowa, and Minnesota.

Illinois Records.—CAIRO: July 12, 1948, L. J. Stannard, 1 ♂. DIXON: June 25, 1947, B. D. Burks, 1 ♂. EAST DUBUQUE: July 3, 1946, Burks & Sanderson, 1 ♀. FREEPORT: June 10–11, 1948, Burks, Stannard, & Smith, 1 ♂. HAVANA: June 17, 1909, 1 ♀; June 1, 1933, at light, C. O. Mohr, 1 ♂; White Oak Creek, near Matanzas Lake, June 2, 1940, B. D. Burks, 4 ♂, 1 ♀; Matanzas Beach, June 25, 1947, Ross & Stannard, 5 ♂, 2 ♀. HOMER: July 4, 1943, H. H. Ross, 1 ♂. HOMER PARK: June 30, 1925, T. H. Frison, 1 ♀. JERSEYVILLE: June 2, 1938, T. H. Frison, 1 ♂. KANKAKEE: Aug. 3, 1938, Burks & Boesel, 1 ♂. KAPPA: June 22, 1943, H. H. Ross, 1 ♂. MAHOMET: June 8, 1940, H. H. Ross, 1 ♂. MAZON: Mazon Creek, June 25–27, 1938, B. D. Burks, 3 ♂, 2 ♀. MILAN: Rock River, June 4, 1940, Mohr & Burks, 5 ♂, 2 ♀. MOMENCE: June 22, 1938, Ross & Burks, 1 ♂. MOUNT CARMEL: June 18, 1947, B. D. Burks, 1 ♂, 1 ♀. MUNCIE: May 22, 1942, Ross & Burks, 1 ♂. PEORIA: June 23, 1938, F. F. Hasbrouck, 1 ♂. ROCKFORD: June 12, 1938, at light, Ross & Burks, 1 ♂; June 29, 1938, at light, B. D. Burks, 1 ♂; June 11, 1948, Burks, Stannard, & Smith, 13 ♂, 1 ♀. ST. JOSEPH: July 29, 1922, T. H. Frison, 1 ♀.

PULLA Group

3. *Heptagenia pulla* (Clemens)

Ecdyurus grandis Clemens (1913:147). Nomen nudum.
Ecdyurus pullus Clemens (1913:330).

MALE.—Length of body 10–11 mm., of fore wing 11–12 mm. Head light yellow, with a transverse, brown mark crossing face below antennal bases, and vertex shaded with brown. Pronotum dark brown; mesonotum and thoracic sternum light red-brown, pleura yellow. Legs yellow, with apexes of femora and bases of tibiae red-brown, tarsi with articulations stained with red-brown; wings hyaline, veins and crossveins of each fore wing brown. Abdomen yellow, tergites shaded with red-brown on broad, longitudinal, median area, this dark area interrupted by a narrow, yellow, median line and a pair of lunate, submesal marks on each tergite; posterior margins of tergites shaded with dark brown; sternites yellow, with a broad, light red, shaded area at posterior margin of each; genitalia, fig. 365, yellow, shaded with red at apexes; caudal filaments almost white, articulations brown.

Nymph.—Length of body 11–13 mm. Head dark brown, with a white area on either side between compound eye and lateral margin of head. Each tarsal claw with a large basal tooth, ventral denticles wanting. Dorsum of abdomen mostly dark brown, with prominent, white markings: tergites 1 and 2 mostly white, tergites 4 and 8 each with a large, quadrate, white spot on meson at posterior margin, other tergites each with a pair of submesal and a pair of posterolateral, round, white spots; gills relatively small and oval, with filamentous, ventral tufts well developed and present in all gills; caudal filaments alternately brown and white throughout.

Known from Manitoba, New York, Ohio, and Ontario.

FLAVESCENS Group

4. *Heptagenia marginalis* Banks

Heptagenia marginalis Banks (1910:198).

Male.—Length of body and of fore wing 9–10 mm. Head tan, with black markings along margin of frontal shelf, just below each antennal base, at either side of median ocellus, on vertex just posterior to each lateral ocellus, and along posterior margin of head; compound eyes separated on meson by a space as wide as one lateral ocellus. Thorax cream colored, with narrow, black lines on pleura; legs light yellow, almost white, each femur with a prominent, dark brown ring at apex, fore tibia and fore tarsal segments shaded with brown at apex; first fore tarsal segment one-sixth as long as second; wings hyaline, with veins and crossveins brown. Abdomen white, each tergite with a narrow, black band across posterior margin and a pair of oblique, sublateral, black marks; genitalia, fig. 366, white; caudal filaments very light gray, with articulations slightly darker.

Female.—Length of body 9–10 mm., of fore wing 10–11 mm. Color pattern very similar to that of male, as all black marks of male are apparent in female, ground color of body entirely white; caudal filaments white.

Nymph.—Length of body 10–11 mm. Head light brown, with small, white spots. Each tarsal claw with basal tooth, but ventral denticles wanting. Dorsum of abdomen light brown, with a narrow, black crossband at posterior margin and a pair of sublateral, black streaks on each tergite; tergite 1 mostly white, following tergites each with a pair of sublateral, round, white spots; tergite 8 with a large, median, white blotch; abdominal sternum white to cream colored; gills semiovate, with fibrillar ventral tuft well developed on all segments;

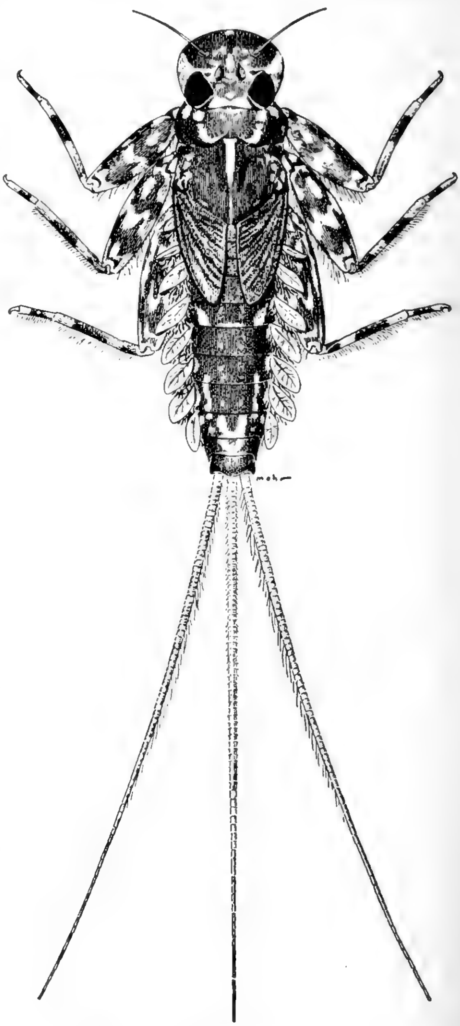


Fig. 384. — *Heptagenia flavescens,* mature nymph, dorsal aspect.

caudal filaments with alternating brown and white banding.

Known from New York, North Carolina, Ohio, Pennsylvania, Virginia, and West Virginia.

5. *Heptagenia patoka* Burks

Heptagenia patoka Burks (1946:612).

Male.—Length of body and of fore wing 9 mm. Head tan; compound eyes separated on meson by a space as wide as lateral ocellus. Thorax brown, pleura yellow; each fore leg light tan, fore femur with red-brown shading in middle and at apex, brown shading at apex of fore tibia and at articulations of tarsus, first fore tarsal segment one-third as long as second; wings hyaline, veins and crossveins brown, with crossveins in costal and subcostal interspaces of fore wing broader and darker than others. Abdomen red-brown on dorsum, light yellowish tan on venter; tergites 1–3 each with a pair of yellow, submesal, round spots near anterior margin, following tergites with these spots more elongate and progressively darker and more vague, becoming scarcely distinguishable from dark ground color; a faint, median, yellow line present on tergites 1–5; sternites unmarked; apical three segments shaded with tan; genitalia, fig. 367, tan, with brown shading at edges; caudal filaments tan, articulations brown.

Nymph.—Unknown.

The species is known only from Illinois.

Illinois Record.—Patoka: July 19, 1945, Ross & Sanderson, 1 ♂.

6. *Heptagenia flavescens* (Walsh)

Palingenia flavescens Walsh (1862:373).

Male.—Length of body 8–11 mm., of fore wing 10–13 mm. Head yellow, vertex shaded with tan; compound eyes grayish yellow-green, the two eyes separated on meson by a space slightly wider than a lateral ocellus. Thorax mostly red-tan, with pleura mostly yellow. Legs yellow, each fore femur shaded with red-brown in middle and at apex, fore tibia and tarsal segments shaded with gray-brown at apexes, first tarsal segment one-fifth as long as second segment; middle and hind femora shaded with brown at apexes; wings hyaline, veins and crossveins brown, those of hind wing slightly lighter brown, basal costal crossveins of fore wing weak or virtually wanting. Abdomen yellow, with a broad, median, gray-brown band on tergites 1–7, a narrow, dark gray, transverse band at posterior margin of tergites 1–7 or –8; apical three tergites orange-tan, apical two sternites shaded with orange-tan; genitalia, fig. 368, with forceps tan or yellow and penis lobes rose-pink; caudal filaments white or pale yellow, articulations brown or tan.

Female.—Length of body 9–12 mm., of fore wing 11–15 mm. Head and thorax entirely yellow, or mesonotum faintly stained with tan; legs as in male; abdomen yellow, without dark, dorsal shading or with median, dorsal area faintly tan stained, a narrow, transverse, gray line present at posterior margins of tergites 1–8 or –9; terminal abdominal sternite more deeply cleft on meson of posterior margin than in *diabasia*; caudal filaments white.

Nymph.—Fig. 384. Length of body 12–16 mm. Head mostly dark brown, with a prominent, triangular, white mark extending from anterolateral angle of each compound eye to lateral margin of head. Thorax brown, with small, irregular, white spots, each tarsal claw with a prominent basal tooth, but no ventral denticles. Abdomen dorsally dark brown with, typically, a pair of submedian, a pair of sublateral, and a pair of anterolateral, white spots on each of tergites 2–7; tergite 1 mostly white; submedian spots of tergite 4 and of 5 enlarged so as to coalesce at posterior margin; tergites 8 and 9 each white in median area, brown laterally; tergite 10 usually entirely brown; gills borne by seventh segment with well-developed ventral tuft of filaments; entire venter white, except that posterior margin of sternite 9 has a brown border; caudal filaments alternately banded brown and white.

Known from Georgia, Iowa, Illinois, Kansas, Manitoba, Minnesota, and Texas.

Illinois Records.—Billett: May 6, 1942, Burks & Mohr, 2 ♀. Calvin: May 26, 1942, Mohr & Burks, 1 ♂. Dixon: June 27, 1935, DeLong & Ross, 1 ♂. Freeport: June 10, 1948, Burks & Stannard, 1 ♂. Havana: May 18, 1894, Hart, 1 ♂. Mount Carmel: April 22, 1946, Mohr & Burks, 2 ♂, 1 ♀. Oregon: July 9, 1925, T. H. Frison, 14 ♂, 17 ♀; July 13, 1926, Frison & Hayes, 2 ♂; July 19, 1927, Frison & Glasgow, 3 ♂. Prophetstown: July 19, 1927, Frison & Glasgow, 1 ♂; Rock River, June 26, 1947, B. D. Burks, 1 ♂; July 24–25, 1947, Burks & Sanderson, 1 ♂. QUINCY: June 7, 1939, Burks & Riegel, 1 ♂. ROCKFORD: May 22, 1941, Ross & Burks, 1 ♂, 1 ♀; May 15, 1942, Ross & Burks, 1 ♂. ROCK ISLAND: 12 ♂, 4 ♀ (Walsh 1862:374). ROCKTON: Rock River, June 25, 1947, B. D. Burks, 1 ♂. SHAWNEETOWN: July 14, 1948, Mills & Ross, 1 ♂. STERLING: at light, May 21, 1925, D. H. Thompson, 1 ♂; May 22, 1941, Ross & Burks, 1 ♂.

7. *Heptagenia cruentata* Walsh

Heptagenia cruentata Walsh (1863:205).

The types of this species are lost, but there are a male and female in the collection at the Museum of Comparative Zoology which were determined as of this species by Walsh. They were collected a year after the description was published.

MALE.—Length of body 7–8 mm., of fore wing 9–11 mm. Head usually entirely shaded with red; compound eyes pearl-gray, the two eyes separated on meson by a space slightly narrower than a lateral ocellus. Thorax with notum light red-brown, pleura and sternum deep yellow. Legs yellow, femora and tibiae extensively stained with red, this red shading more intense in middle and at apex of each femur and on basal half of each tibia; tarsi grayed toward apexes; first fore tarsal segment one-fourth as long as second; wings hyaline, with membrane in costal and subcostal interspaces washed with yellow; all longitudinal veins and crossveins in hind wing golden, crossveins dark brown in fore wing, those in costal and subcostal interspaces broadened and darker. Abdomen deep yellow, with a broad, longitudinal, median, red-brown stripe on dorsum, this interrupted on each of tergites 2–8 by a longitudinal, median, yellow line and a pair of lunate, submedian, light streaks; genitalia, fig. 369, with forceps yellow and penis lobes red-tan; caudal filaments light yellow, with articulations light red-brown.

FEMALE.—Length of body 8 mm., of fore wing 10 mm. General color as in male, but yellow of body lighter, and red- and brown-shaded areas less conspicuous; legs colored as in male except that red shading is obscure on tibiae; dorsum of abdomen only lightly shaded with red-tan; posterior margin of terminal abdominal sternite only slightly incised on meson; caudal filaments light yellow, articulations sometimes faintly darkened.

NYMPH.—Unknown.

The species is known from Illinois, Manitoba, and Nebraska.

Illinois Records.—ANNA: at light, July 22, 1938, Burks & Boesel, 1 ♂. DIXON: June 27, 1935, DeLong & Ross, 1 ♂. PROPHETSTOWN: Rock River, July 24–25, 1947, Burks & Sanderson, 5 ♂, 1 ♀; June 26, 1947, B. D. Burks, 1 ♂. QUINCY: June 8, 1939, Burks & Riegel, 11 ♂, 13 ♀; July 13, 1937, Mohr & Burks, 1 ♂, 3 ♀. ROCK ISLAND: 4 ♂, 3 ♀ (Walsh 1863:205); June 7, 1937, Burks & Riegel, 1 ♂. ROCKTON: Rock River, June 25, 1947, B. D. Burks, 4 ♂.

LUCIDIPENNIS Group

8. *Heptagenia rusticalis* McDunnough

Heptagenia rusticalis McDunnough (1931*b*:92).

MALE.—Length of body and of fore wing 5–6 mm. Head yellow on face, shading to brown on vertex; compound eyes contiguous on meson. Dorsum of thorax brown, blending into deep yellow on pleura and sternum; legs dull, deep yellow, femora suffused with brown; wings hyaline, veins and crossveins colorless. Abdominal tergites dull brown, venter deep yellow, anterior tergites each with a faint, longitudinal, median, yellow line and a pair of submesal, longitudinal, yellow streaks; genitalia, fig. 370, smoky yellow; caudal filaments gray.

FEMALE.—Length of body 5–6 mm., of fore wing 6–7 mm. In appearance, similar to male, but head entirely light red-brown; entire thorax dull yellow; abdominal tergites lightly washed with red-brown, sternites yellow; posterior margin of terminal abdominal sternite evenly rounded from side to side; caudal filaments pale yellow.

NYMPH.—Unknown.

The species is known from New York, Ohio, and Quebec.

9. *Heptagenia inconspicua* McDunnough

Heptagenia inconspicua McDunnough (1924*b*:118).

MALE.—Length of body 4–5 mm., of fore wing 5–6 mm. Head tan; compound eyes light gray, contiguous on meson. Thoracic notum dull, light brown, pleura and sternum yellow. Legs yellow, apex of each fore femur and fore tibia, and fore tarsus shaded with dull brown, first fore tarsal segment one-third as long as second; wings hyaline, veins and crossveins colorless. Abdominal tergites shaded with orange- or red-brown, this shading more intense at posterior margins of tergites; genitalia, fig. 371, yellow, apical two forceps segments slightly smoky; caudal filaments white or faint yellow, with basal articulations red-brown.

FEMALE.—Length of body 4–5 mm., of fore wing 6–7 mm. Head tan, stained with orange; legs, thorax, and abdomen colored as in male; posterior margin of terminal abdominal sternite produced on meson, truncate; caudal filaments white.

NYMPH.—Unknown.

This species is known from Illinois, Indiana, Manitoba, Missouri, Ohio, and Wisconsin.

Illinois Records.—DIXON: June 27, 1935, 2 ♂, 2 ♀; at light, June 25, 1947, B. D. Burks, 1 ♂. LAKE GLENDALE: May 16, 1947, B. D. Burks, 1 ♂. OAKWOOD: June 6, 1925, T. H. Frison, 2 ♂; June 9, 1926, T. H. Frison, 6 ♂; June 23, 1948, B. D. Burks, 4 ♂; June 24, 1948, Mills & Ross, 1 ♂. OREGON: July 18, 1927, Frison & Glasgow, 1 ♂. RICHMOND: June 20, 1938, B. D. Burks, 1 ♂; Aug. 15, 1938, Ross & Burks, 3 ♂, 5 ♀. ROCKFORD: June 29, 1938, B. D. Burks, 1 ♂. SOUTH BELOIT: July 2, 1931, Frison, Betten, & Ross, 1 ♂. ST. CHARLES: at light, July 8, 1948, Ross & Burks, 1 ♂, 1 ♀. URBANA: at light, July 5, 1907, 1 ♂; July 8, 1931, H. H. Ross, 1 ♂. WAUKEGAN: Aug. 15, 1938, Ross & Burks, 5 ♂.

10. *Heptagenia lucidipennis* (Clemens)

Ecdyurus lucidipennis Clemens (1913:329).

MALE.—Length of body 6 mm., of fore wing 7 mm. Head with face yellow, shaded with brown, vertex dark brown or red-brown; compound eyes contiguous on meson. Thoracic notum brown, pleura and sternum yellow. Legs yellow, fore femur shaded with brown, first fore tarsal segment one-fourth as long as second; wings hyaline, costa and subcosta of fore wing slightly grayed, other longitudinal veins and all crossveins colorless. Dorsum of abdomen dark brown, venter yellow; each basal tergite with dark-shaded area vaguely interrupted by a lighter, longitudinal, median line and a pair of obscure, submedian streaks; genitalia, fig. 372, yellow; caudal filaments light yellow, almost white, with faint, gray shading in basal halves.

FEMALE.—Length of body 6 mm., of fore wing 8 mm. Color pattern very similar to that of male, but slightly lighter, the yellow areas almost white and the brown areas tan or reddish; caudal filaments white.

NYMPH.—Length of body 7–8 mm. Head as wide as pronotum, dark brown, with numerous small, white spots. Thorax predominantly white, with numerous dark brown spots on dorsum; each tarsal claw with large basal tooth and several ventral denticles. Abdominal dorsum predominantly brown, each tergite typically white along posterior margin, two submedian and two anterolateral, white spots in brown area near anterior margin; gills of anterior segments each with ventral, filamentous tuft well developed; pair of gills on segment 6, each with filamentous tuft small and reduced; pair on segment 7 without ventral, filamentous tufts; caudal filaments white, unmarked.

Known from New York, Ohio, and Ontario.

11. *Heptagenia perfida* McDunnough

Heptagenia perfida McDunnough (1927*b*:301).

MALE.—Length of body 5.5–6.5 mm., of fore wing 6.5–7.5 mm. Head yellow, with red-orange shading; compound eyes bluish gray, contiguous on the meson. Thoracic notum chestnut brown; pleura tan, paling to yellow ventrally, sternum yellow. Legs yellow, apical half of fore femur red-brown, fore tibia and fore tarsus shaded with faint gray; wings hyaline, veins and crossveins colorless except that costa and subcosta of fore wing sometimes show faint, yellow staining. Abdominal tergites a deep, rich brown, with anteromesal area of tergites 2–8 yellow-brown, a longitudinal, median, yellow line and a pair of submedian, yellow streaks often visible within this yellow-brown area; venter yellow; genitalia, fig. 373, yellow, apical margin of forceps base with a pair of sublateral, prominent, setose projections; caudal filaments light yellow, basal articulations brown.

FEMALE.—Length of body 5.5–6.5 mm., of fore wing 7.5–8.5 mm. Head yellow, with

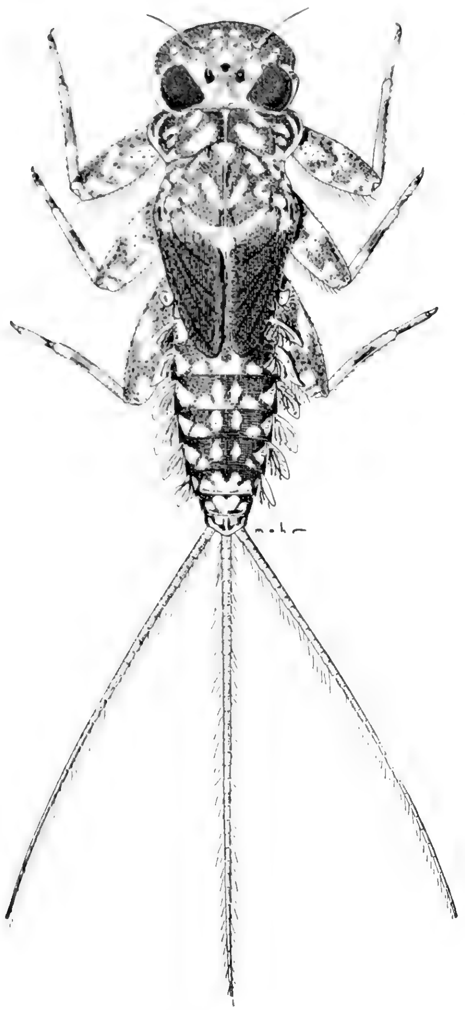


Fig. 385. — *Heptagenia perfida,* mature nymph, dorsal aspect.

orange shading. Thorax dull brown dorsally, light yellow ventrally. Abdomen dull brown dorsally, darker at posterior margins of tergites, sternites light yellow; posterior margin of terminal sternite produced and truncate on meson; caudal filaments light yellow, basal articulations tan.

Nymph.—Fig. 385. Length of body 6–8 mm. Head slightly wider than thorax, dorsal side of head brown, with a pair of submesal, white spots on anterior margin, a second small pair of white spots just posterior to these, three fairly large spots between eyes and posterior to antennal bases, and a white streak extending from anterolateral angle of each compound eye to margin of head. Thorax brown, marked with obscure, paler spots; each tarsal claw with basal tooth virtually wanting and only three to five ventral denticles. Dorsum of abdomen brown, tergites 1–7 each with a pair of submedian, white streaks, usually a pair of small, white dots at posterior margin lateral to submedian streaks, and a pair of posterolateral, white, triangular marks; median area of tergites 8 and 9 each with a large, white blotch; filamentous tuft absent in gills borne by seventh segment, tuft borne by sixth pair of gills reduced in size; abdominal sternites each with a slightly irregular, brown crossband at anterior margin; caudal filaments tan, unmarked.

Known from Illinois and Ontario.

Illinois Records.—Alto Pass: May 31, 1940, B. D. Burks, 2♂; Union Springs Church, May 12, 1939, Burks & Riegel, 2♂; June 1, 1940, B. D. Burks, 1♂, 1 N; May 3, 1946, Burks & Sanderson, 2♂, 1♀; May 15, 1946, Mohr & Burks, 2♂, 2♀; branch of Clear Creek, May 19, 1946, Mohr & Burks, 2♂, 1♀. Cora: May 3, 1946, Burks & Sanderson, 1♂, 1♀. Eddyville: Lusk Creek, June 6, 1946, Mohr & Burks, 1♂. Golconda: May 13, 1939, Burks & Riegel, 2♂, 2 N. Jonesboro: branch of Clear Creek, May 15, 1946, Mohr & Burks, 7♂. Oakwood: Salt Fork River, May 22, 1942, Ross & Burks, 1♂. Wolf Lake: Hutchins Creek, May 15–June 1, 1940, B. D. Burks, 4♂, 2 N.

MACULIPENNIS Group

12. *Heptagenia umbratica* McDunnough

Heptagenia umbratica McDunnough (1931*b*:92).

Male.—Length of body 7–8 mm., of fore wing 8–9 mm. Frontal shelf of head stained with brown, and with a transverse, black streak across base, face above frontal shelf yellow, vertex brown; compound eyes separated on meson by a space as wide as a lateral ocellus. Thoracic notum and pleura dull brown, sternum yellow. Legs light yellow, fore femur, tibia, and tarsus shaded with brown; first fore tarsal segment one-fourth to one-fifth as long as second segment; wings hyaline, veins and crossveins in costal half of fore wing brown, others colorless. Abdomen yellow, tergites with posterior margin black and dorsal area shaded with brown; tergites 2–6 each with a transverse, black streak at posterior margin and a pair of large, posterolateral, brown triangles; apical three segments brown; genitalia, fig. 374, with forceps pale yellow, shaded with brown toward apexes, penis lobes tan; caudal filaments white.

FEMALE.—Size as in male; color generally identical with that of male except that brown shading is less intense; posterior margin of terminal abdominal sternite produced, and evenly rounded from side to side.

NYMPH.—Length of body 9 mm. Head and dorsum of body extremely dark brown, with lighter markings obscure or virtually wanting; each tarsal claw with a small basal tooth and a few ventral denticles; gills uniformly dark purplish gray, those of seventh pair lacking ventral, filamentous tufts; caudal filaments dark gray.

Known from Quebec.

13. *Heptagenia hebe* McDunnough

Heptagenia hebe McDunnough (1924*b*:122).

MALE.—Length of body 6–7 mm., of fore wing 7–8 mm. Frontal shelf of head stained with brown, a black, transverse streak across base of shelf; face yellow, vertex brown; the compound eyes pearl-gray, separated on meson by a space slightly wider than a lateral ocellus. Thorax yellow-brown dorsally, pleura yellow, with a longitudinal, brown streak just dorsad of each coxa; sternum yellow. Legs yellow, apexes of femora shaded with tan; an obscure, dark brown, ventral streak usually present near apex of each femur; fore tibia shaded with tan in apical half, fore tarsus tan; first fore tarsal segment one-fifth as long as second segment; wings hyaline, all veins of fore wing tan, crossveins dark brown, those in costal and subcostal interspaces surrounded by a dark brown cloud, another cloud at base of outer fork; often these clouds surround virtually all crossveins in fore wing; veins and crossveins of hind wing hyaline. Abdomen yellow, tergum heavily shaded with dark brown, this shading sometimes uniformly and completely covering tergites, but usually tergites 2, 3, and 8 each with a pair of submedian, yellow streaks, tergites 4–7 each with large, round, median, yellow spot; genitalia, fig. 375, yellow, with median, discal spines extremely long; caudal filaments light yellow.

FEMALE.—Length of body 5–6 mm., of fore wing 7–8 mm. Head almost entirely yellow. Thorax yellow, with dark brown, longitudinal stripe on each pleuron above coxae; legs light yellow, fore femur lightly shaded with tan; wings with crossveins in costal and subcostal interspaces surrounded by dark brown clouds, other crossveins in fore wing dark brown, veins white or a faint yellow. Abdomen light yellow, with a pair of broad, submarginal, lunate, dark brown streaks on each of tergites 1–7; posterior margin of terminal abdominal sternite produced, evenly rounded from side to side; caudal filaments white.

NYMPH.—Length of body 5–7 mm. Head brown, with dark brown freckles and three white spots on margin just anterior to either eye, and a pair of submedian, white spots on posterior margin of vertex. Thorax brown, with numerous small, white spots; each tarsal claw with a small, acute basal tooth and 3–5 ventral denticles. Dorsum of abdomen brown, with prominent, white markings; tergite 1 almost entirely white, tergite 2 white on median area and on posterolateral triangles, tergites 3 and 6 each with four white dots, tergites 4 and 5 white on broad, median area and on lateral triangles at posterior margins, tergite 7 white across posterior half, tergite 8 almost entirely white, tergite 9 with a white stripe across anterior margin and with a pair of circular, posterolateral, white spots, last tergite with a median, white spot at posterior margin; venter entirely white except for a brown mark at each posterolateral angle of terminal abdominal sternite; gills borne by seventh segment without ventral, filamentous tufts; caudal filaments tan, alternating articulations brown.

Known from Connecticut, Illinois, Indiana, Iowa, Maryland, Michigan, Minnesota, New York, Ohio, Ontario, Pennsylvania, Quebec, and Tennessee.

Illinois Records. — DOWNS: Kickapoo Creek, June 22, 1943, H. H. Ross, 1♂. EICHORN: June 6, 1946, Mohr & Burks, 1♂. HOMER: Salt Fork River, June 30, 1925, T. H. Frison, 4♀; July 19, 1924, T. H. Frison, 1♀. KANKAKEE: Kankakee River, June 17, 1939, B. D. Burks, 1♂; July 10, 1925, 1♂; July 10, 1925, T. H. Frison, 3♂, 2♀. LA GRANGE: June 17, 1938, J. S. Ayars, 2♂. MAZON: Mazon Creek, June 23–28, 1938, Ross & Burks, 1 ♂, 9 ♀, 5 N. OAKWOOD: Salt Fork River, June 6, 1925, T. H. Frison, 6 ♂, 1 ♀; June 14, 1930, T. H. Frison, 2 ♂; Camp Drake, June 24, 1948, Mills & Ross, 1 ♂. QUINCY: Mississippi River, June 7, 1939, Burks & Riegel, 1 ♂; June 8, 1939, T. E. Musselman, 1 ♂. URBANA: at light, July 29, 1947, L. J. Stannard, 1 ♀; July 5, 1907, 1 ♀. WILMINGTON: at light, Aug. 6, 1947, Burks & Sanderson, 5 ♂.

14. *Heptagenia maculipennis* Walsh

Heptagenia maculipennis Walsh (1863:206).

The male lectotype of this species is in the Museum of Comparative Zoology. It is badly broken, but the remaining fragments indicate that the present concept of the species is correct.

MALE.—Length of body 4.5–6.0 mm., of fore wing 6.5–8.0 mm. Head yellow; vertex stained with red-brown and having a brown stripe at posterior margin; compound eyes greenish gray, with a brown stripe across middle of each, eyes separated on meson by a space almost twice as wide as a lateral ocellus. Thorax cream colored, almost white, with a longitudinal, mesal, brown stripe on mesonotum; a dark brown stripe on each pleuron extending from mesocoxa to pronotum and a lighter brown stripe extending ventrally from fore wing base to sternum. Legs pale yellow to white, fore femur yellow, ventral side with a black mark at apex, apexes of fore tibia and fore tarsal segments shaded with gray; first fore tarsal segment one-sixth to one-fifth as long as second segment; wings hyaline, anterior veins of fore wing tan, all crossveins brown, those in costal and subcostal interspaces surrounded by brown clouds, fig. 318; posterior veins of fore wing and all veins and crossveins of hind wing colorless. Abdomen white, with tergites 7–9 and basal half of 10 shaded with bright orange- or red-brown; genitalia, fig. 376, white; caudal filaments white.

FEMALE.—Length of body 5.0–6.5 mm., of fore wing 7.0–8.5 mm. Head as in male. Thorax much as in male except that brown shading is reduced in area, the longitudinal, mesal, brown shading of mesonotum is usually confined to anterior half of sclerite; legs as in male, but fore tibia and tarsus with no dark shading; wings hyaline, all veins colorless, anterior crossveins of fore wing brown. Entire abdomen light yellow to white; posterior margin of terminal abdominal sternite produced on meson, evenly rounded; caudal filaments white.

NYMPH.—Length of body 5.0–6.5 mm. Head wider than pronotum, anterior, dorsal portion gray-brown, freckled with dark spots, three white spots on either margin just anterior to compound eye, three large, round, white spots on vertex between eyes. Thoracic notum gray-brown, with numerous white spots; each tarsal claw with a small, acute basal tooth and four or five ventral denticles. Abdomen dorsally gray-brown, with large, white markings; tergite 1 almost entirely white; tergites 2, 3, and 6 each with a pair of submedian, white streaks, a pair of posterior, white triangles, and a pair of lateral triangles; tergites 4 and 5 each with a large, median, white area, a pair of posterior triangles, and a pair of lateral triangles; tergites 7 and 8 with a confluent, median, white blotch, and each with a pair of posterior and a pair of lateral triangles; tergite 9 brown on posterior two-thirds, white anteriorly, three marginal, white dots in brown portion; tergite 10 brown, with a pair of large, submedian, white marks; sternites entirely white; gills borne by seventh segment lacking ventral, filamentous tufts; caudal filaments white, articulations brown, these latter alternately of lighter and darker tones.

Known from Illinois, Manitoba, Missouri, Ohio, Ontario, and Tennessee.

Illinois Records.—Specimens, collected June 3 to September 8, are from Antioch, Aurora, Beardstown, Dixon, Effingham, Elizabethtown, Hardin, Harrisburg, Havana, Homer, Hoopeston, Illini State Park (La Salle County), Kankakee, Lewistown, Mahomet, Momence, Monmouth, Monticello, Mount Carmel, Muncie, Oakwood, Oregon, Ottawa, Pontiac, Prophetstown, Quincy, Rockford, Rock Island, Rockton, Rossville, St. Charles, Shawneetown, Shelbyville, South Beloit, Sterling, Urbana, Waukegan, and Wilmington.

15. *Heptagenia walshi* McDunnough

Heptagenia walshi McDunnough (1926:193).

MALE.—Length of body and of fore wing 6 mm. Head brown, a light tan or yellow crossband just below antennae; compound eyes separated by a space almost as wide as one compound eye. Thorax brown on dorsum and pleura, sternum tan. Legs yellow, each femur with a black streak at apex, fore tibia and fore tarsus shaded with brown; first fore tarsal segment one-fourth as long as second segment; wings hyaline, veins and all crossveins but those posterior to Cu_1 in fore wing brown, with brown clouds surrounding crossveins in costal and subcostal interspaces as well as those posterior to bulla; stigmatic area stained with brown; veins and crossveins of hind wing almost or quite colorless. Abdomen white, each tergite tinged with tan in posterior half; a black crossline at posterior margin of each tergite; genitalia, fig. 377, light tan to white; caudal filaments white.

NYMPH.—Unknown.

This species is known from Ohio and Ontario.

16. *Heptagenia juno* McDunnough

Heptagenia juno McDunnough (1924*b*:121).

MALE.—Length of body 5.5–6.5 mm., of fore wing 6.5–7.5 mm. Head white, with a narrow, brown crossline at base of frontal shelf and at posterior margin of vertex; compound eyes separated on meson by a space as wide as one eye. Thorax cream colored, a longitudinal, black line on each pleuron above coxae, and a vague, dark streak at bases of each pair of wings; legs light yellow, each femur with a dark streak at apex, first fore tarsal segment one-fourth as long as second; wings hyaline, all veins except anterior ones of fore wing hyaline, crossveins of fore wing anterior to Cu_1 brown, others hyaline, crossveins in costal and subcostal interspaces of fore wing surrounded by brown clouds. Abdomen white, a black line at posterior margin of each tergite 1–7; apical tergites each vaguely darkened in mesal area with brown; venter white; genitalia, fig. 378, white; caudal filaments white.

FEMALE.—Length of body 5 mm., of fore wing 6.5 mm. Coloration similar to that of male, but light yellow of thorax becoming white or almost white; transverse, black marks at posterior margins of abdominal tergites faint or wanting, terminal three tergites not darkened; posterior margin of terminal abdominal sternite produced on meson as an obscure, blunt point; caudal filaments white.

NYMPH.—Length of body 6 mm. Head dark gray-brown, slightly wider than pronotum, three white spots on margin just anterior to either compound eye. Thorax dark grayish-brown, with numerous white spots, each tarsal claw with a small, basal tooth and four or five ventral denticles. Abdomen dark gray-brown, with white spots, tergite 1 mostly white, tergites 7 and 8 with a coalescing, median, white blotch, tergite 9 white at anterior margin, dark posteriorly; sternites 8 and 9 each with a transverse, dark brown mark on meson of anterior margin; caudal filaments white, articulations brown.

This species is known from Kentucky, New York, Pennsylvania, Quebec, and Tennessee.

17. *Heptagenia minerva* McDunnough

Heptagenia minerva McDunnough (1924:121).

MALE.—Length of body 6 mm., of fore wing 7 mm. Head yellow, with a black, transverse line at base of frontal shelf and at posterior margin of vertex; compound eyes separated on meson by a space as wide as one eye. Thorax cream colored, with a median, brown streak on anterior third of mesonotum and a very dark brown spot on either side of base of mesoscutellum; a longitudinal, black line on each pleuron above coxae. Legs yellow, fore femur with a median, reddish spot and an apical, black streak; wings hyaline, veins of fore wing brown, crossveins darker brown, crossveins of costal and subcostal interspaces surrounded by brown clouds, as are those posterior to bulla; outer fork with brown cloud at base. Abdomen faint yellow or white, each of tergites 1–7 with a transverse, black line at posterior margin and a pair of sublateral, elongate, brown triangles; apical three tergites shaded with red-brown; venter, genitalia, fig. 379, and caudal filaments white.

FEMALE.—Length of body 7 mm., of fore wing 8 mm. Coloration similar to that of male, but generally lighter, with light yellow of thorax becoming white; dark shading of abdominal tergites much reduced, terminal tergites white.

NYMPH.—Unknown.

The species is known from Maryland and Ontario.

18. *Heptagenia aphrodite* McDunnough

Heptagenia aphrodite McDunnough (1926*a*:194).

Male.—Length of body 6 mm., of fore wing 7 mm. Head with face yellow, vertex red-brown, with black shading around ocelli and at posterior margin; compound eyes separated on meson by a space as wide as one eye. Thorax with pronotum yellow, mesonotum chestnut brown, with yellow shading laterally; pleuron yellow, with a broad, red-brown, longitudinal stripe above coxae; sternum yellow; legs yellow, each femur shaded with tan at apex, fore femur also with a black, apical streak; wings hyaline, all longitudinal veins but C, Sc, and R_1 of fore wing colorless, crossveins of fore wing anterior to Cu_1 brown, those in costal and subcostal interspaces surrounded by brown clouds. Abdomen yellow, tergites 1–7 each with a black, transverse line at posterior margin and a pair of large, brown, elongate, sublateral triangles; terminal three tergites very dark brown; genitalia, fig. 380, light yellow; caudal filaments light yellow in color.

Female.—Length of body 6–7 mm., of fore wing 7–8 mm. Coloration similar to that of male, but generally lighter. Thoracic notum yellow, with vague, brown darkening on meson at anterior margin of mesonotum. Abdomen yellow, tergites 1–9 each with a minute, transverse, black line at posterior margin, tergites 2–7 each with a pair of sublateral, oblique, dark brown streaks; terminal abdominal sternite with posterior margin produced on meson in form of a Tudor arch; caudal filaments white.

Nymph.—Length of body 7 mm. Head dark brown, slightly wider than pronotum, three white spots at margin on either side just anterior to compound eye. Thorax dark brown, with numerous white spots; each tarsal claw with small, acute basal tooth and 4–6 ventral denticles. Abdomen dorsally mostly brown, with white markings; tergite 1 mostly white, tergites 7 and 8 with a median, coalesced, white blotch, tergite 9 with a white, median triangle based on anterior margin; abdominal sternum uniformly tan, entire margin of sternite 9 brown; caudal filaments tan, articulations brown.

This species is known from Georgia, Illinois, Indiana, New York, North Carolina, Ontario, Tennessee, West Virginia, and Wisconsin.

Illinois Record.—Momence: at light, July 17, 1914, 1 ♂.

43. *EPEORUS* Eaton

Epeorus Eaton (1881:26).

The species of the genus *Epeorus* (*s. lat.*) can be grouped into four subgenera: *Epeorus* Eaton (*s. s.*), *Iron* Eaton (1883, pl. 24, fig. 44), *Ironodes* Traver (1935*b*:32), and *Ironopsis* Traver (1935*b*:36). The last two subgenera include only western species in North America.

In the adult males of this genus, the compound eyes are contiguous on the meson; the fore leg is approximately as long as the body, the fore tarsus is one and one-sixth to one and one-half times as long as the fore tibia, and the first segment of the fore tarsus is as long as, or slightly longer than, second segment; the two fore tarsal claws are either of equal size and blunt, or unequal, with the larger claw blunt and the slightly smaller claw hooked at the apex. In both sexes, the first segment of the hind tarsus is as long as, or slightly longer than, the second segment. The wing venation is typical for the family, fig. 319, with the crossveins in the basal area of the costal interspace of the fore wing extremely weak or absent and the stigmatic crossveins anastomosed or not. In the hind wing, vein M_2 diverges from M_1 slightly basad of the center of the wing. In the male genitalia, the forceps are four-segmented, with the second segment longer than the third and fourth segments combined; the penis lobes, fig. 387, are fused on the median line about one-half of the distance to the apexes. These penis lobes are simple or are provided with median hooks or spines; there may also be lateral prongs on the lobes. In the females, the posterior margin of the terminal abdominal sternite, fig. 361, is cleft on the meson.

In the nymphs, fig. 386, the frontal margin of the head is not incised on the meson; the apical segment of the maxillary palp is enlarged, but relatively acute at the apex, and has a dense row of hairs on the outer margin; the apex of the galea-lacinia of the maxilla bears three stout, curved teeth. The apical segment of the labial palp has a dense row of hairs on the outer margin and, be-

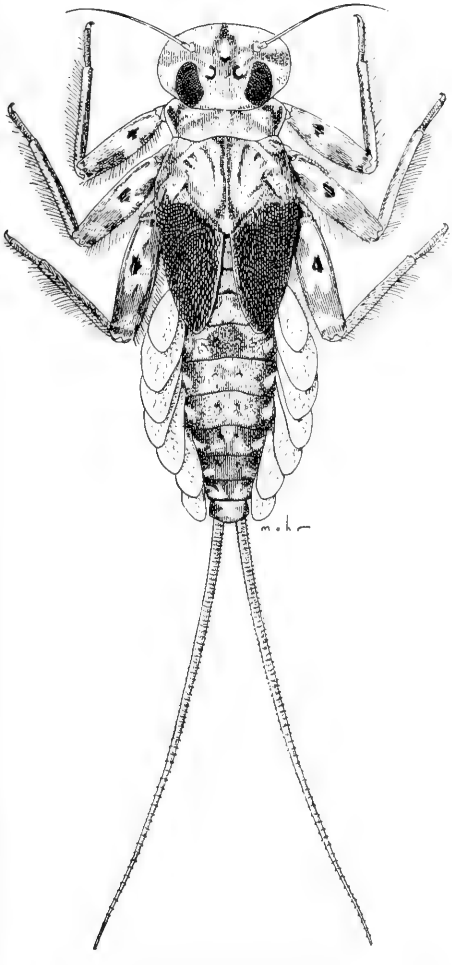


Fig. 386.—*Epeorus namatus*, mature nymph, dorsal aspect.

low this, a bank of pectinate spines. In the legs, the femora are relatively long and slender, with a closely set row of bristles along the posterior margin of each; each tarsal claw is short, rather slender at the base, and has two to six extremely minute, ventral denticles near the tip. Gills are borne by abdominal segments 1–7; each gill, fig. 327, is composed of a ventral, platelike element and a much-reduced, dorsal tuft of filaments; the anterior and posterior pairs of gills may or may not project beneath the abdominal venter to form, with the intermediate gills, a partial or complete, ventral, adhesive disc. There are only two long caudal filaments; the median one is atrophied.

The nymphs of *Epeorus* inhabit shallow, cool or cold, rapidly flowing water.

The genus *Epeorus* is well represented in the western and northeastern states, but is extremely rare in the Midwest. *Epeorus namatus* (Burks) (1946:607), figs. 386, 387, was described from Indiana and *vitrea* (Walker) (1853:555) is known from Manitoba, Michigan, New York, Ontario, Pennsylvania, and Quebec. Either or both of these might eventually be collected in Illinois.

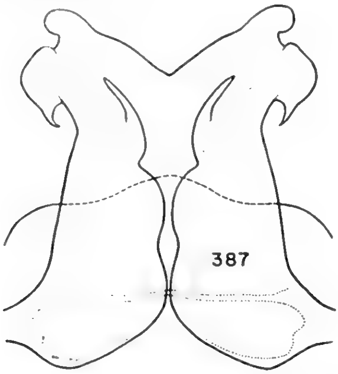
44. *CINYGMULA* McDunnough

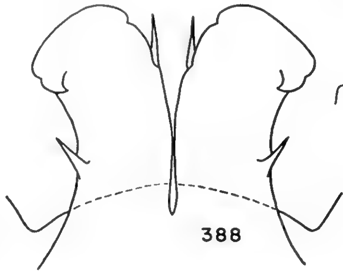
Cinygmula McDunnough (1933*b*:75).

In the adult males of *Cinygmula,* the compound eyes are large, but are not quite contiguous on the meson; each fore leg is about as long as the body, with the femur three-fourths as long as the tibia and the tarsus one and one-fourth to one and one-half times as long as the tibia; the first tarsal segment is from three-fifths to three-fourths as long as the second segment. The wing venation in both sexes is typical for the family, with the stigmatic crossveins of the fore wing not at all, or only slightly, anastomosed; the wing membrane often is suffused with a gray or yellow tint. Vein M_2 in the hind wing diverges from M_1 in the center of the wing. In the male genitalia, the forceps have four segments, the second of which is the longest and is about as long as the third and fourth segments combined; the penis lobes, fig. 388, are rather long and slender, have conspicuous lateral and mesal spines, and are either entirely separate or fused on the meson at the base only. The terminal abdominal sternite of the female has a V-shaped, median indentation on the posterior margin.

In the nymphs, the frontal margin of the head is emarginate on the meson, exposing a small portion of the labrum when viewed in dorsal aspect. The femora are relatively long, narrow, and flattened, and the tarsal claws are short, stout, and bear only three to five minute, ventral denticles. A pair of gills is present on each of abdominal segments 1–7; these gills are similar on all segments, each being platelike, with the fibrillar portion either entirely wanting or reduced to two or three filaments, fig. 328; the gills normally are held against the sides of the abdomen and project over the tergites but do not extend beneath the venter at all. The median caudal filament is slightly longer than the lateral ones.

with the frontal margin of the head entire. The tarsal claws are relatively short and stout at the bases; each claw has only two





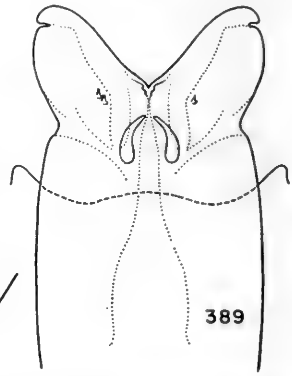


Fig. 387.—*Epeorus namatus*, male genitalia. Fig. 388.—*Cinygmula atlantica*, male genitalia. Fig. 389.—*Cinygma integrum*, male genitalia.

The species of *Cinygmula* are principally western and northern in distribution. *C. altantica* (McDunnough) (1924*b*:131) occurs in New York and Nova Scotia.

45. *CINYGMA* Eaton

Cinygma Eaton (1885:247).

In the adult males of this genus, the compound eyes are large, but do not quite meet on the meson; each fore leg is as long as the body, the femur and tibia almost or quite equal in length, the tarsus twice as long as the tibia, and the first tarsal segment from three-fifths to three-fourths as long as the second tarsal segment. In both sexes, the wing venation is typical for the family, with the stigmatic crossveins, fig. 322, numerous and anastomosed in such a way that a fine, slightly irregular line, parallel with vein C, divides the costal interspace into two parts; the costal crossveins of the fore wing in the basal area are quite weak. Vein M_2 in the hind wing diverges from M_1 in the center of the wing. The male genital forceps have four segments, the second of which is longer than the other three combined; the penis lobes, fig. 389, are broad and fused on the meson almost to the tips, and there is a small, median spine on each penis lobe at a point midway from the base to the apex. In the females, the posterior margin of the apical abdominal sternite is broadly rounded, and has a median notch.

The nymphs are typical for the family, or three ventral denticles near the tip. A pair of gills is borne by each of abdominal segments 1–7; each gill, fig. 329, is composed of a broad and platelike, dorsal element and a small ventral tuft of filaments; the gills do not extend over the abdominal sternites; the three caudal filaments are all of practically the same length.

The species of *Cinygma* known at present occur only in the western states. *C. integrum* Eaton (1885:248) is known from British Columbia, Oregon, and Washington.

45. *RHITHROGENA* Eaton

Rhithrogena Eaton (1881:23).

In the adult males of this genus, the compound eyes are contiguous on the meson; each fore leg is slightly longer than the body, with the tibia one and one-third times as long as the femur, and the tarsus one and one-fourth to one and one-half times as long as the tibia; the first segment of the fore tarsus is only one-fifth to one-third as long as the second segment. In both sexes, the wing venation is typical for the family, fig. 320, but the costal crossveins in the basal area of the fore wing are very weak, and, in Nearctic species, the costal, stigmatic crossveins are anastomosed, fig. 323. In the hind wing, vein M_2 diverges from vein M_1 slightly basad of the middle of the wing. In the male genitalia, the four-segmented forceps arise from a base which has a shallow, median indentation with a broadly

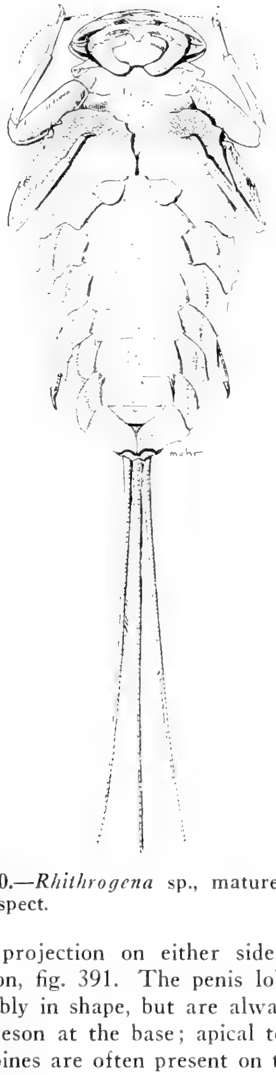


Fig. 390.—*Rhithrogena* sp., mature nymph, ventral aspect.

rounded projection on either side of this indentation, fig. 391. The penis lobes vary considerably in shape, but are always fused on the meson at the base; apical teeth and lateral spines are often present on the penis lobes. The posterior margin of the apical abdominal sternite of the female is broadly rounded, without a median emargination.

In the nymphs, fig. 390, the frontal margin of the head is very slightly emarginate on the meson, exposing a small part of the labrum when viewed in dorsal aspect; each maxillary palp has the distal segment broad and clavate, with the apex obliquely truncate and bearing multiple rows of pectinate spines and teeth on the inner surface and a dense row of hairs on the outer margin; the crown of each maxillary galea-lacinia bears a row of minute, stout teeth or spines; the apical segment of each labial palp is greatly enlarged and has a dense row of fine hairs along the outer, apical margin, below which is a bank of pectinate spines. In the legs, the femora are only moderately flattened, and have a row of closely set bristles along the posterior margin of each; each tarsal claw is short, broad at the base, and bears one or two ventral spines near the base and two or three ventral denticles near the tip. The gills are borne by segments 1–7, each gill being composed of a ventral, platelike element and a dorsal tuft of filaments, fig. 324. The platelike element of each gill has the outer margin irregularly fissured. The gills are held spread out beneath the venter of the abdomen in such a way as to form an adhesive disc, the first and last pairs of gills meeting on the meson to complete this disc at the anterior and posterior ends of the abdomen. The median caudal filament is somewhat longer than the cerci; all filaments are bare except for minute setae on the mesal margin of each cercus.

The species of *Rhithrogena* are relatively numerous and common in the western states and in the Northeast. Only one species has been collected in Illinois.

Rhithrogena pellucida Daggy

Rhithrogena pellucida Daggy (1945:383).

MALE.—Length of body and of fore wing 6–7 mm. Compound eyes in life dark gray-green; scape and pedicel of each antenna light yellow, flagellum shaded with gray; vertex and frontal shelf of head dark brown, except for a light yellow, transverse band extending from eye to eye at level of bases of antennae. Pronotum dark red-brown; mesonotum dark brown, almost black, with faint, greenish tinge, apex of scutellum red-brown; pleura brown, with yellow markings. Legs yellow or tan-yellow, each femur with a vague, brown, median band, and each tarsal segment shaded with gray-brown at apex; first fore tarsal segment one-third as long as second; wings hyaline, veins C, Sc, and R of fore wing shaded with gray-brown at bases, all other veins and all crossveins hyaline; stigmatic crossveins only slightly anastomosed. Abdominal tergites 2–6 each with a pair of large, brown, lateral spots; tergites 7–10 brown, with faint orange cast; sternites dirty white or yellow; genitalia, fig. 391, greatly reduced, the penis lobes lacking all spines, teeth, or tubercles; caudal filaments white, articulations not darkened.

Female.—Size as in male. Color similar to that of male, but generally lighter, the dark brown of the male being replaced by lighter brown, and light yellow being replaced by white.

Nymph.—Length of body 6.5–7.5 mm. Head, thoracic dorsum, and abdominal tergites 1–7 and 10 dark chestnut brown, tergites 8 and 9 yellow except at lateral margins. Thoracic sternum white, with narrow, brown lines at edges of sclerites; each femur light brown, variegated with white in middle and at either end, and with scattered, dark brown dots in basal two-thirds; tarsal claws brown at tips. Abdominal venter tan or yellowish, sternites 2–8 each with a brown, median patch and a dark brown, transverse line at the posterior margin, and a brown-shaded area near lateral margins; lamellate portion of each gill white, fibrillar portion faintly stained with tan; caudal filaments tan.

This swift-water species is known from Illinois, Michigan, and Minnesota.

Illinois Records.—Como: Elkhorn Creek, June 18, 1925, D. H. Thompson, 2 N; Rock River, July 6, 1925, 2 N; Aug. 12, 1924, 1 N. Dixon: Rock River, May 12, 1925, D. H. Thompson, many exuviae; May 22, 1925, 1 N. Erie: Rock River, July 23, 1925, D. H. Thompson, 1 N. Grand Detour: Rock River, May 27, 1927, 9 N. Hillsdale: Rock River, July 29, 1925, D. H. Thompson, 1 N. Lyndon: Rock River, July 8, 1925, D. H. Thompson, 28 N; July 15, 1925, 5 N; Aug. 5, 1924, 1 N. New Milford: Rock River, at mouth Kishwaukee River, July 14, 1927, D. H. Thompson, 5 N. Oregon: Rock River, below bridge, May 24, 1927, D. H. Thompson, 1 N; July 11, 1929, T. H. Frison, 1 N. Portland: Rock River, July 21, 1925, D. H. Thompson, 1 N. Roscoe: Rock River, Aug. 20, 1925, D. H. Thompson, 7 N. Sterling: Rock River, Aug. 7, 1924, D. H. Thompson, 1 N.

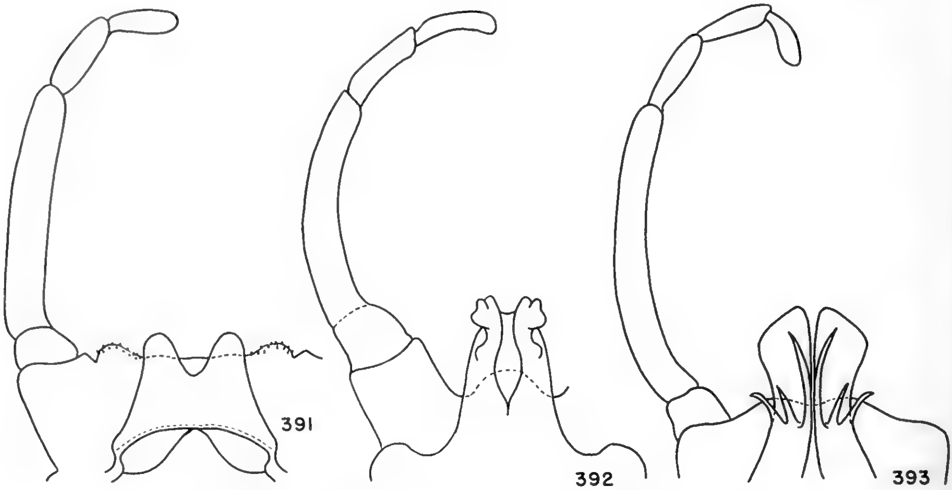

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Fig. 391.—*Rhithrogena pellucida,* male genitalia.
Fig. 392.—*Anepeorus simplex,* male genitalia. (After McDunnough.)
Fig. 393.—*Arthroplea bipunctata,* male genitalia.

47. *ANEPEORUS* McDunnough

Anepeorus McDunnough (1925*b*:190).

In the males of *Anepeorus*, the compound eyes are only moderately large and are separated on the meson by a space at least as great as the width of one eye; each fore leg is only slightly longer than the middle or hind leg; the fore tibia is one and one-third times as long as the fore femur, and the fore tarsus is only two-thirds as long as the fore tibia; the second tarsal segment is one and one-half times as long as the first, slightly longer than the third, and one and one-half times as long as the fourth, the fifth segment being slightly shorter than the fourth segment. In both sexes, the wing venation is typical for the family, with the stigmatic crossveins in the costal interspace relatively few in number and sometimes partly anastomosed. In the hind wing, vein R_5 diverges from R_4 at a point the same distance proximad of the outer wing margin that R_3 diverges from R_2; vein M_2 diverges from M_1 at a point only one-third the distance from the base to the outer wing margin. The male genitalia consist of a pair of four-segmented forceps arising from a medianly

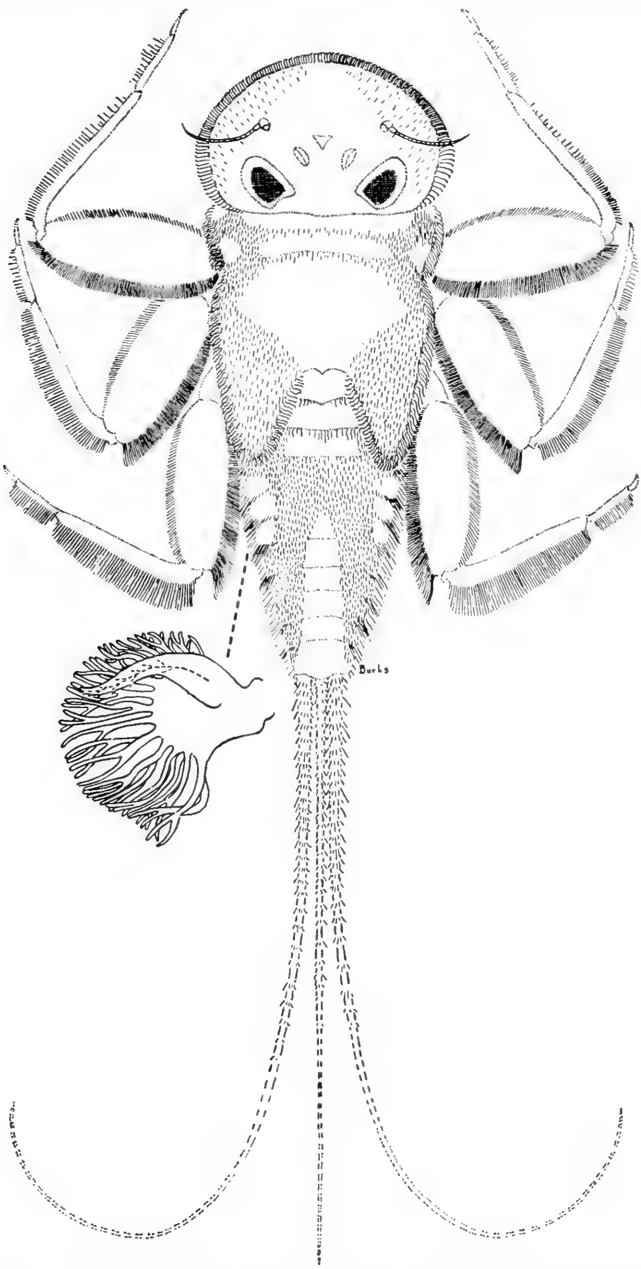

Fig. 394.—Nymph questionably placed as that of *Anepeorus;* nearly mature nymph, dorsal aspect. The small figure at left shows detail of gill borne on venter of fifth abdominal segment.

excavated base, fig. 392; the penis lobes are fused at the meson, on the ventral side, and bear a cluster of thin, somewhat convoluted laminae at the apexes.

The nymphs are not known with certainty, but fig. 394 shows an extremely rare form that may be a nymph of this genus. Only three specimens of this form have been collected in Illinois over a period of more than 20 years. It has not yet been possible to rear it.

This supposed nymph of *Anepeorus* has the head extremely broad and flat, with the compound eyes located near the posterior margin; the anterior and lateral margins bear a dense fringe of hair; the mouth-parts are evidently those of a predator, as the mandibles have long, slender incisors, and the broad, grinding, molar surfaces are absent; the fanglike structure of the maxillae and labium clearly fits them for predacity. The pronotum has lateral, flangelike projections; the legs are flattened and have a dense fringe of long hairs along the posterior margins of all femora and the middle and hind tibiae; the anterior margins of the femora bear dense fringes of shorter hairs; the claws are long, slender, and edentate; the wingpads show the heptageniid pattern of veins. The abdomen is flattened dorsoventrally and is relatively broad; the tergites are clothed with dense, somewhat woolly hairs; each of the first seven abdominal segments has a pair of ventral gills, fig. 394, which are all of the same general shape; the apex of the terminal abdominal segment is produced as a broad lobe; the three caudal filaments are all of approximately equal length, and their length is greater than that of the entire head and body; the caudal filaments are virtually bare, each clothed with short, sparse setae only in the basal area. Both male and female specimens have been collected, the male nymph showing the rudimentary forceps at the posterolateral angles of the projecting lobe on the posterior margin of the terminal abdominal sternite.

The short, thickset abdomen and the shape of the terminal abdominal sternite eliminated this nymph from consideration as the possible naiad of the genus *Pseudiron*. The nymph here considered to be that of *Anepeorus* bears a superficial resemblance to the nymph of the Russian *Behningia ulmeri* Lestage (Behning 1924; Chernova 1938).

Anepeorus simplex (Walsh)

Heptagenia simplex Walsh (1863:204).

Mayflies of this species are almost identical in appearance with those of two other heptageniid species: *Heptagenia persimplex* and *Stenonema integrum*. In both *persimplex* and *integrum*, however, the fore tarsus in the males is much longer than the fore tibia. *A. simplex* is actually an extremely rare species, and some of the published records of it have been based on misidentified specimens.

I agree with McDunnough (1929:179) that the Walsh specimen in the Museum of Comparative Zoology now labeled lectotype of this species is not *simplex* as defined by Walsh himself. There is another male specimen in the type lot at the M.C.Z. which is, in my opinion, the true *simplex*, as it agrees closely with Walsh's original description. The abdomen is, unfortunately, lacking from this specimen; so I was not able to examine the genitalia when I saw the specimen in 1942. I am basing my treatment of the species on McDunnough's redescription (1929:179), based on a single pair, now in the Illinois Natural History Survey collection, which was collected on the Rock River a few miles upstream from Rock Island, and on a single male subimago from Mount Carmel, on the Wabash River.

MALE.—Length of body 6–8 mm., of fore wing 7–9 mm. Head faintly suffused with pink, almost white; antennae white; eyes greenish yellow in life, according to Walsh. Entire thoracic notum a very faint yellowish pink; pleura and sternum white. Legs white, with yellow or brown shading on entire fore femur, at apexes of middle and hind femora, at bases of all tibiae, at apex of fore tibia, and at apexes of all tarsal segments; wings hyaline, with crossveins in costal half of each fore wing stained tan; three to five costal crossveins basad of bulla in fore wing, seven or eight stigmatic crossveins present in each fore wing. Abdomen white; genitalia, fig. 392, faintly yellow, caudal filaments white.

FEMALE.—Length of body 7–9 mm., of fore wing 8–10 mm. Coloration identical with that of male, except that yellow-brown shading of each fore femur is confined to a middle stripe and small area at apex; abdomen yellowish (due to color of eggs), posterior margin of terminal abdominal sternite produced as a broadly rounded lobe, without median emargination or excavation; caudal filaments faintly tan stained on basal articulations.

Known from Illinois and Iowa.

Illinois Records. — MOUNT CARMEL: Wabash River, June 10, 1947, Burks & Sanderson, 1 ♂. OREGON: Rock River, July 9, 1925, T. H. Frison, 1 ♂, 1 ♀. ROCK ISLAND: 10 ♂, 9 ♀ (Walsh 1863:204). Records of supposed nymph: DIXON: Rock River, May 22, 1925, D. H. Thompson, 1 N. MOUNT CARMEL: Wabash River, May 25, 1942, Mohr & Burks, 1 N; May 28, 1942, Mohr & Burks, 1 N.

48. *ARTHROPLEA* Bengtsson

Arthroplea Bengtsson (1908:239).
Remipalpus Bengtsson (1908:242).
Haplonia Blair (1929:254).

In the adult males of *Arthroplea*, the compound eyes are almost contiguous on the meson; the first fore tarsal segment is two-thirds as long as the second segment, and the entire tarsus is twice as long as the fore tibia. In both sexes, the venation of the fore wing is typical for the family, with the basal crossveins in the costal interspace rather weak and the stigmatic costal crossveins well developed but relatively few in number and not anastomosed. The hind wing, fig. 321, has the vein R_{4+5} unbranched throughout its length. The male genitalia, fig. 393, consist of a pair of five-segmented forceps and a pair of semirectangular penis lobes; each lobe bears three long, filamentous appendages. In the females, the apical abdominal sternite has the posterior margin evenly rounded from side to side, not indented on the meson.

The nymphs, fig. 395, are unique among American mayflies in that the labial and maxillary palps are considerably lengthened. Each maxillary palp has two segments and is as long as the head and thorax combined; each labial palp has two segments and is one-half as long as the maxillary palp. Normally, the maxillary palps are held extended posteriorly, over the thoracic notum, but the labial palps are concealed beneath the head. Each tarsal claw is short, stout at the base, and bears a row of minute bristles on the ventral side in the basal area. A pair of single gills is present on each of abdominal segments 1–7; each gill is platelike, with a point at the apex. There are three long caudal filaments.

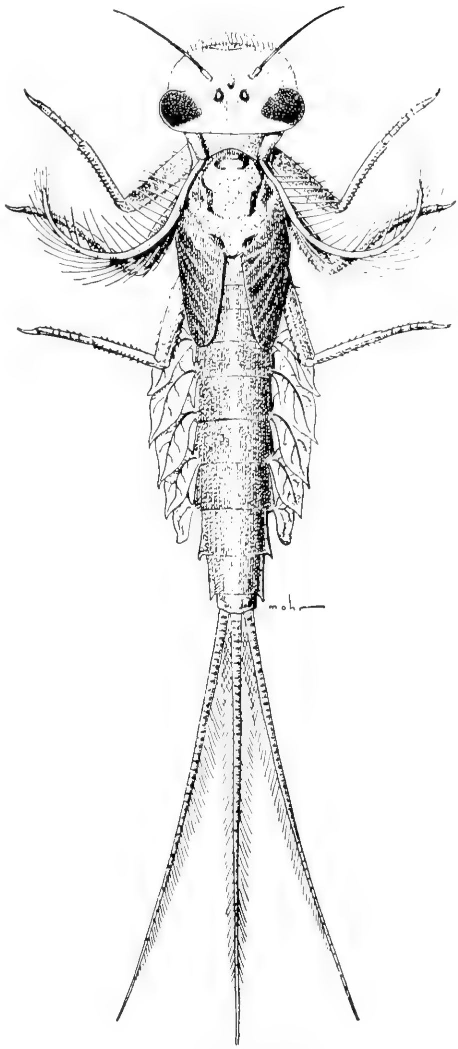

Fig. 395.—*Arthroplea bipunctata*, mature nymph, dorsal aspect.

Arthroplea is represented by only one North American species, *bipunctata* (McDunnough) (1924*c*:76), known from Connecticut, Maine, New Hampshire, Ontario, and Quebec.

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Largemouth Bass in Ridge Lake, Coles County, Illinois

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CONTENTS

Illinois angler with catch of largemouth bass from Ridge Lake.

Largemouth Bass in Ridge Lake, Coles County, Illinois

GEORGE W. BENNETT

IN 1941, when Ridge Lake, in Fox Ridge State Park, Coles County, Illinois, was completed, it was set aside as a study area for the largemouth bass, *Micropterus salmoides* (Lacépède). Initially, the largemouth was the only species of fish involved in the study. Later, in 1944, the bluegill, *Lepomis macrochirus* Rafinesque, was added as a companion species for the largemouth, and in 1949 the warmouth, *Chaenobryttus coronarius* (Bartram), was introduced.

At the time the study was begun, little was known of the factors that control the numerical size of populations of the largemouth, or the maximum total poundage of this species that a lake or pond could support. Extensive censusing of pond fish populations was in progress in various parts of the United States, and some fisheries investigators (Meehean 1942:193; Swingle & Smith 1941:274; Swingle 1950:14) assumed that, because in many ponds the total weight of largemouth bass exhibited relationships to the total weight of prey fish present of, say, 1 to 3 or 1 to 4, such relationships represented the "normal" or optimum ratios. These investigators further assumed that such ratios should be duplicated as nearly as possible in stocking new ponds.

The hypothesis of "normal" ratios between the weight of largemouth bass populations and the weight of populations of prey fish coexisting with the bass was based partially on the assumption of a direct predator-prey relationship between the two groups of fishes. Seemingly logical at the time was the further assumption that growth in a population of largemouths cannot remain "normal" if the population of prey fish drops below a certain predator-prey ratio. Both of these assumptions had to be discarded when research demonstrated that largemouths, once defined as piscivorous, are in fact relatively omnivorous and are able to maintain populations at high numerical and poundage levels when species of fish believed to furnish their principal sources of food are not present. In several artificial ponds in Illinois, largemouth bass populations isolated from other fishes maintained high numerical and poundage levels (Bennett 1951:235, 239 and unpublished records). Conversely, in some Illinois ponds in which largemouth bass were coinhabitants with other species of fish, the bass populations dwindled in both numbers and poundages.

In early decades of the present century, the phenomenon of declining populations of largemouth bass, a phenomenon early appreciated by fisheries personnel of the period, was largely responsible for the extensive development of hatchery propagation of these bass and for the imposition of certain fishing restrictions, including a closed season, a 10-inch minimum length limit, and a creel limit of 10 fish, first put in force in Illinois on July 1, 1923.

Fisheries workers in Illinois have observed often the ability of largemouth bass to expand their populations suddenly to take advantage of new territory. A new impoundment is particularly favorable to the successful reproduction of largemouths (Bennett 1946:9). When, for example, a new reservoir is stocked with equal numbers of adult largemouths, white crappies or black crappies, bluegills, and black bullheads, usually the largemouths, during the first spawning season, populate the shore shallows with tremendous numbers of young. Throughout this first season, the young of the other species of fish included with the bass may be so few in number that none can be collected. Probably few workers who have observed this sudden population expansion of bass have recognized its true significance in the production of superior fishing for largemouths, or how to make use of it in managing the species.

There is little reason to doubt that the "bonanzas" of largemouth fishing that are experienced occasionally by certain anglers in certain locations in certain years have stemmed from the development of superior populations of largemouths. These populations appear usually as a result of a relatively high survival of bass spawn during a season 2 to 4 years prior to the "bonanza" year. Such spawning success may be brought about by stocking a new reservoir with a few spawners.

Under natural conditions, any catastrophe which severely decimates a fish population that includes largemouth bass, but which allows the survival of a few bass spawners along with small numbers of adults of other species, will almost always be followed by an unusually large production of young bass. Such a phenomenon as a severe drought or drawdown, winterkill, abnormal predation, disease, or a combination of these might severely reduce a mixed population of fishes and set the stage for the production of a dominant bass brood.

Ridge Lake was stocked with 100 adult largemouth bass on April 30 and May 1, 1941. A few weeks later, a very large brood of young was produced. When the numerical size of this brood was estimated,

Fig. 1.—Ridge Lake, aerial view toward east. The dam, surface spillway, and tower spillway are at the lower end of the lake. The laboratory is visible within an indentation in the shore-line vegetation on the south bank of the lake.

it was believed that, unless the numbers were greatly reduced, food competition would become severe and growth would be slow. Consequently, 335 yearling bass were introduced into Ridge Lake on June 18, 1941. This introduction of yearling bass was ineffectual in thinning the numbers of bass fingerlings sufficiently, and, by 1942, bass of the 1941 brood had stopped growing.

In 1943, a culling technique, in which small or otherwise undesirable fish were permanently removed from the lake, as described in the section titled "The Draining Census," was adopted and used in alternate years to allow bass spawners to produce an abundant crop of young at intervals of 2 years. The culling technique allowed no single year-class to become dominant, because many large bass were present and actively preying upon the young as they reached fingerling sizes. This technique could be depended upon to assure the production of bass to replace those caught by anglers (who after 1945 were not restricted to the 10-inch length limit for bass) and those removed with other small fishes in the biennial culling operations.

The present publication is essentially a description of the culling technique of management and its effect upon the largemouth bass in Ridge Lake for an approximate 10-year period beginning with the spring of 1941 and ending after the bass spawning season but before the angling season of 1951. This technique, which is being employed in all recreational lakes built by the state of Illinois, may be depended upon not only to maintain good bass fishing over an indefinite period but to produce superior angling for fish of other warm-water species inhabiting these lakes.

Acknowledgments

Nearly everyone who has been employed on the permanent or temporary staff of the Aquatic Biology Section of the Illinois Natural History Survey since 1941 has assisted in some capacity in the Ridge Lake investigation. In the early years, Mr. Bruno von Limbach, Dr. Louis A. Krumholz, and Dr. Philip W. Smith contributed much time to general collections. On draining censuses, the staff usually consisted of six to eight individuals, and over the five censuses (1943–1951) included Dr. Donald Hansen, Mr. von Limbach, Dr. Krumholz, Mr. Jacob H. Lemm, Mr. Daniel Avery, Mr. Paul G. Barnickol, Dr. Arthur Witt, Jr., Mr. Leonard Durham, Dr. R. Weldon Larimore, Dr. William C. Starrett, Dr. James S. Jordan, Mr. Walter H. Hart, and Mr. William Nuess. Included among the several members of the staff of the State Department of Conservation who helped with these censuses were Mr. Sam A. Parr, Mr. William J. Harth, Mr. Glee Fogelman (deceased), Mr. James Holmes, Mr. Quentin Pickering, Mr. George Kuhn, Mr. Ora Price, and Mr. Bruce Muench.

As members of the staff of the Illinois Natural History Survey, several persons made special contributions to this study. Mr. Robert G. Rennels, Dr. Smith, Mr. Vernon A. Anderson, Mr. Charles D. Kemp, Mr. John Jedlicka, Jr., and Mr. W. W. Fleming took limnological samples and statistics on the anglers' catch. Mr. Frank C. Bellrose, Mr. G. H. Boewe, and Mr. Fleming made special studies on the flora of the lake. Dr. Witt and Mr. Durham studied the growth of Ridge Lake bass and bluegills from scale collections. Mr. James S. Ayars edited the manuscript. The author fully acknowledges the assistance given by those listed above.

Characteristics of Ridge Lake

Ridge Lake, fig. 1, was constructed by damming Dry Run Creek, an intermittent stream flowing through a steep-sided ravine within the boundaries of Fox Ridge State Park, 7 miles by road south of Charleston. The original area of the lake at overflow level in late 1941 was 18.1 acres. Water is supplied by drainage from 902 acres of the watershed of Dry Run Creek, which is a small tributary of the Embarrass River. Much of the land within the watershed of the Embarrass River in this immediate region is unusual in that medium slopes are rare; level lands break into steep-sided ravines with slopes of more than 30 per cent. In the Ridge Lake watershed, slopes of less than 4 per cent are found on 64.6 per cent of the area;

on 33.2 per cent of the area, slopes are in excess of 30 per cent (Stall *et al.* 1951: 20). Agricultural misuse of the watershed has created a serious silting problem within the lake. In 1949, Stall *et al.* (1951: 12) found that the lake had an average annual capacity loss of 1.29 per cent, representing an annual erosion of 4.36 tons of soil per acre of watershed.

The amount of soil loss from the watershed depends primarily upon the nature of the soils, slopes, and land use or farming practices. Erosion occurs in two forms, sheet erosion and gully or channel erosion. Pasturing of some of the ravines above the lake contributes to the erosion. The slipping of earth from ravine sides into the valley floor occurs even where the ravines are entirely unpastured. Most of the soil that drops off the hillsides as a result of slipping eventually comes to rest on the bottom of Ridge Lake. In 1950, about 4 acres of the upper lake area were covered with water of less than a foot in depth; this same area was covered with water 3 to 4 feet in depth when the water was impounded in 1941. An effort is now being made to organize a soil conservation district that will include the lake watershed and that will slow down the rate of sedimentation within the basin.

The fill impounding the water of Ridge Lake is a 450-foot earthen dam running north and south across the valley of Dry Run Creek; a concrete surface spillway 70 feet wide was constructed over a natural bank at the north end of the fill, fig. 2. The primary overflow structure, however, is a tower spillway designed so that it removes water from the bottom of the lake rather than from the surface. Inside the tower is a spillway wall parallel to the dam that divides the tower into an east and a west section; the overflow lip, the top of this wall, is 8 feet long; its elevation above sea level is 595 feet. The elevation of the crest of the surface spillway is 596 feet above sea level, so that, on small rises of the lake level, all the overflow water passes through the tower. As the tower is open at the bottom, water from the bottom of the lake rises in the east section of the tower to correspond to the lake level. When the lake level exceeds the overflow lip, the water spills over into the west section of the tower, the section nearer the dam, and passes through a rectangular concrete tunnel 5 feet wide and 7 feet high to that part of Dry Run Creek on the downstream side of the dam. In summer, when the waters of the lake are thermally stratified and the bottom waters are devoid of oxygen, rises in the lake level allow stagnant bottom water to escape from the lake.

A gate valve, 4 feet square, located at the base of the spillway wall in the tower, allows the lake to be drained. This gate was first closed on April 17, 1941, when construction of the dam was completed.

In 1940, a brick laboratory and a boat dock were constructed on the south shore of the lake about 800 feet up the lake from the dam, fig. 3. At the same time, two single-post concrete towers were built, one in the center of the lake opposite the laboratory and the second about two-thirds of the distance up the lake from the dam to the upper end of the basin. These towers, which were supplied with wooden floors and railings, have been used to support recording thermographs and other weather instruments.

The maximum lake depth, 25 feet, is in the old stream channel near the dam; the valley floor of the lake near the dam is 4 to 6 feet above the bottom of the old stream channel. From the old stream channel near the dam, the floor of the valley gradually rises until, about 2,500 feet up the lake from the dam, it exceeds the 595-foot level of the overflow lip of the tower spillway. The width of Ridge Lake varies from about 400 feet at the dam to 200 feet at the upper end. The steep side walls of the lake basin tend to make much of the lake comparatively deep, except in the upper end, where sedimentation is now extensive.

Limnological Characteristics

Limited work on the limnology of Ridge Lake defined the range of variation of some physical and chemical characteristics of this body of water during the summer periods of 1941–1951, somewhat longer in 1942 than in the other years; some quantitative biological sampling was done in 1948 when Fleming (1949) was investigating the characteristic forms of plankton

Fig. 2.—The dam, tower spillway (left), and surface spillway (right) as seen from the surface of Ridge Lake.

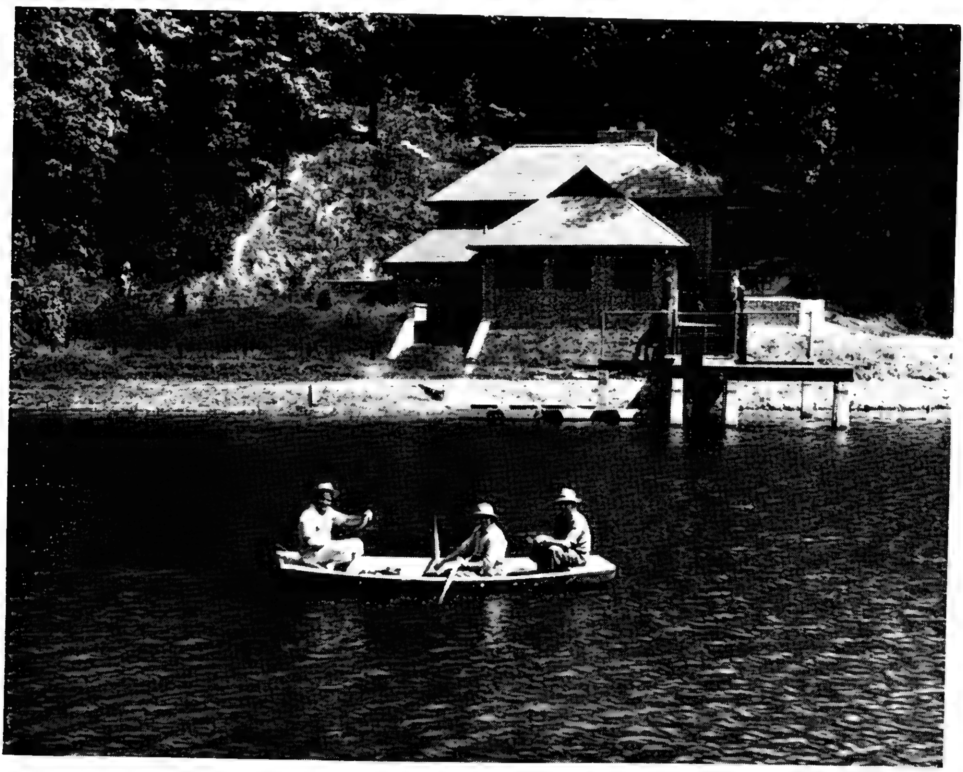

Fig. 3.—Illinois Natural History Survey laboratory and boat dock at Ridge Lake in the summer of 1949. After the March draining of that year, the lake failed to refill completely until December.

and bottom fauna associated with growths of rooted aquatic vegetation.

Throughout the periods when biologists were stationed at the laboratory (summers, 1941–1951), recording thermographs were operated to measure fluctuations of air temperatures and of water temperatures at various depths, fig. 4. Daily records were made of rainfall; these were compared with the fluctuations in water levels recorded on a continuous water level recorder and with changes in the transparency of the water as determined by Secchi disc readings. In 1942, when a biologist was stationed at the laboratory throughout the greater part of the year, analyses for dissolved oxygen were made on waters collected at frequent intervals from late February to the third week in October at depths of 0, 3, 6, 9, 12, 15, and 18 feet. Because physical and chemical data were collected for a longer continuous period of time in 1942 than in any other year, the records for 1942 have been used to illustrate the relationships between these data, figs. 5 and 6. Fig. 5 shows the average weekly air temperatures and the average weekly water temperatures at a depth of 4 feet (by recording thermographs) from the third week in March through the greater part of October; also, water levels, transparencies of water, and rainfall for approximately this same period.

Rainfall, Water Levels, and Transparency.—The drainage basin of Ridge Lake is large in proportion to the capacity of the lake basin. This fact, coupled with the fact that most slopes in the drainage basin are steep and that some of them are overgrazed, insures a rapid runoff of rainfall carrying a relatively large load of silt, most of which passes into the upper end of the lake basin, where the heavier particles of silt are dropped. Fine clay particles disperse throughout the waters of

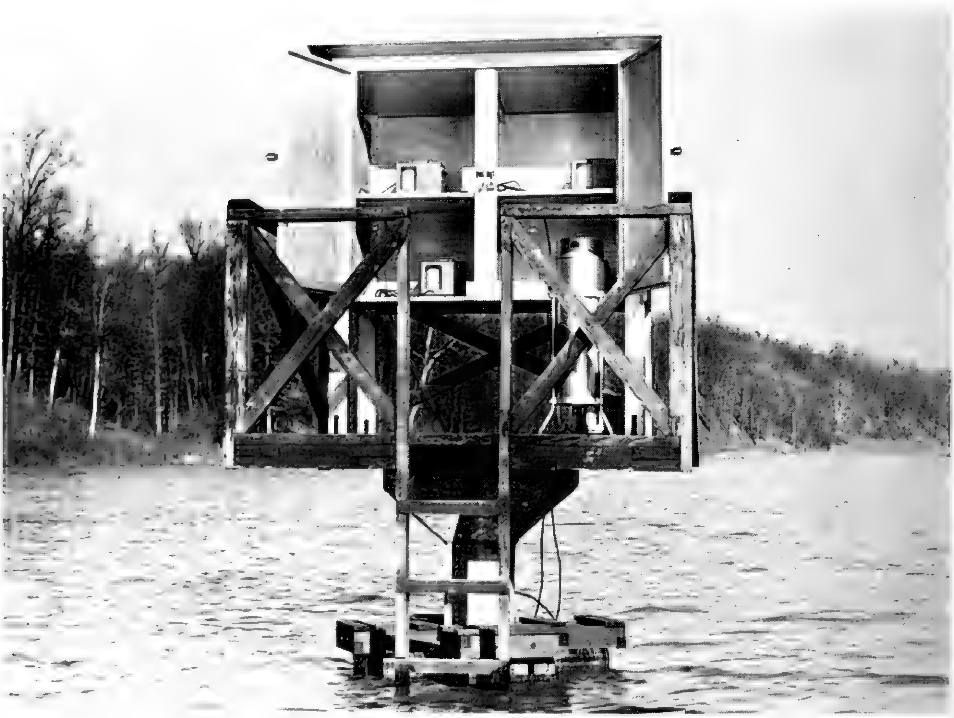

Fig. 4.—Recording thermographs on instrument tower in Ridge Lake opposite the laboratory. These thermographs were used to record air temperatures and water temperatures at various depths. The bulbs of water temperature recorders were suspended from a float built around the concrete tower so that they would rise and fall with changing lake levels. The rain gauge shown here, when in use, was placed on a second tower in the upper part of the lake. A water-level recorder was located on the boat pier in front of the laboratory.

the lake and increase the turbidity. During periods between rains, these clay particles settle out, and the lake becomes clear.

In 1942, the lake was most turbid on March 12, fig. 5, when a Secchi disc would disappear at 0.7 foot below the surface. Transparencies of less than 2 feet were recorded also on March 16, 19, and 22; on April 8, 9, and 10; on May 7; and on June 14, 15, 16, and 17. While all rains of as much as 0.5 inch influenced the transparency of the water to some extent, most rains of 1 inch or more were followed by periods of very low transparency of water, showing Secchi disc measurements of less than 2 feet. Such low transparency, during the fishing season, interfered with fishing success. Once the transparency approached 1 foot, about 5 or 6 days free from rain were required for the water to reach a maximum of transparency.

The amount of silt entering the lake and the muddiness of the water varied not only with the condition of the vegetative cover on the watershed (influenced by the seasons) but also with the type of rainstorm. For example, on June 26, 1942, a rain of 2.0 inches was recorded as having fallen throughout a period of 10 hours; transparency readings made on that day and on days following showed that the lake had greater transparency on the first and second days after the rain than on the day of the rain. In another instance (September 19, 1942), a violent rain of short duration amounting to only 0.65 inch caused a drop in transparency from 10 feet to 3.7 feet, apparently without raising the water level of the lake.

The maximum transparency of the water was measured at 14 feet on June 4, 1942, after 15 days of little or no rainfall. Later, in the summer and fall of the same year, water transparency did not exceed 10 feet. During this period, the transmission of light was reduced by plankton (mostly blue-green algae) rather than by particles of clay.

In 1942, the water level of Ridge Lake never dropped lower than 0.4 foot below the overflow lip of the tower spillway. The drainage basin of 1.41 square miles (902 acres, or about 50 acres of drainage basin per acre of lake) is large enough to fill the lake basin with runoff water from normal rainfall several times during a single year. Even in late summer, a time of infrequent rains, the runoff is sufficient to prevent severe drops in the lake level.

The tower spillway, fig. 2, which removes water from the bottom of the lake, has a capacity of 25 cubic feet of water per second. If the water inflow from the drainage basin exceeds this capacity, the level of the lake rises and, if the lake level exceeds the crest of the surface spillway, a foot higher than the lip of the tower spillway, the water flows over into a stilling basin and then into the section of Dry Run Creek below the dam. The capacity of the surface spillway is so great that runoff waters from even the heaviest rains do not create a flow of water exceeding about a foot in depth on the crest of this spillway. Within a matter of minutes after a rain, or at most a few hours, the lake level drops below the crest of the surface spillway.

In 1942, the water level of the lake rose above the crest of the surface spillway eight times, fig. 5, after rainfalls of approximately 1 or more inches. Water continued to run out of the lake through the tower spillway all through the spring and summer until August 22. On September 8, a rain of 2.2 inches, which fell during a period of 12 hours, raised the water level in the lake 0.7 foot, and water again flowed through the tower spillway. The maximum fluctuation of the lake level throughout the spring, summer, and fall of 1942 was 2.5 feet.

Thermal Stratification and Dissolved Oxygen.—Ridge Lake would probably show characteristics of a eutrophic lake except for the occasional loss of substantial quantities of water from the lower strata following heavy rains. As mentioned previously, an inflow of runoff water from the lake watershed in amounts large enough to cause a significant rise in the lake level above the lip of the tower spillway is followed by a loss of water through that outlet from the cold, oxygen-deficient stratum immediately above the lake bottom. Except after rains so heavy that water flows over the surface spillway, the volume of bottom water lost is approximately equivalent to the volume

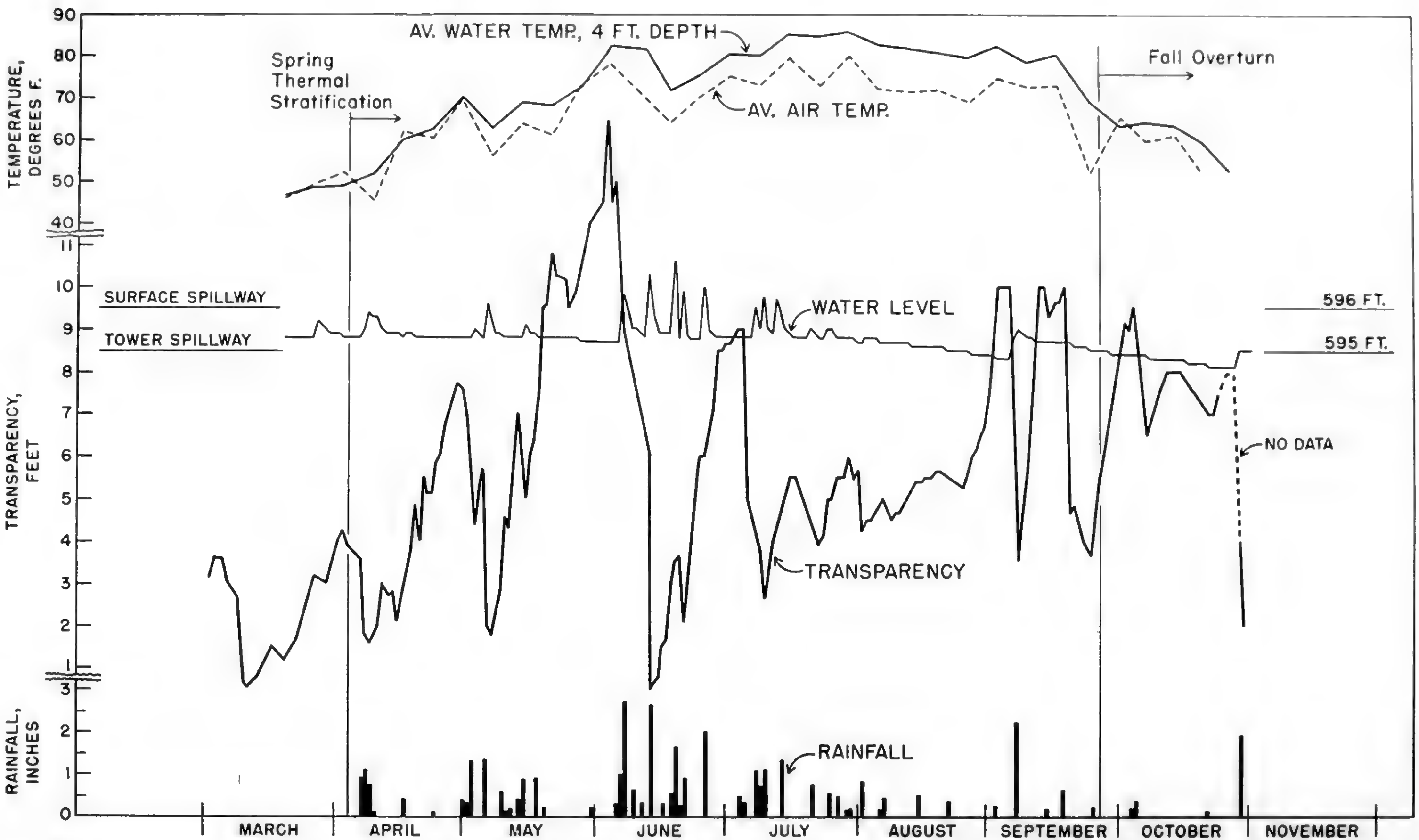

Fig. 5.—Air and water temperatures, water levels, water transparencies, and rainfall recorded at Ridge Lake, March to late October, 1942, arranged to show the interrelationships of these physical phenomena.

of runoff water flowing into the lake. After large rains, this exchange of water is extensive. Most of the runoff water, when warmer than the bottom water, flows from the upper end of the lake toward the lower end at surface or near-surface levels. The bottom water is replaced by water from strata lying immediately above; the lowest and coldest layers are lost through the tower spillway. The magnitude of change (increase) in the temperature and dissolved oxygen content of waters in the bottom strata of the lake following a period of rainfall is dependent upon the volume of runoff water draining into the lake from the watershed. When the volume of runoff water is great enough to exceed the capacity of the tower spillway and raise the lake level above the crest of the surface spillway, the water discharge from Ridge Lake becomes a combination of surface water and bottom water.

In 1942, persistent thermal stratification of Ridge Lake, characteristic of the warm seasons, began on April 4, figs. 5 and 6. Prior to this date the lake appeared to be thermally stratified for short periods; in each of these periods, the stratification was broken up by cold weather, which usually was accompanied by heavy rainfall.

Annually, during the period of summer thermal stratification, Ridge Lake shows a surface layer of warm water (epilimnion) of 3 to 5 feet in thickness. In the thermocline, the layer of water below the epilimnion, the temperatures gradually become lower toward the bottom. The thermocline may show a temperature gradient of 10 to 18 degrees F. within a perpendicular distance of only 18 feet. No indication is given of a hypolimnion, or stratum of water of uniform temperature lying directly above the lake bottom.

Early in April, 1942, the temperature of the water at a depth of 18 feet was 46.5 degrees F., while the temperature of the water at the surface was 59.0 degrees F. Between the first week in May and the first week in June, the temperature at 18 feet rose from 50.0 to 63.5 degrees F. while that at the surface rose from 70.5 to 87.0 degrees F. The maximum temperatures for the 18-foot depth during the latter half of July and throughout August in 1942 ranged from 71.7 to 74.0 degrees F. During this same period, surface temperatures varied between 80.0 and 88.0 degrees F.

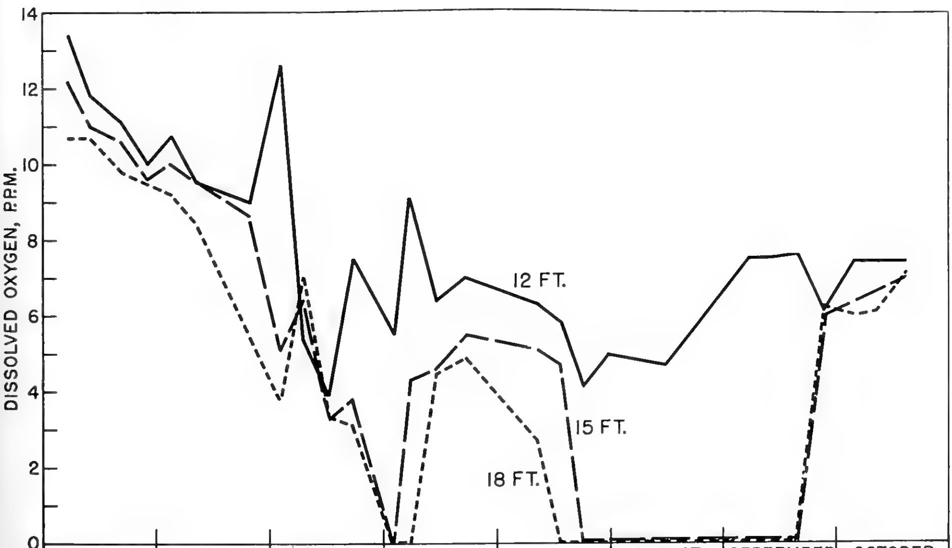

Fig. 6.—Dissolved oxygen, parts per million, at 12-, 15-, and 18-foot depths in Ridge Lake, early March to late October, 1942. The rise in oxygen during the month of June was due to the replacement of stagnant bottom water forced out of the lake through the spillway tower by surface water entering the lake from rains that fell on the watershed.

Throughout the entire period of stratification there was at least 0.5 degree difference between temperatures at 15- and 18-foot depths and at least 1 degree difference between temperatures at 12- and 15-foot depths. Usually the differences were 1 to 3 degrees between the 15- and 18-foot depths and 1.5 to 4 degrees between the 12- and 15-foot depths.

The first period of rapid increase of water temperatures at the 15- and 18-foot depths occurred in early May following heavy rains of May 3 and 6. At the beginning of this period, the temperatures at the 15- and 18-foot depths were 51.0 and 50.0 degrees F., respectively. By early June, the temperatures at the 15- and 18-foot depths had risen to 64.0 and 63.5 degrees F., respectively. By June 7, when rains were resumed after a period of very low precipitation, temperatures at the 15- and 18-foot depths had dropped to 61.0 and 58.0 degrees F., respectively. Heavy rains occurred at rather frequent intervals from June 7 to July 14, and during this period the temperature of water at the 15-foot depth rose from 61.0 to 72.0 degrees F. and at the 18-foot depth from 58.0 to 70.5 degrees F. During this same period, the temperature of the surface water dropped from a high of 87.0 degrees F. on June 2 to 82.5 degrees F. on July 14.

The fact that periods of rapid temperature rise in the water close to the lake bottom corresponded to periods of heavy rainfall indicated that the loss of the cold bottom water through the spillway tower was largely responsible for these temperature increases.

Fluctuations in the dissolved oxygen content of the deeper waters of Ridge Lake were even more striking than those in temperature. Following the beginning of prolonged stratification in April, 1942, the supply of dissolved oxygen at the 15- and 18-foot depths gradually became less, except when, during the second week in May, two rains, each exceeding 1 inch of precipitation, fig. 5, apparently forced out of the lake a large volume of the bottom water containing a reduced supply of dissolved oxygen. This water was replaced by that lying nearer the surface and containing a greater amount of oxygen. Thus, there was a temporary increase of oxygen at the 15- and 18-foot depths; but, because of the oxygen demand of organic material on and above the lake bottom, the new supply rapidly was used up until by early June no dissolved oxygen remained. On June 7, a period of heavy rainfall began, fig. 5, which ended July 14; there were 7 consecutive days (last 4 days in June and first 3 days in July) when no rain fell. The heavy rains of this period forced the oxygen-deficient waters out of the lake and almost immediately increased the available dissolved oxygen to more than 4 parts per million at the 15-foot depth and considerably more at the 12-foot depth, fig. 6. Samples for oxygen analyses taken at these depths and at the 18-foot depth (this sample was taken 8 inches off the bottom) on July 11 showed that the dissolved oxygen was 6.3 p.p.m. at 12 feet, 5.1 p.p.m. at 15 feet, and 2.7 p.p.m. at 18 feet. Before the end of the third week in July, the dissolved oxygen at 15- and 18-foot depths had again dropped to zero, where it remained until the fall overturn began on September 27, as a result of abnormally cold weather during the preceding week. At the time the fall overturn began, water temperature at a depth of 4 feet was 62.0 degrees F.

The biological effect of the removal of stagnant water from the lower levels of Ridge Lake is unknown. Certainly it must temporarily increase the volume of water inhabitable by fish. Evidence from oxygen determinations made in 1948 by Fleming (1949:20) and by other workers in 1942 and 1943 shows that, after periods of flushing, the increased oxygen supply is rather rapidly used up, probably too soon for the invasion of those bottom organisms that require dissolved oxygen. The increase in water temperatures may speed up the growth of midge larvae (*Chaoborus*) that normally inhabit oxygen-deficient bottoms. It is probable that the perpendicular extent of the oxygen-deficient stratum of water above the bottom is, on the average, somewhat less than it would be without the tower spillway arrangement for loss of bottom water.

Fertility of Water.—Ridge Lake probably ranks intermediate in fertility when compared with other lakes within the boundaries of Illinois. Judged by fish production, most ponds and lakes in central and northern Illinois are more fertile and many in southern Illinois are less fertile (Bennett 1943:361 and unpublished fish censuses of ponds and lakes). Comparisons of the mineral analyses of the water of several Illinois lakes, and the poundages of fish these lakes support, with measurements of soil fertility on the watersheds show that a large part of the nutrient materials of each lake may have entered the lake with runoff water from the watershed and become trapped within the basin. A part of these materials may be buried under silt deposits. In addition to the nutrients that enter from the watershed, there is within the lake itself an accumulation of organic materials resulting from the death and disintegration of plants and animals, all of which adds to the fertility. More nutrients and organic matter are gained through inflowing water and through accumulation than are carried away in overflow, and thus impoundments, many of which are built over soils of comparatively low fertility, tend to become more fertile as they age.

Table 1 shows two partial mineral analyses of water made by the Illinois State Water Survey: one of the water of Dry Run Creek prior to impoundment and a similar one of lake water after impoundment. A comparison of these two analyses shows large differences in the amounts of almost all of the minerals. These two water samples were taken approximately 3 years apart, and during this length of time changes may have taken place in land use within the watershed, opening up new areas to erosion and leaching.

Table 1.—Partial mineral analysis of water from Dry Run Creek, April 7, 1938, prior to impoundment, and of water from Ridge Lake soon after gate valve was closed, April 22, 1941.

Mineral	Dry Run Creek, April 7, 1938, Parts per Million	Ridge Lake, April 22, 1941, Parts per Million
Iron	2.0	3.2
Manganese	0.0	0.5
Silica	21.0	9.5
Calcium	5.2	72.1
Magnesium	24.3	22.9
Sodium and potassium	59.6	11.0
Sulfate	18.5	40.1
Nitrate	1.2	1.8
Chloride	1.5	5.0
Methyl orange alkalinity	220.0	248.0
Total hardness	113.0	272.0

A study of Ridge Lake (Stall *et al.* 1951:24–5) showed that a large part of the sediment deposits of the lake originated probably from the Hennepin gravelly loam which occurs on the steep, heavily eroded slopes of the watershed. These deposits contain amounts of potassium and phosphorus adequate for farm crops, but they are low in nitrogen.

The soils of the flat uplands of the Ridge Lake watershed are planted usually to row crops—corn and soybeans. These soils are much less fertile (judged on the basis of the crops they produce) than are most of those farther north in Illinois; while the northern soils average a corn-production rate of approximately 75 bushels per acre, those in the region of Dry Run Creek average not more than 25 bushels per acre.

Growing Season for Fishes.—In experiments with largemouth bass, Markus (1932:210) found that the rate of digestion was very slow in fish held in water below 50 degrees F., but that it increased rapidly with increasing temperatures up to about 72 degrees F. Observations on growth of the largemouth bass in Illinois ponds indicate that growth begins each spring when water temperatures range between 50 and 60 degrees F. Average water temperatures at the 4-foot depth in Ridge Lake in 1942, fig. 5, first exceeded 55 degrees F. during the week of April 13–19 (April 15) and did not again drop to 55 degrees F. until the week of October 27–November 2 (October 29). These temperature readings showed that the growing season for bass at Ridge Lake was nearly 6.5 months long in 1942. Similar measurements of water temperatures in Fork Lake (Bennett, Thompson, & Parr 1940:13, 15) in 1939 showed that the growing season in this pond was 6 months. The site of Fork Lake, which lies within 65 miles of Ridge Lake, is only about 25 miles farther north, and its seasonal cycle of temperatures probably is comparable to that of Ridge Lake.

There is evidence that in 1942 the growing season at Ridge Lake began unusually early. The average weekly water temperatures (at 4 feet) of 62.6 degrees F. recorded for the week of April 20–26, 70.2 degrees F. for April 27–May 3, and 82.5 degrees F. for June 1–7 are unusually high for these times of year, fig. 5. Further, the first schools of bass fry in 1942 were seen on May 14 and the maximum number of schools was counted on May 19. In all other years except 1941 and 1951, schools of bass fry were not in evidence until after June 1. For these reasons, we considered that the 1942 season was abnormally long. In most years of this study, the growing season at Ridge Lake did not exceed 6 months.

Aquatic Plants.—A large number of marsh and moist-soil plants were to be found growing along Dry Run Creek before Ridge Lake was built. In March, 1941, prior to the closure of the gate valve in the dam, G. H. Boewe and Frank C. Bellrose of the Illinois Natural History Survey staff collected plants in the lake basin and reported on the species to be found there. Among the marsh plants were the following:

- Bulrush, *Scirpus atrovirens* Willdenow and *Scirpus,* probably *polyphyllus* Vahl
- Common cattail, *Typha latifolia* Linnaeus
- Horsetail, *Equisetum* sp.
- Sandbar willow, *Salix interior* Rowlee
- Sedges, *Carex* spp.
- Virginia wildrye, *Elymus virginicus* Linnaeus

Early in the period of impoundment, from April, 1941, until midsummer, 1942, little aquatic vegetation was in evidence, although cattail, American waterplantain, *Alisma subcordatum* Rafinesque, horsetail, and some sedges had appeared at the upper end of the lake. Leafy pondweed, *Potamogeton foliosus* Rafinesque, was collected in several places in the upper end of the lake on September 5, 1942, and by September 15 it was becoming abundant.

In 1941 and subsequent years, any cattails that appeared were cut off at the roots. Consequently, in the years that the lake has existed, these plants have never increased in abundance beyond a few scattered individuals.

Scattered bunches of *Potamogeton foliosus* were growing in the shallows in front of the surface spillway and in the upper end of the lake in early June, 1943. By August, dense mats of fine-leaved potamogeton were abundant in water up to 6 feet in depth, and scattered bunches of *P. nodosus* Poiret, sago or fennelleaf pondweed, *P. pectinatus* Linnaeus, cattail, waterplantain, and several species of arrowheads, *Sagittaria* spp., including common arrowhead or duck potato, *S. latifolia* Willdenow, were growing in shallow water.

In 1944 and 1945, the vegetation was essentially of the same species as those found in 1943; in addition, the naiad, *Najas flexilis* (Willdenow) Roskovius & Schmidt, and Canada waterweed or elodea, *Anacharis canadensis* (Michaux) Planchon, were first collected in 1945.

In 1946, a vegetation die-off occurred for the first time in Ridge Lake. A similar die-off, which occurred each year from 1946 on, usually had begun by the tenth of July. A coating of blue-green algae seemed to envelop the plant mats, which began to sink in some places, forming deep ravines of open water between ridges of dying plants. These open-water areas gradually increased in extent until much of the lake that had been choked with vegetation in June was open water by the end of July.

In 1948, when among the most abundant plants were sago pondweed and elodea, these plants completely disintegrated within 2 weeks of the time they were first observed to be affected (July 8). Dragging a garden rake on parts of the lake bottom, where the thickest mats had been, produced only wisps of decaying plant stems. By July 23, the entire lake was open water except for small beds of elodea in shallow water at the upper end of the lake and at the surface spillway. These were second-growth plants, as the original plants had died there also. Both sago pondweed and elodea gradually came back, until by August 25 the plants had grown to the surface again in much of the area formerly filled with them. However, the growth was not so thick as the first growth had been.

In 1949, when the lake refilled only to about the 11-acre contour after the March draining, the mats of aquatic vegetation and the midsummer die-off were similar to those of preceding years except that, with the shallower water, the beds were farther down the lake toward the dam. By August 5, the exposed bottom of the upper end of the lake was grown up shoulder-high with smartweed and rice cutgrass, *Leersia oryzoides* (Linnaeus) Swartz. The upper end of the lake was not again reflooded until late November.

The plant cycle of 1950 was similar to that of 1948.

Fleming (1949) studied the dissolved oxygen content, carbon dioxide content, and plankton of the water within the mats of vegetation and compared the data he obtained there with similar data from open water. He found a daily oxygen cycle in the plant mats, in which the dissolved oxygen reading usually was highest in the early afternoon and lowest at about 5 A.M. (Fleming 1949:18–9). Entomostraca and rotifers were less common in the vegetation than in the open water, but the plant mats, particularly of elodea, harbored considerable food for small fishes.

The mats of plants in the upper end of Ridge Lake harbored unknown numbers of small fish (usually both bass and bluegills) that appeared to stay within the plant-growth area throughout the entire summer season. These fish made poor growth; some bass fingerlings collected in this part of the lake in September, 1948, were less than 2 inches in length, although 3.5 months of age. The midsummer die-off of aquatic plants probably reduced the number of small fish living within the confines of the vegetation by forcing these fish into open water at a time when they could be utilized by larger bass. Thus, the July die-off of vegetation was probably a wholly desirable phenomenon from the standpoint of fish management.

The Creel Census

Ridge Lake was first opened to public fishing in June, 1942, and, with the exception of 1943, it has been opened each year since, under a system designed to give a complete record of all fish caught, the time spent in fishing, and the types of gear and kinds of bait used.

In most years of this study, the opening date for fishing was in June, as soon as possible after the bass fry were actively schooling, and the lake was kept open until August 31. Exceptions were in 1942, when the lake, opened to fishing in June, was kept open until October 31; in 1944, when the lake was opened on August 9 and closed on October 1; and in 1946, when the lake was opened on Saturday and Sunday of each week from April 6 until June 1, when it was opened for 5 days each week.

Except as noted above, public fishing periods were from 6 to 10 A.M. and from 3 to 8 P.M., Wednesday through Sunday of each week. The lake was closed on Mondays and Tuesdays. All fishing was done from seven boats owned by the Natural History Survey; for use of the boats no rental charge was made. The demand for these boats was so great that usually it was necessary for fishermen to make reservations for them in advance by mail or phone, particularly early in the season. Requests for boats during the first few days of the season were filled by drawing names from among those of the many applicants.

Fishermen coming from distances greater than 25 miles were allowed to reserve boats for both the morning and afternoon periods of any day on which they were permitted to fish. Those driving distances of less than 25 miles were limited to either a morning or an afternoon period of any day for which they were given permits. No bank fishing was allowed, because such fishing would have made impossible the collecting of complete fishing records and because the banks bordering the lake are very steep and the control of bank erosion was and is a problem difficult of solution.

All boats were stationed at the pier or boat dock immediately below the laboratory. Before each fishing period, fishermen having reservations for that period were checked in at this pier, where each submitted his state fishing license in return for a Ridge Lake fishing permit. On each permit were recorded the fisherman's name, his address, and the time of day when he began fishing. At the end of the fishing period or sooner, if he became tired, the fisherman returned to the pier,

Fig. 7.—Ridge Lake fisherman with his catch arranged for the rapid taking and recording of pertinent data. As anglers brought in their catches, the length, weight, and fin-clip mark of each fish were recorded by an employee of the Illinois Natural History Survey. A sample of scales from each fish was taken for age determination, and a record was made of time spent in fishing and kinds of bait on which the fish were caught.

fig. 7, where the time of day was recorded on his lake fishing permit card. The fisherman was questioned about the baits and tackle he used, and the information obtained was recorded on the permit card. If the fisherman had brought in fish, these were weighed and measured, and a few scales from each were taken for later use in studies of age and growth rates. The scales from each fish were placed in a small envelope, and the length and weight of the fish were recorded in appropriate spaces on the outside. Any fin mark (clipped fin) was noted, both on the fishing permit card and on the scale envelope. After all pertinent data were recorded, the fisherman was given his state license and the legal-sized fish of his catch and allowed to make a future reservation. Fishermen were very co-operative, once the system was known, particularly those who lived within a radius of a few miles and fished the lake often.

Previous to 1946, fishermen were not allowed to take largemouth bass of less than 10 inches. But in 1946 and following years, they were asked to bring in all bass, as well as all bluegills, they caught, regardless of sizes. Bass of less than 10 inches in length were not considered in a fisherman's limit of 10 legal-sized fish; so that a fisherman was allowed to catch and bring to the boat dock 10 legal-sized bass and any number of illegal-sized ones. The bass of less than 10 inches in length were left with the census taker at the boat dock. No creel limit was placed on bluegills, but no one fisherman ever exceeded the Illinois Fish Code limit of 50 in a single day. Since July 1, 1939, there has been no length restriction on bluegills taken by fishermen in Illinois.

Prior to 1945, the use of live minnows for bait was prohibited by regulation at Ridge Lake. This regulation, the object of which was to prevent the introduction into the lake of undesirable species of fishes, resulted in much dissatisfaction among fishermen. In 1945, and thereafter, fishermen were allowed to fish with live minnows after their minnow buckets had been inspected at the boat dock for young carp, suckers, and goldfish, which were removed when found.

The periods in which the lake was open to public fishing during the years 1942 through 1950 (this report does not extend into the 1951 fishing season) were as follows:

1942—June 17 through October 31 (5 days a week, but fishermen were present on the lake on only 15 days in September and October)

1943—No public fishing

1944—August 9 through October 1 (5 days a week)

1945—June 20 through August 31 (5 days a week)

1946—April 6 through August 31 (week-ends, 2 days a week, during April and May; 5 days a week in other months)

1947—June 11 through August 31 (5 days a week)

1948—June 10 through August 29 (5 days a week)

1949—June 15 through August 31 (5 days a week)

1950—June 15 through August 31 (5 days a week)

The Draining Census

In March of 1943, and thereafter at intervals of 2 years (1945, 1947, 1949, and 1951), Ridge Lake was drained, the fish population was censused, and selected fish were fin-clipped and returned to the lake as soon as a sufficient amount of water had collected behind the dam. Through such an operation, the population was culled of small or otherwise undesirable fish. Draining was usually done during the latter part of March, when the water was cold and fish could be handled with little or no loss. In most years, spring rains could be counted upon to refill the lake basin within a few weeks, often before the exposed bottom had had sufficient time to dry out below a surface crust. Only in 1949, when local spring rains were less than normal, did the lake fail to refill by May 15, following a March draining. In that year, the water covered an area of about 11 acres on June 1 and remained practically constant until November.

For the 1943, 1945, and 1947 censuses, a temporary fish screen was built, about 100 yards below the dam, across the section of Dry Run Creek that served as the outlet channel for the lake, fig. 8. This screen was made of 1-inch-mesh poultry netting, two 4-foot widths long enough to extend across the outlet channel. The two 4-foot widths were overlapped 1 foot on one edge and fastened with small hog rings to make a single strip of netting 6 feet wide. One edge of the netting was supported 3 feet above the stream bed on steel fence posts driven at intervals across the stream channel; the free or lower edge of the netting was brought well upstream from the posts and staked in the bottom of a 1-foot trench dug across the channel. Then the trench was filled with gravel, which buried the lower edge of the netting so deep that it would not pull loose.

On all censuses, the stilling basin at the base of the concrete surface spillway was used for holding fish to be returned to the lake. Weep holes in a 4-foot header wall across the lower end of this basin were plugged, and the basin above the wall was pumped full of water from the lake before any water was released through the outlet valve.

Through tests run in the first two draining operations, it was discovered that no fish came through the outlet valve until the lake level had been lowered more than 10 feet (lake depth 25 feet from the spillway crest to the bottom of the outlet). As the valve gate is 4 feet square, the lake probably could be drained in 24 hours with the valve wide open. However, the flow resulting from a wide-open valve would top almost any screen that could be built across the stream channel and cause erosion of the stream banks below the outlet. The most the valve was ever open in actual draining operations was 36 inches and then only for a matter of minutes. Draining of the lake was accomplished in about 4 or 5 days with the valve open usually 18 to 24 inches and with frequent closing of the valve for cleaning the screen. The valve was never left open at night or when it was unattended.

When the lake level was down 12 to 15 feet, fish came through the outlet valve in small numbers; it was not until the lake level was down 18 to 20 feet that the fish came through in quantity. When the lake level was down about 18 feet, the valve was opened for a few minutes, and then closed while the fish that had come through were being handled. Fish to be saved for restocking the lake were separated out and moved immediately into the spillway stilling basin. Those of value for stocking new lakes and ponds were weighed, counted, and placed in a tank truck. All other fish were sorted by species and sizes, and representative samples were weighed and measured individually; the rest were weighed in groups of 100 to 200 and counted. When all or most of the water, except that constantly running in the stream channel, had flowed out of the lake basin, the valve was closed, and water was allowed to collect behind the valve for an hour or so. The water was then released, and usually more fish were washed through with it. This pro-

Fig. 8.—Temporary fish screen used in draining censuses. For fish censuses in 1945 and 1947, a temporary screen constructed of 1-inch-mesh poultry netting was installed across the stream channel below the outlet of Ridge Lake.

cedure was repeated four or five times, until no more fish came through. In the meantime, a crew of several men walked over the lake basin to collect fish that had become stranded.

As the temporary screen described above was located 100 yards below the lower end of the outlet tunnel, on each draining operation several pools in the stream channel between the lower end of this tunnel and the screen had to be pumped out and the fish collected. In 1948, a permanent concrete base and slotted posts to hold removable screens were built only a short distance below the lower end of the outlet tunnel, so that the 1949 and 1951 draining and censusing operations were simplified, fig. 9.

The concrete outlet tunnel had been poured before the dam was constructed; it was located in an excavation near the opposite end of the dam site from, and parallel to, the natural stream channel. While the tunnel was being built, runoff water was flowing in the natural stream channel across the dam site. After the concrete tunnel had been completed and before any clay was moved to the dam site for the fill, a diversion ditch was dug between the upper end of the concrete tunnel and the stream channel, to enter the latter about 150 yards above the dam site. The stream flow was then directed through the diversion ditch to the concrete tunnel, and the dam was built across the stream channel, leaving a blind channel or ditch (the old stream channel), about 100 yards long and several feet across, between the head of the diversion ditch and the dam. This blind channel was never filled in and still contained 5 inches of water when the rest of the lake basin was drained in 1943; it was believed to have been the hiding place of an estimated 473 small bass that escaped the first census, 87 of which appeared in

Fig. 9.—Improved type of fish screen used in draining censuses. A permanent screen was built below the outlet of Ridge Lake in 1948. It consisted of a wide concrete base, wing walls, and a center post double slotted to hold removable screen frames and planks. Planks placed below the screen frames created a head of water in the basin between the outlet and the screen and reduced the water pressure on the screen if the latter became partially clogged with debris. Screen frames could be raised for cleaning.

1943 as unmarked fish (see page 241). Attempts to seine this ditch were futile because of the hip-deep mud.

By the time of later drainings (1945, 1947, 1949, and 1951), silting and sloughing-off of the banks had reduced the depth of water in this blind channel to 3 inches or less; here large fish, the backs of which could be seen readily, were caught with dip nets. Some small fish probably have escaped each census by staying in this blind channel. Poisoning of this channel was considered impractical because fish held in the spillway basin had to be returned to the refilled diversion ditch in the lake basin after only a small volume of water had collected behind the gate of the outlet valve.

An attempt in 1949 to poison Dry Run Creek within the lake basin was a failure, presumably because of the low water temperature. It is probable that none of the toxicant entered the blind channel near the dam, as the outlet valve was not kept closed long enough for water to back up into this channel from the diversion ditch.

On each census after the lake was drained and all fish were collected (that could be collected), the outlet valve was closed and water was allowed to collect in the diversion ditch above this valve. When this ditch was bank-full of clear water for 150 or more yards above the valve (usually about 12 hours after the valve was closed), the amount of water

Fig. 10.—Handling fish at Ridge Lake. When Ridge Lake was ready for restocking after a draining operation, selected fish to be returned to the water were handled in lots of 50 to 100. The fish, held in the stilling basin at the lower end of the concrete surface spillway, were captured and placed in a stock tank (left of center). From this they were removed individually and weighed, measured, "scaled" (had a few scales removed for later age determination), marked (fin-clipped), or had previous marks recorded, and placed in a second stock tank (lower left). When the second tank became crowded, the fish were transferred quickly to covered tubs on a horse-drawn sled, hauled over the dam, and replaced in the lake.

Fig. 11.—Marking bluegill at Ridge Lake. Each new fish (unmarked) returned to the lake after a draining census was marked by the removal of one fin. Most bluegills live only about 4 to 5 years, and few of them appeared in more than one of the spring censuses after being marked. Many bass appeared in several censuses, because their normal life span in Ridge Lake is 8 to 10 years.

was considered sufficient to begin restocking the lake with the fish held in the stilling basin at the base of the surface spillway. As the fish selected for the restocking had not been previously processed, a work station was set up on the edge of the spillway stilling basin with two large stock-watering tanks filled with clean water and supplied with aerating pumps, fig. 10. A table, measuring boards, and weighing scales were set up nearby. The fish were moved, 50 to 100 at a time, from the stilling or holding basin to one of the stock tanks; from this they were removed individually and weighed, measured, "scaled" (8 to 10 scales removed from side of fish below the dorsal fin), fin-clipped (or had previous fin-clip recorded), and placed in the second stock tank. When this second tank became crowded, the fish in it were transferred quickly to covered tubs on a horse-drawn sled, hauled over the dam, and replaced in the lake. No fish that appeared sluggish or emaciated, or that showed evidence of injury from its passage through the outlet valve and tunnel, was used in the restocking. On no census was there any evidence of undue mortality among the fish that were returned to the lake. Operational mortality was believed to have been rather low, because a large percentage of the marked bass returned to the lake after each census were either caught by fishermen or recaptured in subsequent censuses.

In the 1943, 1945, and 1947 censuses, when 1-inch-mesh poultry netting was used for the temporary fish screen, many small fish passed through this screen with the water. An estimate was made of the number of these fish in 1945 and 1947, but not in 1943, when, because a dominant brood of 5- to 8-inch bass was present, the number was probably lowest.

When the permanent concrete frame for fish screens was built below the dam in 1948, the removable screens to fit this frame were covered with quarter-inch-mesh hardware cloth. This small mesh was no more satisfactory for gaining an accurate count of the small fishes than was the 1-inch mesh, as thousands of small bluegills became gilled in the screen mesh. The fish impeded the flow of water through the screen and stopped draining operations until they could be removed. It became an impossible task to make any count of these young. For the 1951 census the screen frames were covered with 1-inch-mesh hardware cloth, and no attempt was made to estimate the numbers of small bluegills less than 2 inches long that went through; however, toward the end of the draining operation a fine-mesh dip net, held in the flow below the screen for 1 minute, caught 381 small bluegills weighing 2.75 pounds.

As mentioned previously, fish were fin-clipped prior to their being returned to the lake following a census, fig. 11. The fin clipped in the 1943 census was the left pectoral; in the 1945 census the right pectoral; in the 1947 census the left pelvic; in the 1949 census the dorsal; and in the 1951 census the left pectoral. In each census, only the fish that had not been fin-clipped previously were marked. Thus, all fish more than 22 months old (except the few that as small fish had escaped capture by staying in the lake basin) bore marks that assigned them to specific 2-year periods; for example, a 3.5-pound bass caught in 1949 showed the left pectoral fin missing, which indicated that it had been spawned in 1941 or 1942 and marked when being returned to the lake after the 1943 census.

Population Dynamics

The 435 largemouth bass with which Ridge Lake was stocked in 1941 were wild fish netted from Craborchard Lake near Carbondale, Lake Chautauqua near Havana, and Lake Glendale near Robbs, all in Illinois. Table 2 lists the lakes from which these bass were taken, the numbers, weights, and length ranges of the bass, and the dates of their introduction into Ridge Lake.

Before being released, all the bass were fin-clipped for later identification. From each Craborchard Lake bass, the left pectoral fin was clipped, from each Lake Chautauqua bass, the right pectoral, and from each Lake Glendale bass, the dorsal.

Table 2.—Source, number, weight, and length range of largemouth bass used in stocking Ridge Lake.

Source of Fish	Number	Weight, Pounds	Range of Lengths, Inches	Date of Stocking
Craborchard Lake	58	24.1	6.5–11.5	April 30, 1941
Lake Chautauqua	42	42.9	8.5–17.0	May 1, 1941
Lake Glendale	335	29.5	5.0–7.0	June 18, 1941
Total	*435*	*96.5*	—	—

No largemouth bass from outside sources have been placed in Ridge Lake since the original 435 were introduced in 1941. Evidence presented later (pages 265 and 266) indicates that many of these original bass were sufficiently injured during netting operations or in transportation to Ridge Lake to cause them to die within a short time after their introduction into the lake, particularly the Lake Glendale fish that were caught and moved in June.

Bluegills were first placed in Ridge Lake on June 27, 1944, when 107 of these fish, 4.5 to 7.5 inches in length, were brought in from Lake Chautauqua. Of these, 7 were dead or dying on arrival, but 100 were released. Later in the same year, on July 13, 29 bluegills between 5 and 6.5 inches in length were brought to the lake from a strip-mine pond near Danville, Illinois. No weights were taken of either group of bluegills. From each Lake Chautauqua fish was clipped the left pectoral fin and from each Danville fish the right pectoral. No other stocks of bluegills have been introduced since these 129 were released in 1944.

In April, May, and June of 1949, three groups of warmouths, *Chaenobryttus coronarius* (Bartram), totaling 138 fish were placed in Ridge Lake to test the ability of these fish to expand their popu-

Table 3.—Largemouth bass, bluegills, and other fish that were permanently removed from Ridge Lake by angling and in draining operations during the 1941–1951 study period. Not included in figures for the draining censuses were fish, less than a year old, so small that accurate counts were not possible.

Year	Permanently Removed by Angling						Permanently Removed in Draining Censuses					
	Largemouth Bass		Bluegills		Other Fish		Largemouth Bass		Bluegills		Other Fish	
	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds
1941.	51	8.23	—	—	—	—	—	—	—	—	—	—
1942.	485	271.67	—	—	—	—	—	—	—	—	—	—
1943.	32	17.82	—	—	—	—	2,783	482.60	—	—	36	9.10
1944.	466	270.46	—	—	32	37.03	—	—	—	—	—	—
1945.	409	356.87	2	1.22	7	5.15	994[1]	197.01	10,000[2]	100.00[2]	762	463.21
1946.	362	263.35	1,686	228.03	284	45.97	—	—	—	—	—	—
1947.	181	195.80	644	111.61	38	5.65	2,117	79.62	64,868	3,194.97	663	566.22
1948.	648	460.03	5,831	826.03	241	103.95	—	—	—	—	—	—
1949.	594	540.51	15	2.92	6	2.82	1,012	102.97	19,714	1,564.31	110	52.11
1950.	515	330.28	895	120.31	276	85.38	—	—	—	—	—	—
1951[3]	—	—	—	—	—	—	707	136.34	51,307	1,761.90	1,079	154.12
Total[4]	*3,743*	*2,715.02*	*9,073*	*1,290.12*	*884*	*285.95*	*7,613*	*998.54*	*145,889*	*6,621.18*	*2,650*	*1,244.76*

[1] Figure includes an estimated 500 very small fish.
[2] Figure estimated.
[3] This report does not include the angling season of 1951.
[4] Total largemouth bass, 11,356 weighing 3,713.56 pounds; total bluegills, 154,962 weighing 7,911.30 pounds; total other fish, 3,534 weighing 1,530.71 pounds; grand total of fish, 169,852 weighing 13,155.57 pounds.

lation when introduced into water inhabited by a dominant bass population and a reduced population of bluegills. The warmouths varied in length between 3 and 9 inches and were fin-clipped for later identification.

Neither largemouth bass, bluegills, nor warmouths are indigenous to Dry Run Creek. An application of fish poison to the part of the creek within the lake basin, prior to the impoundment of the water, resulted in a kill of the following species:* stoneroller, *Campostoma anomalum* (Rafinesque); creek chub, *Semotilus atromaculatus* (Mitchill); creek chubsucker, *Erimyzon oblongus* (Mitchill); silverjaw minnow, *Ericymba buccata* Cope; green sunfish, *Lepomis cyanellus* Rafinesque; longear sunfish, *Lepomis megalotis* (Rafinesque); bluntnose minnow, *Hyborhynchus notatus* (Rafinesque); white sucker, *Catostomus commersonnii* (Lacépède); yellow bullhead, *Ameiurus natalis* (Le Sueur); and black bullhead, *Ameiurus melas* (Rafinesque).

* Names from American Fisheries Society (1948), except the scientific name for the black buffalo and the common and scientific names for the silverjaw minnow, all of which are from Hubbs & Lagler (1947).

None of these appeared in the lake in numbers during the 1941–1951 study period except the green sunfish, the black bullhead, and the yellow bullhead. Carp, *Cyprinus carpio* Linnaeus, and one black buffalo, *Ictiobus niger* (Rafinesque), appeared in the 1947 draining census. A few carp appeared in the 1951 census. These fish are believed to have moved up Dry Run Creek from the Embarrass River and to have entered the lake by swimming up over the surface spillway during periods of high water.

Each time the lake was drained, fish of the species indigenous to Dry Run Creek (largely green sunfish and black bullheads) were removed, but within the next 2 years following each draining a few more of these species had worked down into the lake from the stream above and had produced small numbers of young. Although green sunfish never became a substantial part of the population, usually some were present. Black bullheads were particularly numerous during the 1943–1946 period and many taken by fishermen were more than a pound in weight.

The numbers and weights of fishes per-

Table 4.—Largemouth bass, bluegills, and other fish taken in draining censuses of Ridge Lake in 1943, 1945, 1947, 1949, and 1951. The bass and bluegills were separated into groups on the basis of previous fin markings or lack of such markings. The other fish were separated into groups on the basis of size: green sunfish and warmouths were considered large if 6 inches or longer, bullheads if 7 inches or longer, and carp if 12 inches or longer. No fish except some of the bass and bluegills (and warmouths in 1951) were returned to the lake after any of the censuses. The numbers of bass and bluegills returned are shown in table 5.

Group	1943 Census		1945 Census		1947 Census		1949 Census		1951 Census	
	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds
Bass										
1941 stock	17	55.10	10	39.63	1	6.75	1	7.00	—	—
1941–1942	4,754[1]	812.30[1]	543	416.20	63	153.75	23	91.17	4	19.65
1943–1944[2]	—	—	1,088[3]	256.98[3]	20	48.33	9	33.46	2	9.09
1945–1946	—	—	—	—	2,425	357.94	77	201.74	11	44.12
1947–1948	—	—	—	—	—	—	1,929	574.46	173	362.68
1949–1950	—	—	—	—	—	—	—	—	1,320	463.09
Total	*4,771*	*867.40*	*1,641*	*712.81*	*2,509*	*566.77*	*2,039*	*907.83*	*1,510*	*898.63*
Bluegills										
1944 stock	—	—	61	25.74	2	0.85	—	—	—	—
1944–1946	—	—	10,000[4]	100.00[4]	66,627[5]	3,478.22[5]	90	30.62	—	—
1947–1948	—	—	—	—	—	—	19,624	1,533.69	663[6]	132.47[6]
1949–1950	—	—	—	—	—	—	—	—	51,300[7]	1,760.25[7]
Total	—	—	*10,061*	*125.74*	*66,629*	*3,479.07*	*19,714*	*1,564.31*	*51,963*	*1,892.72*
Green Sunfish										
Large	5	0.98	162	30.74	—	—	58	13.02	—	—
Small	8	0.82	56	3.36	124	8.10	—	—	—	—

WARMOUTHS										
Large	—	—	—	—	—	—	—	—	47[8]	13.17[8]
Small	—	—	—	—	—	—	—	—	869	57.97
Total	—	—	—	—	—	—	—	—	*916*	*71.14*
BLACK BULLHEADS										
Large	23	7.30	336	404.11	209	139.27	52[9]	39.09[9]	100	61.15
Small	—	—	208[4]	25.00[4]	273	23.60	—	—	59	4.93
Total	*23*	*7.30*	*544*	*429.11*	*482*	*162.87*	*52*	*39.09*	*159*	*66.08*
CARP										
Large	—	—	—	—	57[10]	397.25[10]	—	—	4	16.90
Small	—	—	—	—	—	—	—	—	—	—
Total	—	—	—	—	*57*	*397.25*	—	—	*4*	*16.90*
GRAND TOTAL	4,807	876.50	12,464	1,301.76	69,801	4,614.06	21,863	2,524.25	54,552[11]	2,945.47[11]
Per acre	267	48.7	692	72.3	3,878	256.3	1,215	140.2	3,030.7	163.6

[1] Figure includes estimated 473 bass weighing estimated 80.41 pounds that escaped the 1943 census.
[2] Some of the fish in this group were spawned in 1941 or 1942, escaped the 1943 draining census, and appeared as unmarked fish in the census of 1945, when they were given the same mark as the fish spawned in 1943 and 1944.
[3] Figure includes an estimated 500 bass from 2 to 5 inches long weighing 10 pounds.
[4] Estimated summer spawn of 1944.
[5] Figure includes 6,873 large bluegills (6 or more inches in length) weighing 1,104.53 pounds, 49,754 small bluegills (3 to about 6 inches in length) weighing 2,223.69 pounds, and estimated 10,000 very small bluegills (1.5 to about 3 inches in length) weighing estimated 150 pounds.
[6] Complete removal of bluegills was attempted in the 1949 census. The large bluegills reported here were fish that escaped the census of 1949 and re-established the population in the lake following that census.
[7] Figure includes estimated 1,000 very small bluegills (1.5 to about 3 inches in length) weighing 35 pounds.
[8] Warmouths were first placed in the lake in 1949. Included in the figure reported here are some of the original stock and individuals of the first spawn.
[9] Figure includes 18 yellow bullheads weighing 7.36 pounds.
[10] Figure includes 1 black buffalo weighing 7.5 pounds.
[11] Figure does not include 22 minnows weighing 1.95 pounds and consisting of various species used for bait by fishermen.

manently removed from the lake during the 1941–1950 period by angling (yield) and of those permanently removed in the 1943–1951 draining censuses (culling operations) are shown in table 3. Not included in figures for the draining censuses were fish, less than a year old, so small that accurate counts of them were not possible. In 1941 and 1943, the lake was not opened to the public, and the angling records for both years are those of Natural History Survey personnel who were taking samples of fish for growth studies. Many additional bass were taken by Survey personnel and released alive in 1941 and 1943; those listed in table 3 were fish so severely hooked as to make their survival uncertain.

The fact that, from original stocks of only 435 bass and 129 bluegills, more than 11,300 bass and more than 154,000 bluegills were removed from Ridge Lake during a 10-year period of operation is good evidence that both species are capable of expanding their populations to approach the carrying capacity of waters into which they are introduced and of maintaining these populations indefinitely under a system of operation such as has been followed at Ridge Lake. In this experiment, the bluegills showed a higher reproduction rate than did the bass. Other species, primarily black bullheads and green sunfish, were able to survive and in some years to increase their numbers under the predation pressure of a strong bass population.

Whereas table 3 lists the numbers and weights of fishes permanently removed from the lake by angling and in the draining censuses, table 4 lists the numbers and weights of fishes taken in these draining censuses and table 5 lists the numbers and weights of fishes returned to the lake following the censuses. Both tables 4 and 5 are arranged to show data on the individual fin-clip groups of largemouth bass and bluegills for each of the five censuses in which they were involved. Green sunfish, bullheads, and other indigenous fishes, removed from the lake on each census, and also introduced warmouths, have been separated in the census tabulations, table 4, into "large" and "small" categories. Any green sunfish or warmouth of 6 inches or more in length

Table 5.—Largemouth bass and bluegills returned to Ridge Lake following each of five draining censuses. Fish were separated into groups on the basis of previous fin markings or lack of such markings.

Group	1943 Census		1945 Census		1947 Census		1949 Census		1951 Census	
	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds
Bass										
1941 stock	15	47.90	9	35.08	1	6.75	1	7.00	—	—
1941–1942	1,973[1]	336.90[1]	496	379.59	61	148.95	23	91.17	3	14.90
1943–1944[2]	—	—	142	101.13	20	48.33	9	33.46	2	9.09
1945–1946	—	—	—	—	310	283.12	77	201.74	9	36.10
1947–1948	—	—	—	—	—	—	917	471.49	170	335.05
1949–1950	—	—	—	—	—	—	—	—	619	367.15
Total	*1,988*	*384.80*	*647*	*515.80*	*392*	*487.15*	*1,027*	*804.86*	*803*	*762.29*
Per acre	110	21.4	36	28.7	22	27.1	57	44.7	45	42.4
Bluegills										
1944 stock	—	—	61	25.74	2	0.85	—	—	—	—
1944–1946	—	—	—	—	1,759	283.25	—	—	—	—
1947–1948	—	—	—	—	—	—	—	—	—	—
1949–1950	—	—	—	—	—	—	—	—	656	130.82
Total	—	—	*61*	*25.74*	*1,761*	*284.10*	—	—	*656*	*130.82*
Per acre	—	—	3	1.4	98	15.8	—	—	36	7.3

[1] Figure includes estimated 473 bass weighing estimated 80.41 pounds that escaped the 1943 census.
[2] Some of the fish of this group were spawned in 1941 or 1942, escaped the 1943 draining census, and appeared as unmarked fish in the census of 1945, when they were given the same mark as the fish spawned in 1943 and 1944.

was considered "large," and any bullhead of 7 inches or more in length was placed in the same category. The 57 carp taken in 1947 averaged almost 7 pounds each and those in 1951 about 4 pounds each; no "small" carp (less than 12 inches in length) were taken.

Comparison of tables 3, 4, and 5 will show that following each draining census many bass and bluegills were not returned to the lake. Only in the year 1943 were bass smaller than 8 inches total length returned to the lake. Most of the fish making up the early 1943 population of small bass (bass other than the 1941 original stock) were 6 to 9 inches in length. In the 1943 census operation, the population of small bass was reduced by about 58 per cent (4,754 reduced to 1,973, according to tables 4 and 5). Only 1,500 of the 4,281 bass actually taken in the 1943 census were returned to the lake as marked fish. However, other small bass were later found to be in the lake. During the summer of 1943 when Ridge Lake was not opened to the public, Natural History Survey personnel took, and released, 363 bass of the size range of the 1941 and 1942 broods; 276 of these were fish that had been marked and 87 were unmarked fish. On the basis of the relationship between unmarked fish and marked fish in the catch it was calculated that, in the lake, there were about 473 of these small bass that had escaped capture, possibly by remaining, at the time of the census, in the blind stream channel between the mouth of the diversion ditch and the dam. This number and their interpolated weight were added to the census tabulation, table 4, and to the tabulation of small bass actually replaced in the lake following the census, table 5.

In the 1949 census, there was a large number of unmarked bass ranging between 9 and 10 inches in length. These fish could be expected to grow to 10 inches or larger during the 1949 fishing season and, as fishermen were asked to bring in all bass caught, regardless of size, it was assumed that these fish might add to the 1949 yield, even though they failed to reach the 10-inch legal length. For these reasons, bass of 9 inches or larger were returned to the lake following the 1949 census. In the 1951 census, 277 unmarked bass 8 to 10 inches long were marked and returned to the lake, along with 342 unmarked bass of 10 inches or longer, table 5.

At the time of the 1945 draining census, only 61 of the 129 bluegills with which Ridge Lake was stocked in 1944 were recovered, table 4. These had produced a large number of young in 1944, ranging in size from 1.5 to 2.5 inches by March of 1945. A rough estimate of the number that came through the screen below the outlet was 10,000, weighing 100 pounds. Others probably remained within the lake basin, although the blind stream channel near the dam had filled in considerably since the 1943 draining.

The 61 bluegills remaining from the 1944 stock were returned to the lake following the 1945 census. In the 1947 census 2 years later, the bluegill population was found to consist of 2 of these 61 fish; 6,873 other bluegills of 6 or more inches in length, weighing 1,104.53 pounds; 49,754 bluegills of 3 to about 6 inches in length, weighing 2,223.69 pounds; and approximately 10,000 bluegills of 1.5 to about 3 inches in length, weighing approximately 150 pounds. These groups made a total of 66,629 fish, weighing 3,479.07 pounds, table 4.

Following the draining operation in 1947, 1,759 of the larger unmarked bluegills were fin-clipped (left pelvic fin) and returned to the lake along with the 2 fish from the original stock of 1944, making a total of 1,761 fish weighing 284.1 pounds, table 5. When the fish population was censused again in 1949, only 90 of these marked bluegills were retaken and the entire bluegill population, exclusive of an unestimated number of fish about 1 inch in length, numbered only 19,714 fish, weighing 1,564.31 pounds, table 4. This poundage was less than half of that collected in the 1947 census.

An attempt was made in the 1949 draining census to remove all bluegills from the lake. Although 19,714 of these fish were removed, table 4, and none returned, and the stream channel and diversion ditch were treated with a heavy dosage of cubé (5 per cent rotenone) to poison the escaped fish, the attempt was unsuccessful. In March, 1951, when the fish population was again censused, nearly

52,000 bluegills were found to be present, showing that many small fish had escaped the treatment. Small bluegills that survived the 1949 draining and poisoning operations must have been subjected to heavy predation from bass, because in that year the large bass population that had developed in the 1947–1948 period was concentrated in 11 acres of water having much less than one-half of the volume of the full lake. At the time of the draining, these small bluegills may have lived in eddies of the flowing creek, or in shallow pools on the lake bottom where water was trapped by uneven deposition of silt, until the rising water behind the dam flooded their hiding places and released them to the open water. Scales collected from a number of the larger bluegills taken in the 1951 census indicated that these fish must have been survivors of the 1949 census. Since 663 large bluegills appeared in the 1951 census, table 4, it seems quite probable that the number that escaped the 1949 census may have numbered several thousand, most of which were eaten by bass. As it was quite obviously impossible to rid the lake of bluegills without allowing the basin to dry out thoroughly, it was decided to return 656 of the larger bluegills to the water following the 1951 census, table 5.

Table 6.—Numbers and poundages of largemouth bass, bluegills, green sunfish, and black bullheads taken by fishermen from Ridge Lake, 1941–1950. In addition to the fish included in this table were 5 large warmouths, weighing 1.98 pounds, caught in 1949, and 50 small warmouths, weighing 3.12 pounds, and 3 large warmouths, weighing 1.07 pounds, caught in 1950.

Year	Largemouth Bass				Bluegills			
	Ten Inches or Longer		Less Than 10 Inches		Six Inches or Longer		Less Than 6 Inches	
	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds
1941[1]	1	1.25	50	6.98	—	—	—	—
1942	323	225.74	162	45.93	—	—	—	—
1943[1]	3	7.92	29	9.90	—	—	—	—
1944	466	270.46	—	—	—	—	—	—
1945	409	356.87	—	—	2	1.22	—	—
1946	206	233.04	156	30.31	733	144.29	953	83.74
1947	149	186.57	32	9.23	416	95.07	228	16.54
1948	363	396.00	285	64.03	2,301	509.71	3,530	316.32
1949	577	535.21	17	5.30	12	2.76	3	0.16
1950	236	255.46	279	74.82	386	83.30	509	37.01
Total	*2,733*	*2,468.52*	*1,010*	*246.50*	*3,850*	*836.35*	*5,223*	*453.77*

Year	Green Sunfish				Black Bullheads			
	Six Inches or Longer		Less Than 6 Inches		Seven Inches or Longer		Less Than 7 Inches	
	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds	Number	Weight, Pounds
1944[2]	2	0.70	—	—	30	36.33	—	—
1945	1	0.38	—	—	6	4.77	—	—
1946	79	19.31	185	12.90	17	13.60	3	0.16
1947	9	2.02	27	2.34	2	1.29	—	—
1948	108	26.56	63	7.40	67	69.51	3	0.48
1949	—	—	—	—	1	0.84	—	—
1950	17	4.38	19	1.14	187	75.67	—	—
Total	*216*	*53.35*	*294*	*23.78*	*310*	*202.01*	*6*	*0.64*

[1] Lake not open to public fishing in this year.
[2] No green sunfish or black bullheads were caught in years prior to 1944.

The tabulation of fishes removed by angling, table 3, includes all of the fish taken on hook and line, regardless of whether they were large enough to interest anglers. In table 6, the information on yield has been expanded to show the relative numbers and weights of fishes of desirable and undesirable sizes. During the period between the opening of Ridge Lake and June 30, 1951, the minimum legal length for largemouth bass in Illinois was 10 inches. In 1946 and subsequent years, fishermen at Ridge Lake were requested to bring in all fish they caught, regardless of size. In table 6, bass are separated into those of 10 inches or more in length and those of less than 10 inches.

Minimum lengths for desirable sizes of fishes of other species caught at Ridge Lake have been set arbitrarily at 6 inches for bluegills, green sunfish, and warmouths, and 7 inches for bullheads. Table 6 shows that among the largemouth bass and bullheads taken by anglers the numbers of fishes of desirable sizes far outnumbered those of undesirable sizes. Among the bluegills and green sunfish, however, the smaller fishes taken by anglers outnumbered the fishes of desirable sizes.

The poundages of fish per acre of water are shown in table 7 for the draining censuses and for the fish returned to the lake after censusing, and in table 8 for the annual catches by fishermen. Of particular interest in table 7 is the gradual reduction in poundage of bass supported by the lake from March, 1943, to March, 1947, and the rapid recovery that took place between March, 1947, and March, 1949. This reduction and recovery in poundage of bass appears to bear no relationship to the annual catch of bass made by anglers, table 8 (although combined bass yields of 1945 and 1946 were higher than the combined yields of 1943 and 1944); the bass yield in 1948 (25.6 pounds per acre) was considerably higher than that in any prior year and yet, after this high yield of 1948, the draining census of 1949, table 7, showed a bass population that exceeded that found in any other census.

The actual gain in poundage of largemouth bass during each of the four 2-year periods may be determined by subtracting the poundage of the original stock or the poundage of the bass replaced in the lake after any given draining census from the poundage taken on the next census following, table 7, and to this figure adding the poundage of fish taken by anglers during the fishing seasons between these two censuses, table 8.

Figured on this basis, the bass gain in the 1941–1943 period was 58.5 pounds per acre; in the 1943–1945 period, 34.2 pounds per acre; in the 1945–1947 period, 37.2 pounds per acre; in the 1947–1949 period, 59.8 pounds per acre; and in the 1949–1951 period, 53.5 pounds per acre. Thus, although the bass population reached a low point in the 1947 census, the actual gain of the 1945–1947 period was greater than that of the 1943–1945 period.

The bass gains of the 1941–1943 period, the 1947–1949 period, and the 1949–1951 period exceeded those of the other two periods, and it seems probable that with these gains the bass population approached the maximum poundage that the lake would support (approximately 50 pounds per acre).

Figured on the same basis as that used for bass, tables 7 and 8, the gain in bluegills was 204.7 pounds per acre in the 1945–1947 period, 123.2 pounds in the 1947–1949 period, and 112.1 pounds in the 1949–1951 period. It is difficult to estimate the maximum poundage of bluegills the lake will support, but, figured on the basis of the 1947 census, it might exceed 200 pounds per acre.

As may be seen in table 7, the total poundages of fish supported by Ridge Lake at the times of the various censuses varied widely. Because largemouth bass of the 1941 year-class made little or no growth in 1942, it is assumed that at the time of the census in 1943 the largemouth population was approaching the carrying capacity of the lake for this species. Theoretically, when other species are present along with largemouth bass, the total poundage of fish that can be supported by the lake may be greatly increased; except in 1947, when the bluegill population may have been nearing the potential maximum for bluegills alone, the populations of fishes other than bass prob-

Table 7.—Pounds of fish, per acre of lake, taken in draining censuses of Ridge Lake and pounds, per acre of lake, returned following each census, 1943–1951. The area of the lake was assumed to be 18 acres.

Year	Taken in Draining Census				Returned Following the Census		
	Large-mouth Bass	Bluegills	Other Fish	Total in Census	Large-mouth Bass	Bluegills	War-mouths
1941 (original stock)	—	—	—	—	5.3	—	—
1943	48.2	—	0.5[1]	48.7	21.4	—	—
1945	39.6	7.0	25.7[1]	72.3	28.7	1.4	—
1947	31.5	193.3	31.5[2]	256.3	27.1	15.8	—
1949	50.4	86.9	2.9[3]	140.2	44.7	—	—
1951	49.9	105.2	8.7[4]	163.8	42.4	7.3	2.9

[1] Black bullheads and green sunfish.
[2] Black bullheads, green sunfish, carp, and one black buffalo.
[3] Black bullheads, yellow bullheads, and green sunfish.
[4] Warmouth bass, black bullheads, carp, and miscellaneous minnows.

Table 8.—Pounds of fish per acre of lake (18 acres) taken by fishermen and fishing pressure at Ridge Lake, 1941–1950.

Year	Yield, Pounds per Acre				Fishing Pressure, Man-Hours per Acre
	Largemouth Bass	Bluegills	Green Sunfish	Black Bullheads	
1941[1]	0.5	—	—	—	—
1942	15.1	—	—	—	212
1943[1]	1.0	—	—	—	—
1944	15.0	—	+[2]	2.0	90
1945	19.8	0.1	+[2]	0.3	105
1946	14.6	12.7	1.8	0.8	168
1947	10.9	6.2	0.2	0.1	155
1948	25.6	45.9	1.9	3.9	320
1949	30.0	0.2	—	+[2]	220
1950	18.3	6.7	0.5[3]	4.2	224

[1] Lake not open to public fishing in this year.
[2] Less than 0.1 pound per acre.
[3] Consists of 0.3 pound per acre of green sunfish and 0.2 pound per acre of warmouths.

ably were much below the potential maximum.

In a review of table 7, this question may immediately arise: If a determination could be made of the maximum poundage of each of several fish species that can be supported individually by a lake, and then if all of these species could be placed together in the lake, what would be the relationship between the maximum poundage of this composite population of fishes that can be supported by the lake and a summation of the maximum poundages of fishes supported by the lake as individual species?

The data in table 7 cannot give a satisfactory answer, but they advance the suggestion that, while the diversification of species may improve the degree of utilization of available food and space and thereby add to the poundage of fish the lake can support, the maximum poundage of a composite population will be considerably less than the summation of the maximum poundages of individual species. Even in a bass-bluegill combination in which, in theory, the young of the bluegills should improve the food supply of bass, there is no evidence from this study that the bass population is able to expand to a poundage significantly greater than the lake supports when bluegills are absent. Rather, there is some indication that a large bluegill population has a depressing effect upon the bass population and that interspecific competition may exist.

Bass Spawn Inventory

The idea for an annual inventory of schools of largemouth bass fry at Ridge Lake originated on May 29, 1941, when the first schools of young of that year appeared. On this date, three separate schools of very small bass fry were located in shallow water close to the inner face of the dam; on May 30, what appeared to be the same schools were found in about the same locations, and several other schools were found in other parts of the lake.

From May 30 to June 7, 1941, a daily search for schools of largemouth bass fry was made. Two men in a small rowboat moved slowly around the lake shallows, one man rowing the boat backwards (stern foremost), and the other standing up in the stern for maximum vision. In this way, it was possible to spot the schools in the clear water at distances of about 25 feet and, at closer range, to make rough estimates of the total numbers of fry in the schools and to plot on a map of the lake the approximate position of each school.

On each succeeding day after May 29, the count of schools and the estimate of fry increased, until, on June 5, 38 separate schools were counted. (The fry in these schools had been spawned from survivors of the 100 sexually mature bass placed in the lake on April 30 and May 1, table 2.) On June 6, 26 schools were counted, and, in addition, many small groups of fry were seen scattered along the shore shelf,* indicating that some of the schools had broken up. On June 7, larger numbers of fry were observed scattered along the shore shelf than had been seen on the previous day, and fewer schools were enumerated. School counts were discontinued June 7.

* A shore shelf is a narrow ledge of earth cut by wave action at the water line in parts of the lake where the slope of the natural bank is steep. Water over this shelf varies between one-half and 2 inches in depth, and small fish, when over the shelf, are relatively safe from larger fish.

The figure accepted as the estimated number of bass fry for the spawning season, table 9, was the number for June 5, 76,000, the highest number recorded for any single day of the spawning season.

This technique of counting schools of bass fry and estimating numbers of young fish cannot be depended upon to give more than a very rough measure of the success of spawning at Ridge Lake for any given year. It is based on the assumption that all mature bass inhabiting this small body of water reach a condition of ripeness and spawn within a period of a few days. If eggs were deposited over a period longer than 6 or 7 days, the first eggs deposited would hatch, the young would school, and the schools would break up before the last nests of eggs were hatched. Once the fry in the schools begin to scatter, it is difficult to estimate the numbers of young, although a rough census of scattered fry can be made at Ridge Lake by counting small groups of fry along the shore shelf.

The estimates made of the numbers of bass fry in the individual schools are probably conservative. It was not considered desirable to capture and count these young fish, and visual estimates of numbers leave much to be desired. In the Ridge Lake censusing, no schools of fry were estimated to contain more than 3,000 fish, with the exception of one huge school found around the concrete spillway tower in 1951. The estimates for most schools ranged below 2,000.

Most schools of bass fry were found near shore in water of 1 to 6 feet in depth. A few were found well out from shore in the open water of the lake. Ordinarily, the schools of fry were seen fairly close to the surface of the water. Occasionally they were observed to sound and disappear from view for several minutes before reappearing near the surface. Most of the censusing work was done within a strip of water extending about 35 feet out in the lake from the water edge, and it is probable that some schools, ranging farther out, were missed. On each day of censusing, some schools may have escaped being censused because they were submerged.

The efficiency of censusing may be reduced by turbid waters, floating mats of algae, and rooted aquatic vegetation, either submergent or emergent. For example, in 1944, when the spawn estimate was only 1,000 fry, table 9, and in 1949, when it was 24,000, the censusing operation was handicapped by mats of floating algae. In both of these years, the enumeration of young bass was continued, after the schools had broken up, by counting the fry scattered along the shore shelf. In 1945, when the peak spawn was recorded, few floating algae were present, but dense beds of submerged aquatic plants (not at the time reaching the surface) were in the lake. In 1946 and in 1947, turbid water during the height of the spawning seasons so reduced the visibility that not until 3 or 4 days after the first schools were observed was it possible to make a comprehensive census.

Despite many possible sources of inaccuracies, the fairly uniform technique of censusing that was continued each year after it was established in 1941 gave comparative data that are very useful. The results of bass fry estimates, 1941 through 1950, were reported in a previous paper (Bennett 1951:237) and are repeated in table 9, along with an estimate of the 1951 spawn and the actual dates when the first schools of bass fry were seen in each year. Table 9 has been set up in two sections to emphasize the striking difference in the abundance of spawn between years in which the population was culled of small "yearling" fish (fish spawned the previous year) and years in which many of these fish were present.

Although the numbers shown in table 9 may be far from accurate, if these numbers are taken as indices of the relative abundance of young bass from year to year, it is believed that they are highly significant. In 1941, when the lake was first stocked with adult bass and in years when the lake was drained and restocked with only the larger fish, the average of the estimated numbers of fry (50,500) was about 8.6 times the average of the estimated numbers of fry found in alternate years when the lake was not drained and the fish population was not culled of small "yearling" fish. The difference between average numbers would have been much greater if the spawn count of 1942 had been omitted. The "yearling" fish present in 1942 (largely bass ranging in size from 6 to 11 inches) averaged larger than those present in any other comparable year (1944, 1946, 1948, or 1950). These bass were little interested in nest robbing or in predation on fish of fry sizes. They decimated the 1942 spawn, but their predation is believed to have taken place after the 1942 bass fry had grown to fingerling sizes.

Table 9.—Estimates of numbers of largemouth bass fry to reach schooling stage in years in which Ridge Lake fish population was culled of small "yearling" fish (fish spawned the previous year) in spring draining censuses, and similar estimates in years in which no draining censuses were made and many small "yearling" fish were present. The earliest dates on which bass fry were observed are listed.

Data for Years in Which Small "Yearling" Fish Were Removed in Spring Draining Censuses			Data for Years in Which Small "Yearling" Fish Were Present; Lake Not Drained		
Year	Estimated Number of Bass Fry	Earliest Date of Fry Appearance	Year	Estimated Number of Bass Fry	Earliest Date of Fry Appearance
1941	76,000[1]	May 29	1942	26,000[1]	May 14
1943	18,000[1]	June 10	1944	1,000[1]	June 4
1945	116,000	June 3	1946	2,500	June 5
1947	37,000	June 4	1948	0[2]	None
1949	24,000	June 3	1950	0[2]	None
1951	32,000	May 25	—	—	—
Total	*303,000*	—		*29,500*	—
Average	50,500	—		5,900	—

[1] Few fish other than largemouth bass were present in the lake.
[2] No schools of young bass could be found in 1948 and 1950. Extensive seining with a minnow seine produced no small bass in 1948; in 1950, one small bass was taken in one of five minnow seine hauls in the upper part of the lake.

Although, in 1948 and 1950, conditions were relatively good for censusing, no schools of bass fry were observed in either year. In 1948, a careful search was made for fry and fingerlings at approximately 2-day intervals from May 28 to June 20. The search included the area along the shore shelf late in this period, when schools, if they existed, should have broken up. "Yearling" bluegills and bluegill fry were abundant in all parts of the lake. On July 7, six hauls with a quarter-inch-mesh minnow seine in six locations in the upper end of the lake brought up hundreds of "yearling" bluegills and bluegill fry but not a single fingerling bass.

In 1950, the search for bass fry and fingerlings extended over approximately the same period as in 1948 (May 29 to June 12), with results approximating those of 1948. One bass fingerling was taken in one of five minnow-seine hauls made in the upper part of the lake on June 25, indicating that a few young bass of the current spawn were present in the lake. Small bluegills were numerous in these seine hauls, in spite of the fact that an attempt had been made to eradicate the bluegill population from the lake at the time of the 1949 census.

In 1951, bass fry first were observed on May 25, when six schools that were located contained an estimated 16,000 fish. The maximum count was made on May 29: 12 schools containing an estimated 32,000 fry. On this date, the largest school of bass fry ever observed at Ridge Lake was found over deep water (14 to 20 feet) around the concrete spillway tower near the dam. This school extended completely around three sides of the tower, a linear distance of about 30 feet, and was approximately 8 feet broad throughout its extent. It was estimated to have contained 10,000 bass, and it remained close to the tower until it began to break up on June 2. Only a remnant of this school could be found around the tower on June 6.

Spawning Success and Population Density

Few persons will question the assumption that variations in the physical and chemical characteristics of an aquatic environment during the time that fish are spawning may influence the success of spawning. Sudden fluctuations in water levels, in turbidity and rate of silting, in dissolved salts, and in temperature have singly, or in combination, been held responsible for good or poor production of young.

Little has been published, however, on the relationship between the composition and density of a fish population and the success of the spawning attempts of one or several species comprising that population. In my opinion, information on this relationship is of great importance in the management of lakes for angling, because of the probability that the disappearance of a species considered of high value for angling may be associated with the inability of that species to produce a successful spawn under certain types and degrees of competition.

At Ridge Lake, fairly reliable population estimates of fish larger than 3 inches long could be made at any given bass spawning period. Estimates of population could then be compared with inventories of schooling bass fry.

Population estimates of fish, not including those fish of less than 1 year of age, were made as follows: For any given year of the series of years beginning with 1941, when the lake was stocked, and continuing in 1943, 1945, 1947, 1949, and 1951, when it was restocked following draining in March, the population estimate included only the fish actually placed or replaced in the lake in that year (except for 1943 when an estimate of the number of unmarked bass was added, table 5, note 1). For any given year of the series of years 1942, 1944, 1946, 1948, and 1950, the population estimate included all fish, except those spawned in the given year, that were recovered in the draining census of the following spring; to these were added the fish recorded as being caught by fishermen during the summer of the given year, which were obviously in the lake at spawning time of that year. These estimates do not include fish lost from the population through natural mortality and from such causes as death resulting from undetected injury during the previous censusing operation, escape over the spillway, or poaching. Although it is recognized that the population estimates and inventories of spawn at Ridge Lake are far from exact, it is believed that both have value because of a year-to-year uniformity of technique used in gathering data.

Table 10 shows the total numbers per acre of largemouth bass, bluegills, and other fish (mostly green sunfish and black bullheads) for each year, along with an estimate of the bass spawn per acre. Bass are separated into those of 10 inches in length or larger and those smaller; bluegills into those of 6 inches in length or larger and those smaller.

In a study of the relationship between population density and spawning success, consideration should be given to the spawning and feeding habits of the species involved.

In Illinois and other northern states, largemouth bass of 10 inches or more in length may not be capable of spawning unless they are at least 2 years old. Fish of this species larger than about 7 inches in length are usually not interested in food items as small as bass fry. Bluegills of 6 inches in length are capable of spawning. Fish of this species 3 inches in length or longer may feed on bass fry.

In 1941, at the time 100 bass of spawning age were placed in Ridge Lake, the lake area was only about 9 acres, giving an assumed adult population of 11 bass per acre. The resulting spawn was the second largest recorded and the largest per acre: 38 broods estimated at 76,000 fry (8,444 per acre, table 10). The relatively sparse population of adult bass had little or no interference with their spawning.

Table 10.—Estimated numbers of largemouth bass, bluegills, and other fish per acre shortly prior to spawning time, and of largemouth bass fry at spawning time, for each of the years 1941–1951 at Ridge Lake. Calculations involving acreage were based on a water area of 18 acres except where stated otherwise.

Year	Largemouth Bass, Per Acre		Bluegills, Per Acre		Other Fish, Per Acre		All Fish, Per Acre		Estimated Bass Fry, Per Acre
	Ten Inches or Longer	Less Than 10 Inches	Six Inches or Longer	Less Than 6 Inches	Large	Small	Large	Small	
1941	11[1]	—	—	—	—	—	11	—	8,444
1942	24[2]	266	—	—	2	—	26	266	1,444
1943	6	104	—	—	—	—	6	104	1,000
1944	57	33	—	—	29	15	86	48	56
1945	36	—	3	—	—	—	39	—	6,444
1946	34	53	476	2,858	17	32	527	2,943	139
1947	22	—	98	—	—	—	120	—	2,056
1948	77	72	299	1,120	16	4	392	1,196	0
1949[3]	70	23[4]	—	—	—	—	93	—	2,182
1950	42	31	58	2,878	20	56	120	2,965	0
1951	29	16[5]	36	—	3[6]	31[6]	68	47	1,778

[1] Calculations for this year based on actual water area (about 9 acres) at spawning time.
[2] Figure includes only 3 bass of spawning age per acre.
[3] Calculations for this year based on actual water area (about 11 acres) during summer.
[4] None less than 9 inches long.
[5] None less than 8 inches long.
[6] Warmouths only.

Forty of the bass placed in Ridge Lake in 1941 were recorded as being caught by fishermen after June, 1942, table 19. Seventeen were taken in the first draining census, in 1943, table 4. So at least 57 of the original Ridge Lake bass must have been present during the 1942 spawning period (about 1.3 per cent of the bass taken in the 1943 draining census, table 4). These 57 bass, plus a large number of "yearling" bass 5 to 11 inches in length, made up most of the 1942 population prior to spawning time; this population is calculated to have averaged 290 bass per acre, table 10. Fourteen schools of fry were counted on May 29; they were estimated to contain 26,000 young fish (1,444 per acre). No larger counts were made after this date. The smaller number of broods in 1942 than in 1941 may have been due to a smaller number of spawners, to interference with their spawning by "yearling" bass, or to a less favorable spawning season. Very few bass of the 1942 brood appeared in the 1943 draining operation. From this fact it was assumed that most of them became food for the 1941 brood during the summer.

With the removal of 2,783 small bass of the 1941 brood in the spring of 1943, the population was reduced by more than 50 per cent, tables 3 and 4. Bass of the 1941 brood were old enough to spawn in 1943, but many were rather badly stunted. The sexually mature bass, which included 15 of the original stock, produced a relatively small spawn estimated at 18,000 fry (1,000 per acre, table 10).

In 1944, Ridge Lake contained a relatively large population of adult bass. Attempts to census the young were only moderately successful (page 246); the highest estimate of young seen on any one day never exceeded 1,000, or about 56 per acre, table 10.

In the years when the fish population of Ridge Lake during the bass spawning season was one essentially of largemouth bass only (1941–1944), the bass spawn became progressively smaller each year, although in each year some spawn was produced, table 10. Bluegills were introduced into Ridge Lake after the bass spawning season of 1944, and, when the lake was drained in the spring of 1945, only large bluegills were replaced in the lake along with all of the legal-length bass, table 5. Several hundred bluegill fry produced in late summer of 1944 undoubtedly escaped the census by remaining in the stream channel and in pools within the lake basin when the draining operation of 1945 was completed. These later escaped to the lake as it refilled.

The bass spawn of 1945 was the largest ever produced after the lake basin was full—an estimated 116,000 fry (6,444 per acre, table 10), spawned by a population of 36 adult bass per acre, table 5. However, on a per-acre basis, the 1945 spawn was not as large as that of 1941, when the lake area was about 9 acres. From the 1947 draining census, table 4, it is evident that the 61 adult bluegills returned to the lake in 1945 and their progeny of 1944 that escaped the 1945 census produced large numbers of young in 1945 and 1946. Moreover, the survival rate of the young bluegills must have been high in spite of the presence of unusually large numbers of small bass. These young bass might have been expected to control the survival of bluegill fry in 1945 and 1946, but it is evident that they did not.

At the beginning of the spawning season of 1946, Ridge Lake contained a large population of both bass and bluegills, plus somewhat larger populations of bullheads and green sunfish than had been present in previous years. The estimated total population of fish was 3,470 per acre in 1946 prior to spawning and the bass spawn was estimated to be about 139 fry per acre, table 10.

The 1947 spawn of bass was estimated at 2,056 fry per acre, table 10. Following the draining census in March, 392 legal-sized bass and 1,761 large bluegills had been returned to the lake, table 5, giving a population of 120 fish per acre. The 1947 bass spawn per acre was much smaller than that of 1941 or 1945 and slightly smaller than that of 1949, but larger than that of other years, table 10.

There was no visible indication that bass fry developed to the schooling stage in 1948 or 1950. In 1948, several adult female bass caught by Natural History Survey personnel early in June contained well-developed eggs; female bass caught by anglers later, after the lake was opened to fishing, appeared to be spent. Yet no schools of bass fry were seen by Survey personnel in making daily trips around the lake, and no young bass were taken in extensive seining in the shallow upper end of the lake. Yearling bluegills and bluegill fry were abundant.

An estimate of the 1948 fish population, based on the anglers' catch of 1948 and the 1949 census, gave 149 bass and 1,419 bluegills per acre, table 10. This is a large population but considerably less than that of 1946, when the lake contained 3,470 fish per acre (87 bass, 3,334 bluegills, and 49 other fish).

In 1949, 1,027 bass were returned to the lake following the March census, table 5, about 25% of which were between 9 and 10 inches in length. The lake area by June 1 was only 11 acres. An attempt had been made to remove all bluegills in March. After the census, the bass population, which had developed in 18 acres of water with a large available food supply in the form of crayfish, bluegills, and aquatic insect nymphs, was concentrated into 11 acres of water containing a much reduced food supply. Bass caught throughout the summer were thin, and many of those less than 10 inches long in March were still below that length when caught in July and August. The bass spawn was relatively small; the estimate was 24,000 fry (2,182 per acre, table 10).

In 1950, small bluegills were again abundant, most of them having originated from the 1949 spawn of those fish that had remained in the lake basin during the 1949 draining operation. The estimated population of small bluegills was 2,878 per acre; this was comparable to the number present in 1946 and more than twice the number present in 1948, table 10. However, in 1948 the large bluegills numbered 299 per acre as compared with 58 in 1950. In 1950, as in 1948, the survival of bass to the fry stage apparently was very low.

The number of bass replaced in the lake after the 1951 census amounted to 29 large fish per acre, plus an additional 16 per acre that ranged between 8 and 10 inches long, a total of 45 per acre, table 5. The bluegills replaced averaged 36 large fish per acre. The large warmouths replaced averaged about 3 per acre and the small warmouths 31 per acre. Small warmouths were replaced in an attempt to build up the population of these fish. In this year the estimated number of bass fry produced per acre amounted to more than 1,700, table 10.

Several factors related to density of population appear to have influenced the production of largemouth bass spawn. During the years 1941 to 1944, inclusive, when the fish population was essentially one of largemouth bass alone, the spawn estimate decreased each year without any apparent relationship to the number of bass of spawning age present in the lake. Later, when bluegills were present, the years of good spawn production were those in which the bluegill population (particularly of small fish) was greatly reduced at the time of the spring draining census (1945, 1947, 1949, 1951). There is strong evidence here that a large bluegill population may control the survival of the spawn of bass (1946, 1948, 1950). If this relationship of bass with a crowded bluegill population were allowed to continue over a period of years, the bass population might become gradually smaller because of the lack of adequate replacement for the adults lost. Interference with spawning and attacks on bass eggs and fry by small fish (of other species as well as the bluegill) may be the most important single factor responsible for poor bass populations and poor bass fishing in Illinois lakes.

The level of survival of young bass throughout the first year of life may not be correlated very closely with the level of spawn production. In 1942 and 1943, moderate numbers of young were observed, but age determinations made from scales removed from bass taken by fishermen and from bass handled during the draining censuses in later years indicated that very few fish of the 1942 and 1943 broods survived the postfry stage. In 1946, the number of bass fry was relatively small, but quite a number of fish from the brood of this year appeared in the catches of later years, in spite of the fact that this brood could have been eliminated entirely through draining operations of March, 1947. Bass of the 1946 brood that appeared in the catches of 1947 and 1948 and as unmarked fish in the 1949 draining census must have remained in the lake basin or in the feeder stream above the lake during the 1947 census.

How often must a successful spawn be produced to maintain a largemouth bass population that approaches the maximum a body of water will support? At Ridge Lake the bass population was maintained at a high level throughout most of the 10-year study period by relatively good spawns in most odd-numbered years (1941, 1943, 1945, 1947, 1949, and 1951) alternating with relatively poor spawns in most even-numbered years (1944, 1946, 1948, 1950), table 9. In this 10-year period small bass were removed in draining censuses and, from the summer of 1946 on, by fishermen.

A relatively small number of fish are required to replace those taken by fishermen or lost through natural mortality and other causes of death. That even this relatively small number may not be produced, or may not survive the period of high vulnerability to predation, is suggested by the spawn inventories of 1948 and 1950, table 9, and the almost complete disappearance of the large number of bass fry produced in 1942. Largemouth bass are capable of rapid growth. Thus, if small bass are available, the replacement of a large loss among bass of desirable sizes may take place in a comparatively short time.

With estimates of the numbers of bass spawned and with age determinations of the bass taken by fishermen and in draining censuses, it is possible to show the relationship between the number of fry in each brood and the subsequent catch of members of the brood as larger fish. In table 11 are shown estimates of the numbers of bass fry per acre appearing in the years 1941, 1943, 1945, 1947, and 1949; for each brood or year-class, the number of bass taken by angling in the year of the spawn and the year following; and also the number taken in the draining census made approximately 21 months after the spawn appeared. The captured bass were fish, 6 to 12 inches in length, that had survived long enough to grow to sizes too large for "easy" predation. The most favorable calculated survival ratios of number of fry to number of bass subsequently captured were 29 to 1 for 1941 and 30 to 1 for 1947; the 1943 and 1949 ratios of 40 to 1 and 34 to 1, respectively, were only slightly less favorable. The poorest survival occurred in the 1945 brood, in which the ratio was 195 fry to 1 bass recovered. All of these survival ratios may have represented a higher rate of survival than would have occurred had the same numbers of schooling fry (as estimated in table 11) been subjected to predation from more nearly "normal" (unculled) populations of fishes.

Table 11.—Estimated number of largemouth bass fry in each of five year-classes or broods produced by the original stock in Ridge Lake and by adult bass returned to the lake following draining censuses, the number of bass of designated year-class taken by fishermen in the next two fishing seasons after spawning, plus those taken in the next draining census about 21 months after spawning, and the ratio of spawn to fish subsequently taken. Calculations involving acreage were based on a water area of 18 acres except where stated otherwise.

Year-Class or Brood	Estimated Number of Fry, per Acre	Number, per Acre, of Bass of Designated Year-Class Taken in the 21 Months Succeeding Spawning			Ratio of Spawn to Subsequent Take
		By Fishermen	In Draining Census	Total	
1941[1]	8,444	28	266[2]	294	29 to 1
1943	1,000	—	25	25	40 to 1
1945	6,444	15	18	33	195 to 1
1947	2,056	17	51	68	30 to 1
1949[3]	2,182	20	45	65	34 to 1

[1] Calculations for this year based on actual water area (about 9 acres) at spawning time.
[2] Figure includes an estimated 473 bass that escaped the 1943 census.
[3] Calculations for this year based on actual water area (about 11 acres) during summer.

Growth of Bass

At Ridge Lake the permanent removal, or culling out, of small fish by the Natural History Survey staff during draining operations in alternate years and by anglers during most fishing seasons reduced competition for food among surviving fish in the lake and thereby allowed for relatively rapid growth.

If all bass of less than 8 to 10 inches in length could have been permanently

Fig. 12.—Taking a sample of scales from largemouth bass handled in Ridge Lake draining census. Scales collected from bass and bluegills taken in draining censuses or caught by anglers were placed in small envelopes and later used for aging these fish.

removed from the lake at 2-year intervals, selection would have been continuously in favor of the rapidly growing fish. However, in each year the lake was drained, some small bass remained in the lake basin and survived by staying either within the blind end of the old stream channel near the dam or in undrainable water pockets that appeared in the lake bottom as a result of uneven deposition of silt. After water was again impounded behind the dam, these bass escaped to mingle with the population of selected fish that were returned to the lake. Probably many of the escaped fish were eaten by the larger returned fish, but those that survived found conditions optimum for rapid growth. On the next census 2 years later, they made their appearance as the larger individuals of the group of unmarked fish.

During the period 1941–1951, scale samples, fig. 12, were collected from 4,305 bass that were taken by fishermen or that were returned to the lake following draining censuses. Later these bass were aged and separated into broods (year-classes). Growth curves were constructed for the individual broods by use of the average lengths of the fish at the time of capture. The growth curves for 4,273 of these fish are shown in fig. 13. The numbers of fish in the year-classes represented in this figure are given here: 1941, 1,780 fish; 1944, 96 fish; 1945, 580 fish; 1946, 286 fish; 1947, 1,038 fish; 1948, 203 fish; and 1949, 290 fish. The 1942 and 1943 broods were represented by only 17 and 15 fish, respectively, too few for use in the construction of valid growth curves for these broods. Average lengths of 1941 brood bass in 1942 were based largely on fish of legal length kept by anglers; therefore the growth curve for the 1941 brood in 1942 is not truly representative.

The evidence furnished by the 1942 creel, the 1943 draining census, and fish samples taken by Natural History Survey staff members in 1943 indicates that, even after drastic thinning in 1943, the 1941 brood of bass dominated the fish

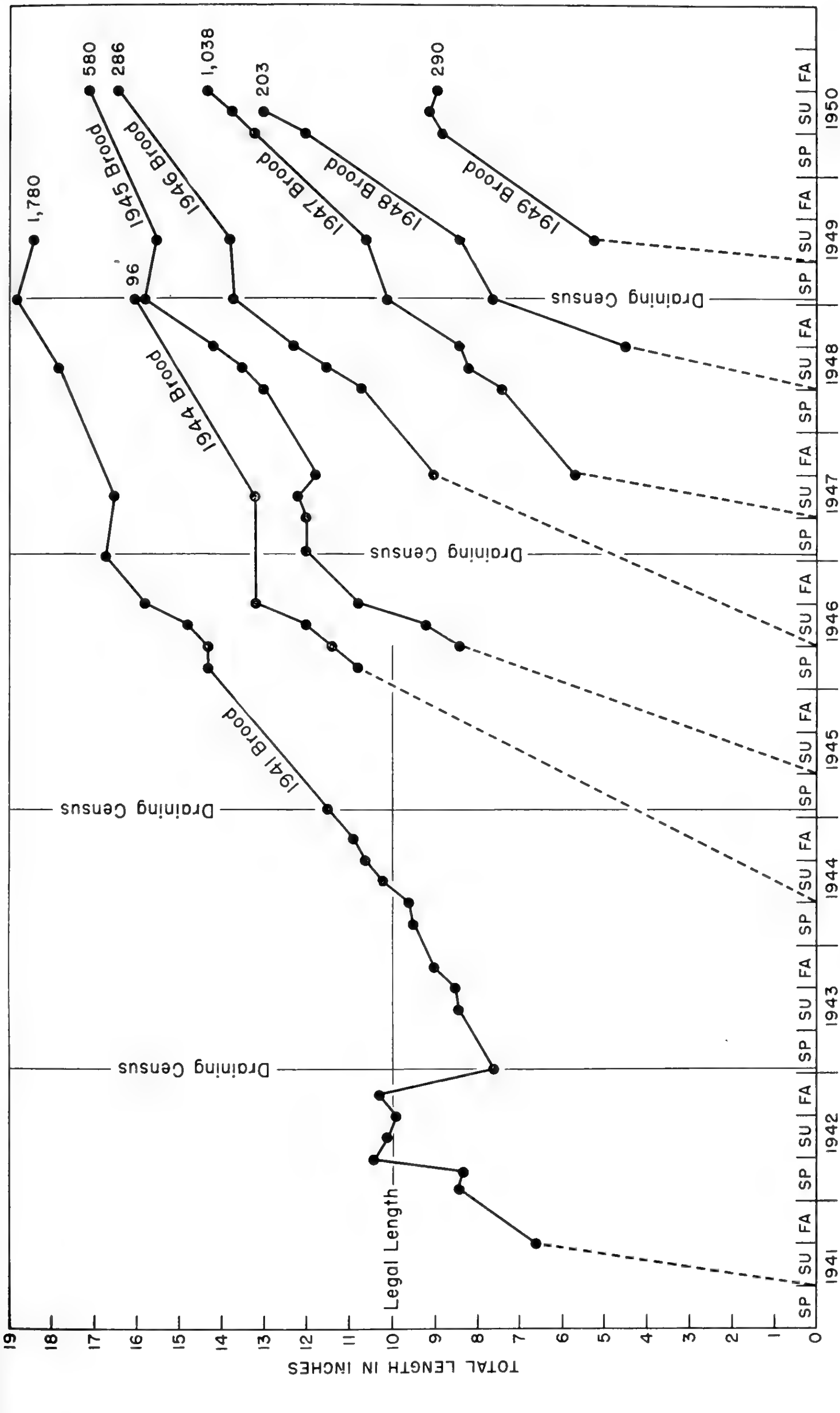

Fig. 13.—Growth rates of largemouth bass spawned in Ridge Lake, 1941–1949; lengths based on measurements of fish in anglers' catches and in draining censuses (SP, spring; SU, summer; FA, fall). The 1942 data are based largely on legal-length fish kept by anglers.

population of the lake. The survival of spawn in 1941 was very high, and the new lake contained adequate forage for these small bass throughout the 1941 growing season, so that their growth rate in 1941 was rapid, table 12, even though the lake basin did not completely fill until December.

In four collections in the spring of 1942, consisting of a total of 148 fish, 21.6 per cent of the bass were 10 inches or longer; on the basis of this sample, it was decided to open the lake to fishing in the summer of that year.

In the fishing season of 1942, anglers took 323 bass of 10 inches or longer belonging to the 1941 brood, table 6, and released 3,604 smaller fish they had caught. Apparently the larger fish were the cannibals of the brood. It was not until the draining census of 1943, after the fish of the 1941 brood had completed two growing seasons, that the average length in the brood could be placed accurately; it was 7.6 inches, table 13. Scale studies support the hypothesis that most of this growth was made in 1941 and that the fish remained about the same size throughout 1942. Growth was resumed in the 1943 season at a relatively slow rate, following the spring reduction in population. It was not until late in the summer of 1944 that a large part of the 1941 brood exceeded the 10-inch length. In the draining census of 1945, after four growing seasons, this brood averaged only 11.5 inches total length. The condition of overpopulation and stunting of bass that existed in Ridge Lake early in 1942 might have been quickly rectified had fishermen been allowed to take the 3,604 bass of less than legal length (10 inches) that were caught and released in that year.

As mentioned in the section "Spawning Success and Population Density," very few bass of the 1942 and 1943 broods survived the postfry stage. The first brood of bass after that of 1941 to be represented in anglers' catches by fair numbers of fish was that of 1944. Ninety-two fish of this brood unexpectedly appeared as unmarked individuals in the hook-and-line catch of 1946. The survival of 1944 brood fish, supposedly removed from the lake in the draining operation of 1945, may be theorized as follows: Bass of the 1941 brood were about 10 inches in length in 1944 and were not particularly interested in bass fry as food. Few bass of smaller sizes (1942 and 1943 broods) were present. Bluegills were placed in the lake in June of that year and immediately produced a large spawn. The small bluegills may have acted as a buffer, reducing bass predation on bass. The upper part of the lake had developed a dense stand of the pondweed, *Potamogeton foliosus,* and other plants into which some of the 1944 brood bass moved and lived throughout the summer. Individuals of this group made poor growth (as shown by the scale pattern of the brood) because of food competition among the fish within the mass of plants. At the end of the first growing season most of these bass were less than 2 inches in length (calculated from scale measurements at later dates).

Table 12.—Numbers of 1941 brood of largemouth bass of various lengths taken with fly-rod lures at Ridge Lake, on August 20 and on October 14 and 21, 1941.

Total Length, Inches	Number Taken, August 20	Number Taken, October 14 and 21
3	0	0
3½	1	1
4	3	2
4½	2	9
5	1	1
5½	1	0
6	9	4
6½	11	1
7	9	2
7½	5	5
8	6	9
8½	2	11
9	0	20
9½	0	9
10	0	7
10½	0	2
Total	*50*	*83*

Some of the small bass of the 1944 brood escaped the 1945 draining census by remaining in pools or in the blind stream channel between the mouth of the diversion ditch and the dam until after the draining census was completed and water was again impounded. These fish then escaped from the confines of the blind stream channel or the pools. As

Table 13.—Average total lengths of largemouth bass at, or approximately at, ends of named growing seasons, Ridge Lake, 1941–1949.

Year-Class or Brood	Number of Samples	Average Total Length in Inches at End of Named Growing Season							
		1st	2nd	3rd	4th	5th	6th	7th	8th
1941	1,780	8.3[1]	7.6[1]	9.2	11.5	14.3	16.7	17.4	18.8
1944	96	—	—	13.2	—	—	—	—	—
1945	580	8.4	12.0	13.0	15.8	—	—	—	—
1946	286	—	10.7	13.7	—	—	—	—	—
1947	1,038	7.4	10.1	13.2	—	—	—	—	—
1948	203	7.6	11.0	13.0	—	—	—	—	—
1949	290	8.8	—	—	—	—	—	—	—
Total	*4,273*	—	—	—	—	—	—	—	—
Average[2]	—	8.1	10.3	12.6	13.7	14.3	16.7	17.4	18.8

[1] Average for end of first growing season based on small number of samples taken by angling. Average for end of second growing season based on fish taken in 1943 draining census.
[2] Average of average lengths at ends of named growing seasons.

soon as the fry of the 1945 spawn appeared, the escaped fish had an abundance of food available to them. After June of 1945, they made rapid growth, and in 1946, when they were caught as unmarked fish, they ranged from 10.5 to 13.5 inches in length (the scales indicated a 7- to 11-inch increment for 1945).

The ability of the 1941 brood of bass to curtail the survival of postfry bass seems to have been lost in 1944, and no brood produced from 1944 on was able to control the survival of young bass to an extent comparable to the control exercised by the 1941 brood in 1942 and 1943.

In spite of the relatively small bass spawn observed in 1946, and the apparent absence of surviving bass spawn in 1948, the 1946 brood was represented in scale collections by 286 fish and the 1948 brood by 203 fish, table 13.

Scale studies indicated that although the numbers of spawn surviving in years in which the lake was not drained were relatively small, they contributed in some degree to the numerical size of the bass population in later years.

Plateaus in the growth curves in fig. 13, corresponding to early summer periods following March drainings, suggest that the draining operations greatly reduced the food resources of the lake for the large bass replaced in it, and that, in spite of the fact that the poundage of bass returned after each draining census was smaller than that taken in the census, several months were required before the fish resumed their growth. In 1949, the food shortage was more severe than usual because the lake basin failed to refill completely until fall.

The average lengths attained by indi-

Table 14.—Average total lengths of bluegills at, or approximately at, ends of named growing seasons, Ridge Lake, 1944–1949.

Year-Class or Brood	Number of Samples	Average Total Length in Inches at End of Named Growing Season				
		1st	2nd	3rd	4th	5th
1944	15	—	—	6.9	7.5	7.8
1945	1,304	5.8	6.3	6.5	7.7	—
1946	267	—	5.6	6.9	—	—
1947	106	—	5.3	8.0[1]	—	—
1948	44	3.6	7.6	—	—	—
1949	211	—	6.4	—	—	—
Total	*1,947*	—	—	—	—	—
Average[2]	—	4.7	6.2	7.1	7.6	7.8

[1] Measurements actually taken in May, 1950, beginning of fourth growing season.
[2] Average of average lengths at ends of named growing seasons.

viduals of the various broods of bass at or approximately at the ends of the various growing seasons are shown in table 13. Growth for the first year was fairly uniform for all broods; average lengths at approximately the end of the year ranged between 7.4 and 8.8 inches. Growth for the second year was slow for the 1941 brood, which was stunted in this year of life, but the average lengths for second-year bass of other broods ranged between 10.1 and 12.0 inches. All broods except that of 1941 attained an average length of at least 13.0 inches the third year, and the 1945 brood averaged 15.8 inches the fourth year. After the slow start made by the 1941 brood during its first 4 years, the rate of growth improved, so that, during the next 4 years, the average weight of individuals of this brood increased from about 1 pound at the beginning of the 1945 growing season to about 4 pounds at the beginning of the 1949 season.

Fishermen prefer to catch large bass but are satisfied with fish of sufficient size to produce an appreciable bend in a fly rod or bait rod. Small bass ordinarily strike more readily than do large ones and for this reason are easier to catch. Thus, from the standpoint of bass management, the growth rate of a bass after the fish has reached a catchable size is of secondary importance; the primary objective is to bring the maximum number of bass fingerlings up to sizes attractive to fishermen in the shortest possible time.

Growth of Bluegills

Except for a short period in 1949, Ridge Lake probably contained fairly large populations of bluegills after the spawning season of 1945. In the draining operation of March, 1949, the bluegills were reduced to a low population level because an attempt was made at that time to get rid of them completely.

The growth rates of the several year-classes or broods of bluegills produced in the lake have been determined by aging scales from 1,947 of these fish collected in the years 1946–1950, table 14.

Growth of the first two year-classes of bluegills produced in the lake was rapid, fig. 14. In the 1946 growing season, 1944 year-class fish averaged 6.9 inches total length (at about 32 months of age) and 1945 fish averaged 5.8 inches (at about 19 months of age). Bluegills representing 1946, 1947, and 1948 year-classes grew less rapidly than those representing preceding year-classes, and fish of each of these year-classes grew at a less rapid rate in their first year than fish of the year-class preceding, fig. 14. Poorest recorded first-year growth occurred in 1948; bluegills spawned in that year averaged only 3.6 inches total length in March, 1949, before second-year growth had started.

The growth stimulus produced by the severe thinning of the bluegill population in 1949 is shown clearly in the 1947, 1948, and 1949 year-classes among fish that were spawned after, or that managed to escape, the draining operation of 1949, fig. 14. Bluegills of the 1947 year-class, which averaged 5.3 inches in length in March of 1949 (equivalent to end of second growing season), had grown to an average length of 8.0 inches by May of 1950 (shortly after start of fourth growing season); fish of the 1948 year-class, which averaged about 3.6 inches in length after one season of growth, grew to an average length of 7.6 inches before the third growing season was well under way; and fish spawned in 1949 matched second-year growth with the 1945 year-class by reaching 6.4 inches in length within the 1950 season. In 1949, the year in which maximum growth rates were attained by bluegills, the total number of these fish was so small that, creel records indicate, few could be caught by anglers, table 3.

Catch Rate Versus Fishing Pressure

In observing the catch of largemouth bass at Ridge Lake year after year, it was noticed that the rate of catch dropped off rather rapidly early in the season and that, after about the first 3 weeks, most of the bass taken were caught by a relatively small number of fishermen. This phenomenon was particularly pronounced in 1949 when, following the March draining census, the bass returned to the lake were concentrated in a reduced volume of water. At this time Ridge Lake contained at least 1,046 bass large enough to be attractive to fishermen (1,027 fish returned after March census, plus unknown number of unmarked fish, 19 of which were caught during the summer). The total catch and rate of catch for preseason fishing, daily fishing during the first week, and fishing by weeks throughout the rest of the summer fishing season are shown in table 15, along with man-hours of fishing and calculated number of bass available.

In the June period before the lake was opened to the public (June 1–14), members of the Illinois Natural History Survey aquatic biology staff fished for bass needed for another phase of the study. Fishing periods (preseason) for one or two men were usually not more than 2 hours in length for any one day. With this very light fishing intensity, 50 bass weighing 52.49 pounds were taken in 17.75 man-hours, at the rate of 2.96 pounds of bass per man-hour, or approximately a pound of bass for each 20 minutes of fishing. On the first day the lake was opened to the public, 67 bass, weighing 78.56 pounds, were taken in 156.0 man-hours of fishing, at the rate of 0.5 pound per man-hour. On the second day, only 22 bass, weighing 22.31 pounds, were taken in 121.5 man-hours of fishing, at the rate of 0.18 pound per man-hour. The rate of catch was still lower during the next 3 days of fishing that completed the first fishing week. In this week a total of 121 bass weighing 140.67 pounds were taken in 633.5 man-hours of fishing. The

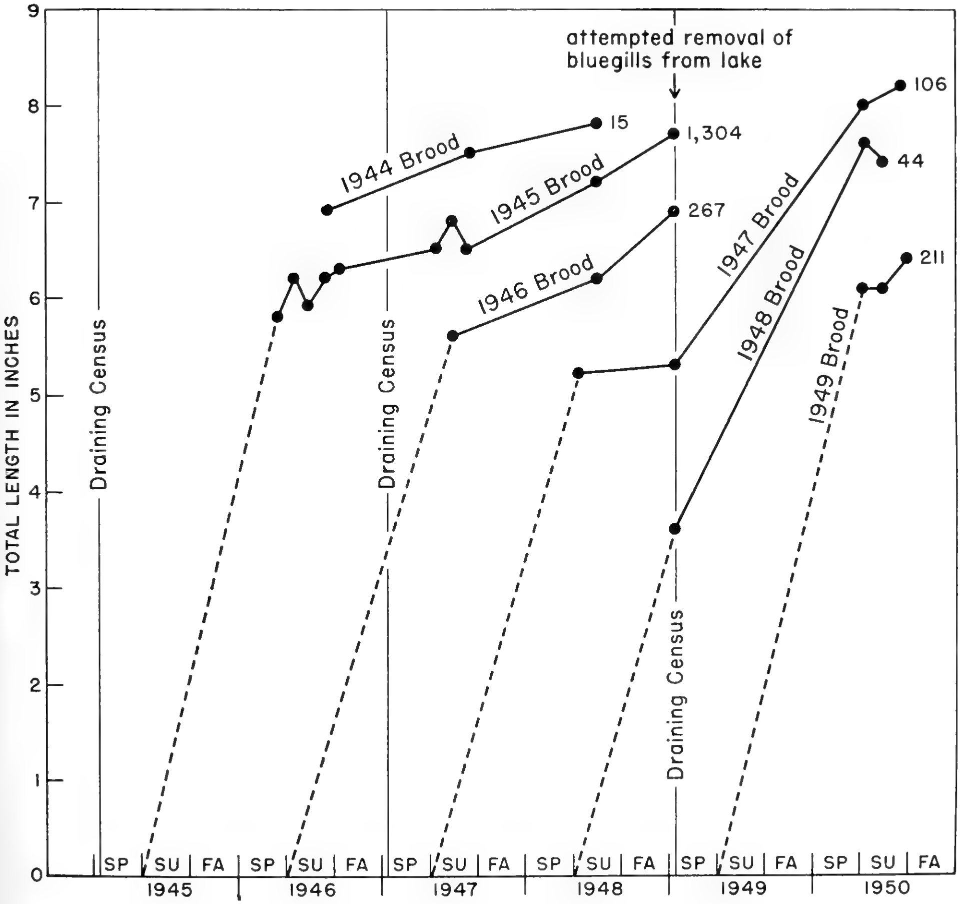

Fig. 14.—Growth rates of bluegills spawned in Ridge Lake, 1944–1949; lengths based on measurements of fish in anglers' catches and in draining censuses (SP, spring; SU, summer; FA, fall).

rate of catch from the third day of fishing to the end of the week was nearly as poor as the average rate for most weekly periods through the remainder of the summer. This poor rate of catch for the last 3 days of the first week followed an accumulation of fishing hours over a 2-day period of about 25 man-hours per acre. Less than 10 per cent of the bass available at the beginning of the public fishing period had been taken by the end of the second day and there was still a bass population of at least 82 fish per acre. When the lake was closed after 11 weeks of fishing, there were still about 451 bass available (41 per acre); the hook-and-line yield represented 56.9 per cent of the number of fish of 9 inches or more in length that were available when preseason fishing was begun on June 1.

The apparent drop in rate of catch in 1949 from preseason fishing to the rate of even the first day of public fishing, table 15, suggested that bass were rather quickly influenced by an acceleration of fishing activity. Consequently, fishing data were reassembled to show average rates of catch (by weight) for half-day fishing periods for the first week of fishing during each of the seasons of 1942, 1944, 1947, and 1949—years in which the fish populations were made up entirely or principally of bass. These average rates of catch are shown in table 16 and fig. 15. The season of 1945 was omitted because muddy water early in the first week,

Table 15.—The 1949 creel at Ridge Lake, with figures arranged to show rapid drop in success of angling associated with intensive fishing. Bass listed as available were at least 9 inches in length. Calculations involving acreage were based on the actual water area of 11 acres.

Period and Date	Man-Hours of Fishing	Available Bass		Catch				
		Total	Per Acre	Number	Total Weight, Pounds	Hours to Catch One Bass	Hours to Catch 1 Pound of Bass	Pounds of Bass per Man-Hour of Fishing
Preseason 6/1–14	17.75	1,046[1]	95	50	52.49	0.4	0.3	2.96
First Week of Regular Season								
1st day 6/15	156.00	996	90	67	78.56	2.3	2.0	0.50
2nd day 6/16	121.50	929	84	22	22.31	5.5	5.4	0.18
3rd day 6/17	111.25	907	82	8	8.87	13.9	12.5	0.08
4th day 6/18	96.50	899	82	10	11.44	9.6	8.4	0.12
5th day 6/19	148.25	889	81	14	19.49	10.6	7.6	0.13
Regular Season								
1st week 6/15–19	633.50	996	90	121	140.67	5.2	4.5	0.22
2nd week 6/22–26	627.50	875	79	95	82.73	6.6	7.6	0.13
3rd week 6/29–7/4	561.00	780	71	77	66.77	7.3	8.4	0.12
4th week 7/6–10	357.00	703	64	73	54.04	4.9	6.6	0.15
5th week 7/13–17	391.50	630	57	52	45.52	7.5	8.6	0.12
6th week 7/20–24	376.25	578	52	25	25.50	15.0	14.8	0.07
7th week 7/27–31	317.50	553	50	40	24.54	7.9	12.9	0.08
8th week 8/3–7	263.00	513	47	27	19.28	9.7	13.6	0.07
9th week 8/10–14	154.00	486	44	17	13.85	9.1	11.1	0.09
10th week 8/17–21	139.25	469	43	6	4.72	23.2	29.5	0.03
11th week 8/24–28	128.25	463	42	12	10.40	10.7	12.3	0.08
Total for preseason and season	—	—	—	*595*	*540.51*	—	—	—
Available bass remaining	—	451	41	—	—	—	—	—

[1] This number was derived by adding to the 1,027 bass returned to the lake after the 1949 draining census the 19 unmarked bass caught by fishermen in 1949. Three of these unmarked bass were fish spawned in 1948 that had escaped the 1949 draining census; the others were from the 1949 brood. No allowance was made in this calculation for bass of the 1948 brood that had escaped the 1949 draining census and were not caught; for bass of the 1949 brood that had grown to catchable size (about 6 inches or more) and were not caught; or for bass later unaccountably lost, as through natural mortality.

Table 16.—Rate of catch (by weight) of largemouth bass at Ridge Lake during first 5 days of public fishing in 1942, 1944, 1947, and 1949 when fish population was entirely or principally bass. The season of 1945 was omitted because fishermen were relatively few during the first week and the lake was turbid until late in the week.

Fishing Season	Rate of Catch, Pounds per Man-Hour of Fishing									
	First Day		Second Day		Third Day		Fourth Day		Fifth Day	
	A.M.	P.M.	A.M.	P.M.	A.M.	P.M.	A.M.	P.M.	A.M.	P.M.
1942	0.52	0.16	0.21	0.12	0.16	0.07	0.12	0.02	0.04	0.04
1944	0.39	0.17	0.22	0.29	0.13	0.16	0.16	0.08	0.05	0.04
1947	0.61	0.23	0.33	0.14	0.00	0.12	0.18	0.10	0.00	0.03
1949	0.73	0.32	0.09	0.28	0.05	0.12	0.19	0.06	0.11	0.15
Average	0.55	0.24	0.19	0.20	0.11	0.12	0.16	0.07	0.06	0.07

coupled with an unusually small number of fishermen, made the catch rate for that year appear to be abnormal.

From table 16 it is evident that the rate of catch of bass in the afternoon period of the first day in each of the 4 years was less than one-half that in the morning period. In 3 of the 4 years there was a slight recovery in the morning of the second day, but the rate of catch on the third day (except in 1944) dropped to a level that was less than one-third that

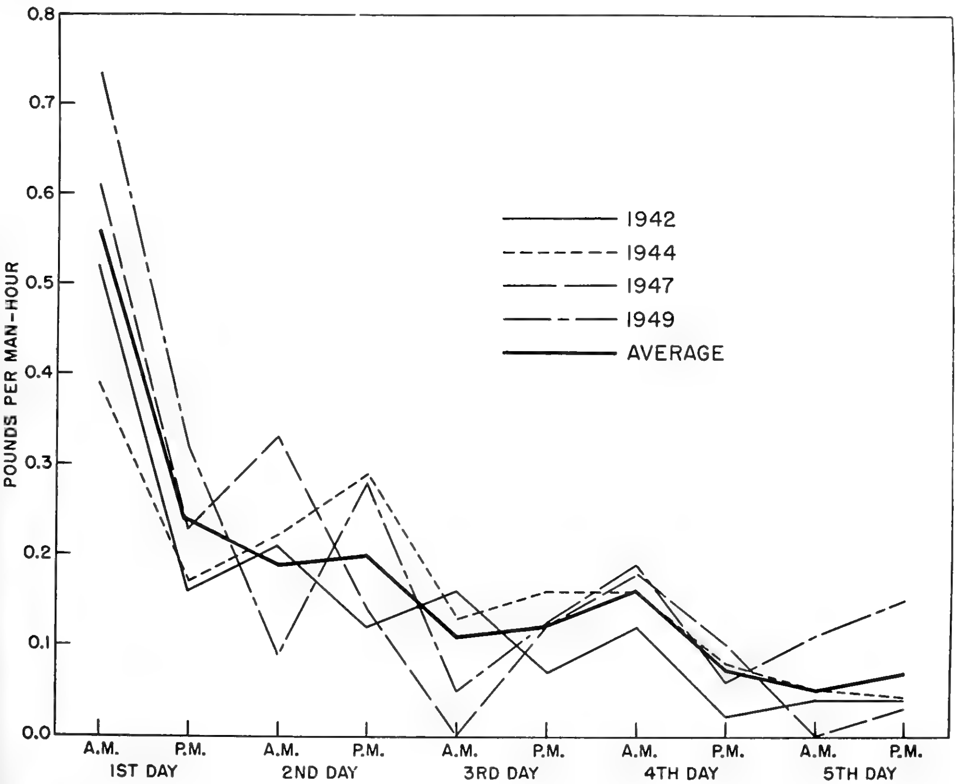

Fig. 15.—Rate of catch (pounds per man-hour) of largemouth bass at Ridge Lake during the first week of public fishing in each of the years 1942, 1944, 1947, and 1949, and the average rate of catch for all of these years.

of the opening morning. In no case was the weight or number of bass taken in the first morning sufficiently great to represent a significant reduction in the total bass population. The catch of highest poundage in relation to total poundage of available bass in the lake was taken during the first morning of the 1949 fishing season; it amounted to approximately 6.3 per cent of the available poundage. The catch of largest number in relation to the total number of available bass in the lake was taken in the first morning of 1947; it amounted to about 4.6 per cent of the available population. The fact that the catch rate of bass dropped in all years within a few hours after the lake was opened to public fishing, and before more than a small proportion of the available bass population had been caught, suggests either that the more aggressive fish were hooked early on the first day or that the fish lucky enough to avoid being hooked during the first few hours became wary of noisy boats and of baits attached to lines.

That the rate of catch (by weight) of bass dropped to a low level within the first few weeks of fishing in each of the years in which public fishing was allowed is shown in table 17. It is obvious that a sudden drop in catch rate occurred in each of these years regardless of when fishing was begun. (See data for 1944, when fishing was begun in August.) Years in which few, or no, bluegills were in the lake and the fishing was mostly for bass (1942, 1944, 1945, 1947, and 1949) are shown in the upper part of table 17; years of considerable fishing for both bass and bluegills are shown in the lower part.

Table 17.—Average weekly rate of catch (by weight) of fish at Ridge Lake. In 1942, 1944, 1945, 1947, and 1949, the population of the lake was principally largemouth bass. In 1946, 1948, and 1950, large numbers of bluegills as well as bass were available.

Fishing Season	Rate of Catch in Pounds per Man-Hour of Fishing														
	June				July				August				September		
	1st Week	2nd Week	3rd Week	4th Week	1st Week	2nd Week	3rd Week	4th Week	1st Week	2nd Week	3rd Week	4th Week	1st Week	2nd Week	3rd Week
Bass[1]															
1942	—	—	0.13	0.06	0.04	0.02	0.06	0.10	0.02	0.01	0.01	0.01	—	—	—
1944	—	—	—	—	—	—	—	—	—	0.16	0.11	0.10	0.32	0.24	0.11
1945	—	—	0.37	0.33	0.15	0.10	0.07	0.18	0.32	0.12	0.11	0.07	0.29	—	—
1947	—	0.18	0.10	0.07	0.07	0.10	0.05	0.03	0.18	0.14	0.11	0.22	0.24	—	—
1949	—	0.22	0.13	0.12	0.15	0.12	0.07	0.08	0.07	0.09	0.03	0.08	—	—	—
Bass and Bluegills[2]															
1946	0.32	0.33	0.24	0.20	0.18	0.21	0.19	0.12	0.17	0.17	0.20	0.18	0.23	—	—
1948	—	0.41	0.25	0.26	0.16	0.21	0.23	0.15	0.24	0.23	0.21	0.19	0.16	—	—
1950	—	—	0.13	0.14	0.13	0.08	0.09	0.07	0.09	0.10	0.25	0.15	—	—	—

[1] The grand average for the years in which fishing was principally for largemouth bass was 0.13 pound per man-hour of fishing.
[2] The grand average for the years in which large numbers of bluegills as well as bass were available was 0.19 pound per man-hour of fishing.

Interesting points suggested by the upper division of table 17 are that in most years the poorest weeks of bass fishing occurred during middle or late July or middle or late August. In 1945, 1947, and 1949, an increase in catch rate (by weight) appeared in either the first or second week in August. In all years shown in the upper part of table 17 except 1942, a rise in catch rate was shown for either the last week in August or the first week in September. This late-season rise probably was associated with a cooling of the lake, resulting from lower air temperatures at night. No explanation is suggested for the striking fluctuations in weekly catch rates that appeared in some years during July and August.

The highest average weekly rate of catch (by weight) for bass was recorded for the first week of the 1945 fishing season (0.37 pound per man-hour), table 17. This catch rate was affected by muddy water during a part of the week, by a low total of fishing hours for the entire week, and by a phenomenal catch of bass made by two expert fishermen who had the lake to themselves during one fishing period. The average rate of catch for the second week of the 1945 season (0.33 pound per man-hour) was nearly as high as for the first; it was higher than the average for the first week of each of the other years in which all or nearly all fishing was for bass. Ricker (1942:228) recorded the rate of catch of bass fishermen at Shoe Lake, Indiana, for the second half of June as being 4.9 pounds per 10 pole-hours (0.49 pound per man-hour); this period was followed by a number of 2-week periods when fishing was much poorer (0.10 to 0.23 pound per man-hour). The average rate of catch for the entire summer period was 2.6 pounds per 10 pole-hours (0.26 pound per man-hour), which is somewhat higher than the rate at Ridge Lake for any single year or for the grand average rate, table 17.

At Ridge Lake, bluegills were more easily caught than were bass and were less seasonal in their biting. Thus, in years when sizable populations of bluegills as well as bass were available to fishermen, the average weekly catch rates (pounds per man-hour) were higher and less subject to severe fluctuations than in years when only bass were available.

As described in the section on the creel census, fishing was done only from the seven boats owned by the Natural History Survey, and the public was not allowed to fish from the lake bank or piers. The boats were assigned to fishermen making advance reservations; a fisherman could use a boat by himself or take one, two, or three other persons with him. Boats were not supplied with anchors, and if a fisherman wished to use an anchor he was expected to provide it.

All occupants of boats were recorded as fishing all of the time they were on the lake. For example, if three men were using a boat, fig. 3, one man manipulating the oars and the other two actually fishing, they were recorded as though all three were fishing all of the time they were on the lake. Two men in a boat were recorded as two fishermen, even though the two alternated between rowing and fishing; one man by himself in a boat was recorded as one fisherman fishing the entire time he was on the water even though he spent about half of his actual time on the lake in keeping his boat in position for fly or bait casting.

It has been estimated that the rates of catch in terms of pounds of fish per man-hour of actual fishing time might be 50 to 100 per cent higher than the rates of catch given in tables 15, 16, and 17.

Factors Affecting Yields of Bass

In table 18, an attempt has been made to show the catch of bass in relation to number and weight of bass available, man-hours of fishing, and available forage in the form of small bass and bluegills. Methods of estimating numbers and weights of bass were the same as are described in the section "Spawning Success and Population Density." The fishing pressures in man-hours per acre include fishing effort directed toward bluegills as well as bass, as the two cannot be separated.

Bass yields varied from 10 to 54 fish per acre and from 10.9 to 49.2 pounds per acre (when the 1949 yield is figured on the basis of the 1949 lake area) and represented 9 to 64 per cent of the number available and 24 to 69 per cent of the weight available, table 18. The highest percentages of catch of available bass occurred in years following the March drainings (1945, 1947, and 1949), when, as a result of draining and culling operations, populations of small bluegills, crayfish, and other bass foods were much reduced. In 1945 the population of small bass was high, in 1947 moderate, and in 1949 low, as a result of the success of the bass spawn in those years. The number of fish designated as a high population for bass was much smaller than the number listed as a high for bluegills. While the yield of bass in numbers and pounds per acre was in some measure dependent on the man-hours of fishing and the available bass per acre, the factor that seemed to have the greatest influence on the total exploitation for a given season was the relative abundance of natural food. In no year in which natural food was "normally" abundant (had not been reduced through artificial means) did the catch of bass exceed 40 per cent of the available crop, either in numbers or pounds, even under a fishing pressure that in one season averaged more than 300 man-hours per acre. It is improbable that greater fishing pressure would have had much effect upon yield under "normal" food conditions. But in 1945, for example, when food conditions were probably considerably below "normal," a fishing pressure of 105 man-hours per acre resulted in a total exploitation of 64 per cent of the number and 69 per cent of the weight of available bass. Thus, the culling technique that was associated with the biennial draining censuses at Ridge Lake not only allowed the fish replaced in the lake to grow rapidly to sizes satisfactory to anglers, but it also increased the rate of catch and the yield in numbers and pounds.

Table 18.—Number and weight of available largemouth bass per acre, catch of bass per acre, fishing pressure, and abundance of bass forage in the form of small fish, Ridge Lake, 1942–1950. Calculations involving acreage were based on a water area of 18 acres except where stated otherwise.

Fishing Season	Available Bass per Acre		Fishing Pressure, Man-Hours per Acre	Available Bass Forage		Catch of Bass per Acre			
	Number	Weight, Pounds		Small Bass	Small Bluegills	Number	Weight, Pounds	Per Cent of Available Number	Per Cent of Available Weight
1942....	290[1]	63.3[2]	212	Low	None	27	15.1	9	24
1944[3]....	90	54.6[2]	90	Very low	Moderate	26	15.0	29	27
1945....	36	28.7[4]	105	High	Low	23	19.8	64	69
1946....	87	46.1[2]	168	Very low	Very high	20	14.6	23	32
1947....	22	27.0[4]	155	Moderate	Low	10	10.9	45	40
1948....	149	76.0[2]	320	None	Very high	36	25.6	24	34
1949....	57	44.7[4]	220	Low	Very low	33	30.0	58	67
1949[5]....	93	73.2[4]	361	Low	Very low	54	49.2	58	67
1950....	73	62.6[2]	224	Very low	Very high	29	18.3	40	29

[1] Only about 24 legal-sized bass per acre. Fishermen took only legal-sized fish; Natural History Survey catches included fish of less than legal size.
[2] Weight estimate based on actual catch plus weight of catchable bass (about 6 inches or more in length) in census of spring following. The estimate is too high, because no adjustment was made for compensatory weight increase as a result of cropping.
[3] Ridge Lake was not opened to public fishing in 1943; public fishing in 1944 was begun in August.
[4] Weight estimate based on weight of bass actually put back into lake following census. Estimate is too low (except possibly that for 1949) because no allowance was made for weight gains between the time bass were returned to the lake and the time they were caught. In 1949, bass may have decreased in weight because they were crowded.
[5] Figured on the basis of a lake area of 11 acres, the actual area for the fishing season.

Unaccountable Mortality and Length of Life

One of the more difficult problems in studying a population of fish is to determine the final disposition of individuals in that population. Marked fish that are caught by co-operating anglers and most of those that are accidentally killed in draining operations are accountable; so are fish that die from accidents or from hooking injuries and are found floating on the water. However, in the Ridge Lake study, many marked fish simply disappeared from the lake. The disappearance of the fish may be attributed to one of the following causes: (1) natural mortality of fish that were unobserved after they had risen to the surface of the water or were torn apart before decay had progressed sufficiently to cause them to float, (2) escape of fish from the lake by way of the surface spillway in time of high water, (3) injury to fish during draining and censusing operations, followed some time later by death and failure of these fish to float, (4) loss of fish that became stranded or buried in the bottom mud at the time of lake draining and were not retrieved, (5) loss of fish through poaching during periods when the lake was closed to public fishing.

As described previously, the first bass placed in Ridge Lake were marked by removal of one fin (left pectoral of bass from Lake Chautauqua, right pectoral of bass from Craborchard Lake, and dorsal of bass from Lake Glendale). Bass spawned in the lake were marked by removal of fins as designated in table 20. Before bass were replaced in the lake following each draining census, those that already carried a fin mark designating original stock or a previous census were recorded as belonging to their respective groups. Unmarked fish were given the fin mark of the census being made.

Marked fish caught by fishermen in the summer fishing period were recorded by the biologist in charge of the creel census. The lake was scouted almost daily in this period for dead fish and, when these were found, their lengths and marks were recorded. Very few dead fish were seen floating on the lake during the fishing periods of the years 1941–1951. Of the small number of dead fish found, most appeared to have died following injuries that resulted from being hooked. A few had died on lost stringers. Data on fish that had died from fishing injuries or on lost stringers and were later found were

Table 19.—Rates of exploitation and unaccountable losses of marked largemouth bass, Ridge Lake, 1941–1951.

Period	Number of Fish	Per Cent of Marked Fish Population of the Period	Exploitation Rate, Per Cent[1]
1941–1943			
1941 original stock	435	—	—
1942 creel	41[2]	9.4	9.4
1943 census	17	3.9	—
Unaccountable loss	*377*	*86.7*	
1943–1945			
1943 restocking	1,515	—	—
1944 creel	469	31.0	31.0
1945 census	553	36.5	—
Unaccountable loss	*493*	*32.5*	
1945–1947			
1945 restocking	647	—	—
1945 creel	404	62.4	62.4
1946 creel	88	13.6	36.2
1947 census	84	13.0	—
Unaccountable loss	*71*	*11.0*	
1947–1949			
1947 restocking	392	—	—
1947 creel	137	34.9	34.9
1948 creel	107	27.3	41.9
1949 census	110	28.1	—
Unaccountable loss	*38*	*9.7*	
1949–1951			
1949 restocking	1,027	—	—
1949 creel	575	56.0	56.0
1950 creel	148	14.4	32.7
1951 census	190	18.5	—
Unaccountable loss	*114*	*11.1*	

[1] Exploitation rate is based on the theoretical number of marked fish present in the lake at the beginning of the fishing season.
[2] Includes one fish taken in 1941.

Table 20.—Numbers of marked largemouth bass originally placed in Ridge Lake, or replaced after draining censuses, and their later disposition, either as components of succeeding creels, of succeeding draining censuses, or as unaccountable losses. Average weights (in pounds) of fish in each marked group at the time of restocking are shown in parentheses.

Fish Group	Original Stock[1]						1941–1942 Group (Left Pectoral)		1943–1944 Group[2] (Right Pectoral)		1945–1946 Group (Left Pelvic)		1947–1948 Group (Dorsal)	
	Left Pectoral		Right Pectoral		Dorsal									
	Number	Per Cent	Number	Per Cent	Number	Per Cent	Number	Per Cent	Number	Per Cent	Number	Per Cent	Number	Per Cent
1941 original stock	58	—	42	—	335	—	—	—	—	—	—	—	—	—
1942 creel	11	19.0	14	33.3	16[3]	4.8[3]	—	—	—	—	—	—	—	—
1943 census	3	5.2	12	28.6	2	0.6	—	—	—	—	—	—	—	—
Unaccountable loss	*44*	*75.8*	*16*	*38.1*	*317*	*94.6*	—	—	—	—	—	—	—	—
1943 restocking	3 (3.40)	—	10 (3.31)	—	2 (2.30)	—	1,500 (0.17)	—	—	—	—	—	—	—
1944 creel	3[4]	100.0	1[4]	10.0	1[5]	50.0	464	30.9	—	—	—	—	—	—
1945 census	—	—	9	90.0	1	50.0	543	36.2	—	—	—	—	—	—
Unaccountable loss	*0*	*0.0*	*0*	*0.0*	*0*	*0.0*	*493*	*32.9*	—	—	—	—	—	—
1945 restocking	—	—	9 (3.90)	—	—	—	496 (0.77)	—	142 (0.71)	—	—	—	—	—
1945 creel	—	—	3	33.3	—	—	337	68.0	64	45.1	—	—	—	—
1946 creel	—	—	0	—	—	—	69	13.9	19	13.4	—	—	—	—
1947 census	—	—	1	11.1	—	—	63	12.7	20	14.1	—	—	—	—
Unaccountable loss	—	—	*5*	*55.6*	—	—	*27*	*5.4*	*39*	*27.4*	—	—	—	—
1947 restocking	—	—	1 (6.75)	—	—	—	61 (2.44)	—	20 (2.42)	—	310 (0.91)	—	—	—
1947 creel	—	—	—	—	—	—	18	29.5	3	15.0	116	37.5	—	—
1948 creel	—	—	—	—	—	—	14	23.0	3	15.0	90	29.0	—	—
1949 census	—	—	1	100.0	—	—	23	37.7	9	45.0	77	24.8	—	—
Unaccountable loss	—	—	*0*	*0.0*	—	—	*6*	*9.8*	*5*	*25.0*	*27*	*8.7*	—	—
1949 restocking	—	—	1 (7.00)	—	—	—	23 (3.96)	—	9 (3.72)	—	77 (2.62)	—	917 (0.51)	—
1949 creel	—	—	1	100.0	—	—	10	43.5	5	55.6	59	76.6	500	54.5
1950 creel	—	—	—	—	—	—	0	0.0	0	0.0	0	0.0	148	16.1
1951 census	—	—	—	—	—	—	4	17.4	2	22.2	11	14.3	173	18.9
Unaccountable loss	—	—	*0*	*0.0*	—	—	*9*	*39.1*	*2*	*22.2*	*7*	*9.1*	*96*	*10.5*

[1] Original stock with left pectoral fin clipped was from Craborchard Lake, that with right pectoral fin clipped was from Lake Chautauqua, and that with dorsal fin clipped was from Lake Glendale.

[2] Some of the fish of this group were spawned in 1941 or 1942, escaped the 1943 draining census, and appeared as unmarked fish in the census of 1945, when they were given the same mark as the fish spawned in 1943 and 1944.

[3] One of these fish was taken in 1941.

[4] [illegible]

added to the creel record. Our biennial inventories of fish allowed an evaluation of most of the losses that occurred.

When the marked fish taken by anglers were added to those found dead and those counted in the succeeding census and the resulting sum was subtracted from the number of marked fish returned to the lake following the preceding census, there was always a shortage—an unaccountable loss of bass that had taken place during the 2-year period. This loss was the result of natural mortality or of the other four undetected decimating factors listed above. The bass that unaccountably disappeared between censuses were simply designated as unaccountable losses.

For each of the 5 biennial periods beginning with 1941 and ending with the draining census of 1951, tables 19 and 20 show the number of marked bass placed in the lake, the number taken by angling in the two fishing seasons, and the number recaptured at the time of the next census. Table 20 lists the original stock separated into groups based on origin and other fish separated into broods to show differences in unaccountable losses in various groups during various periods.

Information on the capture, holding methods, and transportation of the bass introduced into Ridge Lake in 1941 is of particular interest because the unaccountable losses among these bass amounted to 86.7 per cent within the first 2 years, table 19. Table 20 shows the unaccountable losses among the groups of fish obtained from the three sources: Craborchard, Chautauqua, and Glendale lakes.

The Craborchard Lake fish (marked left pectoral) were caught in wing nets on April 27, 28, and 29, 1941; those caught on the first 2 days were held in nets with the funnels closed until the third day, when all of the nets were raised. The fish were placed in a tank truck equipped with an air compressor and transported to Ridge Lake, a road distance of about 150 miles. The weather during the road trip was unseasonably warm. All fish used in stocking the lake were apparently in good condition on arrival, but the unaccountable loss in this group as revealed by the March, 1943, census was 75.8 per cent, table 20.

The Lake Chautauqua fish (marked right pectoral), in which the unaccountable loss as of March, 1943, was only 38.1 per cent, were captured in wing nets in March and April, 1941, and transported to the Department of Conservation's fisheries station at Havana, about 5 miles from the lake in which they were captured. There they were placed in tanks supplied with cold, well-aerated water and held, most of them for several weeks. Fish that were injured in netting probably showed the effects of these injuries during the holding period and were removed from the tanks. On May 1, bass remaining in the tanks were transported to Ridge Lake; the trip by road was begun early in the morning and was completed before the warm part of the day. The distance by road is 145 miles.

The greatest losses occurred among the fish from Lake Glendale (marked dorsal), which were seined on June 17, held overnight in a holding net staked out in Lake Glendale, and transported to Ridge Lake on June 18. The weather was very warm during the trip of about 180 miles. Although all of the Lake Glendale fish placed in Ridge Lake appeared to be in fair shape (fish were thrown out that had died or that showed signs of having become sick on the road), the unaccountable loss among this group of fish was 317 of 335 or 94.6 per cent by March, 1943.

The high loss of fish in the groups of bass moved to Ridge Lake from Craborchard and Glendale lakes suggests the importance of low temperatures and the careful handling of fish being transported from one water to another. None of the transported bass released in Ridge Lake appeared to be sick at the time of release. Yet many of them had evidently sustained injury sufficient to cause death. The unaccountable loss was considerably higher among the bass with which Ridge Lake was stocked in 1941 than among bass spawned in the lake and subjected to no handling except that during biennial draining censuses. Bass are more often transported as fingerlings than as larger fish, and fingerlings may or may not be more subject to injury. The bass transported from Lake Glendale were 5.0 to 7.0 inches in length; those from Craborchard 6.5 to 11.5 inches; and those from Chautauqua 8.5 to 17.0 inches, table 2.

The program of marking and censusing has made it possible to trace the reduction in numbers of each marked group throughout the period of the experiment. The 435 fish of the original stock had been reduced to 17 by the end of the first 2-year period, table 20. As 2 of these fish were killed in the draining operation, only 15 were available for restocking the lake after the census.

All 15 could be accounted for at the end of the next 2-year period (1943–1945): 4 had been caught by fishermen and 1 was found after it had died, evidently as a result of a hooking injury; 10 were recovered in the 1945 census and, of these, 1 was injured in the census and 9 were replaced in the lake after the census. These 9 were fish that had been brought from Lake Chautauqua. At the beginning of the 1945–1947 period they averaged 3.9 pounds each and were probably 7 to 10 years old; during the period 3 were caught, and only 1 was recovered at the time of the 1947 census. Thus, the unaccountable loss in this period was 5 (55.6 per cent) in contrast to no unaccountable loss in the preceding 2-year period. The fish recovered in the 1947 census weighed 6.75 pounds when returned to the lake in 1947. It was recaptured (7.0 pounds) at the time of the 1949 census and was caught by a fisherman (6.5 pounds) in July of 1949. Scales collected at the time of capture indicated that this bass was 10 years of age.

Of the 1,500 marked bass of the 1941 and 1942 broods or year-classes that were returned to the lake following the 1943 census, 464 were taken in the 1944 creel and 543 were retaken in the 1945 draining census, leaving 493 to be accounted for, or a loss of 32.9 per cent. In the next 2-year period (1945–1947), 496 were returned to the lake, and of these 337 were caught in 1945 and 69 in 1946. Sixty-three were taken in the 1947 census, leaving 27 unaccounted for, or a loss of only 5.4 per cent.

During the 1947–1949 period, the number of bass of the 1941 and 1942 broods was reduced by all causes from 61 to 23; the unaccountable loss was 6 fish, or 9.8 per cent of the number returned to the lake in 1947. Only 4 of the 23 bass returned to the lake following the 1949 census were recaptured in the 1951 census. Ten of these 23 fish were caught by fishermen in 1949, none in 1950; 9 were unaccountable losses.

The 1941–1942 group is of particular interest because of its changes in unaccountable losses from 1943 to 1951. In 1945, the losses in this group for the 1943–1945 period were figured as 32.9 per cent. In March, 1943, these bass averaged 0.17 pound each; by 1945, they averaged 0.77 pound; and, by 1947, 2.44 pounds. In the 1945–1947 and the 1947–1949 periods the unaccountable losses were 5.4 and 9.8 per cent, respectively. In the 1949–1951 period, when the bass of this group averaged between about 4 and 5 pounds each, the unaccountable losses were 39.1 per cent. These fish were approaching an age of 10 years and it seems reasonable to believe that natural mortality may have been responsible for much of the relatively high unaccountable loss in the 1949–1951 period.

When the reduction in numbers of bass in the 1941–1942 year-classes that resulted from fishing and all other causes over the period 1943–1951 is compared with a hypothetical 50 per cent annual reduction in numbers, the regressions are found to be quite similar, table 21.

In the Ridge Lake study, the 1941–1942 year-classes constituted the only group of fish large enough and old enough to give satisfactory figures covering the approximate life span of bass. The less comprehensive data from 1945–1946 and 1947–1948 groups failed to follow the reduction pattern of the 1941–1942 group, and it seems likely that the similarity of the regression pattern of the last-named group to a 50 per cent annual reduction pattern may be coincidental.

Exploitation Rates

The rates at which the populations of marked bass were exploited by anglers are shown in table 19. As it was impossible to assign instantaneous times of occurrence to the unaccountable losses that were brought to light when the lake was drained at the end of each 2-year period, the exploitation rate shown in table 19 for any one fishing season is a simple percentage derived from the number of bass

Table 21.—Observed reduction in numbers of marked largemouth bass of the 1941–1942 group in Ridge Lake, 1943–1951, and a hypothetical 50 per cent annual reduction in numbers.

Year	Observed Reduction in Numbers of the 1941–1942 Group of Bass	Fifty Per Cent Annual Reduction in Numbers
1943	1,500	1,500
1945	496	375
1947	61	94
1949	23	24
1951	4	6

caught by fishermen and the number of bass that should have been in the lake during the fishing season if there had been no unaccountable losses. As such losses were undoubtedly occurring throughout each fishing season, the actual exploitation rates must have been higher than figures in the table indicate. This is true particularly of the 1941–1943 period when the unaccountable loss of bass originally placed in the lake was 86.7 per cent. If all of this loss had occurred in 1941, the exploitation rate in 1942 would have been nearly 71 per cent. In any case, the lower the unaccountable loss for a 2-year period, the nearer the calculated exploitation percentage approaches the true figure. It is probable that in the last three biennial periods, in which the unaccountable losses ranged from 9.7 to 11.1 per cent, the calculated exploitation rates are only slightly below the true rates.

The calculated exploitation rates for marked largemouth bass at Ridge Lake were, for all but a single year, higher than the rate of 20 per cent reported by Ricker (1942:248) for Shoe Lake, Indiana, or the rate of 18.5 per cent reported by Eschmeyer (1942:109) for Norris Reservoir. Exploitation rates reported by Ricker and Eschmeyer were based upon recaptures of tagged fish; like the rates for Ridge Lake fish, they were based upon numbers of fish, rather than weights. Exploitation rates based upon weights of bass are usually lower than those based upon numbers, because small bass are more readily caught than are larger ones.

It is significant that the two highest exploitation rates at Ridge Lake were for years in which food was scarce as a result of draining operations, table 19.

Efficiency of Baits

The natural baits (most of them alive) used at Ridge Lake included minnows, crayfish, hellgrammites, earthworms, grasshoppers, catalpa worms, worm and spinner combinations, and canned shrimp. Minnows and crayfish were by far the most efficient in catching large bass (Durham & Bennett 1949:11; 1951:6). For the fishing seasons of the period 1942–1949, minnows had an average catch rate of one desirable bass (10 inches or longer) for 4.0 man-hours of fishing, and crayfish a rate of one desirable bass for 5.3 man-hours (Durham & Bennett 1951:6). The average catch rates for the other natural baits varied from one bass of desirable size for 10.5 man-hours to one for 48.3 man-hours of fishing. Earthworms were used for bait a larger number of man-hours than were any of the other natural baits (2,823 man-hours); this bait caught 55.4 per cent of the bass of less than 10 inches in length that were taken, but only 16.5 per cent of the bass of desirable sizes.

Individual kinds of plugs, spoons, and spinners, used with a casting rod and reel and fished on eight or more trips, caught desirable-sized bass at rates varying between one fish per 1.9 hours and one per 5.7 hours (Durham & Bennett 1951:6). These baits were used during 1,607 man-hours of fishing and caught 586 bass of desirable sizes and 137 smaller ones. More bass were caught on underwater plugs than on floaters, particularly after the month of June, when the surface water of the lake was very warm.

Fly-rod lures accounted for 615 large bass and 469 small ones in 1,892 man-hours of fishing (Durham & Bennett 1951:7). More fishermen used cork-bodied popping bugs and minnows than any other type of bait, and these baits were very efficient in catching bass.

In table 22, the efficiency of natural baits can be compared with that of casting-rod plugs and fly-rod lures in catching bass. Many fishermen using earthworms fished primarily for bluegills, but it seems

Table 22.—Efficiency of natural baits (mostly alive) and of artificial baits for casting rods and fly rods used for catching largemouth bass at Ridge Lake, 1942–1949 (from Durham & Bennett 1951: 7). Desirable bass are those of 10 inches or longer.

Type of Bait	Number of Trips	Man-Hours of Fishing	Bass of 10 Inches or Longer		Bass of Less Than 10 Inches, Number	Ratio of Desirable to Smaller Bass	Total Catch	
			Number	Man-Hours per Fish			Number	Bass per Man-Hour
Live and other natural baits	1,847	6,252	830	7.53	1,383	1 to 1.67	2,213	0.35
Casting-rod lures	744	2,188	768	2.85	211	1 to 0.27	979	0.45
Fly-rod lures	800	2,150	672	3.20	626	1 to 0.93	1,298	0.60
Total	*3,391*	*10,590*	*2,270*	—	*2,220*	—	*4,490*	—

obvious that fishermen had more confidence in live baits, for bass as well as bluegills, than in artificials; they used live baits during nearly three times as many hours of fishing as either casting-rod plugs or fly-rod lures. The catch rate (bass per man-hour) for each of the two groups of artificial baits was superior to that of the natural-bait group, table 22. The figures in this table, however, may not be a fair representation of the relative efficiency of the baits, because fishermen had a tendency to try artificial baits at the start of each fishing period, then switch to natural baits if the artificials were ineffective, and, if the natural baits also failed to catch fish, still continue to use them. Thus, it was possible to build up many "low catch" hours to be assigned to fishing with natural baits.

In laboratory experiments, Brown (1937: 53–4) discovered that the largemouth bass is able to distinguish colors quite readily, particularly red. His experiment suggests that the color-distinguishing ability of the bass eye is comparable to that of the normal human eye when the latter is covered with a yellow filter. The following quotations are from Brown (1937: 53–4):

"Freshly collected bass which have been in the laboratory no more than two days, and fed *Daphnia* during that time, are most attracted by red, then in order of decreasing attraction of the colors used came yellow, white, green, blue and black.

. . . .

"Red appears to be the outstanding color, as such, in the responses of the bass. This color is easily and readily selected from everything else, with the exception of violet."

Colors seemed to be of some importance in stimulating the Ridge Lake bass to strike. While our records of the colors of casting-rod plugs and fly-rod lures used by fishermen at Ridge Lake are incomplete, the available data indicate that, in plugs, red and white combinations attracted more fish than any other colors or combinations; silver alone and black alone in that order were next in apparent effectiveness. For fly-rod lures, yellow was the most effective color; a total of 285 bass were caught on fly-rod lures listed as yellow or as combinations of yellow with other colors. White or combinations of white with other colors were next in effectiveness, followed by combinations of various shades of brown.

After studying the catch records of individual fishermen who fished the lake often, it was apparent that skill played an important role in bass fishing. For example, in 1949 the average rate of catch of bass for all fishermen was 1 pound in 7.1 hours. One man who fished the lake 14 times throughout that summer had a catch rate for bass of 1 pound in 1.76 hours, while another who fished the lake 20 times had a catch rate of 1 pound in 11.1 hours. Both were experienced enthusiastic bass fishermen, both used artificial baits and knew the lake well. Yet one man was more than six times as efficient as the other in catching fish.

During the first few days of public fishing in each year at Ridge Lake, the bass that are not caught have an opportunity to become familiar with the more common methods used by fishermen in presenting artificial baits. Observations on the fishing techniques employed by the most successful bass fishermen suggest that these men vary their techniques much more than do those fishermen who are less successful.

Cost of Fishing

In 1949, a study was made of the amount of money spent for contingent travel, meals, equipment, and licenses by the fishermen who made reservations to fish at Ridge Lake (Bennett & Durham 1951). It was calculated that the average cost of a fishing trip was $1.22 per hour (Bennett & Durham 1951: 13). When the average hourly cost was assigned to the average catch in pounds of bass per hour, the amount of money spent to catch a pound of bass was calculated to be $8.66. The bass population of the lake was assumed to be 1,046 fish at the beginning of the 1949 fishing season, table 15. Fishermen spent about 3,949 hours angling for these bass and caught 594, weighing 540.5 pounds (Bennett & Durham 1951:9). The rate of catch was 0.14 pound per hour or 1 pound per 7.1 hours.

The average bass fisherman probably spends somewhat more than $8.66 per pound for the bass that he brings to creel, because usually he rents a boat (no boat rental charge was made at Ridge Lake); the population of bass at Ridge Lake was unusually high in the year the study was made; and this population, which had developed in 18 acres of water, was concentrated in 11 acres of water.

Discussion

Within the period of study covered by this publication, spring of 1941 through the bass spawning season of 1951, more than 11,000 largemouth bass were permanently removed from Ridge Lake, table 3. These fish were offspring of 435 bass introduced into the lake during the spring of 1941, table 2. Of these 435, only 100 were sexually mature in 1941; the others were yearlings. There is evidence that most of the bass making up the original stock died very soon after being introduced, table 19. Of the bass removed from Ridge Lake previous to the angling season of 1951, 3,743 were taken by anglers and the rest removed in draining censuses as excess small fish, table 3.

Bluegills were placed in Ridge Lake in 1944 (129 adult fish) and, from the summer of 1945 through March, 1951, approximately 155,000 of these fish were removed from the lake (9,073 by anglers), table 3, indicating that bluegills are more prolific than are bass.

In the 8 years of the study period that the lake was open to the public for fishing, the annual bass yield varied between a low of 10.9 pounds per acre and a high of 30.0 pounds per acre, table 8. These figures are based on a lake area of 18 acres. A still higher figure, 49.2 pounds per acre, is derived for 1949 when the reduced lake area for that year, 11 acres, is used as a basis for calculation, table 18. In spite of the fact that Ridge Lake is located in soils of moderately low fertility and cannot be expected to compare in productivity with impoundments in better soils, the yields of bass were 2 to 10 times the yields of bass in unmanaged Illinois waters for which figures are available. A basic requirement for a high yield of bass is a high population of this species; however, because of the behavior idiosyncrasies of the species, a high yield may not be a certainty even when a high population is present.

The history of largemouth bass in new, unmanaged impoundments containing more than one species of fish is one of a high population at first, which gradually becomes smaller, so that, within a span of years equal to that covered by this study, the population may drop to a very low level. At Ridge Lake the population level of bass appeared to increase somewhat, and the highest yields from angling were recorded in 1948 and 1949, near the end of the 10-year period reported here.

When the lake contained only largemouth bass (1941–1944), a satisfactory spawn was produced in each year except 1944. After bluegills were introduced, the years of good bass spawn production were those in which the lake was drained and bluegills and other small fish were removed prior to the bass spawning season. In some of the years in which many small bluegills were present, only a very small number of bass fry could be found; in others, none at all. The high sustained yield of bass at Ridge Lake was a result of successful natural reproduction and satisfactory survival of young bass every other year. There was little relationship between the number of spawners and the number of fry they produced, table 10; there was an inverse relationship between the number of bass fry and the number of small bluegills in the lake at spawning time.

The key to successful management of largemouth bass in Ridge Lake has proved to be the control of the numerical size or the populations of fishes other than bass that inhabit the water. If bass in other waters are similarly influenced by populations of other fishes, it is doubtful if closed seasons, length limits, and creel limits, which have been relied upon for many years to protect and enhance bass populations, have been of any value. The minimum length limit of 10 inches, the creel limit of 10, and a closed season of March 1 to June 15 were first introduced into Illinois in 1923. There is no evidence that these fishing regulations have had any influence on bass fishing in the state.

Ridge Lake was not opened to public fishing in any year until after the bass spawn had been observed or the adults were spent (in a year in which no spawn was seen), so that bass that were spawning in the lake always were protected from human interference. In years when many small fish were present in Ridge Lake and bass spawn production was very low (1944, 1946, 1948, and 1950, table 10), the opening of the lake to intensive angling during the bass spawning season could have had no measurable effect upon the production of young bass. In years when small fish were removed from Ridge Lake in March prior to the bass spawning season and the bass spawn production was high (1943, 1945, 1947, 1949, and 1951), it would have been difficult to measure accurately the effect of heavy angling, during the bass spawning season, upon the production of young bass. Judging from the behavior of bass in response to public fishing at Ridge Lake, however, I believe that the total effects of fishing (removal of some spawning fish and the frightening of spawning and nest-guarding fish) would be less of a limiting factor in the production of young bass than would be the nest-robbing activities of a large population of bluegills.

Estimated survival rates for bass fry in the years 1941, 1943, 1947, and 1949 were 29 to 1, 40 to 1, 30 to 1, and 34 to 1, respectively, table 11. At these rates of survival, the number of fry needed to replace the adults caught by fishermen at Ridge Lake in any single year would probably vary between 5,000 and 20,000. A few males bringing off successful hatches of fry would supply several times either of these numbers. Thus, unless fishermen were able to locate all of the nesting male bass in the lake and make a systematic effort to catch them, some males guarding nests would escape and bring off hatches of young in numbers more than adequate to replenish the population.

The purpose of a size limit on any sport fish is to allow individuals to reach sexual maturity and spawn, but, unless it can be shown that a large number of spawners produce greater numbers of young than a small number of spawners, there is no logic in holding to a minimum length limit. Most species of fish in some measure influence the survival of their own young; that is, when populations are high the success of spawning is low, and vice versa. Thus, if small "yearling" fish (fish spawned the previous year) of a species are taken by anglers without regard to size, the survival of current-season young of that species may be greater than if the "yearling" fish are not cropped. It seems reasonable to assume that, had fishermen been allowed to take bass of less than 10 inches in 1942, survival of the spawns of 1942 and 1943 would have been higher than they were.

The only point that can be made in favor of a creel limit of 10 bass is that on certain very infrequent occasions bass lose their usual wariness and bite very readily. On these occasions, a limit of 10 fish may prevent an overenthusiastic fisherman from taking more fish than he can use.

A characteristic of the largemouth bass that greatly simplifies management is the fact that it spawns somewhat earlier than most other centrarchids with which it may be associated in a pond, and the young bass may be just enough larger than the fry of the other pond fishes to feed heavily upon them. Further, as the quantity of young bass produced is inversely related to the amount of interference with the nesting bass and to actual predation on the eggs and fry, all that is necessary to increase the numerical size of the bass population is to reduce the numbers of fish of the other species inhabiting the water with the bass. The resulting increase in the production and survival of young bass may vary from a few individuals to a brood or year-class so large that it dominates the fish population of the pond. When the individuals of a dominant brood of bass grow to a weight of 0.5 or 0.75 pound each, they may furnish excellent fishing.

There is some possibility that a fish-thinning operation may allow, under some situations, the survival of too large a population of young bass, so that not only is a dominant brood produced, but the individuals may be so numerous that their food requirements exceed their food supply and they become stunted. Such a population of bass was produced in Ridge Lake in 1941. The 1941 year-class, which became stunted in 1942 at an average total length of 7.6 inches, could have been reduced to a numerical level that had food needs approximately commensurate with its food supply had fishermen in 1942 been freed from the state's legal restrictions of a 10-inch minimum length and a creel limit of 10 bass. Overabundant year-classes of bass did not develop in Ridge Lake after 1941 because enough bass of larger sizes were present in the lake to thin out the larger broods before the individuals reached postfingerling sizes. An overpopulation almost certainly would have resulted from the very large brood of bass that appeared in 1945 had not predation on this brood been high when it was in the fingerling stage.

In the 1945 and 1947 draining censuses at Ridge Lake, all bass below 10 inches in length were culled out and all larger bass were returned to the water. In the 1949 census, the minimum length of bass returned to the water was reduced to 9 inches and in the 1951 census to 8 inches. There was no evidence that the reduction in minimum lengths of bass returned to the water after the 1949 and 1951 censuses had a significant effect upon the survival of bass spawn.

In studying the population dynamics of bass and bluegills at Ridge Lake, it is obvious that this combination of fishes in this impoundment would not produce a continuous high yield of bass over a period of years without considerable population adjustment at regular intervals. Bluegill spawning and survival in any 2-year period between draining censuses was excessively high; the bass showed no great ability to control the number of small bluegills. Apparent failure of the bass to keep the bluegill population at a low level probably was related to the presence of a large crayfish population in the lake; the bass seemed to prefer crayfish to bluegills as food. Murphy (1949: 162) found that bluegill fry were not an important item in the diet of the young bass of Clear Lake, Lake County, California, although small bluegills were relatively abundant in the lake at the time his study was made. The preference of bass for foods other than bluegills may be rather general and may have a great deal to do with the variable results that have been obtained from the bass-bluegill combination in some Illinois lakes.

The catch records at Ridge Lake show that bass rapidly lose their vulnerability to angling, so that, within a few days of the beginning of intensive fishing, the catch rate becomes discouraging to a large percentage of the fishermen, and most of the fish caught are taken by anglers who might rate as experts. There is no question that skill is important in catching bass. Records prove that certain fishermen are much more proficient than others. Superior ability to catch bass appears to be associated with the methods of "working" the lures.

The wariness of the largemouth bass is both encouraging and discouraging: encouraging to the aquatic biologist in that he can be certain that this bass will survive in numbers in spite of very heavy angling pressure (Bennett 1945: 385); discouraging to the angler in that, unless he is an expert, his chances of making a good catch of bass in a public lake are rather poor.

The bass at Ridge Lake seemed to retain their wariness during the fall months; even though the lake was closed to public fishing for 3 weeks or a month or more, the rate of catch in postseason test fishing operations was only a little better than during the summer. However, the bass apparently lost their wariness over winter and again became vulnerable to the average fisherman.

Ridge Lake was not opened to the public in 1943 and, in 1944, not until the second week of August. During this closed period, Natural History Survey personnel were taking small samples of bass at regular intervals. These bass were taken by angling (as bass will seldom enter wing nets or traps in clear water), and were caught at a very high rate (average rate about 10 fish per hour). Most of these fish were rather small in size, and small bass are less wary than are large. But preseason fishing for all years, in some of which the average size of fish was much larger than in others, yielded fish at a very high rate. Preseason fishing in 1949 produced bass at the rate of nearly 3 pounds per man-hour, table 15.

Our experience with bass has led us to believe that there is for each body of water a definite level of fishing intensity below which bass do not become "educated," and that it would be possible, in artificial ponds and lakes that are privately owned, for the owners so to regulate the intensity of fishing that small numbers of bass could be caught quickly and with little effort on the part of unskilled anglers.

What such a fishing intensity would be for a given body of water is a question that cannot be answered satisfactorily now. At Ridge Lake, it has been demonstrated that an opening-day fishing pressure of between 1.8 and 5.0 man-hours per acre concentrated within a 4-hour morning period has been followed in the afternoon by a rather severe drop in the catch rate of bass.

Probably the most intensive fishing by Natural History Survey personnel at Ridge Lake was done during the period June 1 to 14, inclusive, in 1949, when 17.75 hours of fishing yielded 50 bass weighing 52.49 pounds, table 15. In this 14-day period, in which the lake was fished on 9 days, the fishing pressure never exceeded 0.36 man-hour per acre for any one day, and usually it amounted to about 0.05 to 0.07 man-hour per acre per day. Somewhere below the rate of 1.8 man-hours per acre per day lies a range of fishing intensity within which bass apparently do not develop wariness. This range probably is influenced by the number of fishing hours per acre per day, by the amount of rest between periods of active fishing, and by the size and conformation of the lake basin. Certainly any lake owner may discover, after a few years of experimental fishing, coupled with a system of complete creel censusing, the approximate fishing intensity at which the catch rate for bass begins to fall off in his lake. It is assumed that during this period the lake is managed to maintain a large population of bass; otherwise, the testing of various fishing intensities would mean little.

The average length of life of its individuals must be considered in the development of a management program for any species of fish. The largemouth bass is a relatively long-lived species, so that a bass of desirable size will probably remain available to the angler for a number of years. In most broods spawned in Ridge Lake, unaccountable losses among the medium-sized bass were usually much lower than among the bass of less than about 0.2 pound or more than about 3.5 pounds in weight, table 20. In a location such as Ridge Lake, where fish may move out of the lake, over the spillway, in time of high water, a large part of the unaccountable loss among small bass may be due to random migration in search of better territory. Larimore (1952: 10) demonstrated that smallmouth bass in streams have definite territorial instincts and that the smaller fish have less well-defined territories than have the larger ones, presumably because the smaller fish are less able to hold desirable territories.

There is some evidence (largely in popular literature on bass fishing) that individual largemouth bass in lakes have been repeatedly recaptured in definite locations over periods of time. If the largemouth is similar to the smallmouth in territorial instincts, it is not difficult to explain the movement of small bass out of a lake when the opportunity arises. This loss of small fish is not considered serious; rather, in many situations it must be considered beneficial, because one objective of a bass management program is to bring the young fish up to desirable sizes as rapidly as possible, and the thinning of a crowded population by loss of individuals over a spillway would allow an improvement in the rate of growth of the fish remaining. That movement of young fish out of Ridge Lake may be random was indicated by the continuation of a crowded population of bass all through the 1942 season, although bass could have moved out of the lake over the surface spillway following seven or eight different storms that occurred in May, June, and July, fig. 5.

The brood of bass spawned in Ridge Lake in 1941 had been reduced to four individuals by 1951, table 20. The age attained by these four bass is probably near the maximum for largemouths in the latitude of Illinois. For the 1941 brood, the unaccountable loss, which includes the loss resulting from natural deaths, was 39.1 per cent in the 1949–1951 period, whereas in the 1947–1949 period it was only 9.8 per cent.

The catches of bass for the individual years 1944 through 1950, which ranged from 31.0 to 62.4 per cent of the marked fish in the lake, table 19, may be considered to represent high exploitation rates for a species of fish that has a normal life span of 8 to 10 years in the latitude of central Illinois. That these exploitation rates were not excessive for the Ridge Lake population was indicated by the fact that there was a comparatively high poundage of bass present when the lake was drained in 1951, table 7, after 7 years of these rates. It is true that in this period the yield of bass in numbers and total poundages, table 6, and pounds per acre, table 8, varied a great deal from year to year, but I can see no upward or downward trends in population abundance that can be clearly associated with rates of exploitation.

So little information is available on exploitation rates of bass in other bodies of water that it is impossible to make a comparative evaluation of the exploitation rates at Ridge Lake. The high bass fry production in alternate years, table 9, was important in that it assured adequate replacements for fish caught, regardless of the exploitation rate.

Today (June, 1954) descendants of the 435 bass with which Ridge Lake was stocked in 1941 are still rising to the lures of some of the fishermen who caught their great-great-great-grandparents in 1942. These present-day fish and the thousands that have inhabited the lake in the period since 1941 are mute evidence that the largemouth bass will respond to a few simple management techniques. The fish technician or the pond owner who knows when and how to apply these techniques need never worry for the future of bass fishing.

Summary

1. Ridge Lake, the dam for which was completed in April, 1941, is an artificial impoundment that at overflow level in 1941 had an area of 18.1 acres and a maximum depth of 25 feet. It was made by damming Dry Run Creek, a tributary of the Embarrass River, in Coles County, Illinois. Both tower and surface spillways were constructed. The tower spillway was provided with a gate valve to be used in draining the lake basin. A permanent laboratory was built on the south shore of the lake about midway between the dam and the upper end. Silting of the lake basin was and is a serious problem, as much of the 902-acre watershed drains into the lake through steep-sided ravines, some of them pastured. The lake is eutrophic-like in character in that it has no dissolved oxygen in the deep water in summer, except when the cool oxygen-deficient water is flushed out of the lake through a tower spillway by the entrance of surface runoff into the lake basin after heavy rains.

2. The lake was stocked in 1941 with 435 bass, table 2, in 1944 with 129 bluegills, and in 1949 with 138 warmouths. In 1942 and most subsequent years, the public was allowed to fish from boats belonging to the Natural History Survey, and a record was made of kinds, numbers, and weights of all fish caught, table 6, time spent in fishing, table 15, kinds of baits, table 22, and the tackle used. A few scales were taken from each of the

bass caught and from most of the larger bluegills and used later for age analyses. The lake was closed to public fishing in 1943 and until August in 1944.

3. At intervals of 2 years, beginning in 1943, the lake was drained in early spring and a census was made of the fish, table 4. Five censuses were made in the 1941–1951 period covered by this study. After each census, the large bass (minimum length 10 inches in most years, 8 or 9 in others) were marked by fin-clipping and returned to the partially refilled lake basin, table 5. After each draining, except that of 1949, the lake basin had completely refilled before the beginning of the summer fishing season. In 1949, the basin had only partially refilled; the water covered an area of about 11 acres on June 1 and remained practically constant in area until November.

4. No stocks of fish, other than the 435 bass released in 1941, the 129 bluegills released in 1944, and the 138 warmouths released in 1949, were introduced into Ridge Lake from other bodies of water. In the study period, which began in the spring of 1941 and ended after the bass spawning season but before the angling season of 1951, more than 11,000 bass and 154,000 bluegills were permanently removed from the lake by angling and in draining censuses, table 3. Of these, 3,743 bass and about 9,000 bluegills were taken by anglers; the others were taken in draining operations as excess small fish. In the 1949–1950 period, few warmouths were caught by anglers and less than 1,000 were taken in the 1951 draining census, table 4. About 3,500 fish other than bass, bluegills, and warmouths were taken from the lake (mostly in draining operations) during the study period, table 3. These, which included green sunfish, black bullheads, yellow bullheads, carp, and a black buffalo, were of species indigenous to Dry Run Creek and the Embarrass River. Although large numbers of bass and bluegills were removed from Ridge Lake during the study period, these fish were as numerous in Ridge Lake in 1951 as they had been at any other time during the 10-year period, table 4.

5. The weight of bass taken in the five draining censuses ranged from 31.5 pounds per acre in the 1947 census to 50.4 pounds per acre in the 1949 census, table 7. In three censuses, those of 1943, 1949, and 1951, the weight of bass was 48.2, 50.4, and 49.9 pounds per acre, respectively. These poundage calculations suggest that the carrying capacity of Ridge Lake for bass may be about 50 pounds per acre. Once the bluegill population had become well established in Ridge Lake, poundages per acre of bluegills varied between 86.9 and 193.3; the largest poundage of bass was found with the smallest poundage of bluegills (1949 census) and the largest poundage of bluegills with the smallest poundage of bass (1947 census), suggesting interspecific competition.

6. Yields of bass taken by angling during years in which the lake (an 18-acre area assumed) was open to public fishing varied between 10.9 and 30.0 pounds per acre, table 8; yields of bluegills varied between 6.2 and 45.9 pounds per acre. Fishing pressure ranged from 90 man-hours per acre in 1944 to 320 man-hours per acre in 1948, table 18.

7. Estimates of numbers of bass fry were made during the spawning season of each year, 1941 to 1951, inclusive, table 9. In years in which the lake was drained and small fish were removed in March, the estimates of numbers of fry varied between 18,000 and 116,000, with an average of 50,500. In years in which the lake was not drained in March and small fish were present, the estimates of numbers of bass fry ranged from 0 to 26,000, with an average of 5,900. Schooling bass fry were observed prior to June 1 in only 3 years out of 11.

8. There was no apparent relationship between the number of bass of spawning age in the lake in any given season and the number of bass fry produced in that season, table 10. Years in which small fish were abundant in the lake (particularly those years in which many small bluegills were present) were years of low production of bass fry.

9. The ratios of numbers of bass fry of a brood to individuals of the same brood taken as larger fish in the 21 months after spawning varied between 29 to 1 and 40 to 1, in 1941, 1943, 1947, and 1949, table 11. In 1945, when the number of bass fry produced was unusually large, the survival ratio was 195 to 1.

10. Bass at Ridge Lake averaged 8.1 inches total length at 1 year of age, 10.3 inches at 2 years, 12.6 inches at 3 years, and 13.7 at 4 years, table 13. Bluegills averaged 4.7 inches total length at 1 year of age, 6.2 inches at 2 years, and 7.1 inches at 3 years, table 14.

11. In 1949, bass fishing dropped from a preseason calculated catch rate of 2.96 pounds per man-hour to a rate of 0.18 pound per man-hour on the second day of the public fishing season, table 15. The calculated rate of catch in the afternoon period of the first day of the fishing season in each year in which public fishing was allowed was less than half that of the morning, table 16. By the third day of the fishing season in each of these years except 1944, the calculated rate of catch was less than one-third that of the opening morning. In no year was the catch in numbers or pounds on the opening morning more than 6.3 per cent of the available number or poundage of fish in the lake. For years in which large numbers of bluegills as well as bass were available, the calculated seasonal catch rate for bass and bluegills together was 0.19 pound per man-hour; for years in which bass were essentially the only fish available, the calculated seasonal catch rate for bass was 0.13 pound per man-hour, table 17. Actual rates of catch were probably 50 to 100 per cent higher than the calculated rates because time spent in rowing boats was counted as fishing time.

12. Some of the factors influencing the yield of bass in any given fishing season were the number and weight of bass available, the fishing pressure, and the amount of natural food available for bass. While all of these factors undoubtedly were important in determining the bass yield, the highest catches, in terms of number and weight of bass available, were made in years when small fishes and other bass foods were reduced through lake draining prior to the fishing season, table 18. In these years, yields of bass from angling varied between 45 and 64 per cent of the number and between 40 and 69 per cent of the weight of bass available. In years (after 1943) when the lake was not drained prior to the fishing season, the yields of bass from angling varied between 23 and 40 per cent of the number available and between 27 and 34 per cent of the weight available.

13. In the 2-year period preceding the first draining census and in each of four 2-year periods between draining censuses, numbers of bass that had been marked by fin-clipping disappeared from Ridge Lake. These bass could have died from injuries or from natural causes without being recovered, they could have moved out of the lake over the surface spillway in time of flood, or they could have been removed through illegal fishing when the lake was closed. The unaccountable losses among the bass with which the lake was originally stocked amounted to 86.7 per cent in the 1941–1943 period, table 19; the losses were so high as to suggest that many of these fish died from injuries received in transportation or handling. Among the bass produced in the lake and later marked, unaccountable losses were lower in the middle age groups than in older and younger age groups. As bass approached the age of 10 years, the unaccountable losses increased, suggesting that the fish were approaching the end of their normal life span.

14. Artificial lures were more effective in catching bass than were live or other natural baits, table 22. Fishermen tended to try artificial baits at the start of each fishing period, switch to natural baits if the artificials were ineffective, and, if natural baits also were ineffective, continue to use them, thus building up many "low catch" hours for the natural baits. Catch records for individual fishermen demonstrated that skill was important to success in bass fishing.

15. For their contingent travel, meals, tackle, and licenses, fishermen at Ridge Lake in 1949 are estimated to have spent an average of $1.22 for each hour of bass fishing. Because they averaged 7.1 hours in catching 1 pound of bass, the calculated cost of their catch was $8.66 per pound.

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Natural Availability of Oak Wilt Inocula

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CONTENTS

Wilt-killed oak trees in a northern Illinois forest area. Dying of trees in "pockets," as illustrated here, indicates that a principal means of spread of the oak wilt fungus from infected to healthy trees is through naturally occurring root grafts.

Natural Availability of Oak Wilt Inocula

E. A. CURL*

IN the past 10 years, oak wilt, caused by *Endoconidiophora fagacearum* Bretz, has become increasingly important as a destroyer of oak trees in the eastern half of the United States. It was first described about 13 years ago as a fungus disease in Wisconsin (Anonymous 1942), but earlier reports of dying oaks indicate that it probably has been present there for the past 20 years.

The American oaks, which number about 300 species, are the most important group of hardwoods in North America, furnishing more native timber than any other related group of broadleaved trees (Finlay 1950). In 1948 the net volume of saw timber in Illinois totaled 10.3 billion board feet (King & Winters 1952). The oak species total was 56 per cent of the net board-foot volume. White oak accounted for 21 per cent of the total, and black oak and northern red oak each made up about 10 per cent. The esthetic as well as the commercial value of oaks must be considered in evaluating the economic importance of oak wilt. Oaks are prized highly as both shade and ornamental trees.

No species of oak yet tested has shown immunity to oak wilt (Kuntz & Riker 1950*b*). Other susceptible species of the family Fagaceae are *Castanea mollissima* Bl., Chinese chestnut; *C. dentata* Borkh., American chestnut; *C. sativa* Mill., European chestnut; *Lithocarpus densiflorus* Rehd., tanbark oak; and *Castanopsis sempervirens* Dudley, bush chinquapin (Bretz & Long 1950, Bretz 1952*a*, Ernst & Bretz 1953). Once infected, trees in the red oak group die rapidly, most of them within 6 weeks. Trees in the white oak group may die slowly over a period of 1 to 3 years.

Since 1942 oak wilt has been reported from 18 states. The results of aerial surveys (Fowler 1951, 1952, 1953) conducted by the United States Department of Agriculture, Division of Forest Pathology, since 1951 and various individual reports (Bretz 1949, Carter 1950*b*, 1952, Cummins 1949, Elmer *et al.* 1953, Fergus & Morris 1950, French & Christensen 1950, Strong 1951, Wysong 1949, Young & Bart 1951) indicate a considerable increase in wilt in most of these states.

In Illinois the disease was first noticed in 1942 (Carter 1950*a*). By the end of 1952 it had been found in 54 of the 102 counties in the state. Most of the counties that are still free of the disease are located in areas where oak timber is not abundant.

The threat of oak wilt was recognized early in Wisconsin (Anonymous 1942, Henry *et al.* 1944) and in Iowa (Dietz & Barrett 1946, Dietz & Young 1948), where some of the first research on the disease was conducted between 1942 and 1948. In 1950 the National Oak Wilt Research Committee (Anonymous 1950) was organized at Memphis, Tennessee, for the purpose of supporting research programs in co-ordination with several universities and with the United States Department of Agriculture, Division of Forest Pathology. Such programs have now been developed in most of the states in which oak wilt is found.

The studies reported herein are intended mainly to supply information concerning the availability of oak wilt inocula and the relative importance of Illinois environmental conditions at different times of the year on the longevity of the causal

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fungus in nature. It seems that such information would be applicable in finding the means of spread of the disease beyond root graft distances and in selecting and developing effective control measures.

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REVIEW OF LITERATURE

A short time after the cause of oak wilt was established as a fungus (Anonymous 1942), the conidial stage was named *Chalara quercina* by Henry (1944). Later Bretz (1951, 1952*b*) succeeded in producing perithecia of the fungus in laboratory cultures and named this stage *Endoconidiophora fagacearum*. Symptoms of the disease have been adequately described by various workers (Henry & Moses 1943, Henry *et al.* 1944, Henry & Riker 1947, Riker 1948, Young 1949).

In 1949 Kuntz & Riker (1950*a*) demonstrated local spread of the disease from diseased to healthy trees through natural root grafts. The means by which the pathogen is transmitted beyond root graft distances has not been determined. While transmission through root grafts is highly important in parts of the Midwest where the disease has become well established, it does not appear to be the primary method of spread in states such as Pennsylvania (Fergus 1953) and Ohio (Young *et al.* 1953). There many isolated single-tree infections occur, indicating long-distance transmission by a spore-carrying vector.

For a decade following the identification of the causal fungus, the form of its fructification in nature was not known. In the summer and fall of 1951 Curl *et al.* (1952) discovered mycelial mats of *Endoconidiophora fagacearum* under the loose bark of diseased oak trees in Illinois. Endoconidia were present in large numbers on these mats. A little later Stessel & Zuckerman (1953) discovered the ascigerous stage on mats in nature. Reports of endoconidium- and perithecium-bearing mats in other states (Barnett *et al.* 1952, Campbell & French 1953, Morris & Fergus 1952, Staley & True 1952) indicate that this type of growth is common on wilt-killed oak trees. The implication of the possible importance of mats in serving as reservoirs of inoculum from which the unknown vector or vectors might spread the disease is readily understood. Curl *et al.* (1953) described the thick, sclerotium-like pad that usually occupies the center of the mycelial mat, and they succeeded in producing a similar structure in laboratory cultures. Zuckerman & Curl (1953) presented proof that the pad is a growth form of *E. fagacearum* and showed that single cells from laboratory-grown pads were capable of continuing growth.

There are many physiological agents that affect the ability of fungus spores to germinate (Gottlieb 1950, Hawker 1950, Lilly & Barnett 1951, Wolf & Wolf 1947). Temperature and moisture have received more attention than other factors since they influence both the germinability of spores and the infection of the host. Many workers (Anderson *et al.* 1948, Heald & Gardner 1914, Heald & Studhalter 1915, Ling 1945, McCrea 1931, Rosen & Weetman 1940) have shown that spores of various fungi usually remain viable longer under comparatively dry conditions than when kept moist, and the resistance of the spores to extremes of temperature is greater under dry conditions. Heat may affect reproduction by hastening the fungus to maturity (Lilly & Barnett 1951).

Weather conditions are known to influence the incidence and relative prevalence of some plant diseases by influencing the availability of inoculum in the field. Ling (1945), working with stripe rust of wheat in China, found that the amount and distribution of rainfall in late winter and spring are most important in determining rust epidemics. On the other hand, Anderson & Rankin (1914) found that winter conditions have little effect on the viability of pycnospores of *Endothia parasitica*.

Wilkins (1938) stated that the age of the spore is probably the most important single factor influencing germination of ascospores of *Ustulina vulgaris*. By making collections of ascospores and conidia of *U. vulgaris* at intervals during the autumn and winter, he showed that the spores soon lose the power to germinate.

Henry (1944) found that the oak wilt fungus grew best within a range of 24 to 28 degrees C. Young (1949) found the optimum range to be 22 to 26 degrees C. The optimum pH range for growth was found by Barnett & Lilly (1952) and Young (1949) to lie between pH 5 and pH 7, and to have limits at pH 3 and pH 9. Young obtained maximum germination of conidia on agar of low dextrose content at 25 to 30 degrees C. Henry obtained best germination of conidia in 1.25 per cent malt solution at 24 degrees C. Little previous work has been reported dealing with germination requirements of ascospores of the fungus. Bretz (1952*b*) found that the ascospores germinated rapidly in 2 per cent dextrose solution at 25 degrees C. Stessel & Zuckerman (1953), using ascospores taken in October from naturally occurring perithecia, obtained 30 per cent germination in 2 per cent dextrose solution at 25 degrees C.

The availability of oak wilt inocula under natural conditions and the effects of environmental conditions on longevity of the fungus have received some attention. McLaughlin & True (1952) reported survival of conidia of the oak wilt fungus for 173 days on a glass surface when kept at 10 degrees C. in controlled low relative humidities. The survival period was much shorter at temperatures above 25 degrees C. Jewell (1953) found that low temperatures and low relative humidity favored the longevity of ascospores of the oak wilt fungus *in vitro*. Curl (1953) reported that the greatest concentration of viable, naturally occurring conidia and ascospores of the oak wilt fungus in Illinois was found during March, April, and May. Young (1949) demonstrated in Iowa that the fungus lives over winter in trees that become infected late in the summer. Young & Spilker (1952) in Ohio failed to obtain the fungus from lumber that had been cut from wilt-killed oaks and piled during the summer, but isolated the fungus from large twigs, slabs, and stump wedges for a period of 3 weeks. Bretz & Morison (1953) found that the survival of the oak wilt fungus in small-diameter infected twig samples is relatively short at temperatures of 20 to 25 degrees C. and above. Fergus (1953) reported the presence of mycelial mats of the fungus in nature in Pennsylvania from March through November, except in April and July. Morris & Fergus (1952) noted the appearance of mats in early March and found them to be viable a month later. They also observed that two mats collected in May continued to produce new perithecia and ascospores for approximately 2 months when kept at 8 degrees C. in a moist chamber. Campbell & French (1953) found mycelial mats of the fungus in Minnesota in November after 2½ months of drought.

The possible significance of mycelial mats of *Endoconidiophora fagacearum* in relation to transmission of the disease has been discussed by various workers. Curl *et al.* (1953) noted the presence of insects, which belonged to three families, beneath the bark of all mat-bearing trees examined in Illinois. Some larvae and adults were seen in direct contact with the fungus. True *et al.* (1952) pointed out that mycelial mats might serve as natural reservoirs of oak wilt inoculum. Craighead & Morris (1952) observed more than 20 species of beetles, flies, and mites on mats of the oak wilt fungus. Morris & Fergus

(1952) in Pennsylvania found evidence of insect and rodent feeding on mycelial mats and pads. Himelick *et al.* (1953) in Illinois and Campbell & French (1953) in Minnesota also reported considerable damage to the fungus pads by rodents. Birds and air currents have received little attention as possible agents of transmission.

The only known practical controls for the oak wilt disease at the present time consist of interrupting root graft systems (Kuntz & Riker 1950*a*) between healthy and infected trees and the practicing of sanitation and eradication (Dietz & Barrett 1946, McNew & Young 1948, Young *et al.* 1953) in oak wilt areas. Hoffman (1952), after investigating oak wilt chemotherapy, reported that several chemicals showed promise in their effectiveness against the pathogen under experimental conditions.

FIELD METHODS

Selection of Trees

Wilt-infected oak trees used in these studies were selected in late September, 1952. They consisted of 19 red oaks, *Quercus borealis* Michx. f., 9 black oaks, *Q. velutina* Lam., 1 bur oak, *Q. macrocarpa* Michx., and 1 white oak, *Q. alba* L., in five major oak wilt areas in the northern half of Illinois where oaks had been dying for several years. These areas were in the Forest Preserve District of Cook County near Chicago; a privately owned 100-acre tract in Ogle County 8 miles south of Rockford; Sinnissippi Forest near Oregon; Detweiller Park at Peoria; and a privately owned 50-acre tract, in Mason County, 10 miles east of Havana. For convenience the study areas will be referred to as the Chicago, Rockford, Sinnissippi Forest, Peoria, and Havana areas.

The total of 30 trees marked for study is a relatively small number compared with the number of wilted trees in all study areas. However, because of the thorough examination given each tree selected and the intensive study made of each mat collected or sampled, a larger number of trees could not be considered. Mycelial mats were collected from a few trees other than those marked for study. These were designated as miscellaneous mats, and they were added to the total number studied. Table 1 shows the kinds and diameters at breast height of trees that were selected for study in each area. The diameters ranged from 8 to 40 inches.

All trees selected for study had been naturally infected and had wilted in 1952 between June 12 and August 25. The initial examination of these trees showed that, in all but three, the trunks were completely sound, the only lethal sign being a slight brown characteristic streaking in the sap wood; the bark was very tight and appeared no different from that of healthy trees. The three trees mentioned above, designated as C-2, R-8, and R-9, were more advanced in their decline than the other trees. On these the bark was very

Table 1.—Wilt-killed oak trees chosen for study in five areas of Illinois. Size of trees is given in inches d.b.h.

Chicago Area			Sinnissippi Forest			Rockford Area			Peoria Area			Havana Area		
Tree	Kind	Inches	Tree	Kind	Inches	Tree	Kind	Inches	Tree	Kind	Inches	Tree	Kind	Inches
C-1	Red	36	S-1	Black	12	R-1	Red	20	P-1	Red	10	H-1	Black	22
C-2	Red	22	S-2	Black	16	R-2	Red	24	P-2	Red	12	H-2	Black	20
C-3	Red	10	S-3	Black	12	R-3	Red	8	P-3	Red	10	H-3	Black	24
C-4	Red	28	S-4	Black	18	R-4	Red	14	P-4	Red	15	H-4	Black	20
C-5	Bur	12	S-5	Black	14	R-5	Red	12	P-5	Red	24	—	—	—
C-6	White	40	—	—	—	R-6	Red	10	P-6	Red	12	—	—	—
—	—	—	—	—	—	R-7	Red	10	—	—	—	—	—	—
—	—	—	—	—	—	R-8	Red	18	—	—	—	—	—	—
—	—	—	—	—	—	R-9	Red	22	—	—	—	—	—	—

Fig. 1.—Examining a wilt-killed oak tree for mycelial mats.

loose, and the condition of the wood appeared to be slightly beyond the optimum for mat development. These trees had wilted early in June.

Examination of Trees

Both standing and felled trees were studied. Five trees, four red oaks and one black oak, were felled to determine the ability of the fungus to fruit on felled timber. The remaining 25 trees were left standing so that a study might be made of their natural decline and the development and deterioration of mycelial mats under natural conditions.

Examination of the standing trees to heights of 20 to 55 feet was facilitated by ladders, fig. 1, constructed on the trunks with green oak slabs obtained from a sawmill. A lineman's safety belt, usually with a one-half-inch rope attached, was used as an added safety precaution. Climbing spurs were not used because of the treacherous nature of loose bark on dead trees. The ladders facilitated thorough examination of the entire main trunks of trees with relative ease and provided safe positions from which some of the lateral branches could be examined.

As excessive removal of bark might have caused infected trees to dry out before mats had a chance to form, these fruiting bodies of the fungus were located at first only by tapping the bark. This proved to be a surprisingly accurate method; in nearly every spot where the bark gave a dull, hollow sound when tapped, a mat was present. After trees have been dead for some time, of course, the entire trunk surface may produce a hollow sound. However, on trees that have reached this stage, few if any new mats will form. Many mats can be located merely by finding cracks in the bark, fig. 2, but these cracks are often so narrow that they are overlooked.

Classification of Mycelial Mats

The fruiting structure of the oak wilt fungus as it appears in nature consists of a light to dark grayish tan, sparse to dense mycelial felt, in the center of which lies a thick gelatinous pad. The mycelial felt with its central pad are referred to to-

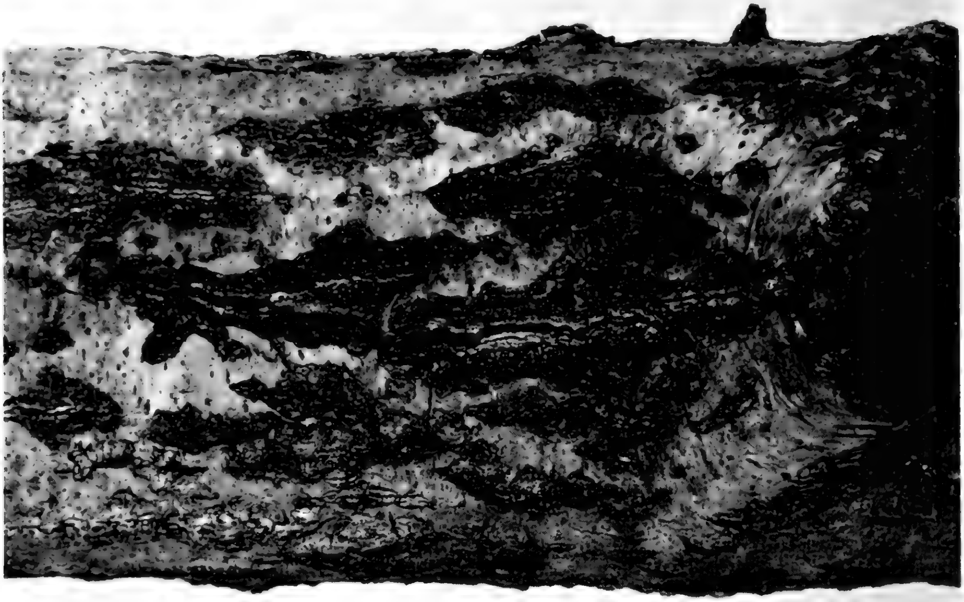

Fig. 2.—Typical crack in the bark of a wilt-killed oak tree. The crack resulted from growth of a fungus mat beneath the bark.

gether as a mycelial mat. The mat varies in size from 1 by 1 cm. to 48 by 14 cm. The central pad is elongated oval to elliptical, dull green to black in color, and has a daedaloid surface. It is pseudoparenchymatous in structure and is usually free of visible loose mycelium.

The following arbitrary classification, based on the stage of development or decline, was given to the mycelial mats examined in the study reported here. A mat of each class is shown in fig. 3.

Class I. An *immature* or fresh mat, still in the rapid growth phase, with mycelium light tan or buff in color and having a firm, light- to dark-colored central pad which shows no sign of decline.

Class II. A *mature* mat, with mycelium and central pad beginning to darken slightly, the pad being firm and showing no definite signs of deterioration; vegetative growth appearing to have ceased or nearly ceased.

Class III. An *aging* mat, with mycelium and central pad becoming darker, the pad beginning to shrink or crack slightly from drying; showing other definite signs of aging but not deteriorating.

Class IV. A *declining* mat; mycelium and pad very dark or black, usually with only parts of the pad remaining intact; showing definite signs of rapid decline.

Class V. A *deteriorating* mat and pad, having lost nearly all consistency and having been reduced to a mass of dry, or wet, black soil-like material.

Methods of Field Sampling

Trees in the five study areas were thoroughly examined twice each month from October 1, 1952, to July 31, 1953. Some mats were examined and, after being sampled, were left on the trees. Others were removed from the trees and taken to the laboratory for study. Still others were tagged and left undisturbed for various periods of time. Metal picnic boxes equipped with ice containers were used for storing and transporting collected material from the field to the laboratory. When the ice containers were kept filled with ice, the temperatures of the boxes were maintained below 16 degrees C., usually between 5 and 12 degrees, even during the hottest days of summer. The time that the material was kept in the iced picnic boxes between the point of collection and treatment in the laboratory never exceeded 5 days.

Mats were sampled on the trees in the following manner. After a mat had been located, a square or rectangular area extending slightly beyond the outer limit of the mat was marked off by driving a sharp chisel through the bark. The bark was then lifted easily and cleanly from the wood, and the mat beneath was exposed.

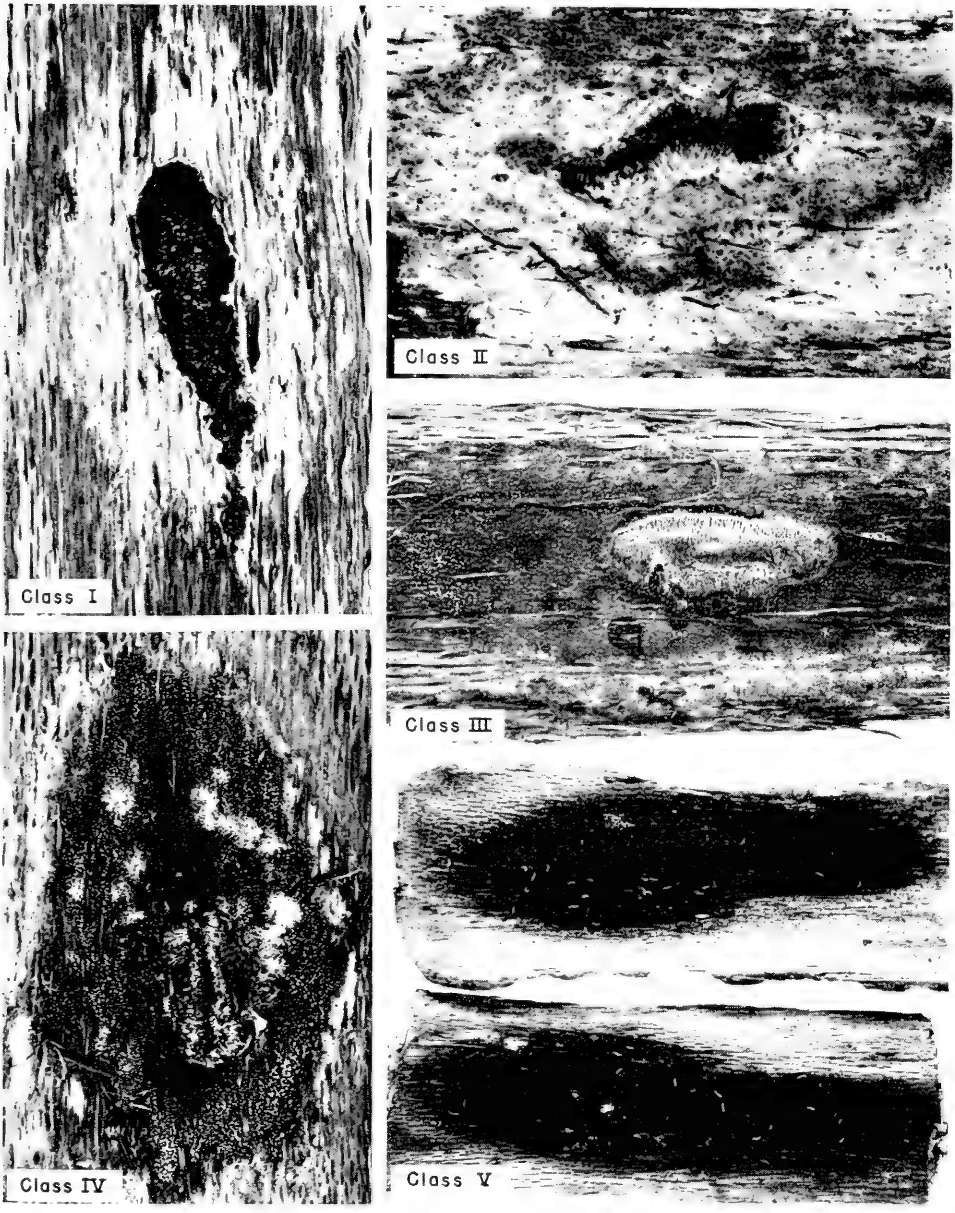

Fig. 3.—Mycelial mats of *Endoconidiophora fagacearum* representative of condition classes arbitrarily established on the basis of mat development and decline: class I, immature; class II, mature; class III, aging; class IV, declining; class V, deteriorating.

The size of the mat and its approximate distance from the ground were recorded. Three disks of mycelium, each 7 mm. in diameter, were cut from the mat with a cork borer. One disk was taken from the periphery of the mat, one from the edge of the central pad, and a third from a point approximately halfway between the other two. When perithecia were present, four additional disks, each 7 mm. in diameter, were taken with the cork borer from within the perithecium-producing "band" on four sides of the pad. Also, a small cross section of the central pad of each mat was taken with a knife. The cork borer and the knife blade were washed in alcohol and flamed before they were used in sampling a mat or pad.

The three mycelial disks were placed in a sterile, 4-ounce glass bottle that contained moist filter paper. The perithecium samples taken from each mat were placed in the bottle with the mycelial disks from the same mat, but they were kept separated from the mycelium by folds in the filter paper. The pad samples from each mat were kept in a separate bottle for later determination of viability of inner cells. All bottles were stored in the iced picnic boxes for transportation to the laboratory. After samples had been taken from a mat, the bark was carefully returned to its original position and nailed down securely with small nails.

Whole mats were removed from trees with a chisel in such a manner that with each was a piece of the wood beneath, approximately one-half inch in thickness. The mats were placed separately in *Lindlene* plastic film bags, most of them two-thirds quart size. These bags were then closed with small rubber bands, to hold in the moisture, and placed in an iced picnic box.

Not all mats were sampled or collected when found. As it was suspected that the lifting of bark over a mat might hasten deterioration or drying of the fungus, some mats were tagged and, for various periods of time, left undisturbed. At 2-week inspection intervals the bark was removed from these mats, several mats at each inspection, and the condition of each compared with the condition of mats of the same age which had been sampled and left on the trees. The lifting of bark from mats, and replacing it, did not noticeably hasten deterioration of the mats.

Wood and Bark on Forest Floor

It has been shown (Curl *et al.* 1952, 1953) that the thick mycelial mats of *Endoconidiophora fagacearum* develop on wood and bark pieces cut from wilt-killed oaks in the mat-producing stage and discarded or placed on the forest floor. Therefore, this type of growth must be considered as one of the possible sources of inoculum from which the disease could be spread.

The mat-producing stage of a wilt-killed tree may be described as the period of decline of the tree during which the bark is moderately loose and the wood beneath is light reddish-brown in color and has a strong amyl acetate or ripe fruit odor characteristic for the fungus. Preliminary tests showed that the ability of the fungus to grow out of the wood and form macroscopic growth is closely related to the presence of the ripe fruit odor.

As wilt-killed trees in the study areas reached the mat-producing stage, pieces of bark and wood measuring approximately 4 by 8 inches (the wood about an inch thick) were cut from the trunks where the ripe fruit odor was present. The bark and the wood were separated. The pieces of bark were placed, inner surfaces down, and the pieces of wood were placed, outer surfaces down, on the forest floor in shaded places. New pieces were cut and laid down about every 2 weeks from November 1, 1952, to July 1, 1953, until the trees had deteriorated to such an extent that they ceased to have the odor that indicated presence of the fungus. Mats that developed on these pieces were sampled in the same manner as those on trees.

Insect Collections

Insects found on mycelial mats were collected at the same time that the mats were sampled. Adults and larvae were placed in small vials and temporarily stored in the metal iced picnic boxes. Mats that were examined and left on the trees afforded a month-to-month opportunity to study insect populations occurring on mats of all ages. The influence of certain species of insects in hastening the decline of mats in nature was followed closely.

Weather Data

An attempt was made to relate average monthly temperatures and precipitation with conidial sporulation, perithecium formation, viability of spores, and general mat deterioration. Weather data were obtained from records of the United States Department of Commerce Weather Bureau for stations nearest the areas being studied. None of the study areas was more than 12 miles distant from the nearest weather station. It is realized that temperature and precipitation may vary to some extent within even this short distance, but it was not feasible to install expensive, unguarded weather-recording equipment in the wilt areas.

LABORATORY STUDIES

Spore Germination

The germination of conidia of *Endoconidiophora fagacearum* by other workers has already been reviewed. For these conidia, solid agar of a low dextrose content and malt solutions have been shown to be good germination media at 25 to 30 degrees C.* However, in the present studies, a medium and a temperature were desired that would insure a high percentage of germination, but that, at the same time, would tend to discourage growth of contaminating fungi and retard the production of secondary endoconidia.

The germinability of laboratory-grown conidia was tested in the following manner. A water suspension of conidia was prepared from a 7-day-old culture of *Endoconidiophora fagacearum* and adjusted to approximately 300,000 spores per ml. Circles were made with a wax pencil on the outside bottoms of Petri dishes containing 2 per cent water agar. One drop of suspension was placed on the surface of the agar within each circle, and each of the dishes was subjected to one of the following incubation temperatures: 7, 16, 25, 28, 31, 34, and 36 degrees at 12-hour intervals for 60 hours. Four hundred spores were counted for each test temperature, and a record was made of the number of spores germinated. Spores were considered germinated if the germ tubes were about the same length as the spores.

Table 2.—Germination of conidia of *Endoconidiophora fagacearum* at various centigrade temperatures on 2 per cent water agar.

Number of Hours	Per Cent Germination at Designated Temperature						
	7°	16°	25°	28°	31°	34°	36°
12	0	0	3	37	9	2	0
24	0	2	19	83	73	16	0
36	0	6	48	93	86	25	0
48	0	11	65	94	91	29	0
60	0	12	74	96	92	35	0

The highest germination rate was 96 per cent at 28 degrees; no germination occurred at 7 degrees nor at 36 degrees during the 60-hour period, table 2. The upper limit of the germination range appeared to be 34 degrees, fig. 4; at that temperature, 35 per cent germination occurred, but the germ tubes did not continue to grow. Secondary sporulation appeared to be most abundant at 16 and at 25 degrees.

The germinability of conidia taken from naturally occurring mycelial mats was determined at 25 and at 28 degrees. Some of the spores were germinated on agar containing 2 per cent of dextrose and some on 2 per cent water agar. Most spore suspensions made from naturally occurring mats contained, in addition to conidia of *Endoconidiophora fagacearum*, spores and hyphal fragments of several other fungi, particularly species of *Penicillium*, *Trichoderma*, and *Graphium*. Drops of the suspension were placed on

* All temperatures given in this report, unless otherwise labeled, are degrees centigrade.

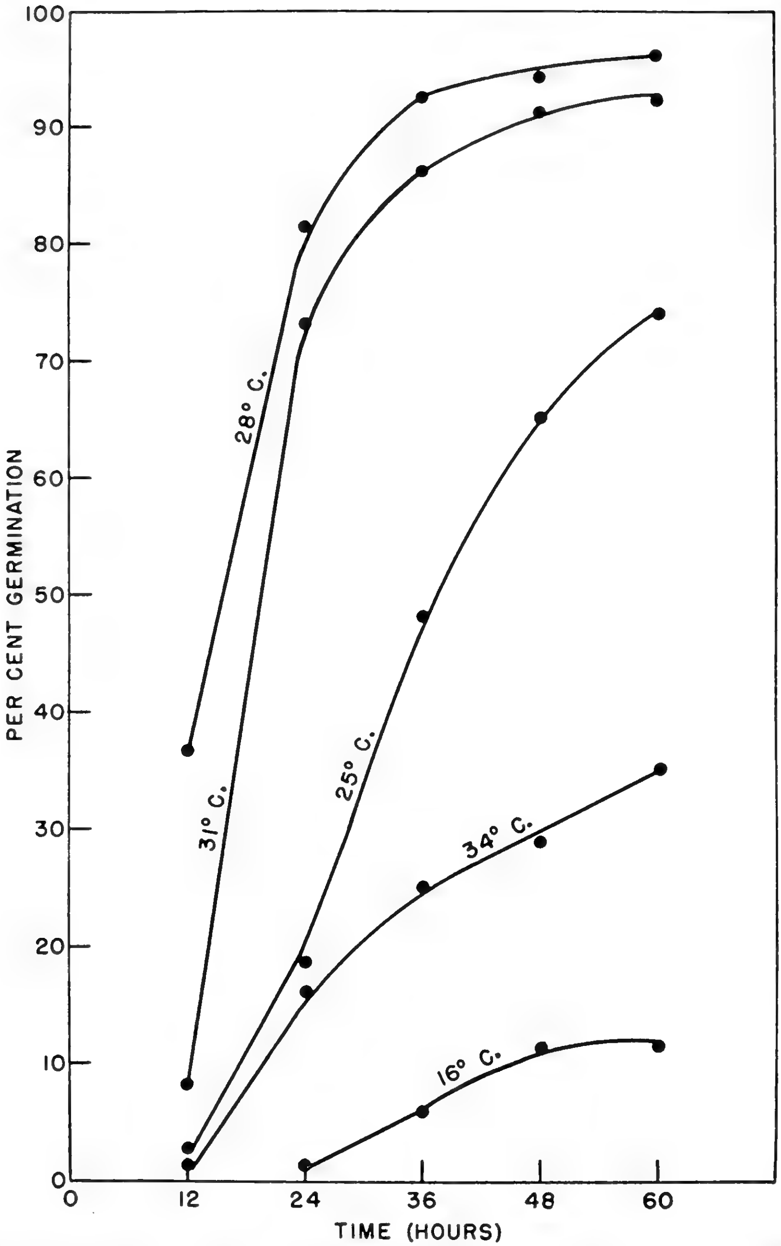

Fig. 4.—Germination of conidia of *Endoconidiophora fagacearum* on 2 per cent water agar at five temperatures.

the surfaces of the media as described for the 7-day-old culture above.

Germination of naturally occurring conidia was slightly higher on the dextrose agar at 28 degrees than on water agar at the same temperature. However, on dextrose agar, the count was confused by the production of secondary conidia after 30 hours, and the contaminants made very rapid growth, further confusing the counting of germinated conidia.

Ascospores from laboratory cultures

Table 3.—Germination of ascospores of *Endoconidiophora fagacearum* at various centigrade temperatures on 2 per cent water agar.

Number of Hours	Per Cent Germination at Designated Temperature						
	7°	16°	22°	25°	28°	31°	34°
12	0	0	20	32	33	14	0
24	0	3	44	47	49	38	0
36	0	20	61	63	68	58	3
48	0	36	—	—	71	60	5
70	7	54	—	—	78	61	8
85	18	64	—	—	—	61	10
120	37	74	—	—	—	68	12

Table 4.—Germination of ascospores of *Endoconidiophora fagacearum* at various centigrade temperatures on 2 per cent dextrose agar.

Number of Hours	Per Cent Germination at Designated Temperature						
	7°	16°	22°	25°	28°	31°	34°
12	0	0	29	46	45	19	0
24	0	1	58	75	69	49	0
36	0	14	69	81	74	60	2
48	0	21	—	—	79	73	4
70	9	53	—	—	84	76	5
85	12	57	—	—	—	78	7
120	23	70	—	—	—	87	8

grown on chestnut agar (30 gm. chestnut meats and 20 gm. agar in 1 l. distilled water) were germinated in Petri dishes, some containing water agar and some 2 per cent dextrose agar; each dish was subjected to one of seven incubation temperatures: 7, 16, 22, 25, 28, 31, and 34 degrees. At most of the temperatures germination was slightly higher on dextrose agar than on water agar, tables 3 and 4 and figs. 5 and 6, the highest germination for any single time interval occurring at 25 and 28 degrees. Secondary conidia started to form at about the same time for each temperature on both media. However, at an incubation temperature of 28 degrees, further production of conidia was retarded, so that at this temperature the counting of germinated ascospores was not confused by germinated conidia until after 70 hours. At incubation temperatures of 22 and 25 degrees, counts of ascospores became confused by germinated conidia after 36 hours. After 120 hours, ascospores incubated at 31 degrees had moderately long, unbranched germ tubes that did not sporulate, and spores incubated at 34 degrees had very short germ tubes that did not continue to grow.

After these tests, it was concluded that a 2 per cent water agar medium and an incubation temperature of 28 degrees for 36 hours would be best for determining germinability of both conidia and ascospores of *Endoconiodiophora fagacearum*.

Sampling

It is recognized that a larger number of samples than the three mycelial disks that were taken from each mat at each sampling might have been desirable in obtaining samples that were representative. However, as some mats were left on trees and sampled several times, the taking of a much larger number of samples would have destroyed the smaller mats.

A short test was run to find how great a difference might be expected between samples taken from different parts of a mat. Four immature (class I) mats were used in the test. Three disk samples (each 7 mm. in diameter) were taken from each

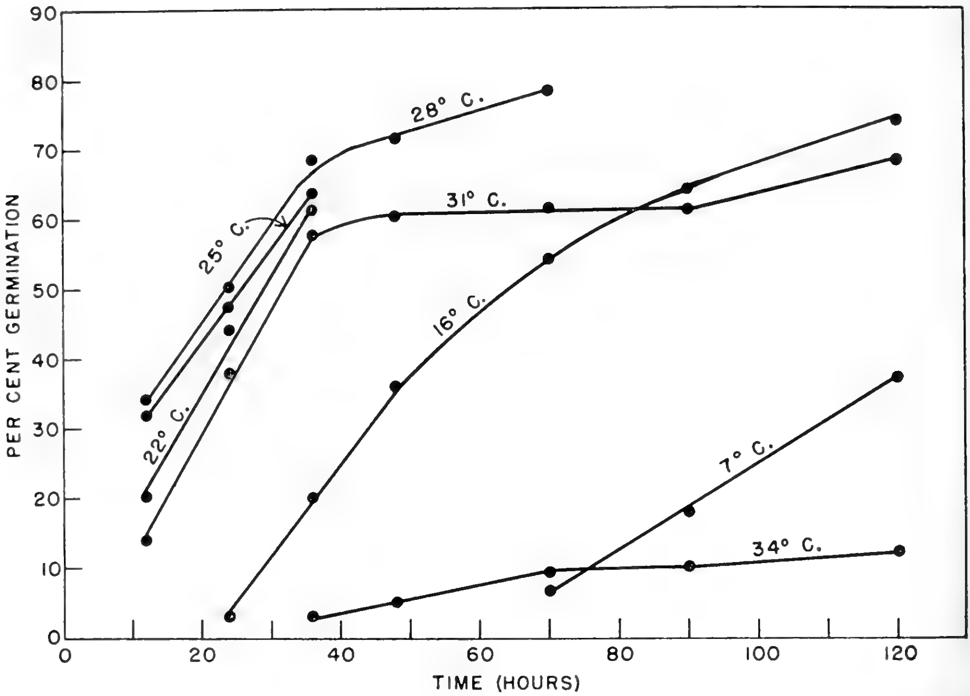

Fig. 5.—Germination of ascospores of *Endoconidiophora fagacearum* on 2 per cent water agar at seven temperatures.

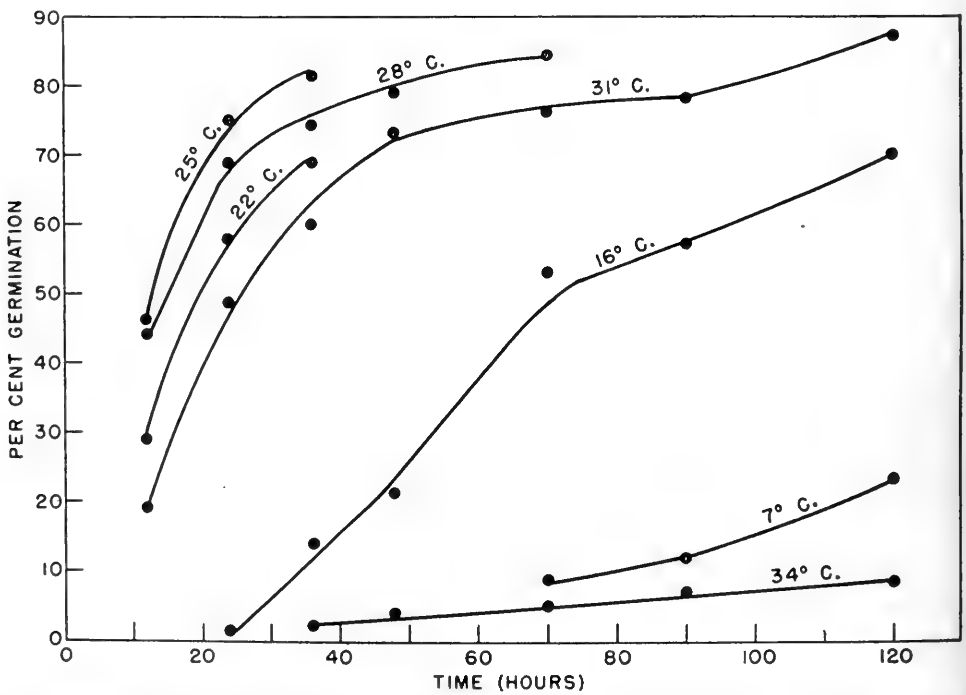

Fig. 6.—Germination of ascospores of *Endoconidiophora fagacearum* on 2 per cent dextrose agar at seven temperatures.

of three sides of each mat from the edge of the central pad to the periphery of mycelial growth. Each group of three disks was placed in a 10-ml. water blank and thoroughly crushed and shaken. The number of conidia in 1 ml. of suspension was then estimated, and the spores were germinated on water agar. The average number and per cent of germination of spores from each three-disk sampling were compared with the number and per cent of germination of conidia from other three-disk samplings on the same mat.

The approximate number of spores found on the four mats ranged on different mats from 280,000 to 1,300,000 in 1 ml. of suspension, and the germination rate ranged from 13 to 41 per cent. In no case was the difference in the average number of spores between any two samplings of the same mat greater than 40,000, and the difference in germination rate did not exceed 5 per cent. It seems unlikely that such differences would be significant. Therefore, it is believed that representative samples were obtained by the method employed in these studies.

Transporting Samples

As it was necessary to store collected samples of the fungus at low tempera-

Fig. 7.—Mycelial mat of *Endoconidiophora fagacearum* grown on sterile oak wood in wheat bran broth.

tures for several days in transferring them to the laboratory, the question arose concerning the possible effects of such temperatures on spore germination. Mycelial mats of *Endoconidiophora fagacearum* were grown in the laboratory in the following manner. Oak wood pieces measuring about 3 inches by 0.5 inch were placed on end in 250-ml. Erlenmeyer flasks which contained a wheat bran broth (8 gm. of wheat bran in 75 ml. of water). The bran broth was steam sterilized, and, when it was cool, a few drops of a spore suspension of the fungus were placed in

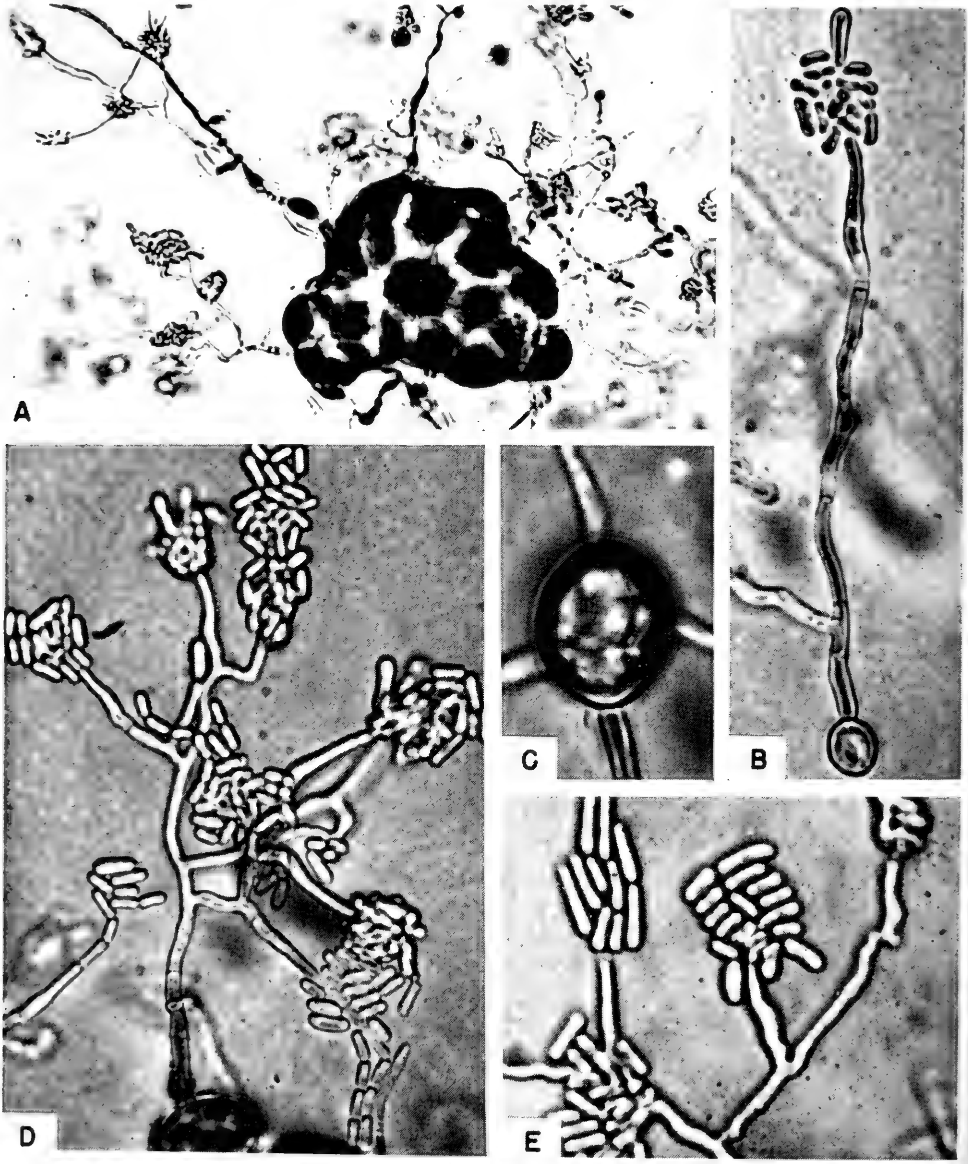

Fig. 8.—Germination of pad cells and conidia of *Endoconidiophora fagacearum*. *A*. Group of germinating pad cells producing abundant endoconidia, ×125. *B*. Small germinating pad cell producing endoconidia after 12 hours at 22 degrees C., ×650. *C*. Four germ tubes extending from a single pad cell, ×800. *D*. Germinating pad cell with abundant sporulation after 48 hours at 28 degrees C., ×650. *E*. Secondary sporulation by germinating conidia after 48 hours at 25 degrees C., ×800.

each flask. After 2 weeks at 25 degrees, one-half to three-fourths of each wood piece was found to be covered with a dense mat of mycelium free from the broth, fig. 7. In this laboratory test, methods of field sampling and storing were duplicated as nearly as possible. Disks of mycelium were taken from some pieces with a cork borer and transferred to moist filter paper in sterilized 4-ounce bottles. Whole pieces were placed in bags of plastic film and closed tightly with rubber bands. Some bottles and bags were then subjected to a temperature of 0 degree and some to a temperature of 16 degrees. For checks, germination counts were made of spores taken from some of the mats before treatment.

After 7 days, germination counts were made of spores in the test material. It was found that storage at 0 and at 16 degrees had no harmful effects on the spores. The germination rates were slightly higher for material stored at either of the two test temperatures than for the checks. Since the storage temperatures for field material were always within the range of 0 to 16 degrees for a period of time not exceeding 5 days, no serious fault could be seen in the storage methods used.

Germination of Pad Cells

Zuckerman & Curl (1953) showed that single cells isolated from laboratory-grown mycelial pads of *Endoconidiophora fagacearum* are capable of producing typical cultures of the fungus on potato dextrose agar. Their finding suggested the possibility that pads on naturally occurring mats might constitute one of the sources of inoculum.

During the summer and autumn of 1953, pad cells from mycelial mats that had been collected from wilt-killed oaks were used in making germination tests. The surface of each pad was cut away with a flamed scalpel, and a small portion of the interior was removed and crushed thoroughly in a sterile water blank to form a suspension of separated cells. Drops of the suspension were placed on the surface of 2 per cent water agar in plates and incubated at 25 degrees.

Good germination was always obtained with cells from the pads of immature (class I) mats in 30 hours. Commonly one or two germ tubes, and frequently four or five, were produced on a single cell, fig. 8*C*. The germ tubes branched prolifically, forming typical conidiophores which produced endoconidia abundantly, fig. 8*A, D*. Cells of all sizes, from 12 by 15 to 45 by 60 microns, germinated readily. The germination rate was in some cases as high as 87 per cent.

Germination of pad cells from mature (class II) mats was obtained only occasionally, and no germination of pad cells was obtained from mats in the more advanced stages of decline. The number of pad cells that appeared to be collapsed or plasmolyzed was greater in pads of advanced condition classes than in pads of classes I and II. Most deteriorating pads consisted of mycelial fragments, bacteria, and spores and hyphae of fungi other than *Endoconidiophora fagacearum*.

The temperature requirements for the germination of pad cells *in vitro* were determined and compared with similar requirements for germination of conidia and ascospores. A suspension of cells was prepared from the interior portion of a pad taken in September from an immature mat on a wilt-killed oak. Drops of the suspension were planted on the surface of 2 per cent water agar in Petri dishes and each dish subjected to one of five incubation temperatures: 8, 15, 22, 28, and 34 degrees. Counts of 200 cells for each temperature were made at intervals of 12 hours.

The highest germination rate of cells was 71 per cent at 22 degrees after 60 hours, table 5. Good germination occurred at 15 and 28 degrees, fig. 9. Among cells incubated at 8 degrees, germination did not begin for 36 hours. Among cells subjected to 34 degrees of temperature, germination did not take place during the 60-hour period, nor later when the temperature was changed to 22 degrees. Production of conidia by the branches, or conidiophores, of the germ tubes occurred in 12 hours at 22 degrees, fig. 8*B*, and 28 degrees, and in 36 hours at 15 degrees. Sporulation seemed to be most abundant at 28 degrees, fig. 8*D*.

The results of the foregoing tests indicate that pad cells of *Endoconidiophora fagacearum* have a slightly lower opti-

Table 5.—Germination of cells from pads of mycelial mats of *Endoconidiophora fagacearum* at various centigrade temperatures on 2 per cent water agar.

Number of Hours	Per Cent Germination at Designated Temperature				
	8°	15°	22°	28°	34°
12	0	6	28	30	0
24	0	28	63	36	0
36	7	57	65	41	0
48	17	60	70	43	0
60	31	60	71	50	0

mum temperature for germination than have conidia and ascospores. Also, the ability of germinated pad cells to sporulate abundantly on water agar seems to equal that of germinated conidia, fig. 8*E*, or ascospores.

Production of Perithecia

In conjunction with the study of perithecium formation under natural environmental conditions, a short experiment was conducted *in vitro* to determine what temperatures most favored the formation of perithecia. A wheat bran agar medium, consisting of 30 gm. of wheat bran and 20 gm. of agar in 1 l. of water, was used. Drops of a spore suspension from each of two compatible strains of *Endoconidiophora fagacearum* were placed approximately one-half inch apart on the surface of the medium near one edge of each plate. The plate was then slanted, forcing the drops to flow parallel with each other to the opposite side of the plate and, thus, distribute spores uniformly on the medium. All plates were incubated at 25 degrees for 7 days, and then placed in groups of six, each group for 16 more days at one of these temperatures: 7, 12, 16, 25, and 31 degrees. Perithecia were counted if the necks could be seen above the substrate with a binocular microscope.

An average of 51 perithecia per plate developed at 16 degrees, 47 at 25 degrees, and 11 at 12 degrees, table 6. At the end of the 16-day incubation period, no perithecia had appeared in plates subjected to either 7 or 31 degrees. Similar results were obtained when the experiment was repeated.

Longevity of Conidia

The following experiment was conducted to determine the extremes of temperature and desiccation at which conidia of *Endoconidiophora fagacearum* may survive. Wooden tree labels, each 3.5 inches in length, were boiled in water for 1 hour. They were then placed on end in 250-ml. Erlenmeyer flasks, each containing 75 ml. of a wheat bran broth, and steam sterilized. The broth was seeded with drops of a conidial suspension and the flasks were incubated at 25 degrees for 2 weeks.

Table 6.—Production of perithecia by *Endoconidiophora fagacearum* at various centigrade temperatures on wheat bran agar.

Replicate No.	Number of Perithecia at Designated Temperature				
	7°	12°	16°	25°	31°
1	0	8	38	91	0
2	0	9	60	16	0
3	0	5	32	51	0
4	0	22	73	*	0
5	0	7	37	66	0
6	0	14	67	10	0
Average	*0*	*11*	*51*	*47*	*0*

* No count possible; agar overrun by *Graphium* sp.

At the end of this time the labels were found to be half covered with a uniform mycelial growth. To serve as a check, a spore suspension was prepared with the fungus from one label of each flask, and the spores were allowed to germinate on 2 per cent water agar at 28 degrees for 36 hours. Eighty-three per cent germination

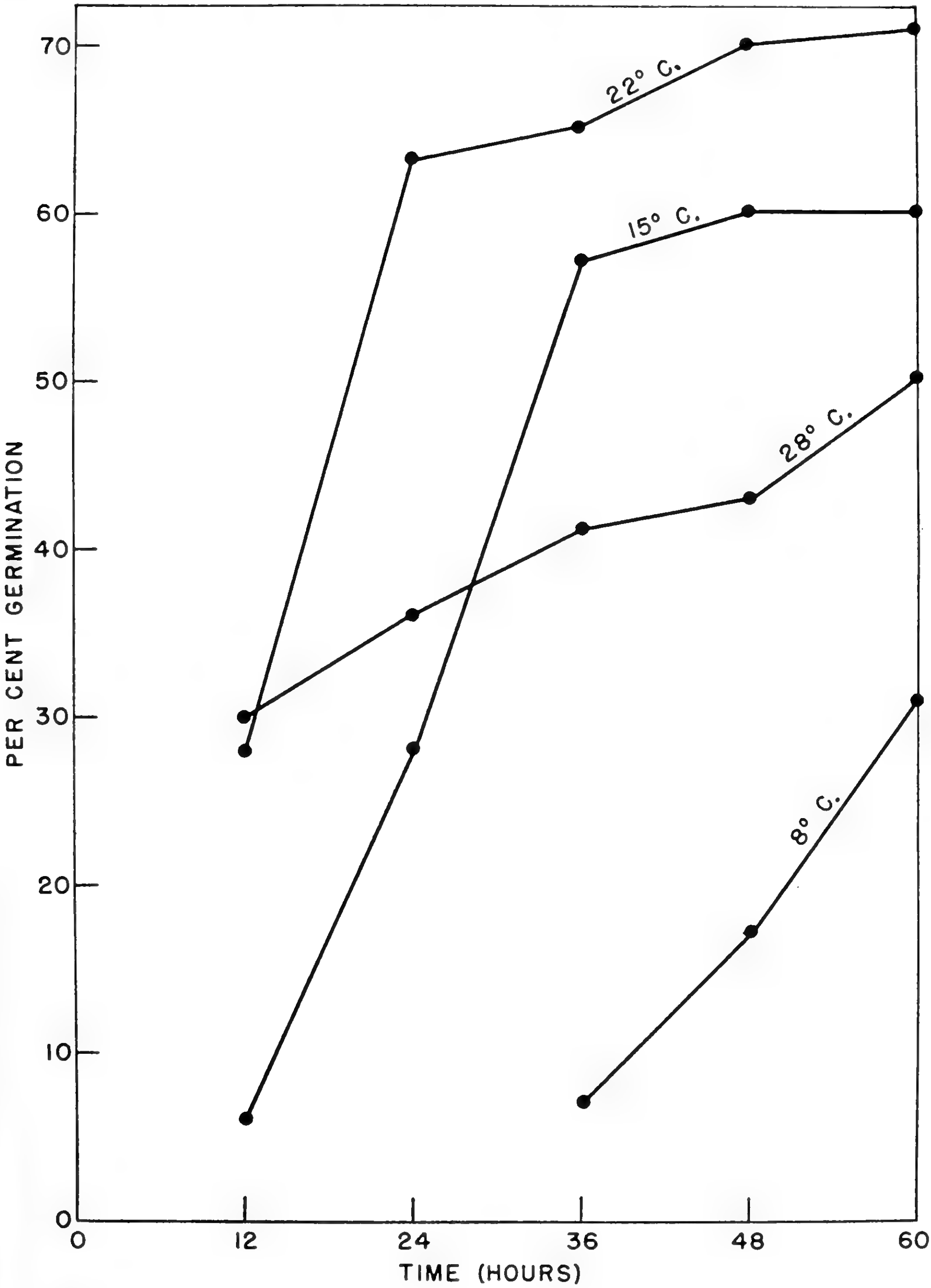

Fig. 9.—Germination of pad cells from naturally occurring mats of *Endoconidiophora fagacearum* on 2 per cent water agar at four temperatures.

Table 7.—Longevity of conidia of *Endoconidiophora fagacearum* grown on sterile wood labels and stored in 100 per cent humidity at various centigrade temperatures.

Number of Days	Per Cent Germination at Designated Temperature					
	0°	12°	16°	25°	31°	34°
0	83	83	83	83	83	83
5	80	70	75	39	40	30
10	71	67	67	31	26	6
15	70	66	57	26	3	1
25	70	60	32	18	0	0
30	55	33	7	0	0	0
35	54	31	4	0	0	0
45	49	17	1	0		
55	49	8	1			
70	45	7	0			
85	21	4	0			
102	10	2	0			
162	0	0				
250	0	0				

Table 8.—Longevity of conidia of *Endoconidiophora fagacearum* grown on sterile wood labels and stored in a dry atmosphere at various centigrade temperatures.

Number of Days	Per Cent Germination at Designated Temperature					
	0°	12°	16°	25°	31°	34°
0	83	83	83	83	83	83
10	58	81	74	54	7	2
20	48	76	74	10	2	1
30	45	22	29	3	1	0
35	41	20	25	3	0	0
40	41	21	22	2	0	0
50	40	14	20	1	0	
70	38	14	17	0		
85	33	13	14	0		
102	30	12	12	0		
162	31	10	8			
250	22	7	3			

was recorded in a count of 300 spores. The remaining labels were transferred from the broth to sterile, dry beakers placed within 12 clean desiccators, 6 of which contained 200 ml. of sterile distilled water and the others 200 gr. of calcium chloride crystals. These desiccators were arranged in pairs (each pair having one desiccator with water and one with calcium chloride), and each pair was subjected to one of the following temperatures: 0, 12, 16, 25, 31, and 34 degrees. Thus, the fungus was subjected to the extreme conditions of 100 per cent humidity and complete, or nearly complete, desiccation at temperatures ranging from freezing to high. At intervals, one label was taken from each desiccator, and a spore suspension was prepared from the fungus on the label. Each suspension was adjusted to 300,000 spores per ml., and drops of it were placed on the surface of water agar within circles marked on the outside of Petri dishes. These dishes were incubated at 28 degrees for 36 hours; then 300 spores were counted for each temperature and moisture condition tested and the per cent of germinated spores was determined.

Viable spores were taken from labels stored at 100 per cent humidity and 0 and 12 degrees temperature for 102 days, but no viable spores were found on labels stored at these temperatures for 162 days, table 7. Spores in the dry atmosphere were still viable after 250 days at 0, 12, and 16 degrees, table 8. The germinability of conidia from both the humid and the dry atmospheres decreased with time at all temperatures, figs. 10 and 11. When the longevity and germinability of spores stored in a dry atmosphere were plotted (number of days on a logarithmic scale), the decrease in germinability of

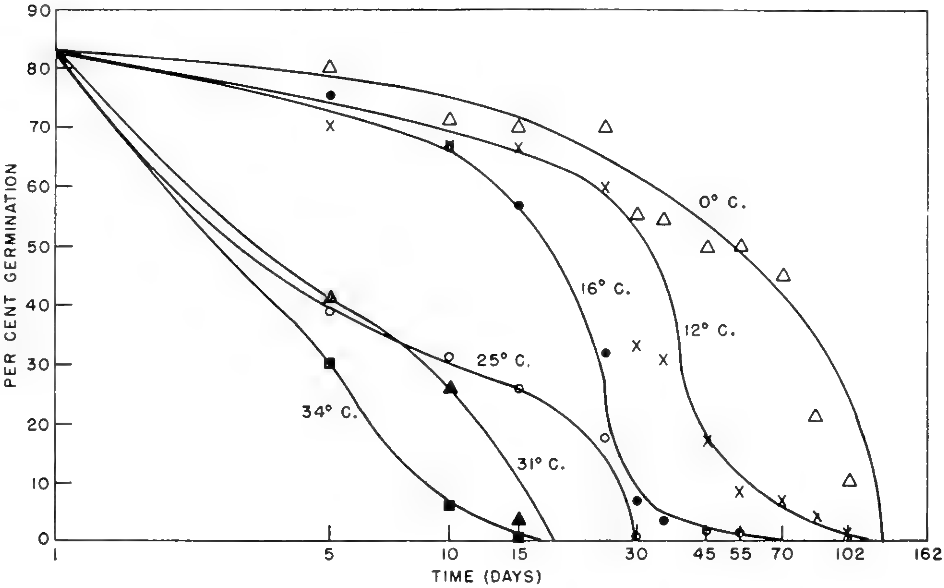

Fig. 10.—Germination of conidia of *Endoconidiophora fagacearum* stored at six temperatures in a water-saturated atmosphere. The curves illustrate the effect of temperature and humidity on longevity of the conidia.

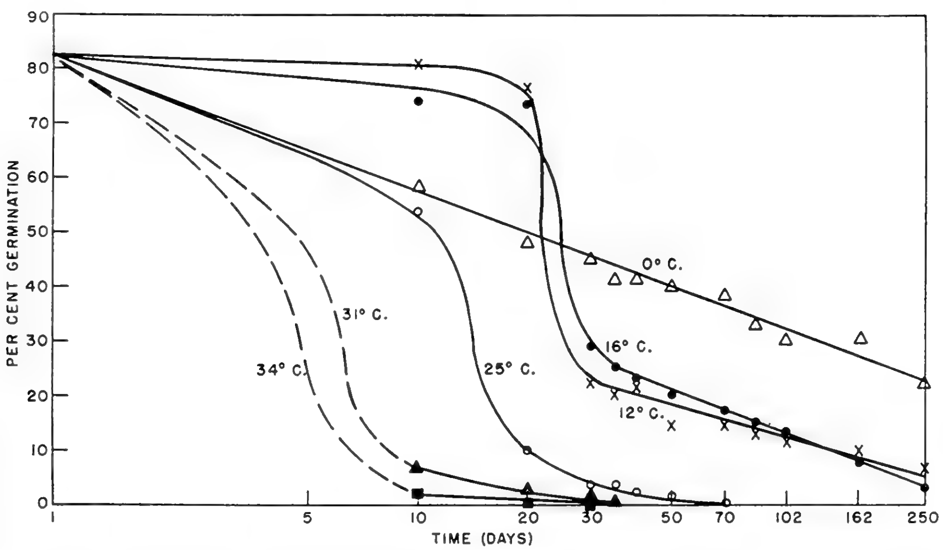

Fig. 11.—Germination of conidia of *Endoconidiophora fagacearum* stored at six temperatures in a dry atmosphere. The curves illustrate the effect of temperature and lack of humidity on longevity of the conidia.

spores stored at 0 degrees was represented by a line that was nearly straight, while decreases in germinability of spores stored at other temperatures were represented by lines that showed abrupt decreases between time intervals.

Ten to 20 days after the last spore germination was observed, cultures of *Endoconidiophora fagacearum* were obtained, from mass transfers to potato dextrose agar, of fungus from the labels that were stored at 25, 31, and 34 degrees under both dry and humid conditions. Possibly these cultures resulted from a few still viable spores that could have been missed in the last germination test, or from some other part of the fungus that might have remained alive.

Treatment of Samples From Nature

Conidia.—Each set of three mycelial disk samples that had been taken from mats in the field was placed in a 10-ml. sterile water blank and thoroughly crushed and stirred with a glass rod to set the spores free in suspension. The approximate number of spores in 1 ml. of the suspension was determined with a Spencer Bright-Line counting chamber. This number divided by 3 gave the average number of spores in 1 ml. of water provided by a single disk sample 7 mm. in diameter. The suspension was then adjusted to about 300,000 spores per ml., and single drops were placed on the surface of water agar. The plates were incubated at 28 degrees for 36 hours and the per cent of germination determined from a count of 300 spores. The mycelial disks sometimes provided fewer than 300,000 spores per ml. of suspension, in which cases the suspensions were plated in their original concentrations, and as many spores as could be found up to 300 were counted.

Mats that were collected whole in the field were sampled in the laboratory with a cork borer, as described on page 284. Approximate numbers of conidia and their germinability were determined as described in the paragraph above.

Perithecia and Ascospores.—Perithecia were counted with the aid of a glass slide, one end of which was marked with black ink into several areas, each measuring 6 mm. square. The slide was placed on the surface of a mycelial disk or whole mat and viewed through a binocular microscope. In the case of disk samples, counts were made of all perithecial necks seen within two to four of the square areas marked on the slide. In the case of whole mats, similar counts were made on each of four slides of the central pad. The average number of perithecia in a 6 mm. square area of surface was determined for each whole mat and for each mat represented by disks.

From each perithecium-bearing mat, exuding masses of ascospores were picked at random from about 15 perithecial necks with a dissecting needle and stirred thoroughly in the well of a hanging-drop slide which contained sterile distilled water. Drops of the suspension were planted on water agar and incubated for spore germination as described for conidia. Data obtained are presented in the section titled "Availability of Fertile Perithecia," beginning on page 315.

Mycelial Pads.—Interior parts of all pads and portions of pads that were collected in the field were transferred to potato dextrose agar to determine the viability of their cells. The plates were incubated at 25 degrees for 7 days. The results are given in table 22.

Further Treatment of Mats.—After the germinability of conidia and ascospores was determined, approximately 100 mats, involving all classes of condition shown in fig. 3, were placed in plastic film bags containing moist cotton; about half of them were stored at 12 and the rest at 16 degrees to determine their ability to renew vegetative growth. Renewed growth occurred only occasionally around the margins of immature mats and on parts of the wood pieces that had no growth previous to being stored. Most of the mats were overrun rapidly by contaminating fungi and bacteria.

Twenty-eight immature (class I) and mature (class II) mats were stored in the laboratory to determine the longevity of conidia and pad cells when mats are protected from natural environmental conditions. Some of these mats were placed in plastic bags with wet cotton and others were wrapped in dry paper toweling. They were then stored, some at 8 de-

Table 9.—Longevity of conidia on mycelial mats of *Endoconidiophora fagacearum* placed in dry storage at two centigrade temperatures.

Mat No.	Storage Temperature	Days in Storage	Per Cent Germination of Conidia
E-10.....	8	30	75
E-17.....	16	30	60
S-1.......	16	150	24
E-15.....	16	175	34
S-2.......	16	205	13
S-3.......	16	330	3

grees and some at 16 degrees temperature, and tested at irregular intervals for viability of conidia and pad cells.

No viable conidia were found after 30 days on mats that were stored in moist bags. Most of these mats were badly deteriorated and overrun by contaminants. One mat, which was stored under dry conditions at 16 degrees, continued to yield viable spores for 330 days, table 9. This mat, from which 3 per cent germination of conidia was obtained after 330 days, was very dry and brittle, and no reading could be registered from the wood with a Delmhorst Model RC-1 moisture detector (accurate to 25 per cent).

Pad cells did not germinate at any time during the storage period. In most instances the cells were colorless and appeared to be collapsed, or they had broken up into fragments.

Insect Feeding Tests

Insects that were found most frequently associated with *Endoconidiophora fagacearum* in the field were collected, identified to species when possible,* and tested in the laboratory for their ability to destroy the fungus by feeding. Mycelial mats of *E. fagacearum* were grown on sterilized sticks of oak wood in flasks of wheat bran broth in the manner described on page 290. The sticks of oak wood bearing the fungus were taken from the broth and placed on moist filter paper in Petri dishes. Some of the insects that had been collected were allowed to feed on this fungus and some on pad material alone; some of the pad material was obtained from naturally occurring mats and some from laboratory-grown pads. Pads were grown abundantly in the laboratory simply by planting the oak wilt fungus on wet wheat bran in Petri dishes and incubating it for approximately 3 weeks at temperatures that ranged between 16 and 25 degrees.†

The only insects found to feed readily and with destructive effect on the mycelium and pads were species belonging to the family Nitidulidae. The species were *Carpophilus niger, C. sayi, Carpophilus* sp. (larvae), *Colopterus truncatus, C. semitectus, Glischrochilus obtusus, G. sanguinolentus,* and an unidentified species of *Glischrochilus* (larvae). Fig. 12 shows the feeding of *Carpophilus* larvae on the mycelium and pad material of *Endoconidiophora.* The ambrosia beetles, *Xyloterinus politus, Monarthrum mali,* and *M. fasciatum,* and members of the order Collembola, or springtails, were observed feeding on mycelial mats, but their effects on the fungus were not macroscopically evident.

FIELD OBSERVATIONS

Development of Mats

During the course of this study, the decline of trees in each wilt area was followed closely over the 10-month study period, October, 1952, through July, 1953. The rate of decline of a wilt-infected oak and the length of time required for the tree to reach a condition favorable for the development of mycelial mats was found to be influenced by the place and time the wilt started. Wilt-infected trees in the more northern study areas, Chicago, Rockford, and Sinnissippi Forest, usually were producing mats 1 to 3 months earlier than trees that wilted at approximately the same time in the Peoria and Havana areas, 125 to 150 miles southward. In the two southerly areas, the average monthly temperature for the 10-month period was slightly higher and

* Identification of all insects was made or arranged for by Dr. Milton W. Sanderson, Associate Taxonomist, Illinois Natural History Survey.

† A method used for growing mycelial pads of *Endoconidiophora fagacearum* on artificial media was developed by E. B. Himelick, Assistant Plant Pathologist, Illinois Natural History Survey.

Table 10.—Mycelial mats of *Endoconidiophora fagacearum* found on individual wilt-killed oaks in the period October, 1952, through July, 1953.

Tree No.	Approximate Time Tree Wilted in 1952	Number of New Mats (Mats Not Found Previously) Found in Designated Month										
		Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Total
C-1	August (L)*	0	0	0	0	0	0	0	0	0	5	5
C-2	June (E)*	0	12	1	1	2	7	0	0	0	0	23
C-3	July (L)	0	0	0	1	3	0	0	9	2	0	15
C-4	August (E)	0	0	0	0	0	0	15	12	10	6	43
C-5†		0	0	0	0	0	0	0	0	0	0	0
C-6†		0	0	0	0	0	0	0	0	0	0	0
R-1	July (E)	0	0	0	5	5	9	0	0	0	0	19
R-2	August (E)	0	0	0	0	0	0	0	36	25	0	61
R-3	August (E)	0	0	0	0	0	0	1	7	4	0	12
R-4	July (L)	0	0	0	0	0	0	1	20	10	0	31
R-5	July (L)	0	0	0	0	0	0	0	3	9	5	17
R-6‡	July (L)	0	0	0	0	0	0	7	23	2	0	32
R-7‡	July (E)	0	0	10	0	0	0	1	0	0	0	11
R-8‡	June (E)	20	7	3	1	1	2	0	0	0	0	34
R-9	June (E)	5	5	0	0	0	0	0	0	0	0	10
S-1	June (L)	0	1	0	0	0	0	0	1	0	5	7
S-2	August (E)	0	0	0	0	0	0	0	5	26	6	37
S-3	August (E)	0	0	0	0	0	0	0	2	0	0	2
S-4	July (E)	0	0	0	0	0	2	4	3	9	21	39
S-5	July (L)	0	0	0	3	3	4	0	5	1	0	16
P-1	July (L)	0	0	0	0	0	3	3	10	4	1	21
P-2	August (E)	0	0	0	0	0	0	0	0	16	0	16
P-3	June (L)	0	0	0	2	1	2	12	31	0	0	48
P-4	June (L)	0	0	0	0	0	0	4	11	6	2	23
P-5	June (L)	0	0	0	0	0	0	0	4	0	0	4
P-6‡	July (L)	0	0	0	0	0	4	3	6	0	0	13
H-1	July (E)	0	0	0	5	18	13	17	5	6	0	64
H-2	August (L)	0	0	0	0	0	0	0	0	2	0	2
H-3	July (L)	0	0	0	0	0	0	0	21	3	0	24
H-4‡	August (E)	0	0	0	0	0	0	0	0	0	0	0
Total		*25*	*25*	*14*	*18*	*33*	*46*	*68*	*214*	*135*	*51*	*629*

* E designates early, or first half of month; L designates late, or second half of month.
† Trees C-5 and C-6 were white oaks that started wilting in the summer of 1951.
‡ Trees designated were felled on the following dates: R-6 on May 5, 1953; R-7 on December 16, 1952; R-8 on November 3, 1952; P-6 on October 21, 1952; H-4 on Sept. 23, 1952.

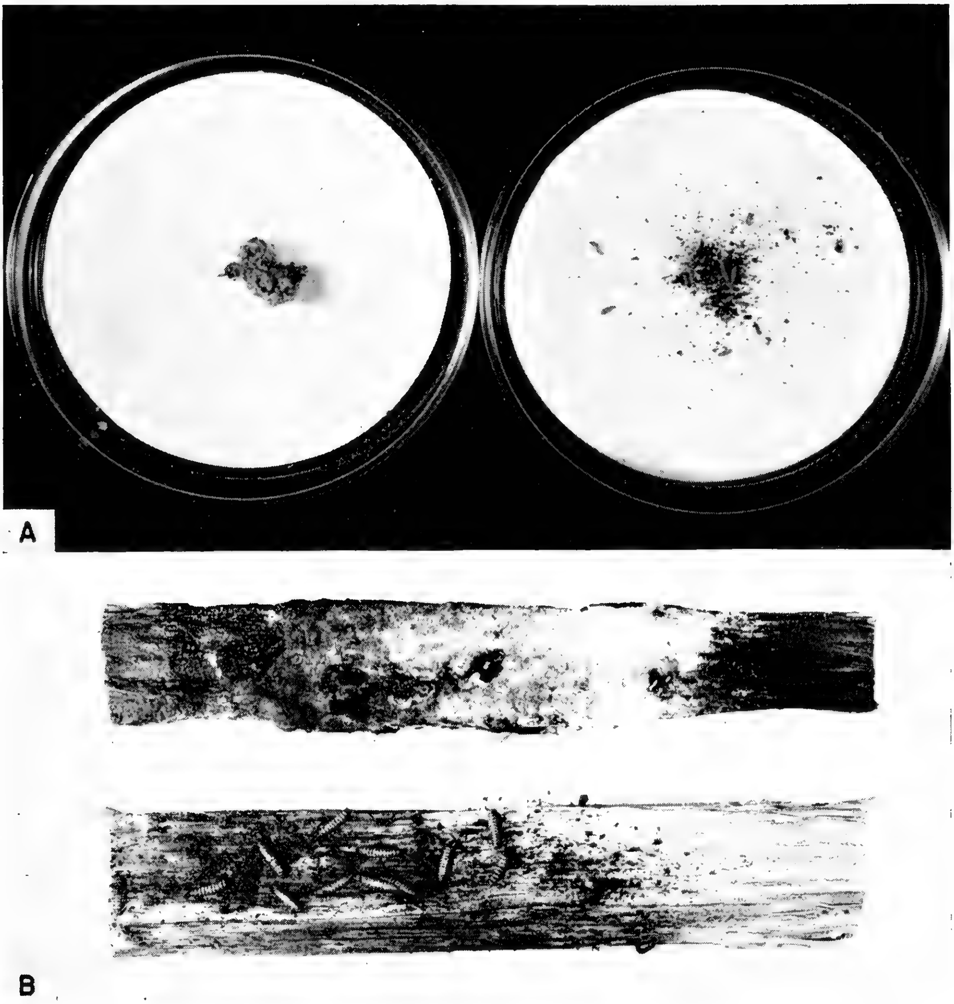

Fig. 12.—*Carpophilus* larvae feeding on *Endoconidiophora fagacearum*. *A*. Portions of laboratory-grown mycelial pad; left, without insects and, right, after exposure for 24 hours to larvae. *B*. Artificially grown mycelial mats; above, without insects and, below, after exposure for 24 hours to larvae.

the average monthly precipitation slightly lower than in the three northern areas. In most cases, trees that wilted in June, 1952, produced their first mats in 4 to 11 months, those that wilted in July produced their first mats in 5 to 10 months, and those that wilted in August produced their first mats in 8 to 11 months and continued to produce new mats for periods of 1 to 4 months, table 10. Most trees that wilted in June and July started producing mats in the fall or winter following and they continued to form new mats for 1 to 7 and 2 to 6 months, respectively, before the wood became too old or dry to support growth of the fungus.

Wilt-killed trees were found to undergo a gradual decline between the time of incipient wilt and the development of the first mats. The first evidence that a tree would soon be in the right condition for mat formation was the appearance of long, dark brown streaks in the sapwood, usually in a narrow strip along one side of the trunk. In some trees this strip started near the base of the trunk and became progressively narrower higher up, in others it appeared first at the top of the bole and progressed downward, and in still others it started at top and base at the same time. In some trees, the browning of the wood occurred in a spiral manner on the bole; with time the brown strip became gradually wider and was followed by loosening of the bark. Two to 5 weeks later the strong characteristic odor of the fungus could be detected. Usually at this stage, mycelial mats formed in a few days if weather conditions were favorable. Several days prior to mat formation, a uniform, very sparse, barely visible mycelial growth was seen on the surface of some of the odoriferous wood. When pieces of this wood were removed and kept moist at 12 degrees, pure cultures of *Endoconidiophora fagacearum* appeared in 3 days. Frequently the first mats to form on a tree followed the decline of the tree so closely that the mats extended from the brown wood under loose bark to the adjacent green wood under tight bark.

In some trees, mats appeared first at the base of the trunk, but, in many trees, they appeared first at the top of the trunk or on some of the large branches. However, as the top part of the tree declined more rapidly than the lower part, and soon became dry, in most trees a larger number of mats formed on the lower half of the bole. The distances at which 355 mats were located above the ground on different trees in all areas were estimated. Of this number, 3 mats were found between 6 inches and 1 foot above the ground, 111 were located between 1 foot and 10 feet, 133 between 10 and 20 feet, 64 between 20 and 30 feet, 33 between 30 and 40 feet, and 11 at heights of 40 to 50 feet.

The areas of loose bark on a tree could be traced accurately by following the dull sound given off when the trunk was tapped lightly with a blunt instrument. Where mats were present the dull sound was pronounced, and close examination revealed small cracks in the crevices of the bark. However, not all cracks that appeared in the bark of wilt-killed oaks were the result of mycelial mat or pad growth. Occasionally very small cracks were found, beneath which the odor of the fungus was strong but where no mats or pads were visible. When the bark of these places was lifted, replaced immediately, and nailed down securely, abundant mycelial growth of *Endoconidiophora fagacearum* developed within 2 weeks. This experience indicated that cracks may precede mat formation. By the time the pressure created by mats growing beneath the bark is strong enough to crack the bark at crevices, the bark has been considerably weakened. During a period of rapid growth in the spring, many pads pushed the bark out so far that small pieces of the bark were dislodged, leaving portions of the pads exposed to the outside. The sizes of cracks in the bark seemed to vary according to the sizes of the mats beneath. In some instances, the combined effects of two mats, one below the other, caused very long cracks to form. The longest crack of this type found measured 3 feet.

The trunks of trees examined in the mat-producing stage did not always have the fungus odor distributed uniformly over the wood. In most trees in this stage, the odor occurred in small, scattered areas along the bole, the wood between these areas having none of the odor. When pieces of wood cut from areas with strong odor were placed in a moist chamber at 16 degrees, abundant mycelial growth of the oak wilt fungus appeared in 3 to 5 days. Wood that was taken from adjacent areas without odor did not produce any visible growth when treated in this manner.

Mats normally formed on the wood surface or on the surface of the inner bark of trees, but several mats were found which had developed entirely within the inner bark. These were typical mats with central pads, the largest measuring 18 by 6 cm.

Mats on Felled Trees

Five wilt-killed trees selected for study of the development of mycelial mats on cut timber were felled at different times of the year. Tree H-4 (Havana area) was felled on September 23, 1952; tree P-6 (Peoria area) on October 21, 1952; tree R-8 (Rockford area) on November 3, 1952; tree R-7 on December 16, 1952; and tree R-6 on May 5, 1953. Trees H-4 and P-6 were felled in an early stage of decline, while the wood was still green and the bark very tight. The other trees had already started to produce mats before they were cut.

Tree H-4 did not produce mats at any time. The bark loosened very slowly, and the fungus odor could never be detected in the wood. Tree P-6 did not produce mats until late in March, 1953, 5 months after it had been felled. Thirteen large mats were found on this tree up to May 5, after which no new mats were found. Twenty mats were found on tree R-8 at the time of cutting, and 14 additional mats appeared over a period of almost 5 months. The last mats to form on this tree were found on March 23, 1953. Tree R-7 had 10 mats when felled and produced only 1 more, which was found on April 21, 1953. Tree R-6 had 7 mats 2 weeks prior to being felled, 23 mats were present at the time of felling, and only 2 developed while the tree lay on the ground, these appearing in the early part of June, 1953.

After trees, whether felled or standing, ceased to produce new mats, the fungus sometimes could still be isolated from wood where the characteristic odor persisted. Where this odor could no longer be detected, the fungus could not be isolated.

Stimulation in Mat Production

Environmental Conditions.—From the time of the initial appearance of mats on a tree to the time when no further mat development occurred, the number of new mats varied from month to month. As each of the 30 trees used in these studies was examined every 2 weeks, all new mats that had formed since the previous examination were counted and tagged, fig. 13. It is believed that few, if any, mats with cracks* were missed; mats with cracks too small to be seen were located by the bark-tapping method.

The data in table 10 show the numbers of new mats found per month on individual trees, the total number of mats found on each tree during the 10-month study period, and the total number found per

Fig. 13.—Wilt-killed oak tree, 10-inches d.b.h., marked with tags to show positions of mycelial mats. This tree was in a study area in northern Illinois.

* Except where otherwise specified, all mats included in these studies were typical mycelial mats with central pads and associated with cracks in the bark of infected trees.

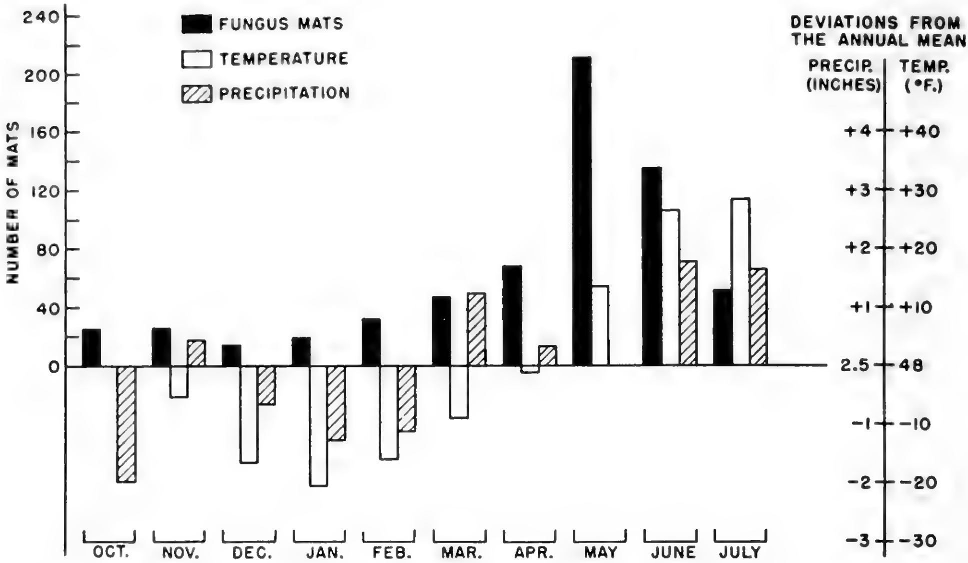

Fig. 14.—Monthly mean temperature and total precipitation, both shown as deviations from the annual means, and the numbers of mycelial mats of *Endoconidiophora fagacearum* found on wilt-killed oak trees in five Illinois study areas, October, 1952, through July, 1953. The bars illustrate the possible influence of monthly temperatures and precipitation on the numbers of mycelial mats of *Endoconidiophora fagacearum* produced on wilt-killed oaks. For temperature in October and precipitation in May there were no deviations from the means.

month on all trees. It can be seen from these figures that mat development was greatly accelerated during April, May, and June. Some of the mats that were found in July were small and dry; many of them consisted only of pad material. They were found by removing bark from the trees. None of these undeveloped mats bore conidia of *Endoconidiophora fagacearum*.

Fig. 14 suggests the influences of monthly temperature and precipitation on mat formation. The average temperatures for May and June, respectively 16 and 22 degrees, approached the optimum temperature (about 25 degrees) for growth of the fungus. The maximum temperatures were 32 degrees in May and 40 degrees in June; each of these occurred on a day near the end of the respective month. Although the average temperature for July was only 24 degrees, a number of days during the month had maximum temperatures of 35 degrees. Thermometer readings showed that the temperature under the bark of wilt-killed oaks in unshaded areas was frequently as high as 40 degrees. During the winter months the highest average temperature for any month was 9 degrees, which is too low for rapid growth of the fungus. The total monthly precipitation for the five study areas during the winter months was generally below the annual mean, but during the spring and summer it was average or above.

The ripe fruit odor associated with *Endoconidiophora fagacearum* was most noticeable during May, probably because of the presence of a large number of mats on the trees. Only at this time of the year could the odor be detected clearly at a distance of 10 feet from the trunks of mat-bearing trees.

Wounds.—The development of macroscopic mycelial growth of the oak wilt fungus was sometimes stimulated by wounds made through the bark of trees that were in or nearing the mat-producing stage. This type of growth, noticeable only during March, April, and May in the study areas, was first seen late in March on tree R-7, which had been felled in December. Where small areas of bark had been cut from trees with an ax 2 weeks previously to check on the condition of the wood, dense masses of fresh mycelium had developed from the edges of the cuts to distances up to 2 feet back under the intact bark. Such patches of mycelium sometimes measured as much as 8 inches in width.

Wound-stimulated mycelial growth was most prevalent during April and May. On any tree that had the fungus odor beneath the bark, macroscopic growth could be induced to form merely by lifting a section of bark and immediately nailing it back in place. From the trunk of felled tree R-7, six pieces of bark, each measuring approximately 8 by 12 inches, were lifted. On two of the areas from which the bark had been lifted, the bare wood was covered with thin plastic, and the bark was replaced and nailed down securely. On two other areas, the inner bark surfaces were covered with plastic and nailed back over the wood. On two other areas the bark pieces were only lifted and immediately nailed back in place.

On the areas where the wood was covered with plastic, abundant growth of *Endoconidiophora fagacearum* appeared within 2 weeks on the under side of the bark only. Two weeks later this growth was old, but still no mycelium had formed on the plastic-covered wood beneath. On the areas which had the inner surface of the bark covered, growth appeared on both bark and wood, more abundantly on the covered surface of the bark than on the wood. On the areas where bark was simply lifted and replaced, good growth occurred on both bark and wood surfaces. Similar results were obtained on felled tree R-8 and on several standing trees.

Wounding not only stimulated free mycelial growth, but it also often hastened the development of typical mats with pads. For typical mats to appear adjacent to previously made cuts was common during April and May. In many cases the pads pushed the bark out at the edges of the cuts, exposing the mats to the outside. Also, mats appeared first on some trees at points where large nails had been driven through the bark in the process of building ladders on the trunks. These observations indicate that mat formation is stimulated by additional air from the outside.

Mats on Bark on Forest Floor

From November, 1952, through July, 1953, 213 bark pieces and 128 wood pieces were taken from wilt-killed oaks and placed on the forest floor in four

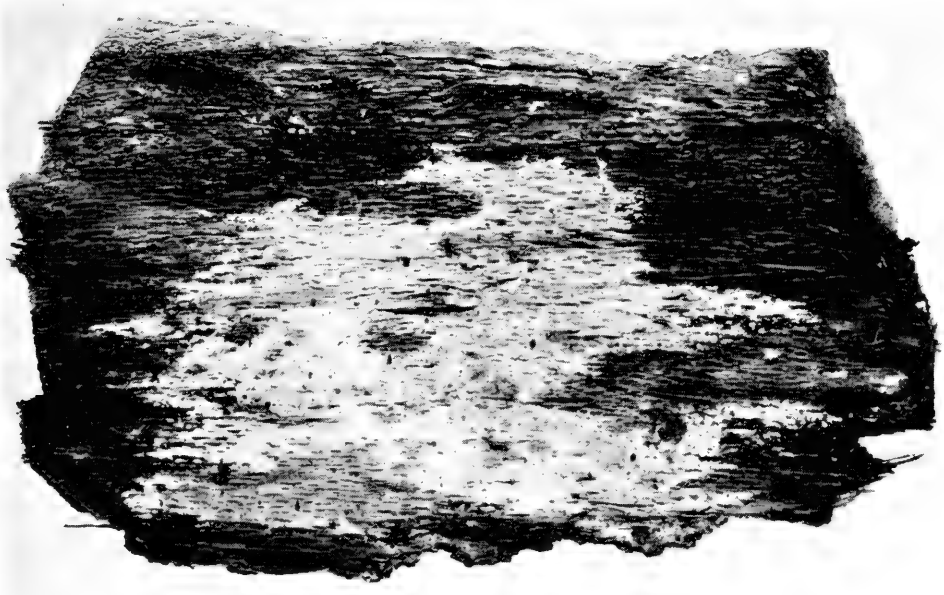

Fig. 15.—Mycelial mat of *Endoconidiophora fagacearum* formed on a piece of bark from a wilt-killed oak while the bark lay on the forest floor.

study areas. Mycelial mats, fig. 15, appeared on only 17 of the bark pieces, table 11. The first such growth known to appear was found on March 24; the last in the early part of April. No visible mycelium of the oak wilt fungus formed on the wood pieces at any time. This absence of growth on the wood is not explained, as it was shown earlier by Curl *et al.* (1953) in Illinois that mats of *Endoconidiophora fagacearum* developed on both bark and wood on the forest floor. All pieces of bark that produced a visible growth of fungus had been placed on the ground 2 weeks before the fungus appeared. Most pieces on which the fungus was not visible after 2 weeks were very dry or were overrun by other fungi. Wood and bark placed on the ground after April dried too rapidly to allow the fungus to develop, at least in visible amounts.

Decline of Mats

The rate of progress of mycelial mats from the immature stage to a deteriorated condition varied considerably according to the time of year when the mats appeared, table 12. Most immature mats found during November, December, and January required 70 to 84 days to reach a stage of deterioration. Mats that were found in the immature condition during February, March, and April became deteriorated in about 42 days, and mats that formed in May, June, and July declined very rapidly, sometimes requiring less than 14 days for complete deterioration.

Table 11.—The development of mycelial mats of *Endoconidiophora fagacearum* on bark and wood pieces that were taken from diseased oaks and placed on the forest floor.

Month (1952–1953)	Bark		Wood	
	Number of Pieces	Number With Mats	Number of Pieces	Number With Mats
November	22	0	20	0
December	20	0	14	0
January	22	0	14	0
February	20	0	9	0
March	40	4	22	0
April	27	13	13	0
May	21	0	14	0
June	21	0	11	0
Total	*213*	*17*	*128*	*0*

Table 12.—The rates of development and decline of mycelial mats of *Endoconidiophora fagacearum* appearing on wilt-killed oaks; as indicated by the condition classes of the mats at 14-day intervals, the rate of development and decline of each mat was influenced by the month in which it first appeared.

Month Mat Appeared	Condition Class* of Mats on Designated Number of Days After First Appearance						
	0 Days	14 Days	28 Days	42 Days	56 Days	70 Days	84 Days
November	I	II	III	IV	IV	IV	V
December	I	II	III	IV	IV	V	
January	I	II	III	IV	IV	V	
February	I	III	IV	V			
March	I	II	III	V			
April	I	II	IV	V			
May	I	II	V				
June	I	V					
July	I	V					

*Condition class I, immature; II, mature; III, aging; IV, declining; V, deteriorating.

As field trips to the oak wilt areas were made only every 2 weeks, many mats that were found during the summer were already in the more advanced stages of decline when first seen.

Mycelial mats that developed on trees in March, April, and May as a result of stimulation by wounds made through bark followed essentially the same rate of decline as typical mats produced in these months. Mats that formed on bark pieces on the forest floor dried rapidly, and some of them disappeared entirely within 2 weeks.

Table 13.—Numbers of mycelial mats of *Endoconidiophora fagacearum* on which individual species of insects were found in the 10-month period October, 1952, through July, 1953. Figures within parentheses indicate the numbers of mats examined.

INSECT GROUP		NUMBER OF MATS WITH INSECTS										
Family	Genus and Species	Oct. (8)	Nov. (20)	Dec. (9)	Jan. (17)	Feb. (44)	March (87)	April (66)	May (109)	June (90)	July (15)	Total (465)
Anthocoridae	*Lyctocoris stalii*	0	0	0	0	0	0	1	2	0	0	3
Blattidae	*Parcoblatta* sp.	0	0	0	0	0	5	5	7	0	0	17
Brenthidae	*Eupsalis minuta*	0	0	0	0	0	0	0	0	19	0	19
Buprestidae	*Agrilus bilineatus*, larvae	0	0	0	0	0	1	0	0	0	0	1
Carabidae	*Pristodactyla impunctata*	0	0	0	0	0	0	4	6	1	0	11
Colydiidae	*Aulonium parallelopipedum*	0	0	0	0	0	0	6	5	7	0	18
	Bothrideres geminatus	0	3	0	0	0	0	0	0	0	0	3
	Synchita parvula	0	0	0	0	0	1	1	1	0	0	3
Cucujidae	*Silvanus bidentatus*	0	0	0	0	0	0	1	16	12	0	29
	Uleiota dubia	0	0	0	0	0	0	1	2	1	0	4
Collembola (order)		0	3	1	2	5	27	9	5	1	0	53
Curculionidae	*Pandeleteius hilaris*	0	0	0	0	0	0	2	0	0	0	2
Elateridae	*Ampedus nigricans*	0	0	0	0	0	0	0	1	0	0	1
	Elater sp.	0	0	0	0	0	0	0	2	0	0	2
Histeridae	*Paromalus bistriatus*	0	0	0	0	0	0	0	27	33	1	61
	Platysoma lecontei	0	0	0	0	0	0	1	20	24	0	45
Mycetophagidae	*Litargus sexpunctatus*	0	1	0	0	0	0	0	1	0	0	2
Nitidulidae	*Carpophilus sayi*	0	0	0	0	0	0	1	15	1	0	17
	Carpophilus sp. (1)	0	0	0	0	0	0	0	3	1	0	4
	Carpophilus sp. (2)	0	0	0	0	1	0	0	0	0	0	1
	Carpophilus sp., larvae	2	8	1	1	8	4	5	7	1	0	37
	Colopterus truncatus	0	0	0	0	0	1	19	18	0	0	38
	Colopterus semitectus	0	0	0	0	0	0	0	31	3	0	34
	Epuraea umbrosa	0	0	0	0	0	0	0	4	0	0	4
	Epuraea terminalis	0	0	0	0	0	0	7	5	0	0	12
	Glischrochilus obtusus	2	2	0	1	1	2	6	15	3	0	32
	Glischrochilus sanguinolentus	0	0	0	0	0	0	0	2	2	0	4
	Glischrochilus sp., larvae	0	0	0	0	0	0	2	16	25	0	43
	Other nitidulid larvae	0	0	0	0	0	0	2	23	17	0	42
Orthoperidae	*Molamba fasciata*	1	0	0	0	0	0	0	2	1	0	4
	Molamba ornata	1	0	0	0	0	0	0	1	0	0	2
Ostomidae	*Tenebroides laticollis*	0	3	0	0	0	0	7	4	0	0	14
Rhizophagidae	*Rhizophagus bipunctatus*	0	1	0	0	0	2	0	3	0	0	6
Scolytidae	*Monarthrum fasciatum*	0	0	0	0	0	0	0	7	3	0	10
	Monarthrum mali	0	0	0	0	0	0	0	8	3	0	11
	Xyloterinus politus	0	0	0	0	0	0	0	16	6	1	23
Staphylinidae	*Atheta* sp.	0	10	2	0	0	0	4	50	5	0	71
	Boletobius quaesitor	0	0	0	0	0	0	0	9	3	0	12
	Coproporus ventriculus	0	0	0	0	0	0	0	3	2	0	5
	Philonthus laetulus	0	0	0	0	0	0	0	4	2	0	6
	Staphylinid larvae	0	0	0	0	0	0	0	2	10	0	12
	Tachinus sp.	0	0	0	0	0	0	0	3	0	0	3
Tenebrionidae	*Cynaeus angustus*	0	0	0	0	0	0	4	0	0	0	4
	Platydema ruficorne	0	0	0	0	0	0	2	1	0	0	3
Trichoceridae	*Trichocera* sp., larvae	0	0	0	0	2	4	4	1	0	0	11

Insects Associated With Mats

The possibility that several insects which are often associated with the fruiting mats of *Endoconidiophora fagacearum* might spread oak wilt inoculum to wounds of healthy trees was pointed out by Norris (1953) in Iowa and by Dorsey *et al.* (1953) in West Virginia. These workers obtained mechanical transmission of oak wilt under experimental conditions with several species of the Nitidulidae. Griswald & Neiswander (1953) in Ohio suggested that the pomace fly, ***Drosophila***

Table 14.—Numbers of mycelial mats of *Endoconidiophora fagacearum* in five condition classes* on which individual species of insects were found in the 10-month period October, 1952, through July, 1953. Figures within parentheses indicate the numbers of mats examined.

Insect Group		Number of Mats With Insects					
Family	Genus and Species	Class I (72)	Class II (63)	Class III (80)	Class IV (123)	Class V (127)	Total (465)
Anthocoridae	*Lyctocoris stalii*	0	0	0	3	0	3
Blattidae	*Parcoblatta* sp.	0	1	1	11	4	17
Brenthidae	*Eupsalis minuta*	0	0	0	7	12	19
Buprestidae	*Agrilus bilineatus*, larvae	0	1	0	0	0	1
Carabidae	*Pristodactyla impunctata*	0	0	3	3	5	11
Colydiidae	*Aulonium parallelopipedum*	0	1	3	11	3	18
	Bothrideres geminatus	0	0	0	1	2	3
	Synchita parvula	0	1	1	1	0	3
Cucujidae	*Silvanus bidentatus*	1	0	5	12	11	29
	Uleiota dubia	0	0	0	2	2	4
Collembola (order)		1	6	6	25	15	53
Curculionidae	*Pandeleteius hilaris*	0	0	0	2	0	2
Elateridae	*Ampedus nigricans*	0	0	0	1	0	1
	Elater sp.	0	0	0	2	0	2
Histeridae	*Paromalus bistriatus*	0	1	9	13	38	61
	Platysoma lecontei	0	0	7	12	26	45
Mycetophagidae	*Litargus sexpunctatus*	0	0	0	2	0	2
Nitidulidae	*Carpophilus sayi*	0	1	9	6	1	17
	Carpophilus sp. (1)	0	0	0	1	0	1
	Carpophilus sp. (2)	0	1	2	0	1	4
	Carpophilus sp., larvae	0	1	5	18	13	37
	Colopterus truncatus	7	8	14	8	1	38
	Colopterus semitectus	0	5	14	13	2	34
	Epuraea umbrosa	0	0	4	0	0	4
	Epuraea terminalis	1	4	6	1	0	12
	Glischrochilus obtusus	1	3	16	5	7	32
	Glischrochilus sanguinolentus	0	0	3	1	0	4
	Glischrochilus sp., larvae	0	3	4	12	24	43
	Other nitidulid larvae	0	1	8	18	15	42
Orthoperidae	*Molamba fasciata*	0	0	0	3	1	4
	Molamba ornata	0	0	0	2	0	2
Ostomidae	*Tenebroides laticollis*	0	0	3	9	2	14
Rhizophagidae	*Rhizophagus bipunctatus*	1	0	0	3	2	6
Scolytidae	*Monarthrum fasciatum*	0	1	5	3	1	10
	Monarthrum mali	0	3	5	2	1	11
	Xyloterinus politus	1	0	13	9	0	23
Staphylinidae	*Atheta* sp.	3	9	18	28	13	71
	Boletobius quaesitor	0	0	5	5	2	12
	Coproporus ventriculus	0	0	0	3	2	5
	Philonthus laetulus	0	0	2	2	2	6
	Staphylinid larvae	0	0	1	0	11	12
	Tachinus sp.	0	0	0	2	1	3
Tenebrionidae	*Cynaeus angustus*	0	3	1	0	0	4
	Platydema ruficorne	0	0	2	1	0	3
Trichoceridae	*Trichocera* sp., larvae	0	0	2	2	7	11

* Condition class I, immature; II, mature; III, aging; IV, declining; V, deteriorating.

melanogaster, which, like the Nitidulidae, is attracted to mycelial mats of the oak wilt fungus and to bleeding wounds on healthy oak trees, might be a vector of oak wilt. In the study reported here, many other insects were found to be associated with naturally occurring fungus mats. From October, 1952, through July, 1953, at least 40 species of insects belonging to at least 33 genera of 19 families (exclusive of Collembola) were collected from mycelial mats on wilt-killed oak trees in Illinois, tables 13 and 14.

Insects associated with mats are not only potential vectors of oak wilt, but they play other roles that affect the life

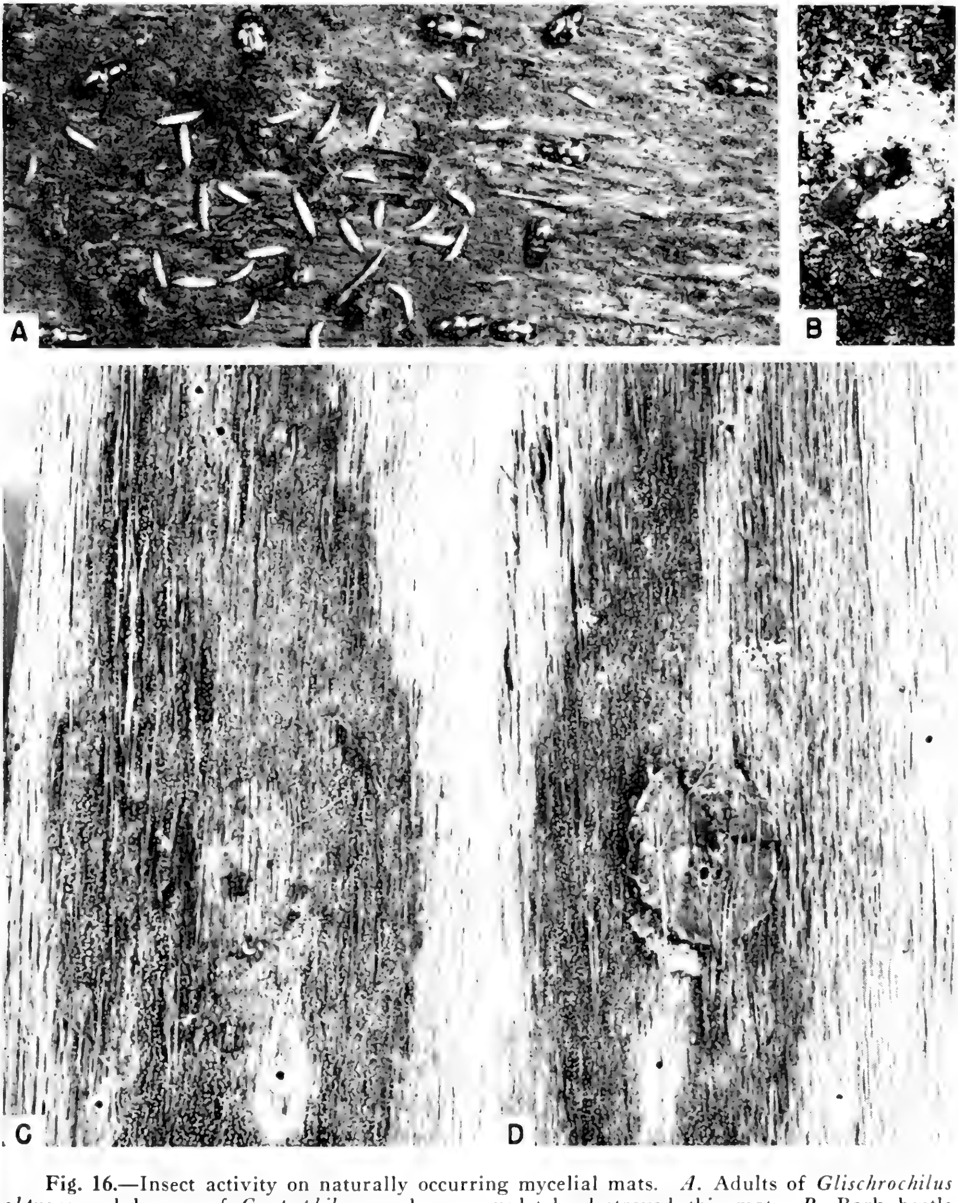

Fig. 16.—Insect activity on naturally occurring mycelial mats. *A.* Adults of *Glischrochilus obtusus* and larvae of *Carpophilus* sp. have completely destroyed this mat. *B.* Bark beetle (Scolytidae) and freshly made hole in fungus mat. *C.* and *D.* Holes made through perithecium-bearing mat and pad on wood and bark by adults of the Scolytidae.

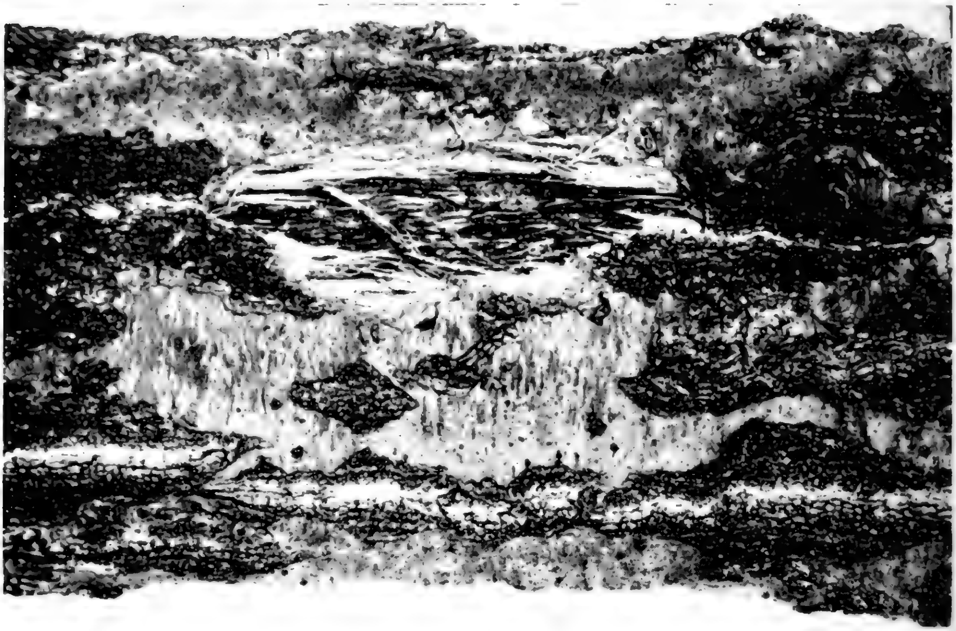

Fig. 17.—Damage inflicted by squirrel or squirrels to the bark of an oak tree and the underlying mycelial pad of *Endoconidiophora fagacearum*.

cycle of the fungus. The destructive feeding habits of some of these insects, particularly the Nitidulidae, on laboratory cultures of *Endoconidiophora fagacearum* were mentioned earlier, page 297. Also, the role of some insects in the destruction of mats in the field was observed, fig. 16*A*.

During the spring three immature mats, which had no insects on them when examined, were covered with clean plastic covers so that no insects could reach the fungus; then the bark, which had been removed for the examination, was replaced over the mats and nailed securely to the trees. Three other immature mats, which had several individuals of both *Glischrochilus obtusus* and *Colopterus truncatus* present, were covered in the same manner.

The mats on which no insects had been seen remained in good condition for between 4 and 6 weeks, after which contamination by bacteria and fungi other than *Endoconidiophora fagacearum* was evident. The mats with insects present declined rapidly, reaching a stage of complete deterioration in 2 weeks. It was observed that, throughout the spring and summer, mats infested by large numbers of Nitidulidae deteriorated rapidly. During the winter months, when insect activity was low, mats lasted much longer.

Another role in which insects may be important is that of spermatizing mats with conidia of opposite compatibility groups, as shown experimentally by Leach *et al.* (1952) with two species of Nitidulidae and one of Orthropidae. Any of the species of insects listed in table 13, or even mites, might conceivably perform this role.

At least 3 of the 40 or more species of insects that were found on mats were present during each of the winter months as well as in the spring and summer, table 13. Several species were prevalent in October and November. During the cold months of January and February only 3 species were constantly associated with the mats; these were adults of the order Collembola and *Glischrochilus obtusus* and larvae of *Carpophilus* sp., which were usually present in large numbers throughout the 10-month period. Although *Carpophilus* larvae were often found embedded in ice on the mats, many of them survived and, on warm days, fed on the fungus. In winter months, *Glischrochilus obtusus* was present usually only in small numbers of 1 to 10 per mat.

In April, large numbers of adult Scolytidae were seen running over the bark surface or making holes through the bark of diseased oaks that were near the mat-producing stage. Later, in May and June, many holes made by these beetles were seen in the wood and bark of most of the mat-bearing trees. It was common to find several holes extending through mycelial mats beneath the bark, fig. 16*B, C*. Many of these holes had been made directly

Fig. 18.—Mats of *Endoconidiophora fagacearum* on which unidentified fungi have overrun all but the central pads.

through the central pads, fig. 16*D*, and some beetles were found embedded there.

Insect activity on mats was greatest during April, May, and June, when more species were found than in any other months. Very few fresh mats were found in July, and insects were seldom found on them.

Few attempts were made to determine exact numbers of insects on mats. Members of the families Nitidulidae, Staphylinidae, and Histeridae, and of the order Collembola, obviously were much more abundant than any of the others. Approximately 75 to 100 adult Nitidulidae and as many larvae were commonly seen on a single mat. Members of the Staphylinidae and of the Collembola, which are much smaller than the Nitidulidae, were even more numerous. Adult insects were found most frequently on class III and class IV mats and larvae on class IV and class V mats, table 14. Insects were seldom present on immature mats, as the cracks in the bark over such mats usually were very narrow, barely perceptible openings that could admit only the smallest insects. Small individuals of the Nitidulidae were often seen making unsuccessful attempts to squeeze through these openings. The fact that immature (class I) mats are not so strongly odoriferous as are mats of the mature and aging classes also may account for the presence of fewer insects on the younger mats.

Other Agents Associated With Mats

Agents other than insects may have been responsible for hastening the decline and deterioration of natural reservoirs of inoculum. Feeding by rodents on mycelial mats of *Endoconidiophora fagacearum* in Pennsylvania was reported by Morris & Fergus (1952). Squirrels caused considerable damage to mycelial mats in Illinois (Himelick *et al.* 1953) during the winter of 1952–53, and new damage of this kind, fig. 17, was seen in May and June of 1953. The rodents seemed to have been interested in only the central pads of young mats, but, to reach the pads, they had torn large holes in the bark, exposing the fungus to other destructive elements, such as insects, wind, rain, and other fungi.

During the summer months, the mat-bearing trees were often exposed to the direct rays of the sun, and temperatures became very high under the bark. The temperatures for one tree at 3:00 p.m. on July 23, 1953, were 32.5 degrees outside and 41.0 degrees under the bark on the sunny side of the trunk, as determined by actual thermometer readings. On the shaded side, the temperatures were 29.5 degrees outside and 30.5 degrees beneath the bark. No further mat production occurred on this tree, and the fungus could not be isolated from the wood. During the winter months, mats were subjected to alternate freezing and thawing. At this time the mats often were continuously wet for several days and finally became slimy with bacteria and other microscopic forms of life.

Many mycelial mats were found to be overrun by wood-rotting fungi, fig. 18, except for the central pad of each, which seemed to repel invasion of these fungi. However, the pads were readily attacked by other fungi. *Graphium*, in particular, throve well in aging pads, where it entangled the pad cells in a thick mass of hyphal strands and produced abundant coremia and slimy masses of spores.

Other agents that were commonly associated with the mats of the oak wilt fungus but that were less destructive were mites, nematodes, and crustacea. Mites were usually abundant during all months on mats in all stages of decline. Nematodes of the genus *Diplogaster** were very abundant on old perithecium-bearing mats. They infested the masses of exuded ascospores of *Endoconidiophora fagacearum*, in some cases hundreds in a single mass. These nematodes had oral openings that measured about 5.6 microns, large enough to admit conidia or ascospores of the oak wilt fungus. However, attempts to entice the nematodes to feed upon the spores of the fungus on the surface of agar were unsuccessful. Crustaceans of the species *Porcellio rathkei* were sometimes found on mycelial mats that had developed on bark pieces on the forest floor, but they were not observed feeding on the fungus of the oak wilt disease.

* Nematodes were identified by Dr. M. B. Linford, Department of Horticulture, University of Illinois.

INOCULA IN NATURE

Sources of Data

A total of 629 mycelial mats of *Endoconidiophora fagacearum* were found beneath the bark of 27 of the 30 wilt-killed oaks that were thoroughly studied over a 10-month period, table 10. The remaining 3 trees, 1 standing white oak, 1 standing bur oak, and 1 felled black oak, did not produce mats. Twenty additional mats were taken from 4 red oaks that were examined only once and that were not included among the thoroughly studied trees. These 20 mats brought the total number of mats found on 31 mat-bearing trees to 649. The figure for mats includes only typical mats with central pads accompanied by cracks in the bark.

The detailed data presented on the following pages were obtained from 365, or 56 per cent, of the total number of mats found. Forty-three of these mats were left on the trees, where each was resampled at 2-week intervals until it reached a deteriorated condition. The total number of additional samplings* that were made of the 43 mats on the trees was 100. Thus, the data came from 465 samplings of 365 mats, table 15. As each additional sampling of a mat was made at a later time than the one preceding and when the mat was more advanced in its development or decline, the data obtained from this sampling were treated as if taken from a separate mat. The figures in table 15 represent mats sampled in all five study areas. More samples were taken during the spring and summer than at other periods of the year, because more mats were produced at that time. Also, more mats of classes IV and V than of other classes were sampled, as they were found more often than mats of the other classes.

* A sampling involved taking three mycelial disks each 7 mm. in diameter from a mat, as described on page 284.

Availability of Conidia

The data regarding numbers and germinability of conidia obtained from samples of naturally occurring mycelial mats of the oak wilt fungus in their different stages of development and decline during 10 months are presented in table 16. The method of counting and germinating conidia is described in another section, "Treatment of Samples From Nature," page 296.

The average number of conidia per mat, as determined from mats of all classes, increased from October to December, 1952, at which time the highest concentration of the 10-month period was reached, fig. 19. The concentration of conidia then decreased steadily during a period of low winter and spring tempera-

Table 15.—Numbers of samplings and average sizes (cm.) of mycelial mats of *Endoconidiophora fagacearum* in five condition classes* sampled in the 10-month period October, 1952, through July, 1953.

Month	Class I		Class II		Class III		Class IV		Class V		Total Samplings	Average Size
	Number	Size	Number	Size	Number	Size	Number	Size	Number	Size		
October	1	15 x 5	2	12 x 5	1	8 x 3	3	9 x 3	1	15 x 7	8	11 x 4
November	4	10 x 5	4	6 x 2	1	15 x 6	8	9 x 4	3	9 x 5	20	9 x 4
December	1	7 x 4	6	11 x 6	1	11 x 5	1	6 x 3	0	—	9	10 x 5
January	3	8 x 4	6	10 x 5	1	9 x 5	5	16 x 6	2	11 x 6	17	11 x 5
February	6	12 x 4	5	10 x 6	10	20 x 6	19	15 x 5	4	12 x 5	44	15 x 5
March	21	7 x 4	12	9 x 5	12	14 x 5	25	11 x 5	17	12 x 6	87	10 x 5
April	19	11 x 4	11	14 x 6	11	15 x 7	12	10 x 4	13	10 x 5	66	12 x 5
May	13	15 x 6	10	16 x 5	30	19 x 6	33	21 x 7	23	23 x 7	109	20 x 6
June	4	13 x 5	5	14 x 5	12	15 x 5	14	17 x 6	55	23 x 8	90	20 x 7
July	0	—	2	9 x 3	1	9 x 3	3	16 x 5	9	12 x 5	15	12 x 5
Total	*72*	—	*63*	—	*80*	—	*123*	—	*127*	—	*465*	—

*Condition class I, immature; II, mature; III, aging; IV, declining; V, deteriorating.

tures until April, 1953, when a sharp rise occurred with a rise in monthly mean temperature. After April, the number of conidia decreased again, as the monthly mean temperatures increased, and no conidia were found on mats that were sampled in July. It is interesting to note in fig. 19 that the peak in conidium concentration in December and a rise in April were preceded by months in which precipitation was above the annual mean.

The time of the highest average per

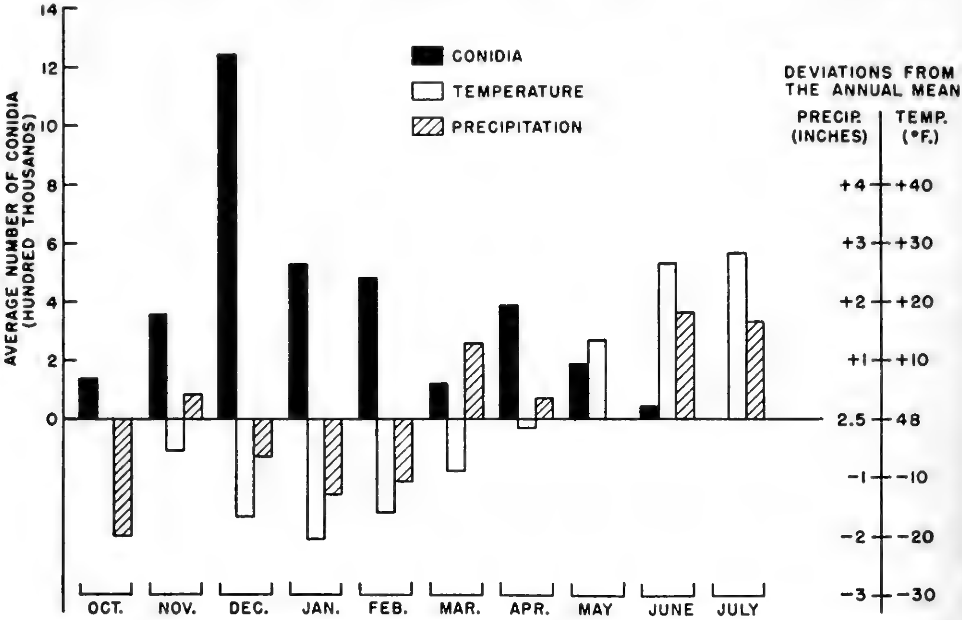

Fig. 19.—Monthly mean temperature and total precipitation, both shown as deviations from the annual means, and average numbers of conidia (per ml. of spore suspension prepared from three-disk sampling of each mat) obtained from samples of mycelial mats of *Endoconidiophora fagacearum*, October, 1952, through July, 1953. For temperature in October and for precipitation in May there were no deviations from the means.

Table 16.—Average number per mat sample* and per cent germination of conidia taken from naturally occurring mats of *Endoconidiophora fagacearum* in five condition classes† in the 10-month period October, 1952, through July, 1953.

Month	Class I		Class II		Class III		Class IV		Class V	
	Number of Spores	Per Cent of Spores Viable	Number of Spores	Per Cent of Spores Viable	Number of Spores	Per Cent of Spores Viable	Number of Spores	Per Cent of Spores Viable	Number of Spores	Per Cent of Spores Viable
October	84,800	58	511,150	15	0	—	0	—	0	—
November	1,079,675	67	608,125	23	106,600	10	29,875	5	0	—
December	122,600	2	1,646,333	4	1,056,000	1	133,000	0	0	—
January	533,000	12	550,433	26	320,000	0	741,120	11	0	—
February	19,442	0	60,740	10	585,410	4	76,453	0	21,250	0
March	413,786	56	70,875	13	25,688	1	12,822	1	3,724	0
April	197,708	61	404,464	34	813,455	40	135,583	6	0	—
May	488,385	39	407,400	6	266,527	9	58,606	1	0	—
June	152,000	67	78,000	15	52,000	9	40,914	5	436	15
July	0	—	0	—	0	—	0	—	0	—

* Figures are calculated averages. Numbers of mat samplings are shown in table 15.
† Condition class I, immature; II, mature; III, aging; IV, declining; V, deteriorating.

Table 17.—Average number per mat sample* and per cent germination of conidia taken from mycelial mats of *Endoconidiophora fagacearum* in five condition classes† in five study areas in the 10-month period October, 1952, through July, 1953.

Study Area	Class I			Class II			Class III			Class IV			Class V		
	Number of Mats	Number of Spores	Per Cent Viable	Number of Mats	Number of Spores	Per Cent Viable	Number of Mats	Number of Spores	Per Cent Viable	Number of Mats	Number of Spores	Per Cent Viable	Number of Mats	Number of Spores	Per Cent Viable
Chicago...	11	144,782	51	16	129,156	19	9	67,956	7	14	19,643	1	26	923	15
Sinnissippi.	12	335,842	49	14	326,421	10	17	371,097	12	24	74,288	3	12	4,442	0
Rockford..	14	500,011	51	17	839,371	10	24	281,083	9	48	117,778	3	46	2,065	0
Peoria.....	20	289,698	51	11	371,009	33	19	421,158	20	16	56,438	5	28	0	—
Havana....	15	481,860	53	5	343,180	18	11	322,227	12	21	65,252	2	15	0	—

* Figures are calculated averages.
† Condition class I, immature; II, mature; III, aging; IV, declining; V, deteriorating.

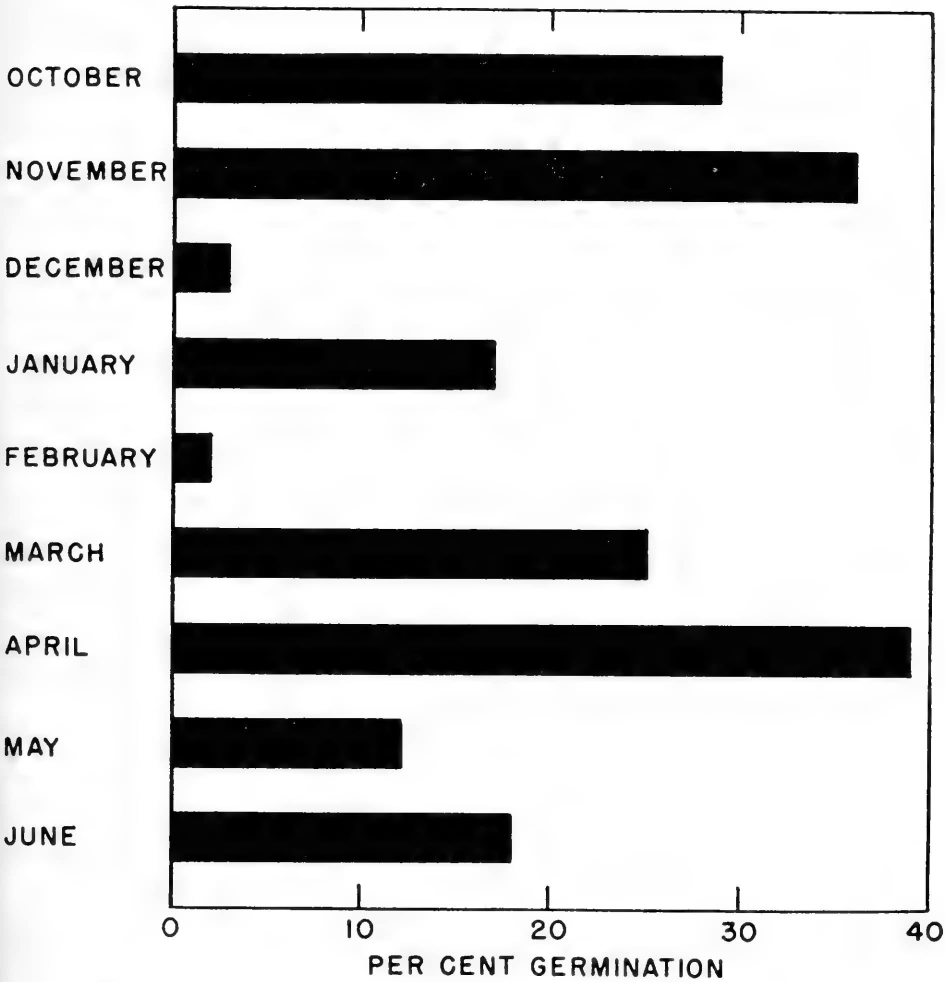

Fig. 20.—Average per cent germination of conidia of *Endoconidiophora fagacearum* taken from mycelial mats, October, 1952, through June, 1953.

cent germinability of conidia taken from mycelial mats during the 10-month period did not coincide with the time of highest concentration of conidia. The best average germination rate (39 per cent) was obtained from conidia that were collected in April, fig. 20. The next best germination rate was obtained from conidia collected in November. A germination rate as high as 80 per cent was not uncommon.

The number and germinability of conidia that were taken from mats of the same condition class did not vary unexpectedly from one study area to another, table 17. All areas included in the study were in the northern half of the state, and the distance between any two areas was not greater than 165 miles.

Pronounced differences were found, in the number and germinability of conidia, between the mats belonging to different condition classes, fig. 21. The highest average numbers of conidia were obtained from mature, or class II, mats. The highest average per cent of germination occurred in conidia from immature, or class I, mats. Both the number and germinability of spores changed as the condition of the mats advanced from class I toward class V or deterioration.

The data dealing with number of conidia on a mat were based upon estimates of the average number of spores in 1 ml. of suspension prepared from a 3-disk sampling of the mat. A rough approximation of the number of conidia on an entire mat could be made by using figures obtained from the samples. The number of conidia in a mature mat which measured 12 by 5 cm. with a central pad which measured 4 by 2 cm. was estimated as follows. The average number of conidia from one disk of mat surface 7 mm. in diameter (38 sq. mm.) contained in 1 ml. of a 10-ml. water blank was 350,000 spores or 3,500,000 spores from the entire disk. The area of the mat, after the area of the central pad (which had few or no spores) had been deducted, was 4,100 square mm. The number of conidia on

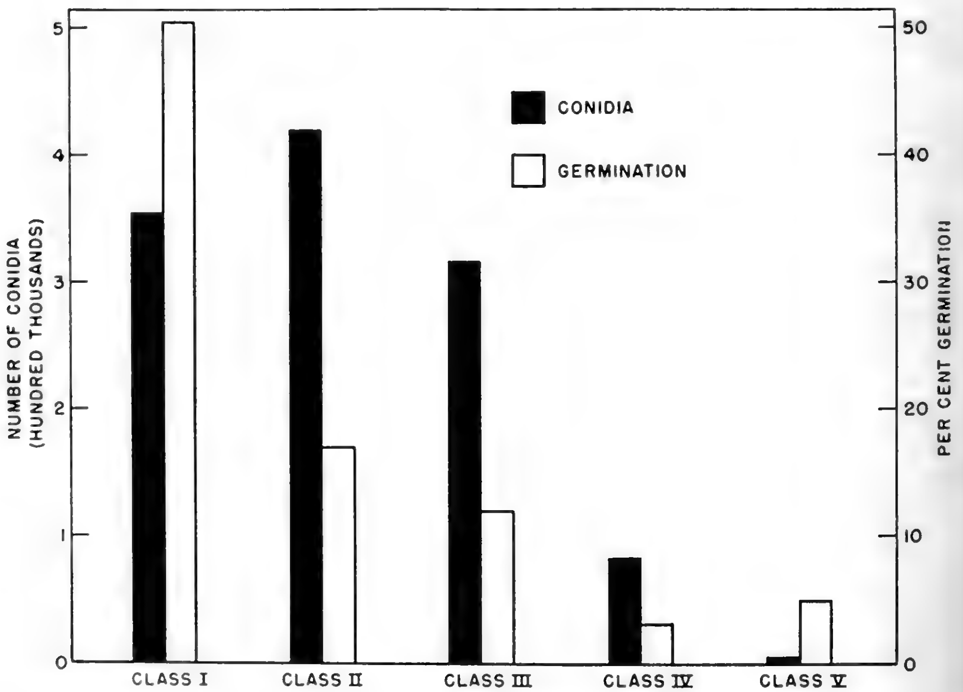

Fig. 21.—Average number and per cent germination of conidia of *Endoconidiophora fagacearum* taken from mycelial mats in five stages of development and decline over the 10-month period October, 1952, through July, 1953; class I, immature; class II, mature; class III, aging; class IV, declining; class V, deteriorating.

the entire mat was estimated as being approximately 378,000,000. Another mat which measured 24 by 10 cm., the pad 6 by 2 cm., and which had the same average number of spores on a disk sample as the mat above, was estimated to have 1,650,000,000 conidia, more than four times as many as the other mat.

From these figures one can appreciate the significance of mat size as well as numbers of mats in accounting for the concentration of conidia in an oak wilt area. It can be seen in table 15, which gives the average sizes of all mats sampled in each month, that the mats of May and June were considerably larger than those of other months. The sizes of the mats sampled in all months ranged from 1 by 1 cm. to 48 by 14 cm.

As pointed out earlier, other possible mycelial sources of oak wilt inoculum might be afforded by the padless mycelial mats that form on bark pieces on the forest floor and by wound-stimulated mycelial growth on standing and felled trees. The conidial sporulation on such mats and the ability of the spores to germinate appear to be equal to those of typical mats with pads, table 18.

Availability of Fertile Perithecia

The total number of mats found with perithecia during the 10-month study period was 90, or 23 per cent of 393 mats studied in detail, table 19. Perithecia were never present on class I mats. The month with the highest percentage of perithecium-bearing mats was December and the next highest May.

Table 18.—Average number and germinability of conidia of *Endoconidiophora fagacearum* obtained from wound-stimulated mycelial mats and from mats on bark pieces on the forest floor during 3 months of 1953.

Month	Wound-Stimulated Mats			Mats on Bark on Ground		
	Number of Mats Sampled	Average Number of Conidia	Per Cent of Conidia Viable	Number of Mats Sampled	Average Number of Conidia	Per Cent of Conidia Viable
March	2	480,000	35	4	256,000	56
April	16	279,000	34	13	38,500	17
May	6	72,000	9	—	—	—

Table 19.—Perithecium-bearing mycelial mats of *Endoconidiophora fagacearum* in four condition classes* found on wilt-killed oaks in the 10-month period October, 1952, through July, 1953.

Month	Class II		Class III		Class IV		Class V		Per Cent of Mats With Perithecia
	Number of Mats Examined	Number With Perithecia	Number of Mats Examined	Number With Perithecia	Number of Mats Examined	Number With Perithecia	Number of Mats Examined	Number With Perithecia	
October	2	2	1	0	3	0	1	0	29
November	4	1	1	0	8	1	3	0	13
December	6	3	1	1	1	0	0	0	50
January	6	0	1	1	5	4	2	0	36
February	5	1	10	1	19	7	4	1	26
March	12	0	12	0	25	2	17	2	6
April	11	1	11	2	12	1	13	0	9
May	10	3	30	21	33	18	23	0	44
June	5	2	12	3	14	8	55	4	20
July	2	0	1	0	3	0	9	0	0

*Condition class II, mature; III, aging; IV, declining; V, deteriorating.

The average number of perithecia on a 6 mm. square area of mat surface and the average germinability of ascospores are presented by months and by mat classes in table 20. Some mature mats had many young perithecia not exuding ascopores,

Table 20.—Average numbers of perithecia on 6-mm. square areas of surface on perithecium-bearing mats of *Endoconidiophora fagacearum* in four condition classes* and per cent germination of ascospores in the 9-month period October, 1952, through June, 1953.

Month	Class II		Class III		Class IV		Class V	
	Number of Perithecia	Per Cent of Ascospores Viable	Number of Perithecia	Per Cent of Ascospores Viable	Number of Perithecia	Per Cent of Ascospores Viable	Number of Perithecia	Per Cent of Ascospores Viable
October	32	27	0	—	0	—	0	—
November	25	†	0	—	50	9	0	—
December	30	0	28	0	0	—	0	—
January	0	—	86	0	16	0	0	—
February	14	0	5	†	42	0	7	†
March	0	—	0	—	5	†	4	†
April	8	†	35	49	3	†	0	—
May	31	36	48	34	42	27	0	—
June	5	†	38	38	16	16	25	11

*Condition class II, mature; III, aging; IV, declining; V, deteriorating.
†Because the surface was infested with nematodes, bacteria, and *Graphium* sp., it could not be told with certainty whether the ascospores had germinated.

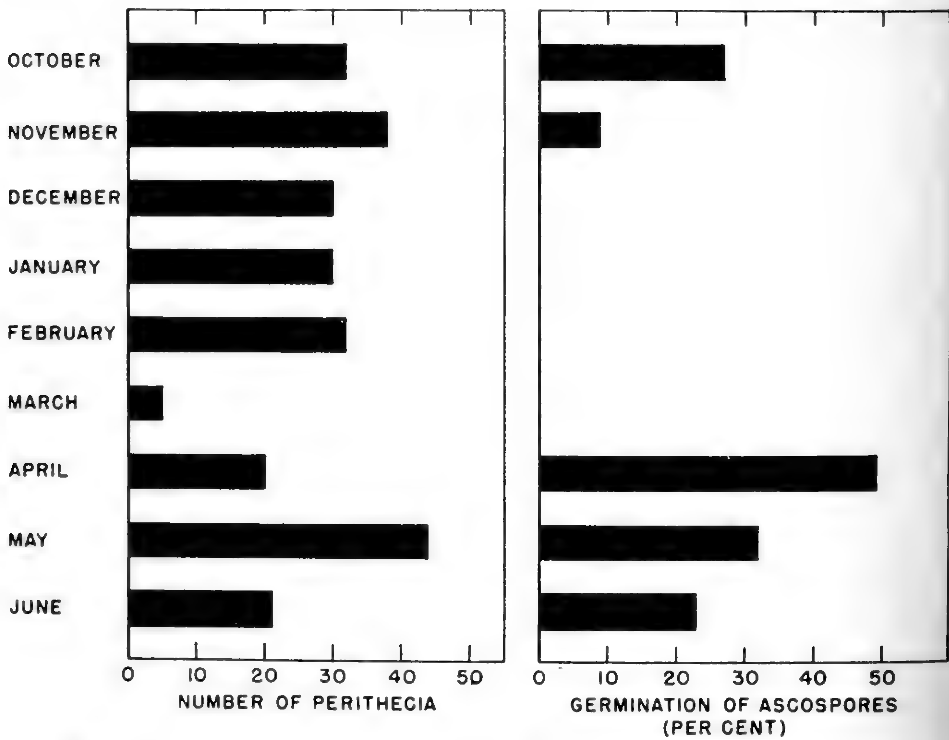

Fig. 22.—Average number of perithecia on a 6-mm. square area of mat surface and average per cent germination of ascospores taken from mycelial mats of *Endoconidiophora fagacearum*, October, 1952, through June, 1953.

Table 21.—Per cent of mats of *Endoconidiophora fagacearum* with perithecia, average number of perithecia on a 6-mm. square area of mat surface, and average per cent germination of ascospores (465 mat samplings in five condition classes*).

Condition Class	Per Cent of Mats With Perithecia	Number of Perithecia on 6-mm. Square Area of Mat Surface	Per Cent Germination of Ascospores
Class I......	0	0	0
Class II.....	21	23	16
Class III....	36	45	33
Class IV.....	33	32	17
Class V......	6	16	11

* Condition class I, immature; II, mature; III, aging; IV, declining; V, deteriorating.

Table 22.—Numbers and per cents of positive cultures obtained by mass transfers of pad cells from mycelial mats of *Endoconidiophora fagacearum* in five condition classes* over the 10-month period October, 1952, through July, 1953.

Condition Class	Number of Pads Sampled	Number Giving Positive Cultures	Per Cent Giving Positive Cultures
Class I......	68	56	82
Class II.....	57	24	42
Class III.....	64	16	25
Class IV.....	112	0	0
Class V......	122	0	0

* Condition class I, immature; II, mature; III, aging; IV, declining; V, deteriorating.

and many old mats had masses of ascospores infested by nematodes, bacteria, and spores of fungi other than *Endoconidiophora fagacearum*. In neither of these types of mats were ascospore germination tests possible.

The average number of perithecia per mat sample and the average percentage of ascospores germinating in four mat classes are treated graphically by months in fig. 22. Perithecia were found in all months except July; the largest average number per mat sample, 44, was found in May. However, germination of ascospores was obtained only in October, November, April, May, and June. The best average germination rate was 49 per cent, obtained with ascospores collected in April; 32 per cent germination was obtained with ascospores collected in May. In some cases, as high as 83 per cent of the ascospores germinated.

Like conidia, perithecia and ascospores were strikingly influenced by the extent of mat development or decline, table 21. Of 465 mat samplings in all areas and all months of the study period, class III, aging mats, had the highest percentage with perithecia, 36 per cent. Mats of this class contained the greatest number of perithecia, an average of 45 on a 6 mm. square area of mat surface, and they had the highest rate of germinating ascospores, 33 per cent. Mats frequently had as many as 90 perithecia on a sample 6 mm. square.

Mycelial Pads

A potential source of oak wilt inoculum which should not be overlooked is that afforded by the highly germinable cells that comprise the central pads of mycelial mats. The ability of these cells to germinate and produce large numbers of conidia was shown in laboratory studies.

From October, 1952, through July, 1953, 423 mycelial pads on mats of all five condition classes were sampled in the field. The results of mass transfers from the interiors of these pads to potato dextrose agar are given in table 22. Eighty-two per cent of the pads from class I mats, 42 per cent of the pads from class II mats, and 25 per cent of the pads from class III mats gave positive cultures of *Endoconidiophora fagacearum*. The living fungus was never isolated from pads of class IV and class V mats.

DISCUSSION

The present study has shown that three potential oak wilt inocula are present in nature in Illinois. These are conidia, ascospores, and mycelial pad cells, all of which are furnished by the macroscopic subcortical fruiting mats of *Endoconidiophora fagacearum* on wilt-killed oaks. The mats on which conidia and perithecia form develop readily on both standing diseased trees and trees felled after symptoms have appeared. Additional conidium inoculum may be created by the formation of padless mycelial mats adjacent to wounds on mat-producing trees and on the inner sides of pieces of bark from diseased trees while these pieces lie on the moist forest floor. Perithecia were never found on such mats.

It was well known before the present study was undertaken that the injection of either conidia or ascospores of *Endoconidiophora fagacearum* into healthy oaks would result in diseased trees. However, it was not realized that the irregularly shaped cells that constitute the pseudoparenchymatous interiors of mycelial pads are capable of rapid germination and abundant sporulation comparable to that of conidia and ascospores. Like conidia and ascospores, the pad cells germinate well on plain water agar, but whether they will germinate and produce oak wilt symptoms when injected into healthy oak trees has not been determined. It has been shown that cultures obtained from pad cells are pathogenic. Pad cells do not seem to be adapted for insect transmission, but the possibility of their spread by squirrels or woodpeckers is not remote. While woodpecker damage to mycelial mats has not been observed in Illinois, damage caused by the feeding of squirrels is common. The spread of fungus diseases by these and other unusual agents has been reported by Gravatt & Marshall (1917), Heald & Studhalter (1914), and Talbot (1952).

The decline of diseased oak trees and the development and decline of the resulting mycelial mats seem to follow a pattern. The brown streaks that are normally found in diseased trees of the red oak group first become more pronounced, usually on one side of the tree; then they increase in width and length until a large area of wood is brown. During this process the bark loses its tight grip on the wood, which begins to emit the characteristic amyl acetate or ripe fruit odor of the fungus. Now having "room" to grow, the fungus appears in a macroscopic form, in most cases in a few days. The time required for the conditioning process to occur before mats appear is dependent on the season of the year. In Illinois the first wilt symptoms of the year are seen on trees early in June. Trees wilting at this time decline rapidly and may produce mats late in August or in September. The decline of trees that wilt in the last part of July or in August is retarded by low winter temperatures, and these trees may not produce mats until the following spring or summer, unless the winter is unusually mild. Mycelial mats of *Endoconidiophora fagacearum* have not been reported on trees of the white oak group in Illinois. The bark on diseased white oaks is thin and adheres to the wood, even after the trees have reached an advanced stage of decline. No ripe fruit odor was detected in the white oaks studied.

In the period of this study, more mats were found during April, May, and June than in other months. These months were the ones during which large numbers of bark beetles (Scolytidae) were boring hundreds of tiny holes through the bark and wood of wilt-killed trees. Such perforating of the bark may have been instrumental in bringing about a subcortical aeration that resulted in a condition favorable for rapid mat development. The inducement of mat formation by intentional wounding of trees that were nearing the mat-producing condition indicated that a supply of air from outside may hasten mat initiation. When the wood surface of mat-producing trees was covered with plastic, the fungus did not grow, at least to a visible form, on the wood but grew abundantly on the uncovered inner bark surface and on other areas of uncovered wood.

Several factors seemed to be influential in determining the occurrence of mycelial mats and the longevity of inocula in nature. Weather conditions affected both the development and decline of the fungus. Mat production on individual trees seemed to be accelerated following periods of cool, rainy weather. Macroscopic growth of the fungus continued over a longer period of time during the winter months than during the summer, and apparently low winter temperatures, along with a minimum of insect activity, increased the longevity of the fungus mats. That the occurrence of new mats in July was rare was due probably to high temperatures plus the fact that wilt-killed trees were, by that time, nearing a state of deterioration which favored the growth of various wood-rotting fungi other than *Endoconidiophora fagacearum*. Observations have shown that new mats are seldom found during August in Illinois.

Apparently the freezing of mats during the winter does not in itself have a marked deteriorating effect on the fungus in nature. Laboratory tests showed that a temperature of 0 degrees C. favored longevity of the fungus in both humid and dry atmospheres; a continuous dry atmosphere was more favorable to the fungus than a continuous humid atmosphere. In the field, the fluctuating temperature and moisture conditions, combined with the effects of mat-invading microorganisms, may account in part for the fact that the germinability of spores collected during the winter months was lower than that of spores collected in spring and early summer. Also, during the winter months, fewer new mats form than in spring and early summer, and it was found that spores from new or immature mats were more highly viable than those from older mats. Perithecia occurred most abundantly on aging mats at temperatures of about 16 degrees C. This was the average temperature for the five study areas in May, 1953, the month during which the greatest number of perithecia occurred.

The data obtained in this study indicate that the greatest inoculum potential of the oak wilt disease may be expected to occur in Illinois during April, May, and June. This indication is made clear by the following facts: (1) The greatest number of mats was found in May and June, (2) more viable conidia were present on mat samples taken in April than in other months, (3) the average size of mats that developed was greater in May and June than in other months, (4) the largest number of perithecia occurred on mats in May, (5) ascospores were most highly viable in April and May, (6) pad cells from immature mats were most highly viable and more mats of this class were found in March, April, and May than in other months. It is also interesting to note, from the standpoint of possible transmission, that insect activity was greatest on mats during April, May, and June.

Insects, particularly the Nitidulidae, in addition to being possible disease vectors and spermatizers of mycelial mats, are probably the most potent destroyers of naturally occurring oak wilt inocula. The feeding of squirrels on mycelial pads appears to be of minor significance in reducing the amount of inoculum on trees, but the possibility of their spreading conidia, ascospores, or pad cells to healthy trees is evident.

The perpetuation of the oak wilt disease seems to be dependent not on the ability of the fruiting mats of the fungus to survive long periods of adverse conditions but rather on the continued existence of the fungus in an oak wilt area where new inocula are produced from time to time. As some trees cease to produce mycelial mats, other trees, more recently wilted, continue the process. Thus, an almost constant supply of fresh inoculum is present. To control the spread of such a disease beyond root-graft distances, it would seem necessary either to prevent the macroscopic fruiting of the fungus, particularly during March, April, May, and June, or to prevent the feeding of insects and other possible vectors on the mycelial mats on both standing and felled trees. The possibility of the extensive spread of the oak wilt disease from fungus development on bark or wood chips on the forest floor seems negligible and might be eliminated altogether by placing the pieces so that they dry rapidly.

SUMMARY

Need for information that would be useful in explaining the spread of oak wilt prompted an intensive study of the availability of oak wilt inocula. This study was made in five major wilt areas in Illinois and covered the 10-month period from October, 1952, through July, 1953.

Results of preliminary laboratory tests showed that a 2 per cent water agar medium and an incubation temperature of 28 degrees C. for 36 hours were best for determining the germinability of both conidia and ascospores of the oak wilt fungus, *Endoconidiophora fagacearum.*

Good germination was obtained with cells from the interiors of pads of *Endoconidiophora fagacearum* mycelial mats that had not started to decline. Mycelial pad cells were found to have a slightly lower optimum temperature for germination than have conidia and ascospores. Germinated pad cells sporulated abundantly on water agar.

Formation of *Endoconidiophora fagacearum* perithecia on a wheat bran-agar

medium was favored by temperatures of 16 and of 25 degrees C.

Tests *in vitro* showed that longevity of conidia of *Endoconidiophora fagacearum* was favored by low temperatures and a dry atmosphere. Under conditions of high humidity, conidia on artificially grown mats remained viable for 102 days at 0 and at 12 degrees C. Under conditions of low humidity, conidia on similar mats were still viable after 250 days at 0, at 12, and at 16 degrees. Conidia on a mat taken from nature and subjected to dry storage at 16 degrees were still viable after 330 days.

Laboratory feeding tests revealed that insects of the family Nitidulidae were effective destroyers of mats of the oak wilt fungus.

The rate at which wilt-infected oaks declined and the length of time required for trees to reach a condition favorable for the development of mycelial mats were found to be closely related to the time of incipient wilt.

The influence of monthly temperature and precipitation on formation of mats of the oak wilt fungus was suggested by accelerated mat development during April, May, and June. The average temperatures for May and June were near the optimum temperature for growth of the fungus.

The development of macroscopic mycelial growth of *Endoconidiophora fagacearum* was readily induced during March, April, and May simply by making cuts through the bark of trees that were nearing the mat-producing stage. This experience suggests a strong air relationship in mat formation.

In March and April, padless mats of the oak wilt fungus formed and grew on 17 of 213 pieces of bark that were taken from diseased oaks and placed on the forest floor. No macroscopic growth formed on any of 128 wood pieces that were treated in the same manner.

The time required for fungus mats on trees to progress from an immature stage to a deteriorated condition varied according to the season in which the mats first appeared. Mats that first appeared during the spring and summer declined rapidly as compared with mats that first appeared during the autumn and winter.

Insect activity on mats in nature was greatest during April, May, and June, when more species of insects were found than in other months. Members of the families Nitidulidae, Staphylinidae, and Histeridae, and of the order Collembola were more abundant than others. Among other agents commonly associated with mycelial mats were nematodes, mites, bacteria, fungi of various kinds, and crustaceans.

A total of 649 typical mycelial mats, each with a pad in the center, were found on 31 selected trees, some of the mats in each month of the 10-month study period. Spore counts from mat samples indicated that the highest concentration of conidia on mats was reached in December, after which there was a steady decrease during a period of low winter and spring temperatures until April, when a sharp rise occurred with the rise in temperature. After April the number of conidia decreased rapidly until, in July, no conidia could be found on mats. In the laboratory, best germination was obtained from conidia that were collected in April and good germination from those collected in October, November, and March. The highest average number of conidia was obtained from mature mats but the highest germination rate of conidia was obtained from immature mats.

The significance of mat size, as well as numbers of mats, in accounting for the concentration of conidia in an oak wilt area was demonstrated from sample data. A mat that measured 24 by 10 cm. was estimated to contain 1,650,000,000 conidia.

Twenty-three per cent of 393 mats (which were presumed to be old enough to have perithecia) contained perithecia. Mats with perithecia were found in all months of the study except July, and the highest average number of perithecia per mat sample was found on aging mats in May. The best germination rate was obtained with ascospores collected from aging mats in April.

Mass transfers of cells from the interior portions of 423 mycelial pads to potato dextrose agar showed that cells from immature, mature, and aging mats were viable; 82 per cent of the pads from immature mats gave positive cultures.

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BULLETIN
of the
ILLINOIS NATURAL HISTORY SURVEY
HARLOW B. MILLS, *Chief*

Efficiency and Selectivity of Commercial Fishing Devices *Used on the Mississippi River*

WILLIAM C. STARRETT
PAUL G. BARNICKOL

Printed by Authority of the
STATE OF ILLINOIS
WILLIAM G. STRATTON, *Governor*

DEPARTMENT OF REGISTRATION AND EDUCATION
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CONTENTS

Cleaning fish in a commercial fish market at Dallas City, Illinois, on the Mississippi River.

Efficiency and Selectivity of

Commercial Fishing Devices

*Used on the Mississippi River**

WILLIAM C. STARRETT†
PAUL G. BARNICKOL‡

IN 1944 and 1946, a fishery survey was made of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa, under the auspices of the Technical Committee for Fisheries, a subgroup of the Upper Mississippi River Conservation Committee. Collections of fish were made with various types of fishing devices at 31 field stations. Based largely on these collections, a report relative to the status of commercial and sport fishing in the Caruthersville-Dubuque section of the river was written and published (Barnickol & Starrett 1951).

The present paper is a statistical analysis of the catch data relative to the efficiency and selectivity of the various commercial fishing devices used during the survey. It is believed that such an analysis could be of value to persons interested in the management of the river's commercial fishery. At the present time, law enforcement is the chief form of fish management practiced in the Caruthersville-Dubuque section of the river.

The fishery survey was financed by the Illinois Department of Conservation, the Illinois Natural History Survey, the Iowa Conservation Commission, and the Missouri Conservation Commission. The Illinois Natural History Survey's laboratory boat, the *Anax,* was used as field headquarters.

The writers are indebted to Dr. George W. Bennett of the Illinois Natural History Survey for suggestions and encouragement in the preparation of this paper and to Dr. Robert Touchberry of the University of Illinois for technical advice in the statistical treatment of the data. The following persons, at the time associated with the Illinois Natural History Survey, aided in the collection of data: Mr. Daniel Avery, Mr. Leonard Durham, Dr. B. Vincent Hall, Dr. Donald F. Hansen, Mr. Don W. Kelley, Mr. Jacob Lemm, Dr. Hurst H. Shoemaker, and Dr. David H. Thompson. Mr. James S. Ayars of the Illinois Natural History Survey edited the manuscript. Many other persons contributed directly in making this investigation possible through their administrative assistance, notably Dr. Harlow B. Mills, present Chief, and the late Dr. Theodore H. Frison, former Chief, of the Illinois Natural History Survey; Dr. G. B. Herndon of the Missouri Conservation Commission; Mr. Sam A. Parr of the Illinois Department of Conservation; and Mr. Everett B. Speaker and the late William E. Albert of the Iowa Conservation Commission. Photographs other than that for fig. 10 were taken by Natural History Survey staff photographers William E. Clark and Charles L. Scott and by the senior author of this paper.

Materials and Methods

In 1944, fish collections were made at 19 field stations on the Mississippi River between Caruthersville, Missouri, and Warsaw, Illinois, and, in 1946, at 12 field stations on the river between Burlington, Iowa, and Dubuque, Iowa, fig. 1. Table 1 contains a list of the field stations, inclusive dates of fishing operations at each

* The investigation on which this paper is based was conducted under the auspices of the Technical Committee for Fisheries of the Upper Mississippi River Conservation Committee.

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station, pool numbers, and the distances of stations from Dubuque.

The survey covered 306 miles of the Mississippi below the mouth of the Missouri River and 383 miles above this point. The lower section extended from the mouth of the Missouri River to Caruthersville and is referred to in this paper as the MR-C section. The upper section extended from Dubuque to the mouth of the Missouri River and is designated as the D-MR section.

Fig. 1.—The Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa; shown is the location of field sampling stations used during the fisheries survey of 1944 and 1946. The river distance between Caruthersville and Dubuque is 689 miles.

In both years of the survey, a key station was established for checking seasonal differences in catches. In 1944, Grafton was the key station and, in 1946, Andalusia. Three sampling periods were spent at each of these stations.

In the fall of 1944, trammel net experiments were conducted at Quincy and at Grafton, Illinois. The data from these experiments are treated separately in this paper.

When, in this paper, reference is made to mesh size of nets and seines, the size of the mesh in inches is indicated; for example, a 1-inch-mesh wing net refers to a wing net having mesh of 1-inch square measure. Square measure mesh size is used throughout this publication. The approximate stretch measure of the webbing can be calculated by multiplying the square measure by two.

The following fishing devices, some of which could not in 1944 or 1946 be used legally by commercial fishermen, were tested by the survey party:

Trammel nets, length of each 80, 100, or 150 yards (mesh of inner net 1½, 1¾, 2, or 3 inches), depth 5 or 6 feet

Seines, length of each 100, 150, or 200 yards (mesh 1 inch), depth 10 feet

Hoop nets (mesh 1 inch, hoop diameters 3½ or 4 feet; mesh 2½ inches, hoop diameters 4 or 4½ feet; mesh 3 inches, hoop diameters 4 or 4½ feet)

Wing nets with and without leads (mesh 1 inch, hoop diameters 2½ to 4½ feet; mesh 1½ inches, hoop diameter 3 feet; mesh 2½ inches, hoop diameters 3½ and 4½ feet)

Trap nets (mesh 1¼ inches)

Basket traps (opening 1½ inches)

Trot lines

The number of each of the various kinds of fish caught and the total lengths of the individuals and their weights, as well as the dates and hours of setting and raising gear, were recorded separately for each type of fishing device (except trot lines) and each mesh size of net (except trammel net) and seine used. The data from trot line sets were too meager for valid analysis. The hoop diameters of wing nets and hoop nets were not considered in this study, and catches made in these nets were not separated on the basis of hoop size.

The common and scientific names of fish caught are listed in table 2.

Characteristics of Area

The Mississippi River in the MR-C section is more turbid and swifter than in the D-MR section. The MR-C section is free of locks and dams, whereas the D-MR section is canalized by a series of 14 locks and dams maintained for navigation.

Detailed descriptions of the physical and fish-faunal characteristics of the Caruthersville-Dubuque section of the Mississippi River and the field stations established during the 2-year survey are contained in the earlier report prepared by Barnickol & Starrett (1951).

In test-net collections, sport fishes were present in greater numbers in the D-MR section of the river than in the MR-C section. In the MR-C collections, smallmouth buffalos and black buffalos were more abundant than bigmouth buffalos. Bigmouth buffalos were more common in the D-MR collections than in the MR-C collections. Blue catfish were found upstream as far as Lock and Dam No. 19 at Keokuk, Iowa. Fish of this species were taken in greater numbers in the Mississippi River below the mouth of the Missouri than above. Flathead catfish were common in both sections of the Mississippi. In 1944, more channel catfish were in test-net collections between Warsaw and the mouth of the Missouri River than in collections from the MR-C section.

Commercial Fishing Activities

At the time of the survey, commercial fishing was conducted along much of the Mississippi River between Caruthersville and Dubuque. According to Starrett & Parr (1951:6), in 1950 there were 248 residents of Illinois who worked either part or full time as professional commercial fishermen on the Mississippi. These

Table 1.—Stations at which fish collections were made in 1944 and 1946 fisheries survey of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa, inclusive dates for each collection, and location of each station.

Station	Inclusive Dates	Miles Below Dubuque Station	Pool No.
	1944		
Caruthersville, Mo.	April 6–12	689	—
Tiptonville, Tenn.	April 15–May 10	665	—
Cairo, Ill.	May 18–24	573	—
Cape Girardeau, Mo.	May 26–31	529	—
Grand Tower, Ill.	June 2–9	499	—
Chester, Ill.	June 11–15	468	—
Ste. Genevieve, Mo.	June 18–24	454	—
Crystal City, Mo.	June 25–30	429	—
Cliff Cave, Mo.	July 2–8	412	—
Mouth of Missouri River, Mo.	July 10–15	383	—
Grafton, Ill.	March 22–30	358	26
Grafton, Ill.	July 17–25	358	26
Grafton, Ill.	Sept. 22–27	358	26
Grafton, Ill. (Experimental)	Oct. 25–29	358	26
Winfield, Mo.	July 27–Aug. 2	337	26, 25
Hamburg, Ill.	Aug. 3–9	320	25
Louisiana, Mo.	Aug. 12–17	295	24
Cincinnati Landing, Ill.	Aug. 19–23	281	24
Hannibal, Mo.	Aug. 25–30	267	22
Quincy, Ill.	Sept. 2–6	256	22
Quincy, Ill. (Experimental)	Oct. 31–Nov. 13	256	22
Canton, Mo.	Sept. 8–13	236	21
Warsaw, Ill.	Sept. 14–19	218	20
	1946		
Burlington, Iowa	April 10–22	178	19
Oquawka, Ill.	April 24–May 5	159	18
New Boston, Ill.	May 7–18	143	18
Muscatine, Iowa	May 19–30	134	17
Fairport, Iowa	June 2–13	118	16
Andalusia, Ill.	April 1–7	103	16
Andalusia, Ill.	June 18–26	103	16
Andalusia, Ill.	Sept. 15–24	103	16
Pleasant Valley, Iowa	June 28–July 9	87	15
Cordova, Ill.	July 11–22	75	14
Fulton, Ill.	July 24–Aug. 4	57	14
Sabula, Iowa	Aug. 6–17	44	13
Bellevue, Iowa	Aug. 19–30	17	12
Dubuque, Iowa	Sept. 1–12	0	12

Table 2.—Accepted common, scientific, and local names of fishes occurring in Mississippi River test-net or other fisheries survey collections made between Caruthersville, Missouri, and Dubuque, Iowa, 1944 and 1946.*

Accepted Common Name	Scientific Name	Local Name
Shovelnose sturgeon	*Scaphirhynchus platorynchus* (Rafinesque)	Hackleback, switchtail, sand sturgeon
Paddlefish	*Polyodon spathula* (Walbaum)	Spoonbill cat, spoony
Longnose gar	*Lepisosteus osseus* (Linnaeus)	Garpike, billfish, billy gar
Shortnose gar	*Lepisosteus platostomus* Rafinesque	Duckbill gar
Alligator gar	*Lepisosteus spatula* Lacépède	Mississippi alligator gar
Bowfin	*Amia calva* Linnaeus	Dogfish, grindle, cypress trout, mudfish
Mooneye	*Hiodon tergisus* Le Sueur	Toothed herring, white shad
Goldeye	*Amphiodon alosoides* Rafinesque	Mooneye
Skipjack	*Pomolobus chrysochloris* Rafinesque	Golden shad, river herring, blue herring
Gizzard shad	*Dorosoma cepedianum* (Le Sueur)	Hickory shad
American eel	*Anguilla bostoniensis* (Le Sueur)	Freshwater eel
Blue sucker	*Cycleptus elongatus* (Le Sueur)	Missouri sucker, bluefish, blackhorse, gourdseed sucker
Bigmouth buffalo	*Megastomatobus cyprinella* (Valenciennes)	Redmouth buffalo, stubnose buffalo, roundhead buffalo, brown buffalo, goarhead, bullhead buffalo, bull-mouth buffalo, bullnose buffalo, slough buffalo, trumpet buffalo
Black buffalo	*Ictiobus niger* (Rafinesque)	Mongrel buffalo, bugler, rooter, reefer, round buffalo, sheepshead buffalo, blue buffalo
Smallmouth buffalo	*Ictiobus bubalus* (Rafinesque)	Razorback buffalo, roach-back buffalo, humpback buffalo, channel buffalo, liner buffalo, quillback buffalo
Quillback carpsucker	*Carpiodes cyprinus* (Le Sueur)	Silver carp, carpsucker, cold-water carp, quillback
River carpsucker	*Carpiodes carpio* (Rafinesque)	Silver carp, carpsucker
Highfin carpsucker	*Carpiodes velifer* (Rafinesque)	Silver carp, river carp, carp-sucker, highfin sucker
White sucker	*Catostomus commersonnii* (Lacépède)	Common sucker, fine-scaled sucker
Spotted sucker	*Minytrema melanops* (Rafinesque)	Striped sucker
Silver redhorse	*Moxostoma anisurum* (Rafinesque)	Silver mullet
Northern redhorse	*Moxostoma aureolum* (Le Sueur)	Des Moines plunger, mullet, common redhorse
Carp	*Cyprinus carpio* Linnaeus	German carp, European carp
Golden shiner	*Notemigonus crysoleucas* (Mitchill)	American bream, roach
Channel catfish	*Ictalurus lacustris* (Walbaum)	Fiddler, catfish, channel cat, spotted cat
Blue catfish	*Ictalurus furcatus* (Le Sueur)	Fulton cat, Mississippi cat, chucklehead cat, coal boater
Yellow bullhead	*Ameiurus natalis* (Le Sueur)	Yellow-bellied cat, greaser
Brown bullhead	*Ameiurus nebulosus* (Le Sueur)	Speckled bullhead
Black bullhead	*Ameiurus melas* (Rafinesque)	Bullhead
Flathead catfish	*Pilodictis olivaris* (Rafinesque)	Hoosier, goujon, shovelnose cat, mudcat, yellow cat, Johnny cat, Morgan cat, flat belly
Northern pike	*Esox lucius* Linnaeus	Pickerel, great northern pike, northern, pike
Grass pickerel	*Esox vermiculatus* Le Sueur	Little pickerel, grass pike, mud pickerel

Table 2.—Concluded

ACCEPTED COMMON NAME	SCIENTIFIC NAME	LOCAL NAME
Yellow walleye	*Stizostedion vitreum vitreum* (Mitchill)	Walleye, yellow pikeperch, jack, jack salmon
Sauger	*Stizostedion canadense* (Smith)	Sandpike, jack salmon
Smallmouth bass	*Micropterus dolomieu* Lacépède	Smallmouth, smallmouth black bass
Spotted bass	*Micropterus punctulatus* (Rafinesque)	Kentucky bass, spotted black bass
Largemouth bass	*Micropterus salmoides* (Lacépède)	Black bass, bigmouth bass, line side, green bass, green trout, largemouth black bass
Green sunfish	*Lepomis cyanellus* Rafinesque	Black perch
Orangespotted sunfish	*Lepomis humilis* (Girard)	
Bluegill	*Lepomis macrochirus* Rafinesque	Bream, sunfish
Warmouth	*Chaenobryttus coronarius* (Bartram)	Goggle-eye, warmouth bass
Flier	*Centrarchus macropterus* (Lacépède)	Round sunfish, longfinned sunfish, round bass
White crappie	*Pomoxis annularis* Rafinesque	Crappie, newlight
Black crappie	*Pomoxis nigro-maculatus* (Le Sueur)	Calico bass, strawberry bass
White bass	*Lepibema chrysops* (Rafinesque)	Silver bass, striped bass, streaker
Yellow bass	*Morone interrupta* Gill	Streaker, barfish
Freshwater drum	*Aplodinotus grunniens* Rafinesque	White perch, perch, sheepshead, gaspergou, grunting perch, croaker

* Because of the pressure of field work, most of the fish handled in the test-net collections could be classified only to species. Some, however, could be classified further, and the following subspecies are believed to have been represented in the sampling: *Lepisosteus osseus oxyurus* Rafinesque, northern longnose gar; *Carpiodes carpio carpio* (Rafinesque), northern carpsucker; *Catostomus commersonnii commersonnii* (Lacépède), white sucker; *Notemigonus crysoleucas auratus* (Rafinesque), western golden shiner: *Ictalurus furcatus furcatus* (Valenciennes), blue catfish; *Ameiurus natalis natalis* (Le Sueur), northern yellow bullhead; *Ameiurus nebulosus marmoratus* (Holbrook), brown bullhead; *Ameiurus melas melas* (Rafinesque), northern black bullhead; *Stizostedion canadense canadense* (Smith), eastern sauger; *Micropterus dolomieu dolomieu* Lacépède, northern smallmouth bass; *Micropterus punctulatus punctulatus* (Rafinesque), northern spotted bass; *Lepomis macrochirus macrochirus* Rafinesque, common bluegill. The spotted gar, *Lepisosteus productus* Cope, if present, was not separated from the shortnose gar. Accepted common and scientific names in the table are from Special Bulletin No. 1 of the American Fisheries Society (1948) or from amendments accepted by the Society (Bailey 1952, 1953); most subspecific names in the footnote are from Hubbs & Lagler (1947).

fishermen reported having caught in that year 2,788,073 pounds of fish valued in the rough at $297,045.23 (Starrett & Parr 1951:7, 10). During 1950, according to the Upper Mississippi River Conservation Committee (1952:35, 37) report, 590 licensed commercial fishermen of Missouri caught 330,488 pounds of fish from the Mississippi River. This same report lists the total Iowa catch from the Mississippi at 839.211 pounds. The Iowa catch was made by 2,200 licensed commercial fishermen. The Iowa report includes data on fishing activities above and below Dubuque.

The most important commercial fishes included in the figures above were carp, black buffalo, smallmouth buffalo, bigmouth buffalo, channel catfish, flathead catfish, blue catfish, freshwater drum, paddlefish, and shovelnose sturgeon.

Hoop nets, seines, basket traps, trammel nets, and trot lines were the principal types of commercial fishing devices employed by these fishermen.

Terminology for Commercial Fishing Devices

The vernacular names of commercial fishing devices used on the Mississippi River are often quite confusing. In an attempt to correct this situation, members of the Upper Mississippi River Conservation Committee (1946:9) defined and classified the commercial fishing devices used on the upper part of the river.

The committee separated the various fishing devices into broad classifications based on the methods by which the devices capture fish. The four principal methods of capture are angling, encompassment, entrapment, and entanglement. Each method is treated separately in the succeeding sections. The terminology recommended by the committee for commercial fishing devices is used in this paper.

Angling Devices

Angling refers to the capture of fish with either single or multiple hooks attached to a line.

Jugs or Floats (Single Hook).—Some fishermen on the Mississippi River use jugs or floats with a hook and bait attached to each, fig. 2. The jugs or floats are floated downstream and are often very effective in taking large catfishes, blue and flathead. These fishing devices provide sport as well as meat, especially when a 25- or 30-pound catfish takes the bait.

Trot Lines (Multiple Hooks).—Trot lines and throw lines are multiple-hook fishing devices common on the Mississippi. Throw lines are favorites among sport fishermen, but they are seldom used by commercial fishermen. Trot lines are of some importance as commercial tackle, fig. 3. They are fished mainly for catfishes in the Caruthersville-Dubuque section and to a lesser extent for carp, bullheads, and freshwater drums.

In 1947, 2.8 per cent of the reported Illinois commercial catch from the Mississippi was taken with trot lines, also known as set lines (Upper Mississippi River Conservation Committee 1948, third section:19). In this same year, 10.4 per cent of the reported Missouri commercial catch from the Mississippi was taken on trot lines (set lines). At the time of the survey, regulations relative to the number of hooks that a fisherman might use varied among the states.

A trot line consists of a heavy cord to which are tied, at intervals of 2 to 3 feet, short drop lines, to each of which is tied a single hook. The ends of the cord

Fig. 2.—Rigging up floats on the Mississippi River for blue catfish. Float fishing, or jug fishing, is more popular on the Mississippi below the mouth of the Missouri River than above.

are secured to stumps or other supports. Each drop line may be a foot or more in length; the length depends upon the depth at which fishing is to be done. Live minnows or small fish (young carp are preferred by many fishermen), cut fish of various kinds, crayfish, spoiled clam meat, and grasshoppers are the common baits used on trot lines for catfish. Dough-balls or corn are the usual baits for carp.

The length of trot lines and number of hooks used seem to vary with the accessibility of bait, number of men to run the lines, and fishing conditions. Evermann (1899:292) reported that he had learned of a trot line 12 miles long in Louisiana. In the Caruthersville-Dubuque section of the Mississippi, the lines seldom exceed 3,000 yards.

During the survey, only a few trot line sets were made. The search for live bait would have consumed more time than could be allotted to one phase of the test-fishing research program. An investigation devoted solely to studying trot line catches in the Caruthersville-Dubuque area would be of value in managing the fishery.

Encompassment Devices

Seines are the only type of encompassment tackle of importance to commercial fishermen in the Caruthersville-Dubuque section of the Mississippi River, fig. 4. Dip nets, another type, are used by hundreds of sport fishermen along this river, but are of little importance as commercial tackle.

Most of the commercial seining in the Caruthersville-Dubuque section of the river is done with short seines. The seines commonly used there are 200 yards in length. In some parts of the river, longer seines are used. A short seine can be operated by two or three men, whereas a longer seine requires more men for efficient operation. The owner of a large seine should be in a position to handle large catches and sell them in distant markets. The operator of a small seine usually can sell his catch locally.

Prior to making a seine haul, a commercial fisherman usually cruises near his selected "seine hauls" or water areas he knows that have bottoms clean enough for seining. If he believes fish are using the

Fig. 3.—Trot lines used by commercial fishermen. On the Mississippi River, trot lines are used chiefly for catfishes. Usually the hooks and lines are secured in a homemade box as shown above.

area, he makes preparations to lay out the seine. A seine haul of 200 or 300 yards can usually be completed within a couple of hours. Handling a big catch in a large seine may require several days.

The survey crew made 25 seine hauls in the Mississippi River between Winfield, Missouri, and Cordova, Illinois. These hauls were made with 100-, 150-, and 200-yard seines of 1-inch square mesh. Time and personnel limited the seining operations to one mesh size.

A summary of the survey seine hauls is given in table 3. Commercial and predatory fishes represented 89.3 per cent of the total weight of all fishes taken with the seine. Sport fishes occurred regularly in the hauls; they represented 11.7 per cent of the total numbers and 3.3 per cent of the total weight of fish in the seine hauls. Crappies made up 82.1 per cent of the number of sport fishes. Only insignificant numbers of other sport species were taken in the seines.

A seine is an efficient fishing device when operated by experienced commercial fishermen. Commercial seines are of larger mesh sizes than the seines employed in the survey. Fishermen generally try to use seines selectively by making hauls in waters they believe are being used by species they desire. The commercial hauls usually are made for carp, buffalofishes, freshwater drums, and paddlefish. However, fishermen using commercial seines frequently catch only a few carp and buffalofishes in a haul and many gizzard shads and gars.

The seine is an important commercial fishing device on the Mississippi River

Table 3.—Composition of catches made with 1-inch-mesh 100-yard, 150-yard, and 200-yard seines in fisheries survey of the Mississippi River between Winfield, Missouri, and Cordova, Illinois, 1944 and 1946.

Kind of Fish	Number of Fish Taken	Per Cent of Total Number Taken	Weight, Pounds	Per Cent of Total Weight
Commercial				
Carp	96	6.5	221.54	16.8
Bigmouth buffalo	16	1.1	26.63	2.0
Smallmouth buffalo	50	3.4	25.16	1.9
Black buffalo	1	0.1	5.93	0.4
Paddlefish	51	3.4	139.80	10.6
Channel catfish	121	8.2	48.56	3.7
Blue catfish	27	1.8	17.04	1.3
Flathead catfish	1	0.1	0.19	—
Carpsuckers	148	10.0	96.05	7.3
Suckers	1	0.1	1.68	0.1
Freshwater drum	88	6.0	29.78	2.2
Subtotal	*600*	*40.7*	*612.36*	*46.3*
Sport				
White crappie	114	7.8	24.96	1.9
Black crappie	28	1.9	5.16	0.4
Bluegill	2	0.1	0.24	—
Yellow walleye	2	0.1	1.99	0.1
Sauger	6	0.4	5.16	0.4
White bass	16	1.1	5.02	0.4
Yellow bass	5	0.3	0.83	0.1
Subtotal	*173*	*11.7*	*43.36*	*3.3*
Predatory				
Shortnose gar	391	26.6	416.06	31.5
Longnose gar	71	4.8	134.73	10.2
Bowfin	6	0.4	17.93	1.3
Subtotal	*468*	*31.8*	*568.72*	*43.0*
Forage				
Gizzard shad	181	12.3	85.06	6.4
Mooneye, goldeye	51	3.5	12.58	1.0
Subtotal	*232*	*15.8*	*97.64*	*7.4*
Total	*1,473*	*100.0*	*1,322.08*	*100.0*

Fig. 4.—Commercial fishermen shipping a seine after completing a haul.

throughout the year. In the D-MR section, large hauls of carp and buffalofishes often are taken from under the ice during the winter months. The seine enables some fishermen in both the D-MR and the MR-C sections of the river to take paddlefish, carp, buffalofishes, and fresh-water drums during periods when few fish are being caught in other devices.

Entrapment Devices

Entrapment devices used in some or all parts of the Caruthersville-Dubuque area of the Mississippi River at the time of the survey included basket traps, hoop nets, wing nets, and trap nets.

Basket traps are constructed of wooden slats and have flexible, wooden throats, fig. 5. Fishermen usually bait these traps with old cheese scrapings and often in the spring they put a live gravid female catfish in each trap to serve as a decoy for unsuspecting males. Basket traps are set in current and are fished in water ranging from 4 to 15 feet in depth. A weight is secured to the tail line of each basket trap to anchor it in place. Some fishermen fish two basket traps or a basket trap and a hoop net by joining the tail lines.

The basket trap is an important fishing device for commercial fishermen of Illinois and Iowa who fish the Mississippi. The state of Missouri does not permit the use of this device. In 1950, Illinois commercial fishermen of the Mississippi River took 52.3 per cent of their reported catfish catch in basket traps (Starrett & Parr 1951:5).

The local terminology often applied to hoop nets, wing nets, and trap nets can be quite confusing. In one area, a hoop net, fig. 6, may be called a buffalo net, in another a fyke net, and in still another a fiddler net. Hoop nets are defined by the Upper Mississippi River Conservation Committee (1946:13) as a "group of devices" "constructed of vegetable fiber netting without fore bay, leads, or wings." The group "includes hoop net, bait net, buffalo net, fiddler net, and *fyke net*." The main differences in the local terminology among these nets result from differences in mesh size and hoop diameter. The fine-mesh nets with small hoops are used for catfish, and the nets with large hoops and large meshes are fished for buffalofishes and carp.

Fig. 5.—A Mississippi River commercial fisherman removing a catfish from a basket trap. In the upper tub is cheese bait.

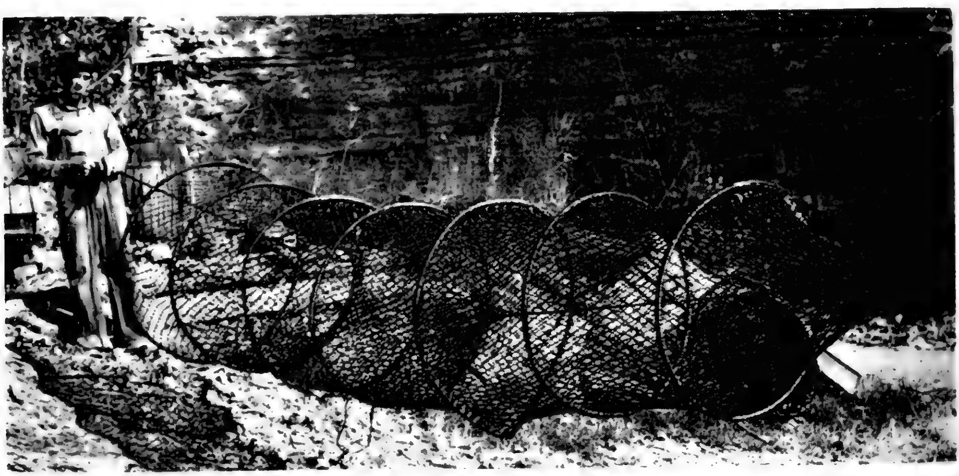

Fig. 6.—A hoop net stretched to show the construction of the net. The hoop net does not have wings.

Hoop nets are fished in the currents of rivers and in depths that cover the nets entirely. Often these nets are baited with cheese scrapings and other wastes purchased from cheese manufacturers, fig. 7. Frequently they are fished in 15 or more feet of water. Each of these nets is anchored by a wire cable or rope attached to a weight, a stake, or a basket trap. The fisherman setting the net takes a mental fix of his location by noting several landmarks. The following day he checks his bearings and locates the approximate place his net was set the previous day. He drags the bottom with a grappling hook until he strikes the net cable, fig. 8. He then re-

Fig. 7.—A commercial fisherman baiting a hoop net with cheese. This fisherman demonstrates a common method of fishing for catfish on the Mississippi River.

Fig. 8.—Searching the bottom of the Mississippi River with a grappling hook for a hoop net and basket trap set. Experienced fishermen quickly locate and retrieve their deep-water sets with a grappling hook.

Fig. 9.—Commercial wing net sets. Wing nets are particularly effective for carp and buffalofishes.

trieves the net and removes the fish from the net.

Hoop nets of 1-, 2½-, and 3-inch mesh were used in the survey. The 3-inch-mesh nets were fished only at the Dubuque station.

The wing net, fig. 9, is identical in construction to the hoop net insofar as the net proper is concerned. Attached to the first hoop of the wing net are two pieces of netting called wings, which give the net its name. The wings are set at about 45 degree angles to the main axis of the net and are secured in position with poles. The wing net is fished either with or without a lead, a piece of netting extending outward from the first hoop and continuing the main axis of the net. It is fished in sloughs, backwaters, and sluggish sections of rivers; also in shallower water than the hoop net. It is held in position by poles. On the Illinois River, the wing net is the net most commonly used by fishermen, whereas on the Mississippi the hoop net is the one most generally fished. The wing net is not popular among commercial fishermen who operate on the Mississippi River.

Wing nets with and without leads were used in the 1944 survey. In 1946, all wing nets were fished without leads. The meshes used in this study were 1 inch, 1½ inches, and 2½ inches. The 1½-inch-mesh wing nets were used only in 1944. The catch data for the 2½-inch-mesh wing nets fished with leads have been combined with the catch data for these nets fished without leads.

About 70 per cent of the commercial fish catch reported from the Illinois section and 59 per cent of that reported from the Missouri section of the Mississippi River for 1947 were taken in hoop nets (Upper Mississippi River Conservation Committee 1948, third section:19). The reports do not differentiate between hoop nets and wing nets; however, the wing net catch comprised only a small fraction of the total annual yield.

The trap net is quite similar to the wing net in construction and operation, fig. 10. It differs from the wing net in that it has a double rectangular wooden frame in front of the first hoop. It is staked out in the same fashion as the wing net. It may be fished either with or without a lead. During the survey, trap nets were fished at only three stations. The mesh used was 1¼ inches. The nets were fished in localities identical to those fished with wing nets.

Analyzing Entrapment Catch Data.—In the Mississippi River survey, entrapment devices were tested more than any of the other devices.

The unit of measurement usually employed in analyzing net catch data is the net-day, and the efficiency of a fishing device is measured by the number of fish and/or the number of pounds of fish it catches per net-day. One net fished for 24 hours is termed one net-day. In this investigation, the number of net-days fished (or trap-days in the case of basket traps) was recorded for each entrapment device.

In some instances, when the catch per net-day of a certain species of fish in one type of net is compared with the catch of this same species in another type of net, the difference is obviously significant. In other instances, it may not be clear as to whether the catch difference is significant, unless the data are tested statistically. In this study, tests for significance of differences in the efficiency of various entrapment devices were made by using the chi-square method of analysis (Snedecor 1946:16). The chi-square was computed from the following formula:

$$\chi^2 = \frac{(X_1 - m_1)^2}{m_1} + \frac{(X_2 - m_2)^2}{m_2}$$

X_1 and X_2 are the actual catches in numbers of commercial-sized fish and m_1 and m_2 are the expected catches. The expected catch for each net of the two nets being compared is that part of the actual total catch of the two nets which is directly proportional to the total number of net-days fished by the net. In table 4 are given catch data on commercial-sized carp, as presented in table 12, and below the table an equation that tests whether there is a significant difference in catch of commercial-sized carp (15 inches or more total length) between 1-inch-mesh wing nets (without leads) and 1½-inch-mesh wing nets (most without leads*) at the 0.05 level with 1 degree of freedom.

The value 21.09 indicates statistically that at the 0.05 level the catch of commercial-sized carp is significantly greater in the 1½-inch-mesh wing net than in the 1-inch-mesh wing net. A chi-square value of 3.841 or more is considered significant at the 0.05 level with 1 degree of freedom. The fish samples were taken at the same stations and the nets were fished simultaneously, thereby eliminating station and seasonal differences with respect to species. However, at each station various habitats were netted, and as a result probably different segments of the population at each station were sampled. This pattern of netting in no way affects the analysis, since the information sought was, in many cases, for the purpose of giving a comparison of efficiency and selectivity of two nets designed for different habitats. For example, the hoop net usually is fished in deeper water than is the wing net and is always fished in the current; the wing net usually is fished in quiet water. Habitat differences of flowing and quiet water are discernible in the catch data, table 5. In the backwater areas and sloughs of the

* Of 156.10 net-days, 8.84 net-days were with leads.

Table 4.—Data (from table 12) on catches of wing nets of two different mesh sizes used in fisheries survey of the Caruthersville-Dubuque section of the Mississippi River, 1944, the data selected and presented to allow comparison of the efficiency of the two mesh sizes in taking carp of commercial sizes.

Net	Number of Net-Days	Per Cent of Total Number of Net-Days	Number of Commercial-Sized Carp Caught	Number of Commercial-Sized Carp in Expected Catch
1-inch-mesh	508.12	76	413	461.32
1½-inch-mesh	156.10	24	194	145.68
Total	*664.22*	*100*	*607*	*607.00*

The following equation is based on the chi-square (χ^2) formula on page 337.

$$\chi^2 = \frac{(413 - 461.32)^2}{461.32} + \frac{(194 - 145.68)^2}{145.68} = 5.06 + 16.03 = 21.09$$

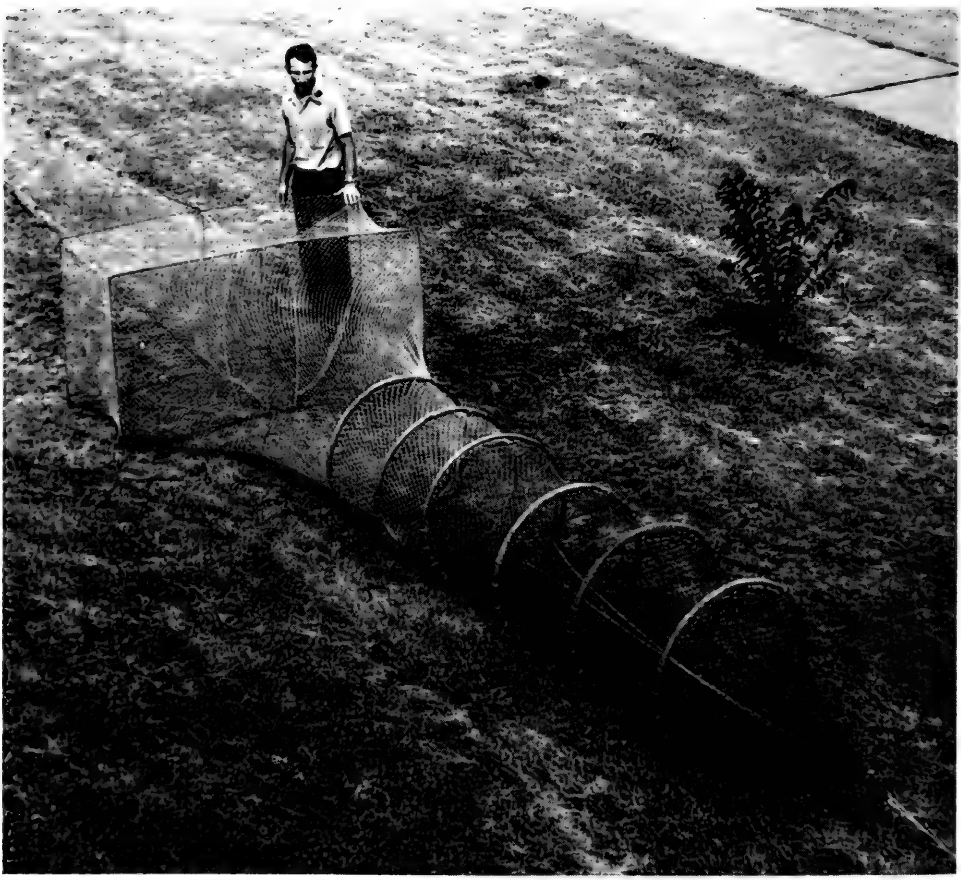

Fig. 10.—Trap net. This net is used by some fishermen who operate on the Mississippi River. Photo courtesy of Dr. John Moyle, Division of Game and Fish, Minnesota Department of Conservation, St. Paul.

upper Mississippi, there is usually a more abundant population of sport fishes than in the river channel.

In figs. 11 and 12, the total catches for all species of fish taken with entrapment devices are presented graphically. Species composition differences between the two sections of the river sampled in 1944 and 1946 account for most of the catch differences reflected in the graphs for the 2 years of test-netting. Differences between 1944 and 1946 in the number of sport fish taken per net-day are apparent in the graphs. The data in table 5 are not suited for detailed analysis, since fishing with the different types of gear was not in all cases done simultaneously.

In order to have some standard for comparing the efficiency and selectivity of the various entrapment devices, it was desirable to select a device that was fished at all the stations. The only entrapment device that met this requirement was the 1-inch-mesh wing net without a lead. In the following catch analyses, the data for the 1-inch-mesh wing net without a lead are used from only those stations at which one or more of the other devices were fished.

The analyses concern largely the catches of the nine most important commercial and sport fishes occurring in the Caruthersville-Dubuque section of the river: carp, bigmouth buffalo, smallmouth buffalo, freshwater drum, channel catfish, flathead catfish, black crappie, white crappie, and bluegill.

In tests for significant differences in numbers of a species caught by various entrapment devices, only fish of commercial or desirable sizes were included. The following minimum total lengths were used: 15 inches for carp, buffalofishes, and channel catfish; 10 inches for freshwater drum; 18 inches for flathead catfish; 8 inches for crappies; 7 inches for bluegill.

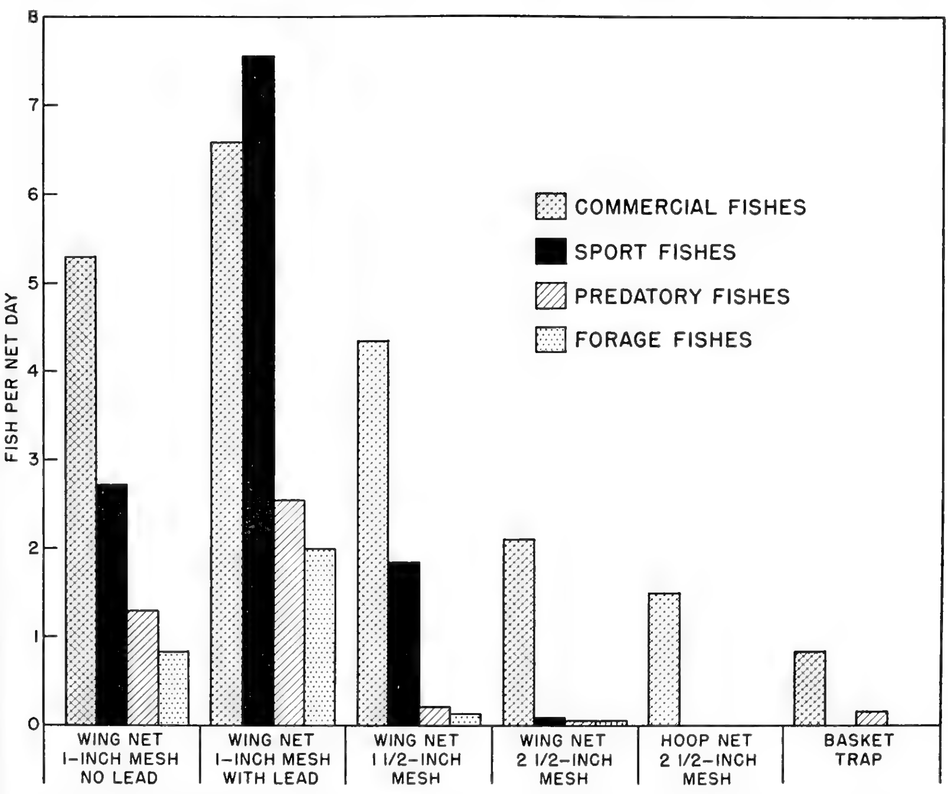

Fig. 11.—The number of fish, all sizes, taken per net-day in entrapment devices fished in the Mississippi River between Caruthersville and Warsaw in 1944.

Table 5.—Number of fish taken per net-day in the various entrapment devices used in fisheries survey of the Caruthersville-Dubuque section of the Mississippi River, 1944 and 1946. Nets fished with leads are so designated, except in the case of some 2½-inch-mesh wing nets; catch data for 2½-inch-mesh wing nets fished with leads in 1944 have been combined with data for such nets fished without leads.

Kind of Fish	Caruthersville-Warsaw Section, 1944					Burlington-Dubuque Section, 1946					
	1-Inch-Mesh Wing Nets (632.37 Net-Days)	1-Inch-Mesh Wing Nets With Leads (175.40 Net-Days)	1½-Inch-Mesh Wing Nets (156.10 Net-Days)	2½-Inch-Mesh Wing Nets (377.63 Net-Days)	2½-Inch-Mesh Hoop Nets (186.81 Net-Days)	1-Inch-Mesh Wing Nets (855.86 Net-Days)	1-Inch-Mesh Hoop Nets (105.97 Net-Days)	2½-Inch-Mesh Wing Nets (421.75 Net-Days)	2½-Inch-Mesh Hoop Nets (730.42 Net-Days)	3-Inch-Mesh Hoop Nets (35.00 Net-Days)	1¼-Inch-Mesh Trap Nets (50.53 Net-Days)
Commercial											
Shovelnose sturgeon	—	—	—	—	—	—	—	—	tr.*	—	—
Paddlefish	tr.*	0.08	—	—	—	—	—	—	—	—	—
American eel	0.05	0.03	—	—	—	0.02	—	—	—	—	0.04
Blue sucker	—	—	—	—	0.02	—	—	—	tr.*	—	—
Suckers, redhorses	0.01	0.05	—	tr.*	0.01	0.09	—	0.01	0.02	0.03	0.30
Bigmouth buffalo	0.03	0.20	0.03	0.07	0.04	0.04	—	0.11	0.07	0.14	—
Black buffalo	0.02	0.06	0.02	0.17	0.02	0.01	—	0.02	0.01	0.03	—
Smallmouth buffalo	0.27	0.64	0.19	0.14	0.34	0.32	0.06	0.12	0.12	0.37	0.06
Carpsuckers	0.85	0.75	0.59	0.21	0.12	0.97	0.11	0.41	0.34	0.09	0.28
Carp	1.50	2.16	2.28	1.14	0.44	0.35	0.08	0.41	0.21	0.42	0.93
Channel catfish	0.48	0.31	0.06	0.02	0.01	1.09	0.59	0.01	tr.*	—	0.20
Blue catfish	0.22	0.31	0.01	0.01	0.01	—	—	—	—	—	—
Yellow bullhead	0.03	0.04	—	—	—	0.01	—	—	—	—	—
Brown bullhead	tr.*	0.01	—	—	—	—	—	—	—	—	—
Black bullhead	0.21	0.50	0.07	—	—	0.07	0.06	—	—	—	—
Flathead catfish	0.61	0.50	0.51	0.07	0.12	0.21	0.42	0.01	0.08	0.03	0.04
Freshwater drum	0.99	0.95	0.58	0.27	0.35	0.74	0.61	0.11	0.21	0.11	1.13
Subtotal	*5.27*	*6.59*	*4.34*	*2.10*	*1.48*	*3.92*	*1.93*	*1.21*	*1.06*	*1.22*	*2.98*
Sport											
Pike	—	—	—	—	—	0.04	—	—	—	—	—
Grass pickerel	—	0.01	—	—	—	—	—	—	—	—	—
Yellow walleye	—	—	0.01	—	—	0.01	—	tr.*	tr.*	0.03	0.02
Sauger	0.07	0.06	0.03	—	—	0.07	0.01	—	—	—	0.14
Spotted bass	—	—	—	—	—	tr.*	—	—	—	—	—
Largemouth bass	0.11	0.27	0.09	0.01	tr.*	0.02	—	tr.*	—	—	—
Green sunfish	0.01	0.01	—	—	—	tr.*	—	—	—	—	—

Bluegill	0.23	2.29	0.19	—	—	0.33	0.02	—	—	—	0.18
Warmouth	0.02	0.24	0.01	—	—	0.01	—	—	—	—	—
Flier	—	0.01	—	—	—	—	—	—	—	—	—
White crappie	0.93	1.04	0.53	0.02	—	2.94	0.13	0.01	tr.*	—	0.63
Black crappie	1.11	3.45	0.81	0.02	—	1.57	0.09	0.01	tr.*	0.03	0.26
White bass	0.22	0.17	0.18	0.01	—	0.16	—	—	—	—	0.26
Yellow bass	tr.*	0.01	0.01	—	—	0.28	—	—	—	—	0.28
Subtotal	*2.70*	*7.56*	*1.86*	*0.06*	—	*5.43*	*0.25*	*0.02*	tr.*	*0.06*	*1.77*
Predatory											
Longnose gar	0.19	0.11	0.03	—	tr.*	0.03	0.01	tr.*	tr.*	—	0.04
Shortnose gar	0.99	1.88	0.08	0.01	—	0.15	0.10	tr.*	—	—	0.08
Alligator gar	0.01	0.43	0.01	—	—	—	—	—	—	—	—
Bowfin	0.10	0.14	0.08	0.02	—	0.13	—	tr.*	—	—	0.02
Subtotal	*1.29*	*2.56*	*0.20*	*0.03*	tr.*	*0.31*	*0.11*	tr.*	tr.*	—	*0.14*
Forage											
Mooneye, goldeye	0.04	0.26	0.03	tr.*	—	0.26	0.08	—	tr.*	—	—
Skipjack	tr.*	0.03	—	—	—	—	—	—	—	—	—
Gizzard shad	0.78	1.70	0.10	0.03	tr.*	0.23	—	—	tr.*	—	—
Golden shiner	tr.*	0.01	—	—	—	—	—	—	—	—	—
Subtotal	*0.82*	*2.00*	*0.13*	*0.03*	tr.*	*0.49*	*0.08*	—	tr.*	—	—
Total	*10.08*	*18.71*	*6.53*	*2.22*	*1.48*	*10.15*	*2.37*	*1.23*	*1.06*	*1.28*	*4.89*

* tr. (trace) indicates that the species was taken but that the take averaged less than 0.01 fish per net-day.

In comparing the efficiency and selectivity of the various entrapment devices, it was necessary to consider the average size of the fish taken, as well as the number of commercial-sized or desirable-sized fish caught. A small-mesh net might take as many fish of commercial species as a large-mesh net; however, the catch of the small-mesh net might be largely of fish under commercial size. The large-mesh net taking only a few fish under commercial size would be a more efficient net to the fisherman since it would require less time for the handling and releasing of small fish.

The mean of the total lengths of indi-

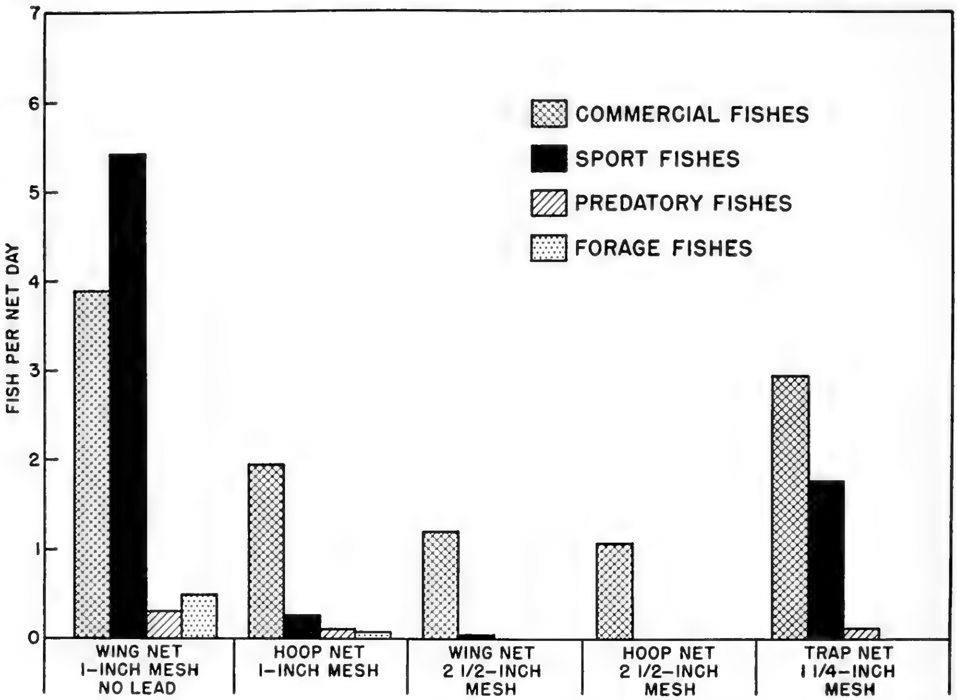

Fig. 12.—The number of fish, all sizes, taken per net-day in entrapment devices fished in the Mississippi River between Burlington and Dubuque in 1946.

Table 6.—Data (from table 13) on catches of wing nets of two different mesh sizes used in fisheries survey of the Caruthersville-Dubuque section of the Mississippi River, 1944, the data selected and presented to allow comparison of the sizes of carp taken by the two mesh sizes.

Net	Mean Total Length (x), Inches	Number of Carp (n)	Standard Deviation (s)
1-inch-mesh	14.47	886	3.34
$1\frac{1}{2}$-inch-mesh	14.96	356	2.37

The following equations are based on the t-test for significance and the degrees of freedom (d.f.) formulas on page 344.

$$t = \frac{14.96 - 14.47}{\sqrt{\frac{(2.37)^2}{356} + \frac{(3.34)^2}{886}}} = \frac{0.49}{\sqrt{0.2839}} = 2.908$$

$$\text{d.f.} = \sqrt{356 \cdot 886} - 1 = 561.6 \text{ or } 562 - 1 = 561$$

Table 7.—Composition of catches made in 74 basket trap sets in fisheries survey of the Mississippi River between Cape Girardeau and Louisiana, Missouri, 1944.

KIND OF FISH	NUMBER OF FISH TAKEN	PER CENT OF TOTAL NUMBER TAKEN	WEIGHT IN POUNDS	PER CENT OF TOTAL WEIGHT
COMMERCIAL				
Carp	2	2.7	2.52	4.0
Blue catfish	18	24.7	8.70	13.9
Channel catfish	32	43.8	32.24	51.7
Flathead catfish	9	12.3	12.98	20.8
Freshwater drum	1	1.4	0.75	1.2
PREDATORY				
Shortnose gar	11	15.1	5.25	8.4
Total	*73*	*100.0*	*62.44*	*100.0*

Table 8.—Composition of catches of commercial-sized or desirable-sized fish taken in basket traps and in 1-inch-mesh wing nets without leads in fisheries survey of the Mississippi River between Cape Girardeau and Louisiana, Missouri, 1944.

KIND OF FISH	BASKET TRAPS (74.0 NET-DAYS)			1-INCH-MESH WING NETS WITHOUT LEADS (236.5 NET-DAYS)			CHI-SQUARE VALUE
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	—	0	—	—	229	0.97	—
Bigmouth buffalo	—	0	—	—	4	0.02	—
Smallmouth buffalo	—	0	—	—	12	0.05	—
Freshwater drum	0.01	1	0.01	0.53	171	0.72	51.71*
Channel catfish	0.34	16	0.22	0.26	31	0.13	2.60
Flathead catfish	0.09	2	0.03	1.93	99	0.42	26.85*
Bluegill	—	0	—	—	21	0.09	—
White crappie	—	0	—	—	187	0.79	—
Black crappie	—	0	—	—	249	1.05	—

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish taken, between basket traps and 1-inch-mesh wing nets at 0.05 level with 1 degree of freedom.

viduals of each species taken in each type of net was computed from measurements of all the fish of that species taken in that type of net. The actual total length of each individual was converted to the nearest one-half inch. The mean of the total lengths and the standard deviation of length of the individuals of a species taken in a particular type of net indicates approximately the size of fish that can be expected in future catches of that net. The presence or absence of dominant year-classes of the various species would be expected to change the species composition and the mean of the total lengths of individuals in the catches from year to year. However, such changes would probably not materially affect the basic differences in efficiency and selectivity of the devices discussed here.

Frequently the differences in the means of the total lengths of fish taken by two types of nets were not apparent. To determine whether the sizes of the individuals of a species taken in one type of net were significantly different from the sizes of the individuals of that species taken in another type of net, a statistical test was desirable. The t-test, derived from a Snedecor (1946:81) formula adapted to groups with different numbers of individuals, appeared to be a satisfactory test for significance of size differences of fish taken in two types of nets. The formula used in computing the t-test for significance is as follows:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{(s_1)^2}{n_1} + \frac{(s_2)^2}{n_2}}}$$

$\bar{x}_1$ and $\bar{x}_2$ are the mean total lengths of the fish; n_1 and n_2 represent the numbers of individuals, all sizes, of the species taken in the gear; and s_1 and s_2 represent the standard deviation. The degrees of freedom were determined by using the geometric mean:

$$\text{d.f.} = \sqrt{n_1 \cdot n_2} - 1$$

From actual net data, table 13, an example is given below table 6 to test if a significant difference exists between the size of carp taken in 1-inch-mesh wing nets and the size of those taken in the 1½-inch-mesh wing nets.

The t-test below table 6 shows that, at the 0.05 level and with 561 degrees of freedom, there is a significant difference in size between the carp taken in the 1½-inch-mesh wing nets and those taken in the 1-inch-mesh wing nets. The 1½-inch-mesh wing nets, on the basis of this test, catch carp which are significantly larger than those taken in the 1-inch-mesh wing nets.

Catches With Basket Traps.—Not a great deal of fishing was done with basket traps during the survey; however, 74 sets were made in the spring and early summer months of 1944. In these sets, the catch was dominated by catfish, table 7. Of a total of 73 fish taken with basket traps, 80.8 per cent were catfish. Channel catfish made up 54.2 per cent of the number and 59.8 per cent of the weight of the catfish catch.

The shortnose gar, the only other fish taken in numbers with basket traps, amounted to 15.1 per cent of the number of fish taken with these traps. No sport fish was taken in the basket traps set by the survey party. However, the writers have observed a few crappies taken in baited basket traps set in one of the bottomland lakes of the Illinois River.

A comparison of the catches of 1-inch-mesh wing nets with catches of basket traps may be made by referring to tables 8 and 9. Fishing was done at the same stations. The channel catfish was the only species of fish taken in greater numbers per net-day in basket traps than in 1-inch-mesh wing nets; the difference was not significant. The catch of flathead catfish was much greater in 1-inch-mesh wing nets than in basket traps. The difference

Table 9.—Size ranges and means of the total lengths of fish taken in basket traps and in 1-inch-mesh wing nets without leads in fisheries survey of the Mississippi River between Cape Girardeau and Louisiana, Missouri, 1944.

Kind of Fish	Basket Traps					1-Inch-Mesh Wing Nets Without Leads					Degrees of Freedom	t Value
	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation		
Carp	—	2	—	—	—	—	631	—	—	—	—	—
Bigmouth buffalo	—	0	—	—	—	—	7	—	—	—	—	—
Smallmouth buffalo	—	0	—	—	—	—	0	—	—	—	—	—
Freshwater drum	—	1	—	—	—	—	377	—	—	—	—	—
Channel catfish	50.0	32	14.16	5.1–19.4	3.64	53.4	58	15.0	2.8–24.5	4.10	42	1.001
Flathead catfish	22.2	9	14.83	8.1–21.6	3.88	39.0	254	17.23	9.4–29.0	4.50	47	1.813
Bluegill	—	0	—	—	—	—	77	—	—	—	—	—
White crappie	—	0	—	—	—	—	366	—	—	—	—	—
Black crappie	—	0	—	—	—	—	365	—	—	—	—	—

* Denotes a significant difference, in sizes of fish taken, between basket traps and 1-inch-mesh wing nets at 0.05 level for degrees of freedom indicated.

in size between channel catfish and flathead catfish taken in 1-inch-mesh wing nets and these same kinds of fish taken in basket traps was not significant.

The basket trap is considered by commercial fishermen of the upper Mississippi as an efficient device for catching catfish. It provides the fisherman with a device that usually does not take sport fish and that can catch channel catfish as efficiently as does the 1-inch-mesh wing net, which is illegal for use in the upper Mississippi. The basket trap was found to be one of the most selective fishing devices tested on the river.

Catches With Wing Nets.—The catches made with wing nets during the survey tend to indicate that commercial fishermen of the upper Mississippi might well increase their catches by using these

Table 10.—Composition of catches of commercial-sized or desirable-sized fish taken in 1-inch-mesh wing nets with leads and in 1-inch-mesh wing nets without leads in fisheries survey of the Mississippi River between Caruthersville and Hannibal, Missouri, 1944.

Kind of Fish	1-Inch-Mesh Wing Nets With Leads (175.40 Net-Days)			1-Inch-Mesh Wing Nets Without Leads (330.51 Net-Days)			Chi-Square Value
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	2.29	152	0.87	2.10	255	0.77	0.99
Bigmouth buffalo	0.26	15	0.09	0.04	3	0.01	18.48*
Smallmouth buffalo	0.41	11	0.06	0.09	7	0.02	5.40*
Freshwater drum	0.26	61	0.35	0.34	146	0.44	2.78
Channel catfish	0.11	13	0.07	0.21	35	0.11	1.32
Flathead catfish	0.75	33	0.19	0.99	68	0.21	0.24
Bluegill	—	175	1.00	—	42	0.13	198.74*
White crappie	—	107	0.61	—	138	0.42	8.11*
Black crappie	—	410	2.34	—	285	0.86	175.86*

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish taken, between the two types of nets at 0.05 level with 1 degree of freedom.

Table 11.—Size ranges and means of the total lengths of fish taken in 1-inch-mesh wing nets with leads and in 1-inch-mesh wing nets without leads in fisheries survey of the Mississippi River between Caruthersville and Hannibal, Missouri, 1944.

Kind of Fish	1-Inch-Mesh Wing Nets With Leads					1-Inch-Mesh Wing Nets Without Leads					Degrees of Freedom	t Value
	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation		
Carp	40.2	378	13.99	5.2–25.6	3.47	40.7	627	14.03	5.2–30.7	3.40	486	0.174
Bigmouth buffalo	42.9	35	14.09	7.0–22.3	3.49	33.3	9	14.72	10.0–21.6	3.99	17	0.433
Smallmouth buffalo	9.7	113	10.58	4.8–22.6	4.05	11.1	72	11.11	5.6–20.9	3.34	89	0.968
Freshwater drum	36.5	167	8.85	4.1–15.1	2.59	35.5	411	8.97	3.8–16.4	2.28	261	0.522
Channel catfish	23.6	55	12.19	6.4–19.6	3.25	27.8	126	12.08	2.5–24.5	4.38	82	0.188
Flathead catfish	37.5	88	16.81	8.4–36.2	4.18	34.3	198	16.04	7.0–41.2	4.85	131	1.367
Bluegill	43.6	401	6.49	3.9– 8.3	0.81	42.4	99	6.59	4.3– 8.2	0.76	198	1.156
White crappie	59.8	182	8.04	4.0–12.7	1.89	52.5	263	7.76	4.6–15.2	1.38	218	1.707
Black crappie	67.8	605	7.86	4.4–11.5	3.09	66.1	431	8.27	4.5–12.0	1.17	510	2.975*

* Denotes a significant difference, in sizes of fish taken, between the two types of nets at 0.05 level for degrees of freedom indicated.

nets more. Wing nets are particularly adapted to fishing backwater and slough areas. In the canalized section of the upper Mississippi, there are now more slough and backwater areas than in years previous to the construction of dams. In periods of low water, when the current is too sluggish for hoop nets, wing nets can be used to advantage.

In that part of the survey made in 1944, several 1-inch-mesh wing nets were fished with leads and others were fished without leads. In table 10 are listed, for each of nine species, the numbers of commercial fish of commercial sizes and sport fish of desirable or usable sizes caught in these nets. The catch per net-day of buffalofishes of commercial sizes was somewhat greater and the catch of crappies and bluegills of desirable sizes was much greater in the nets with leads than in the nets without leads. With respect to each of the other species of fish listed, the difference between the catch

Table 12.—Composition of catches of commercial-sized or desirable-sized fish taken in 1½-inch-mesh wing nets (most without leads) and in 1-inch-mesh wing nets (without leads) in fisheries survey of the Mississippi River between Grand Tower and Warsaw, Illinois, 1944.

Kind of Fish	1½-Inch-Mesh Wing Nets (156.10 Net-Days)			1-Inch-Mesh Wing Nets (508.12 Net-Days)			Chi-Square Value
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	3.09	194	1.24	2.18	413	0.81	21.09*
Bigmouth buffalo	0.09	3	0.02	0.04	6	0.01	0.43
Smallmouth buffalo	—	0	—	0.08	13	0.03	—
Freshwater drum	0.38	72	0.46	0.39	255	0.50	0.71
Channel catfish	0.08	6	0.04	0.20	59	0.12	7.78*
Flathead catfish	1.05	40	0.26	0.78	86	0.17	4.14*
Bluegill	—	12	0.08	—	49	0.10	0.63
White crappie	—	51	0.32	—	319	0.63	21.17*
Black crappie	—	66	0.42	—	496	0.98	46.29*

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish taken, between the two types of nets at 0.05 level with 1 degree of freedom.

Table 13.—Size ranges and means of the total lengths of fish taken in 1½-inch-mesh wing nets (most without leads) and in 1-inch-mesh wing nets (without leads) in fisheries survey of the Mississippi River between Grand Tower and Warsaw, Illinois, 1944.

Kind of Fish	1½-Inch-Mesh Wing Nets					1-Inch-Mesh Wing Nets					Degrees of Freedom	t Value
	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation		
Carp	54.5	356	14.96	7.0–22.7	2.37	46.6	886	14.47	5.2–30.7	3.34	561	2.908*
Bigmouth buffalo	75.0	4	16.88	12.6–22.3	4.45	46.2	13	14.92	10.0–21.6	2.88	6	0.829
Smallmouth buffalo	0.0	29	10.47	7.7–14.0	1.78	7.8	166	11.36	5.6–28.0	2.83	68	2.242*
Freshwater drum	80.0	90	11.23	6.6–16.8	1.93	43.4	588	9.45	3.8–16.4	2.28	229	7.954*
Channel catfish	60.0	10	16.20	11.1–21.1	3.20	24.0	246	12.85	2.8–24.5	3.33	49	3.240*
Flathead catfish	50.6	79	18.38	12.3–31.0	3.71	29.5	292	16.28	7.0–41.2	4.38	151	4.287*
Bluegill	40.0	30	6.57	5.6– 8.0	0.63	33.1	148	6.43	4.2– 8.2	0.79	66	1.058
White crappie	61.4	83	8.39	5.7–12.4	1.50	54.9	581	7.94	4.6–15.2	1.46	219	2.564*
Black crappie	52.4	126	8.08	6.1–10.9	1.07	70.9	700	8.43	4.5–12.0	1.25	296	3.293*

* Denotes a significant difference, in sizes of fish taken, between the two types of nets at 0.05 level for degrees of freedom indicated.

rate of the nets with leads and that of the nets without leads was not great enough to be statistically significant.

Data from the survey indicate that 1-inch-mesh wing nets with leads were the most efficient entrapment gear used for crappies and bluegills. That small-mesh wing nets were effective during the survey in taking sport fishes is shown in table 5. With or without leads, 1-inch-mesh wing nets were effective in catching predator and forage fishes, particularly gars and gizzard shads, table 5.

In table 11 are listed, for each of nine species, the mean of the total lengths of individual fish and the size range of fish caught in 1944 in the 1-inch-mesh wing nets with leads and in similar nets without leads. The mean of the total lengths of black crappies caught in the nets without leads was slightly, but significantly, larger than that of black crappies caught in the nets with leads. With respect to each of the other species of fish, the difference between the mean of the total lengths of fish caught in the nets with leads and that of fish caught in the nets without leads was not great enough to be statistically significant.

Larger catches, per net-day, of carpsuckers were made with the small-mesh nets than with any of the other entrapment devices tested. The species of carpsuckers were considered together because of difficulty in separating them in the field.

Most 1½-inch-mesh wing nets used in test-netting were fished without leads. The species composition of the 1944 catches in the 1-inch-mesh wing nets (without leads) and that of the 1½-inch-mesh wing nets were quite similar, fig. 11 and table 5. The catch per net-day of the 1½-inch-mesh nets, however, was less than that of the 1-inch-mesh nets. The increased mesh size of one-half inch tended to reduce the take of small fish.

The wing nets of 1½-inch-mesh took, per net-day, fewer sport fishes of all sizes, table 5, significantly fewer crappies of usable sizes, and significantly fewer channel catfish of commercial sizes, but significantly more carp and flathead catfish of commercial sizes, than did the nets of 1-inch mesh, table 12. The numbers of bigmouth buffalos caught were too small to permit valid comparisons to be made between the two mesh sizes. No smallmouth buffalo of commercial size was caught in the 1½-inch-mesh nets. The catches, per net-day, of freshwater drums and bluegills were about the same in the nets of 1-inch mesh as in those of the larger mesh.

The mean of the total lengths of the carp caught in nets of each of the mesh sizes was about 15 inches, table 13.

As indicated by the mean of the total lengths of individuals of each species, the sizes of freshwater drums, channel catfish, flathead catfish, and white crappies were greater in catches of 1½-inch-mesh wing nets than in catches of the nets of smaller mesh, table 13. The mean length of black crappies was greater in the nets

Table 14.—Catches of entrapment devices used in fisheries survey of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa, 1944 and 1946. For each device is given the percentage of the catch represented by each of the various classes of fish: commercial, sport, predatory, and forage.

Type of Fish	Basket Traps, 1944	1¼-Inch-Mesh Trap Nets, 1946	1-Inch-Mesh Wing Nets Without Leads, 1944	1-Inch-Mesh Wing Nets Without Leads, 1946	1-Inch-Mesh Wing Nets With Leads, 1944	1½-Inch-Mesh Wing Nets, 1944	2½-Inch-Mesh Wing Nets, 1944	2½-Inch-Mesh Wing Nets, 1946	1-Inch-Mesh Hoop Nets, 1946	2½-Inch-Mesh Hoop Nets, 1944	2½-Inch-Mesh Hoop Nets, 1946	3-Inch-Mesh Hoop Nets, 1946
Commercial	84.9	61.0	52.3	38.6	35.2	66.5	94.8	97.3	81.6	98.8	98.8	95.6
Sport	0.0	36.2	26.8	53.4	40.4	28.5	2.4	1.9	10.4	0.4	0.8	4.4
Predatory	15.1	2.8	12.8	3.2	13.7	3.1	1.1	0.8	4.8	0.4	0.0	0.0
Forage	0.0	0.0	8.1	4.8	10.7	1.9	1.7	0.0	3.2	0.4	0.4	0.0
Total	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*

of 1-inch mesh than in the nets of larger mesh. The writers are unable to explain why the mean length for one species of crappie was greater in nets of 1-inch mesh and the mean length for the other species was greater in the nets of larger mesh.

In the nets of 1-inch mesh, 24.0 per cent of the channel catfish and 29.5 per cent of the flathead catfish were of commercial sizes; in the nets of 1½-inch mesh, 60.0 per cent of the channel catfish and 50.6 per cent of the flathead catfish were of commercial sizes, table 13. The number of commercial-sized fish per net-day was greater for the channel catfish in the nets of 1-inch mesh and for the flathead catfish in the nets of 1½-inch mesh, table 12.

The 2½-inch mesh was the largest mesh tested in wing nets. The 2 years of test fishing indicate that very few sport fishes are taken in nets of this mesh size,

Table 15.—Composition of catches of commercial-sized or desirable-sized fish taken in 2½-inch-mesh wing nets and in 1-inch-mesh wing nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	2½-Inch-Mesh Wing Nets (421.75 Net-Days)			1-Inch-Mesh Wing Nets (855.86 Net-Days)			Chi-Square Value
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	1.76	172	0.41	1.10	238	0.28	14.86*
Bigmouth buffalo	0.31	44	0.10	0.04	13	0.02	50.35*
Smallmouth buffalo	0.21	35	0.08	0.04	16	0.02	29.28*
Freshwater drum	0.22	47	0.11	0.23	210	0.25	25.16*
Channel catfish	0.01	1	0.002	0.10	53	0.06	23.70*
Flathead catfish	0.11	4	0.009	0.27	42	0.05	12.29*
Bluegill	—	0	—	—	97	0.11	—
White crappie	—	6	0.01	—	1,228	1.43	590.01*
Black crappie	—	2	0.005	—	560	0.65	270.87*

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish caught, between the two types of nets at 0.05 level with 1 degree of freedom.

Table 16.—Size ranges and means of the total lengths of fish taken in 2½-inch-mesh wing nets and in 1-inch-mesh wing nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	2½-Inch-Mesh Wing Nets					1-Inch-Mesh Wing Nets					Degrees of Freedom	t Value
	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation		
Carp	100.0	172	20.28	15.4–31.8	2.83	78.5	303	17.55	4.7–30.0	4.85	227	7.747*
Bigmouth buffalo	97.8	45	17.14	13.8–20.1	1.52	39.4	33	13.48	4.5–19.6	3.67	38	5.399*
Smallmouth buffalo	68.6	51	15.74	12.4–26.0	2.30	5.8	277	9.21	4.1–18.4	3.46	118	17.036*
Freshwater drum	100.0	47	15.40	11.4–18.8	1.41	33.2	632	8.79	4.0–18.6	2.93	171	27.961*
Channel catfish	50.0	2	14.25	5.7–23.0	12.37	5.7	936	9.44	2.7–30.1	2.21	42	0.550
Flathead catfish	100.0	4	28.75	18.8–37.0	7.15	23.5	179	15.39	5.6–37.6	5.30	26	3.714
Bluegill	—	0	—	—	—	34.4	282	5.99	3.0– 8.4	1.33	—	—
White crappie	100.0	6	10.42	8.6–13.0	1.85	48.8	2,514	7.36	2.9–13.2	2.30	122	4.045*
Black crappie	100.0	2	10.50	9.1–12.2	2.21	41.7	1,343	7.03	3.0–14.0	2.14	51	2.220*

* Denotes a significant difference, in sizes of fish taken, between the two types of nets at 0.05 level for degrees of freedom indicated.

Table 17.—Composition of catches of commercial-sized or desirable-sized fish taken in 1-inch-mesh hoop nets and 1-inch-mesh wing nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	1-Inch-Mesh Hoop Nets (105.97 Net-Days)			1-Inch-Mesh Wing Nets (855.86 Net-Days)			Chi-Square Value
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	0.48	9	0.08	1.10	238	0.28	13.65*
Bigmouth buffalo	—	0	—	0.04	13	0.02	—
Smallmouth buffalo	—	0	—	0.04	16	0.02	—
Freshwater drum	0.34	32	0.30	0.23	210	0.25	1.22
Channel catfish	0.10	8	0.08	0.10	53	0.06	0.28
Flathead catfish	0.16	5	0.05	0.27	42	0.05	0.06
Bluegill	—	1	0.009	—	97	0.11	9.97*
White crappie	—	9	0.13	—	1,228	1.43	133.34*
Black crappie	—	6	0.06	—	560	0.65	57.12*

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish taken, between the two types of nets at 0.05 level with 1 degree of freedom.

Table 18.—Size ranges and means of the total lengths of fish taken in 1-inch-mesh hoop nets and in 1-inch-mesh wing nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	1-Inch-Mesh Hoop Nets					1-Inch-Mesh Wing Nets					Degrees of Freedom	t Value
	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation		
Carp	100.0	9	21.83	17.2–26.0	2.97	78.5	303	17.55	4.7–30.0	4.85	51	4.162*
Bigmouth buffalo	—	0	—	—	—	39.4	33	13.48	4.5–19.6	3.67	—	—
Smallmouth buffalo	0.0	6	11.75	9.0–13.9	2.09	5.8	277	9.21	4.1–18.4	3.46	40	2.892*
Freshwater drum	49.2	65	10.03	4.9–17.7	3.74	33.2	632	8.79	4.0–18.6	2.93	202	2.593*
Channel catfish	12.9	62	9.15	3.5–18.5	3.62	5.7	936	9.44	2.7–30.1	2.21	240	0.623
Flathead catfish	11.4	44	13.20	4.4–21.0	4.46	23.5	179	15.39	5.6–37.6	5.30	88	2.807*
Bluegill	50.0	2	6.00	5.0– 6.8	1.41	34.4	282	5.99	3.0– 8.4	1.33	23	0.010
White crappie	64.3	14	7.54	4.7–12.4	2.21	48.8	2,514	7.36	2.9–13.2	2.30	187	0.304
Black crappie	66.7	9	7.83	4.3– 9.7	2.02	41.7	1,343	7.03	3.0–14.0	2.14	109	1.183

* Denotes a significant difference, in sizes of fish taken, between the two types of nets at 0.05 level for degrees of freedom indicated.

figs. 11 and 12. Of the total number of fishes taken with the 2½-inch-mesh wing nets, sport fishes comprised only 2.4 per cent in 1944 and 1.9 per cent in 1946, table 14. The number of sport fishes per net-day taken with 2½-inch-mesh wing nets amounted to 0.06 fish in 1944 and 0.02 fish in 1946, table 5. Crappies comprised most of the sport fish catch. The eight crappies taken in the 2½-inch-mesh wing nets in 1946 were all of desirable or usable sizes; of the more than 3,800 crappies taken in the 1-inch-mesh wing nets (without leads) in the same year, less than 50 per cent were of usable sizes, table 16.

Very few predatory and forage fishes, per net-day, were taken in the 2½-inch-mesh wing nets, table 5. The catch in these nets consisted largely of carp, buffalofishes, carpsuckers, and freshwater drums. Thompson (1925:431) states that carp avoid small-mesh nets and traps, but that they are taken readily in large-mesh nets. He writes, "Channel cat and bullheads seem to go most readily into small-mesh nets and basket traps, probably because, being largely nocturnal and hiding during the day, they go into the nets for concealment."

In 1946 test fishing, all of the 172 carp taken in the 2½-inch-mesh wing nets were of commercial sizes, table 16. At the stations at which the 2½-inch-mesh wing nets were fished, only 78.5 per cent of the 303 carp taken in 1-inch-mesh wing nets were of commercial sizes. The catch of commercial-sized carp in the 2½-inch-mesh wing nets amounted to 1.76 pounds per net-day and in the 1-inch-mesh nets to 1.10 pounds per net-day, table 15.

The data indicate that the 1-inch-mesh

Table 19.—Composition of catches of commercial-sized or desirable-sized fish taken in 2½-inch-mesh hoop nets and in 1-inch-mesh wing nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	2½-Inch-Mesh Hoop Nets (730.42 Net-Days)			1-Inch-Mesh Wing Nets (855.86 Net-Days)			Chi-Square Value
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	1.10	150	0.21	1.10	238	0.28	8.42*
Bigmouth buffalo	0.19	45	0.06	0.04	13	0.02	23.30*
Smallmouth buffalo	0.19	59	0.08	0.04	16	0.02	32.22*
Freshwater drum	0.34	152	0.21	0.23	210	0.25	2.35
Channel catfish	0.01	2	0.003	0.10	53	0.06	39.74*
Flathead catfish	0.84	58	0.08	0.27	42	0.05	5.80*
Bluegill	—	0	—	—	97	0.11	—
White crappie	—	3	0.004	—	1,228	1.43	1,037.54*
Black crappie	—	1	0.001	—	560	0.65	474.19*

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish taken, between the two types of nets at 0.05 level with 1 degree of freedom.

Table 20.—Size ranges and means of the total lengths of fish taken in 2½-inch-mesh hoop nets and in 1-inch-mesh wing nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	2½-Inch-Mesh Hoop Nets					1-Inch-Mesh Wing Nets					Degrees of Freedom	t Value
	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation		
Carp	99.3	151	21.28	14.6–31.6	3.31	78.5	303	17.55	4.7–30.0	4.85	213	9.623*
Bigmouth buffalo	84.9	53	16.84	13.2–22.9	2.07	39.4	33	13.48	4.5–19.6	3.67	41	4.804*
Smallmouth buffalo	66.3	89	15.35	10.0–20.0	1.97	5.8	277	9.21	4.1–18.4	3.46	156	20.842*
Freshwater drum	100.0	152	14.66	11.5–18.9	1.39	33.2	632	8.79	4.0–18.6	2.93	309	36.190*
Channel catfish	66.6	3	17.67	6.6–21.9	9.03	5.7	936	9.44	2.7–30.1	2.21	52	1.578
Flathead catfish	95.1	61	26.19	11.8–39.5	6.33	23.5	179	15.39	5.6–37.6	5.30	104	11.972*
Bluegill	—	0	—	—	—	34.4	282	5.99	3.0– 8.4	1.33	—	—
White crappie	100.0	3	10.83	10.6–11.3	0.29	48.8	2,514	7.36	2.9–13.2	2.30	86	20.448*
Black crappie	50.0	2	8.25	7.7– 8.8	1.06	41.7	1,343	7.03	3.0–14.0	2.14	51	1.625

* Denotes a significant difference, in sizes of fish taken, between the two types of nets at 0.05 level for degrees of freedom indicated.

wing nets are much more efficient in taking catfishes than are the 2½-inch-mesh wing nets, table 15. In 1946, only 4 flathead catfish were taken in the 2½-inch-mesh wing nets and 179 (42 of them of commercial sizes, table 15) in the 1-inch-mesh wing nets, table 16. The fish of this species in the 2½-inch-mesh wing net collections ranged in total length from 18.8 to 37.0 inches, and in the 1-inch-mesh wing net collections from 5.6 to 37.6 inches.

More commercial-sized buffalofishes per net-day were caught in the 2½-inch-mesh wing nets than in the 1-inch-mesh wing nets, table 15. In the 2½-inch-mesh wing net catches, 97.8 per cent of the bigmouth buffalos and 68.6 per cent of the smallmouth buffalos were of commercial sizes, table 16. In the 1-inch-mesh wing net sets, only 39.4 per cent of the bigmouth buffalos and 5.8 per cent of the smallmouth buffalos were of commercial sizes.

More freshwater drums of commercial sizes were caught per net-day in the 1-inch-mesh wing nets than in the 2½-inch-mesh wing nets, table 15. On a pounds-per-net-day basis of commercial-sized drums, the catches of the two types of net were almost identical. All of the freshwater drums taken in the 2½-inch-mesh wing nets were of commercial sizes, whereas only 33.2 per cent of these fish taken in the 1-inch-mesh wing nets were of these sizes, table 16. The test-net figures indicate that a fisherman using 2½-inch-mesh wing nets will handle fewer undersized freshwater drums than one using nets of a smaller mesh size.

As indicated in preceding paragraphs, the efficiency and selectivity of wing nets of the mesh sizes used in the survey varied with species and sizes of fish. The small-mesh (1-inch) wing nets were more selective for crappies, bluegills, and catfishes than the 2½-inch-mesh nets, table 15. The 2½-inch-mesh nets were more efficient than the small-mesh (1-inch) nets in taking commercial-sized carp and buffalofishes, table 15.

Catches With Hoop Nets.—In the 1946 test fishing, sport fishes comprised 53.4 per cent of the entire catch with 1-inch-mesh wing nets (without leads), whereas they comprised only 10.4 per cent of the catch with 1-inch-mesh hoop nets, table 14. No attempt was made to fish hoop nets and wing nets of the same mesh in the same habitat to determine if the absence or presence of the wings influenced the catch.

In tables 17 and 18 are listed comparative data on nine species of fish caught in the 1946 test fishing in 1-inch-mesh hoop nets and 1-inch-mesh wing nets (without leads) used at the same stations, although not necessarily in similar habitats.

The numbers, per net-day, of commercial-sized carp and usable-sized bluegills and crappies caught in the wing nets were significantly greater than the numbers, per net-day, of these fish caught in hoop nets, table 17. The numbers, per net-day, of commercial-sized freshwater drums and catfishes did not differ greatly between the two nets. The weights, per net-day, of commercial-sized carp and flathead catfish were greater in the wing net catch, and the weight, per net-day, of commercial-sized freshwater drums was greater in the hoop net catch.

No buffalofish of commercial size was taken in the 1-inch-mesh hoop net sets. The catch of these fishes in the 1-inch-mesh wing nets was small.

The mean of the total lengths for each of three species, carp, smallmouth buffalo, and freshwater drum, was significantly greater for individuals taken in the 1-inch-mesh hoop nets than for those taken in the wing nets of the same mesh, table 18. The mean of the total lengths for flathead catfish was greater for individuals taken in the wing nets. The small number of carp (nine) taken in the hoop nets casts doubt on the value of the test for fish of this species. The mean of the total lengths for bluegills and for crappies was approximately the same for individuals taken in hoop nets as for those taken in wing nets.

In tables 19 and 20 are listed comparative data on nine species of fish taken in the 1946 test fishing in 2½-inch-mesh hoop nets and 1-inch-mesh wing nets (without leads) fished at the same stations, but in most cases in different habitats.

The number of commercial-sized buffalofishes taken, per net-day, was much greater in the 2½-inch-mesh hoop nets than in the small-mesh wing nets, table

19. The 2½-inch-mesh hoop nets were less efficient in taking commercial-sized bigmouth buffalos than were the 2½-inch-mesh wing nets, table 21. The catch per net-day of smallmouth buffalos in the 2½-inch-mesh hoop nets was identical with that in the 2½-inch-mesh wing nets.

Freshwater drums often frequent waters too deep and swift for wing nets. However, such waters are usually suitable for hoop net fishing. Perhaps that is why in 1946 the weights and numbers, per net-day, of commercial-sized drums were higher in the 2½-inch-mesh hoop net catch than in the 2½-inch-mesh wing net catch, table 21. The mean of the total lengths for drums caught in 1946 in 2½-inch-mesh wing nets was greater than for drums caught in the 2½-inch-mesh hoop nets, table 22.

The test-net survey data indicate that the 2½-inch-mesh hoop nets are not effi-

Table 21.—Composition of catches of commercial-sized or desirable-sized fish taken in 2½-inch-mesh wing nets and in 2½-inch-mesh hoop nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	2½-Inch-Mesh Wing Nets (421.75 Net-Days)			2½-Inch-Mesh Hoop Nets (730.42 Net-Days)			Chi-Square Value
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	1.76	172	0.41	1.10	150	0.21	37.22*
Bigmouth buffalo	0.31	44	0.10	0.19	45	0.06	5.91*
Smallmouth buffalo	0.21	35	0.08	0.19	59	0.08	0.002
Freshwater drum	0.22	47	0.11	0.34	152	0.21	15.29*
Channel catfish	0.01	1	0.002	0.01	2	0.003	0.014
Flathead catfish	0.11	4	0.009	0.84	58	0.08	24.82*
Bluegill	—	0	—	—	0	—	—
White crappie	—	6	0.01	—	3	0.004	3.40
Black crappie	—	2	0.005	—	1	0.001	1.13

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish taken, between the two types of nets at 0.05 level with 1 degree of freedom.

Table 22.—Size ranges and means of the total lengths of fish taken in 2½-inch-mesh hoop nets and in 2½-inch-mesh wing nets, both types without leads, in fisheries survey of the Mississippi River between Burlington and Dubuque, Iowa, 1946.

Kind of Fish	2½-Inch-Mesh Wing Nets					2½-Inch-Mesh Hoop Nets					Degrees of Freedom	t Value
	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation	Per Cent Commercial or Desirable Sizes	Number Taken, All Sizes	Mean of Total Lengths, Inches	Size Range, Inches	Standard Deviation		
Carp	100.0	172	20.28	15.4–31.8	2.83	99.3	151	21.28	14.6–31.6	3.31	160	2.897*
Bigmouth buffalo	97.8	45	17.14	13.8–20.1	1.52	84.9	53	16.84	13.2–22.9	2.07	48	0.825
Smallmouth buffalo	68.6	51	15.74	12.4–26.0	2.30	66.3	89	15.35	10.0–20.0	1.97	66	1.016
Freshwater drum	100.0	47	15.40	11.4–18.8	1.41	100.0	152	14.66	11.5–18.9	1.39	84	3.156*
Channel catfish	50.0	2	14.25	5.7–23.0	12.37	66.6	3	17.67	6.6–21.9	9.03	1	0.336
Flathead catfish	100.0	4	28.75	18.8–37.0	7.15	95.1	58	26.19	11.8–39.5	6.33	14	0.698
Bluegill	—	0	—	—	—	—	0	—	—	—	—	—
White crappie	100.0	6	10.42	8.6–13.0	1.85	100.0	3	10.83	10.6–11.3	0.29	6	0.531
Black crappie	100.0	2	10.50	9.1–12.2	2.21	50.0	2	8.25	7.7– 8.8	1.06	1	1.299

* Denotes a significant difference, in sizes of fish taken, between the two types of nets at 0.05 level for degrees of freedom indicated.

cient devices for catching channel catfish, table 5. However, these large-mesh nets were found to be the most efficient devices tested for taking commercial-sized flathead catfish. Of the flatheads taken with these nets in 1946, 95.1 per cent were 18 inches or more in total length, table 20. In the 1-inch-mesh wing net collections of 1946, only 23.5 per cent were 18 inches or more in total length. The mean of the total lengths of flatheads taken in 1946 in the 2½-inch-mesh hoop nets was 26.19 inches, table 20, as compared with 15.39 inches in the 1-inch mesh wing nets and 13.20 inches in the 1-inch-mesh hoop nets, table 18. In the 1946 test-netting, the mean of the total lengths for the 58 flatheads taken in the 2½-inch-mesh hoop nets was about the same as the mean for the 4 flatheads in the 2½-inch-mesh wing net collections, table 22.

The catch of sport fishes in the 2½-inch-mesh hoop nets amounted to less than 0.01 fish per net-day in 1946, table 5. In this same year, the catch of sport fishes was 5.43 fish per net-day in the 1-inch-mesh wing net collections.

Catches With Trap Nets.—Trap nets were fished at only three stations for a total of 50.53 net-days. The nets were all of 1¼-inch mesh. As indicated by fig. 12, the catch with these nets included both commercial and sport fishes. These nets did not take as many sport fishes per net-day as the 1-inch-mesh wing nets, tables 5 and 23; however, they took more than the nets of 2½-inch-mesh. The trap net sets made during this investigation were too few in number to give any conclusive evidence regarding usage of these nets on the Mississippi.

Table 23.—Composition of catches of commercial-sized or desirable-sized fish taken in 1¼-inch-mesh trap nets (with leads) and in 1-inch-mesh wing nets (without leads) in fisheries survey of the Mississippi River between Andalusia, Illinois, and Dubuque, Iowa, 1946.

KIND OF FISH	1¼-INCH-MESH TRAP NET (50.53 NET-DAYS)			1-INCH-MESH WING NET (200.50 NET-DAYS)			CHI-SQUARE VALUE
	Pounds per Net-Day	Number	Number per Net-Day	Pounds per Net-Day	Number	Number per Net-Day	
Carp	2.78	37	0.73	0.96	43	0.21	34.45*
Bigmouth buffalo	—	0	—	—	0	—	—
Smallmouth buffalo	—	0	—	—	2	0.01	—
Freshwater drum	0.29	14	0.28	0.26	56	0.28	0.00
Channel catfish	0.05	2	0.04	0.04	5	0.02	0.32
Flathead catfish	—	0	—	0.15	9	0.05	—
Bluegill	—	2	0.04	—	21	0.10	1.84
White crappie	—	20	0.40	—	131	0.65	4.31*
Black crappie	—	6	0.12	—	137	0.68	22.32*

* Denotes a significant difference, in numbers of commercial-sized or desirable-sized fish taken, between the two types of nets at 0.05 level with 1 degree of freedom.

Entanglement Device

The trammel net is the only entanglement device that was used in the survey. This device is composed of three separate nets secured to a single top and a single bottom line. The two exterior nets (for purposes of explanation called here left-exterior and right-exterior) are made of heavy twine and have a mesh size of 8 to 10 inches. The inner net is a small-mesh gill net loosely sandwiched between the two large-mesh outer nets, fig. 13.

A fish swimming into a trammel net from the left side passes freely through the left-exterior net and strikes the loosely hung inner net with enough force to carry a portion of the inner net with it through a mesh opening of the right-exterior net. The inner net, passing through a mesh of the right-exterior net, forms a pocket in which the fish is enclosed. Similarly, a fish approaching the trammel net from the right side passes through the right-exterior net and becomes trapped in a pocket

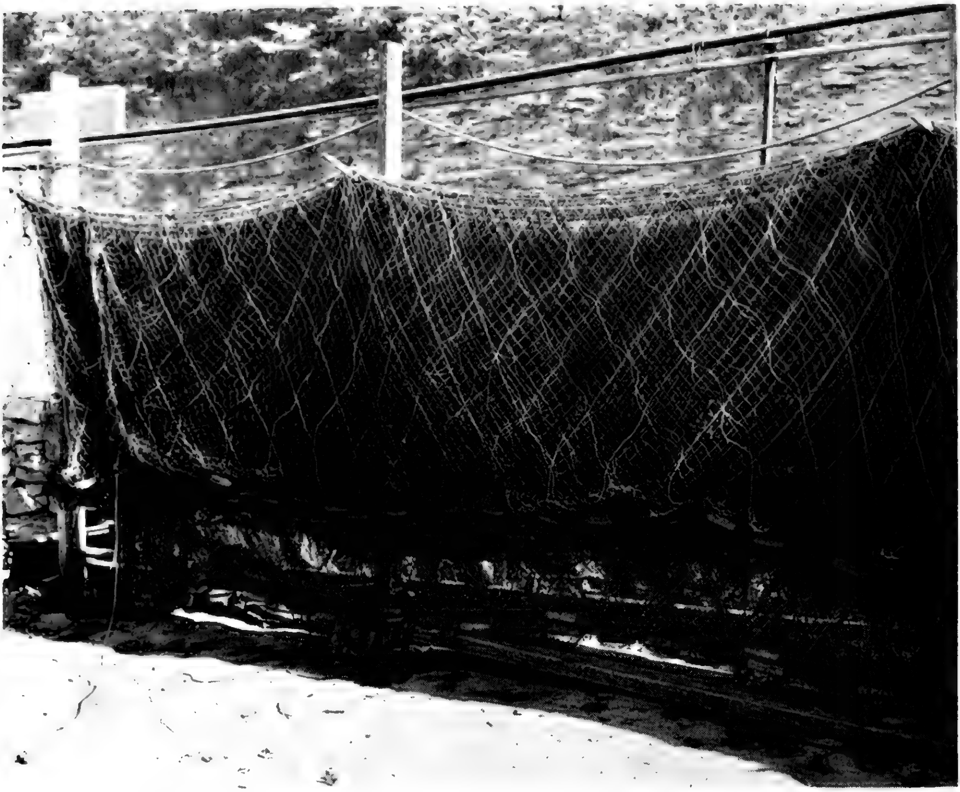

Fig. 13.—View of a trammel net, showing the two exterior large-mesh nets and the inner small-mesh net.

formed when the inner net is carried through a mesh opening of the left-exterior net. The fish is held in the pocket until released by a fisherman, fig. 14.

Trammel nets can be fished in all types of habitats found on the Mississippi. The method by which the trammel net is fished differs with habitat. If a backwater or quiet stretch of the river is to be fished, the net is set, fig. 15. If the river channel is to be fished, the net is floated or drifted downstream.

Trammel net sets and floats were made during the survey at some of the field stations in the D-MR section of the river. A summary of the trammel net fishing data is presented in table 24. Except for data collected from experimental trammel netting at Grafton in October, 1944, and at Quincy in November of the same year, the data relative to catches made in trammel nets of various lengths and mesh sizes were combined. Data from the experimental trammel netting at Grafton and at Quincy were not included in the previous report on the survey (Barnickol & Starrett 1951).

In 1947, trammel nets accounted for 25.1 per cent of the commercial catch from the Missouri section of the river and 14.5 per cent from the Illinois section (Upper Mississippi River Conservation Committee 1948, third section:19).

Catches With Set Trammel Nets.—The set method of trammel netting is the one most generally used by commercial fishermen of the upper Mississippi River. When this method is used, the net is set around a school of fish. Sometimes it is laid out in a zigzag or spiral fashion. Frequently the shore line is used as a backstop for the net. After the net has been set around the fish, a disturbance in the water is created with plungers, fig. 16. Usually the trapped fish become excited and, when they attempt to escape by swimming toward the deep water, they hit the net.

The trammel net can be fished selectively for commercial species by a fisherman familiar with the habits of these fishes. Carp and buffalofishes tend to school in large numbers when spawning or feeding. These fishes ripple the surface of the water or stir up the bottom, revealing their presence to the commercial fisherman searching for signs of fish activity. If the fisherman believes there are quite a few fish of a desired species present, he proceeds to set his trammel net around them. On three occasions, selective netting for one or two commercial species was done by the survey crew. The catches made in these sets are listed in table 25. Carp and buffalofishes dominated these catches. No sport fish was taken in these sets. Trammel net catches taken by commercial fishermen and examined by the writers have been found to contain largely carp and buffalofishes.

Commercial fishes, most of them carp and buffalofishes, dominated the 116 test sets made in 1944 and 1946 with trammel nets, table 26. The trammel net seems to be a very inefficient method for taking catfish. Only three channel catfish and two flathead catfish were netted in the 116 sets.

Bowfins and gars were caught regularly in the sets. These fishes are sold commercially in some areas along the river.

More than 90 per cent of the carp, bigmouth buffalos, and freshwater drums taken in 73 sets of trammel nets in 1946 were of commercial sizes, table 27.

Sport fishermen have long believed and argued that the trammel net is a destroyer of sport fishes. Their belief probably has been influential in outlawing the use of the trammel net in most midwestern wa-

Fig. 14.—A pocketed fish in a trammel net. The inner net forming the pocket around the fish hangs over the cord of one of the exterior nets.

Fig. 15.—Fishermen setting a trammel net around a school of carp on the Mississippi.

ters. Sport fishes amounted to 17.3 per cent of the catches in trammel nets set at the various stations tested along the river in 1944 and 1946, including the late fall, 1944, experimental catches at Grafton, table 26. The majority of the river sets were made with a net having a 1½-inch- or 2-inch-mesh inner net and usually were not made in sites indicating the presence of carp or buffalofishes. Many of the sets were made in areas that appeared especially favorable for sport fishes. In the 116 sets made with trammel nets of various mesh sizes, only 7 bass (*Microp-*

Table 24.—Summary of trammel net sets and floats made in the Mississippi River by the fisheries survey party between Grafton, Illinois, and Dubuque, Iowa, 1944 and 1946.*

Year	Trammel Net Sets					Trammel Net Floats				
	Number of Sets	Length of Net, Yards	Mesh Size, Inches†	Number of Fish Caught	Pounds of Fish Caught	Number of Floats	Length of Net, Yards	Mesh Size, Inches†	Number of Fish Caught	Pounds of Fish Caught
1944	16	100	1½, 2	109	192.08	5	100	1½, 2	6	10.23
1944 (*Grafton Experimental*)	27	150‡	1½, 2, 3	247	336.54	0	—	—	—	—
1944 (*Quincy Experimental*)	0	—	—	—	—	33	100‡	1½, 2	197	250.50
1946	73	100–200	1½, 1¾, 2	961	2,572.41	70	80–100	1½, 1¾, 2	361	591.24
Total	*116*	—	—	*1,317*	*3,101.03*	*108*	—	—	*564*	*851.97*

* Does not include all the sets and floats made by the survey party; certain sets and floats were omitted because of discrepancies in methods of fishing.
† Inner net.
‡ Each mesh size was represented by a 50-yard length of net.

Table 25.—Examples of trammel net sets in which catches of the fisheries survey party were dominated by a single species of fish, Mississippi River, 1946.

Kind of Fish	Burlington, Iowa April 17, 1946 (One Set)		Muscatine, Iowa May 28, 1946 (Two Sets)	
	Number	Pounds	Number	Pounds
Carp	0	0.00	149	527.79
Bigmouth buffalo	31	88.21	1	3.50
Smallmouth buffalo	1	2.10	7	10.39
Carpsuckers	0	0.00	2	2.60
Freshwater drum	0	0.00	7	9.62
Total	*32*	*90.31*	*166*	*553.90*

Fig. 16.—A commercial fisherman using a plunger to create a disturbance in the water in an effort to drive fish into his trammel net.

Table 26.—Composition of catches of trammel net sets and trammel net floats made in the Mississippi River by the fisheries survey party between Grafton, Illinois, and Dubuque, Iowa, 1944 and 1946. Included are catches of the experimental sets made at Grafton and of the experimental floats made at Quincy in the fall of 1944 and all other sets and floats except a few that were omitted because of discrepancies in methods of fishing.

Kind of Fish	Trammel Net Sets (116)				Trammel Net Floats (108)			
	Number of Fish	Per Cent of Total Number	Weight, Pounds	Per Cent of Total Weight	Number of Fish	Per Cent of Total Number	Weight, Pounds	Per Cent of Total Weight
Commercial								
Shovelnose sturgeon	0	0.0	0.00	0.0	383	67.9	473.38	55.5
Carp	584	44.3	1,986.54	64.1	28	4.9	135.21	15.9
Bigmouth buffalo	135	10.3	376.63	12.1	0	0.0	0.00	0.0
Black buffalo	10	0.8	23.76	0.8	0	0.0	0.00	0.0
Smallmouth buffalo	32	2.4	45.42	1.5	2	0.4	3.94	0.5
Bullheads	14	1.1	11.68	0.4	0	0.0	0.00	0.0
Channel catfish	3	0.2	8.37	0.3	2	0.4	10.42	1.2
Flathead catfish	2	0.1	4.45	0.1	7	1.2	11.32	1.3
Suckers and redhorses	4	0.3	7.56	0.2	7	1.2	15.55	1.8
Carpsuckers	67	5.1	84.89	2.7	14	2.5	16.80	2.0
Freshwater drum	50	3.8	63.74	2.1	96	17.0	109.83	12.9
Subtotal	*901*	*68.4*	*2,613.04*	*84.3*	*539*	*95.5*	*776.45*	*91.1*
Sport								
Largemouth bass	1	0.1	0.87	tr.*	0	0.0	0.00	0.0
Spotted bass	6	0.5	6.50	0.2	0	0.0	0.00	0.0
Black crappie	117	8.9	61.35	2.0	0	0.0	0.00	0.0
White crappie	76	5.8	43.04	1.4	0	0.0	0.00	0.0
Bluegill	20	1.5	8.35	0.3	0	0.0	0.00	0.0
Warmouth	2	0.1	0.98	tr.*	0	0.0	0.00	0.0
Sauger	1	0.1	1.52	0.1	5	0.9	8.54	1.0
Northern pike	1	0.1	3.49	0.1	0	0.0	0.00	0.0
White bass	2	0.1	3.45	0.1	0	0.0	0.00	0.0
Yellow bass	2	0.1	0.87	tr.*	0	0.0	0.00	0.0
Subtotal	*228*	*17.3*	*130.42*	*4.2*	*5*	*0.9*	*8.54*	*1.0*
Predatory								
Longnose gar	5	0.4	12.85	0.4	14	2.5	57.49	6.8
Shortnose gar	94	7.1	140.98	4.6	5	0.9	8.66	1.0
Bowfin	51	3.9	171.41	5.5	0	0.0	0.00	0.0
Subtotal	*150*	*11.4*	*325.24*	*10.5*	*19*	*3.4*	*66.15*	*7.8*
Forage								
Gizzard shad	35	2.7	30.33	0.9	0	0.0	0.00	0.0
Goldeye	3	0.2	2.00	0.1	1	0.2	0.83	0.1
Subtotal	*38*	*2.9*	*32.33*	*1.0*	*1*	*0.2*	*0.83*	*0.1*
Total	*1,317*	*100.0*	*3,101.03*	*100.0*	*564*	*100.0*	*851.97*	*100.0*

* tr. (trace) indicates that the species was taken but that the take averaged less than 0.1 per cent of total weight.

Table 27.—Summary of catches of three important commercial fishes in 73 trammel net sets made in the fisheries survey of the upper Mississippi River, 1946.

Kind of Fish	Number of Fish, All Sizes	Number of Fish of Commercial Sizes	Number of Fish of Commercial Sizes per Set	Per Cent Commercial Sizes	Mean of Total Lengths, Inches	Range of Total Lengths, Inches
Carp	537	491	6.73	91.4	16.5	10.6–31.6
Bigmouth buffalo	116	107	1.47	92.2	17.1	10.2–20.8
Freshwater drum	49	46	0.63	93.9	13.5	7.7–17.4

terus spp.) and 20 bluegills were caught. Crappies amounted to 84.6 per cent of the 228 sport fishes taken in the 116 sets.

Experimental Sets at Grafton.—During the regular test-netting program, no specific test was made of the efficiency and selectivity of various mesh sizes of the inner net. However, such a test was conducted in late October, 1944, in a series of 27 sets made with a 150-yard experimental trammel net in several bottomland lakes near Grafton, Illinois. As these lakes were known to have high populations of sport fishes, particularly crappies, they appeared to be especially suited for testing the efficiency and selectivity of various mesh sizes of the inner net in the taking of sport fishes, as well as commercial and other species.

The experimental trammel net was composed of three 50-yard lengths sewed together to form one net 150 yards in length. The mesh size of the inner net of the first section, or length, was 1½ inches, of the second 2 inches, and of the third 3 inches. This experimental net permitted the sampling of a site with three mesh sizes in one set. Each 50-yard section of netting is assumed to have had an equal chance to catch fish and, on the basis of this assumption, the following analysis has been made.

Table 28.—Summary of the catches of fish taken in 27 sets made with a 150-yard experimental trammel net in three bottomland lakes (Flat, Silver, and Royal) near Grafton, Illinois, October, 1944. Figures in parentheses indicate the numbers of fish gilled.

Kind of Fish	1½-Inch-Mesh Net		2-Inch-Mesh Net		3-Inch-Mesh Net	
	Number Caught	Per Cent Gilled	Number Caught	Per Cent Gilled	Number Caught	Per Cent Gilled
COMMERCIAL						
Channel catfish	0 (0)	0.0	2 (0)	0.0	0 (0)	0.0
Black bullhead	12 (1)	8.3	0 (0)	0.0	0 (0)	0.0
Brown bullhead	0 (0)	0.0	1 (0)	0.0	0 (0)	0.0
Carp	1 (0)	0.0	6 (2)	33.3	1 (0)	0.0
Smallmouth buffalo	5 (1)	20.0	3 (0)	0.0	1 (0)	0.0
Bigmouth buffalo	0 (0)	0.0	13 (5)	38.5	5 (1)	20.0
Black buffalo	2 (0)	0.0	3 (1)	33.3	1 (0)	0.0
Carpsuckers	3 (0)	0.0	4 (0)	0.0	0 (0)	0.0
Subtotal	*23 (2)*	—	*32 (8)*	—	*8 (1)*	—
Average	—	**8.7**	—	**25.0**	—	**12.5**
SPORT						
Largemouth bass	1 (0)	0.0	0 (0)	0.0	0 (0)	0.0
Spotted bass	5 (2)	40.0	1 (1)	100.0	0 (0)	0.0
White crappie	8 (0)	0.0	6 (0)	0.0	1 (0)	0.0
Black crappie	53 (8)	15.1	13 (4)	30.8	1 (0)	0.0
Bluegill	4 (1)	25.0	0 (0)	0.0	0 (0)	0.0
Warmouth	1 (1)	100.0	0 (0)	0.0	0 (0)	0.0
Yellow bass	2 (0)	0.0	0 (0)	0.0	0 (0)	0.0
Subtotal	*74 (12)*	—	*20 (5)*	—	*2 (0)*	—
Average	—	**16.2**	—	**25.0**	—	**0.0**
PREDATORY						
Shortnose gar	46 (7)	15.2	2 (0)	0.0	0 (0)	0.0
Longnose gar	2 (1)	50.0	0 (0)	0.0	0 (0)	0.0
Bowfin	11 (0)	0.0	6 (0)	0.0	0 (0)	0.0
Subtotal	*59 (8)*	—	*8 (0)*	—	*0 (0)*	—
Average	—	**13.6**	—	**0.0**	—	**0.0**
FORAGE						
Gizzard shad	8 (3)	37.5	11 (1)	9.1	0 (0)	0.0
Goldeye	1 (0)	0.0	0 (0)	0.0	1 (0)	0.0
Subtotal	*9 (3)*	—	*11 (1)*	—	*1 (0)*	—
Average	—	**33.3**	—	**9.1**	—	**0.0**
Total	*165 (25)*	—	*71 (14)*	—	*11 (1)*	—
Average	—	**15.2**	—	**19.7**	—	**9.1**

The catch of commercial species in the 27 experimental sets was low, since no effort was made to search out such species.

In the 27 sets, 247 fish were caught, table 28. The section with the 1½-inch-mesh inner net caught 165 fish, or 66.8 per cent of the number of fish taken; the section with the 2-inch-mesh inner net took 71 fish, or 28.7 per cent of the total; and the section with the 3-inch-mesh inner net took only 11 fish, or 4.5 per cent of the total.

Of the 165 fish taken in the section with the 1½-inch-mesh inner net, 44.8 per cent were sport fishes, 35.8 per cent were garfishes and bowfins, and 13.9 per cent were commercial species. Crappies comprised 82.4 per cent of the number of sport fishes taken in the section with the 1½-inch-mesh inner net. Of the remaining 17.6 per cent of the sport fishes, six were bass (*Micropterus* spp.), four were bluegills, two were yellow bass, and one was a warmouth. Bullheads were the principal commercial fishes taken in the section with the 1½-inch-mesh inner net. Seven buffalofishes, one carp, and three carpsuckers formed the remainder of the commercial catch.

Commercial species, principally buffalofishes and carp, made up 45.1 per cent of the number of fish caught in the section of the experimental trammel net with 2-inch-mesh inner net. In this section of the net, sport fishes comprised 28.2 per cent of the catch; crappies comprised 95.0 per cent of the number of sport fishes. The section with the 1½-inch-mesh inner net caught 3.7 times as many sport fishes as did the section with the 2-inch-mesh inner net. Only 2 garfishes were taken in the section with the 2-inch-mesh inner net and 48 in the section with the 1½-inch-mesh inner net.

Of the 11 fish caught in the section with the 3-inch-mesh inner net, 72.7 per cent were commercial species. This section of the net caught but 2 sport fishes.

Of the three mesh sizes used in the experimental trammel net, the 2-inch size appeared to be by far the best for commercial fishing. The section of the net having an inner net of this mesh size had the highest catch of commercial species, it had few garfishes, and it had a catch of sport fishes that was low when it is considered that the net was fished in waters known to contain a high population of these fishes, table 28. If sport fishes of larger sizes had been abundant in the waters fished, perhaps the catch of these fishes would have been much higher in this section of the net. The section with the 3-inch-mesh inner net would probably have taken a high catch of large commercial species if fished in a habitat being used by such fishes. This section of the net took very few sport fishes of the sizes then present in the Grafton waters.

In conjunction with the trammel netting experiment at Grafton, 12 net-days of fishing were done with 1-inch-mesh wing nets. Ninety-one bluegills were taken in these wing nets; they ranged in size from 3.8 to 7.6 inches total length. The mean of the total lengths of these bluegills was 5.7 inches. The four bluegills taken in that section of the experimental trammel net having a 1½-inch-mesh inner net ranged from 7.0 to 7.2 inches in length. Evidently most of the bluegills present in the Grafton waters in the fall of 1944 were too small to be taken in the 1½-inch-mesh net. If bluegills of 7 inches and longer had been extremely abundant, the catch in the experimental trammel net probably would have been higher. The mean of the total lengths of bluegills taken in the Mississippi River during the 2-year survey with all types of fishing devices was between 6.1 and 6.5 inches. In the 116 trammel net sets made during the survey, only 20 bluegills were caught, table 26. On the basis of the above discussion, it appears that trammel nets having inner nets with meshes of 1½ inches or larger are quite inefficient in taking bluegills in the Caruthersville-Dubuque section of the Mississippi.

In the 12 net-days of fishing with wing nets at Grafton, 285 crappies were taken. These fish ranged in total length from 4.4 to 11.4 inches; the mean of their total lengths was 7.6 inches. Crappies caught in the section of the experimental net having an inner net of 1½-inch mesh ranged in total length from 7.4 to 12.2 inches; the mean of their total lengths was 9.3 inches. Crappies taken in the section having an inner net of 2-inch mesh ranged [illegible] .9 to 11 [illegible] inches [illegible] total lengths was 10.8 inches. The two crappies taken in the section having an inner net of 3-inch mesh were each more than 11 inches in total length. The mean of the total lengths of white crappies taken at the various stations in the 2 years of test-netting with various commercial devices was between 7.5 and 8.0 inches, and of black crappies between 7.1 and 8.4 inches. As was the case with the bluegills, most of the crappies were too small to be taken in the trammel nets having meshes of 1½ inches or larger. How much the crappie population of the Caruthersville-Dubuque section of the Mississippi fluctuates from year to year in abundance of individuals of different size or age groups is not known; however, the differences in individual lengths between the 1944 and the 1946 samples from the river were not great (Barnickol & Starrett 1951:317).

It was shown by test-netting that, although trammel nets will catch sport fishes, if a mesh of 2 inches or larger size is used, the catch of these fishes is nominal, even when the nets are fished in waters having a high population of crappies and such other common sport fishes as are found in the Caruthersville-Dubuque section of the Mississippi River.

Gilling Experiment With Set Trammel Net.—Some critics of the trammel net have claimed that the net not only captures large numbers of sport fishes, but that sport fishes are killed in the net by gilling. Gilling occurs when a fish strikes the inner fine-mesh net and forces its head through the netting far enough to allow the net twine to become lodged beneath one or both gill covers. The gills may be injured while the fish is trying to escape or while a fisherman is dislodging the fish from the netting. Release of a gilled fish requires of the fisherman more time and patience than does release of a pocketed fish. Pocketed fish are seldom injured in the net.

In the trammel net experiment at Grafton in October, 1944, a record was kept of the section of the net in which each fish was caught, as well as whether the fish was pocketed or gilled in the net. The number and per cent of fishes that were gilled are listed by species and size of mesh in which the fish were caught, table 28. Gilling was relatively greater among the buffalofishes than among any of the other commercial species. The high percentage of gilled buffalofishes might be due to the terrific force with which these fishes hit a trammel net. A fisherman trying to hold buffalofishes alive for a period of time in a crib or holding pond might experience a higher mortality among the gilled fish than among the pocketed fish.

Persons who have fished gill nets know that the sunfishes, including the crappies, the bluegill, and the basses (*Micropterus* spp.), are ordinarily a difficult group to take in large numbers in these nets, whereas the perches and similarly shaped fish are taken readily in them. A low percentage of gilling was recorded for the crappies in the section of the trammel net having a 1½-inch-mesh inner net, table 28. Of 61 crappies taken in this net, only 8 were gilled. These gilled fish ranged in total length from 8.2 to 10.2 inches, and the mean of their total lengths was 8.8 inches. The crappies that were pocketed ranged in length from 7.4 to 12.2 inches, and the mean of their total lengths was 9.4 inches. Although the mean of the total lengths for the pocketed crappies was higher than that for gilled fish, some of the pocketed fish were smaller than any of the gilled fish.

The percentage of gilled crappies in the section of the experimental net with the 2-inch mesh was higher than in the section with the 1½-inch mesh; however, there were twice as many gilled crappies in the section with the 1½-inch mesh as in the section with the 2-inch mesh. No sport fish was gilled in that section of the net with the 3-inch mesh.

Catches With Floated Trammel Net.—Current and a clean river bottom are requirements for fishing with a trammel net that is to be floated or drifted. The floats on the net must be of such buoyancy and the weights of such weight as to hold the narrow axis of the net in a nearly vertical position. The fisherman lays his net in an area of the channel he desires to fish and lets the current carry the net downstream over a clean sand or gravel bottom.

In the D-MR section of the Mississippi

River, fishing with the trammel net floated is limited mainly to the upper ends of the pools where there is enough current to drift the net.

The float method of fishing with the trammel net is limited not only in use but in the kinds of fishes it takes. The shovelnose sturgeon, or hackleback, is the principal species taken by the float method. It may be noted in table 26 and fig. 17 that this species of sturgeon was not taken in the survey collections made with set trammel nets. The trammel net float was the only method by which the survey crew was able to take shovelnose sturgeons in numbers. The only shovelnose sturgeon taken by the survey party with other gear or methods of fishing was a single specimen in a hoop net at the New Boston station. However, in the MR-C section of the river, sturgeons are taken on trot lines by commercial fishermen.

Trammel net floating is an important method available to commercial fishermen interested in fishing for shovelnose sturgeons. This method of fishing makes it possible to harvest a fish crop that might otherwise be lost to man. The freshwater drum was the only other species taken by the float method in large enough numbers to be of importance to commercial fishermen.

Sport fishes are seldom taken in the Mississippi River by the float method. In 108 floats, only 5 sport fishes were taken, of which all were saugers, table 26.

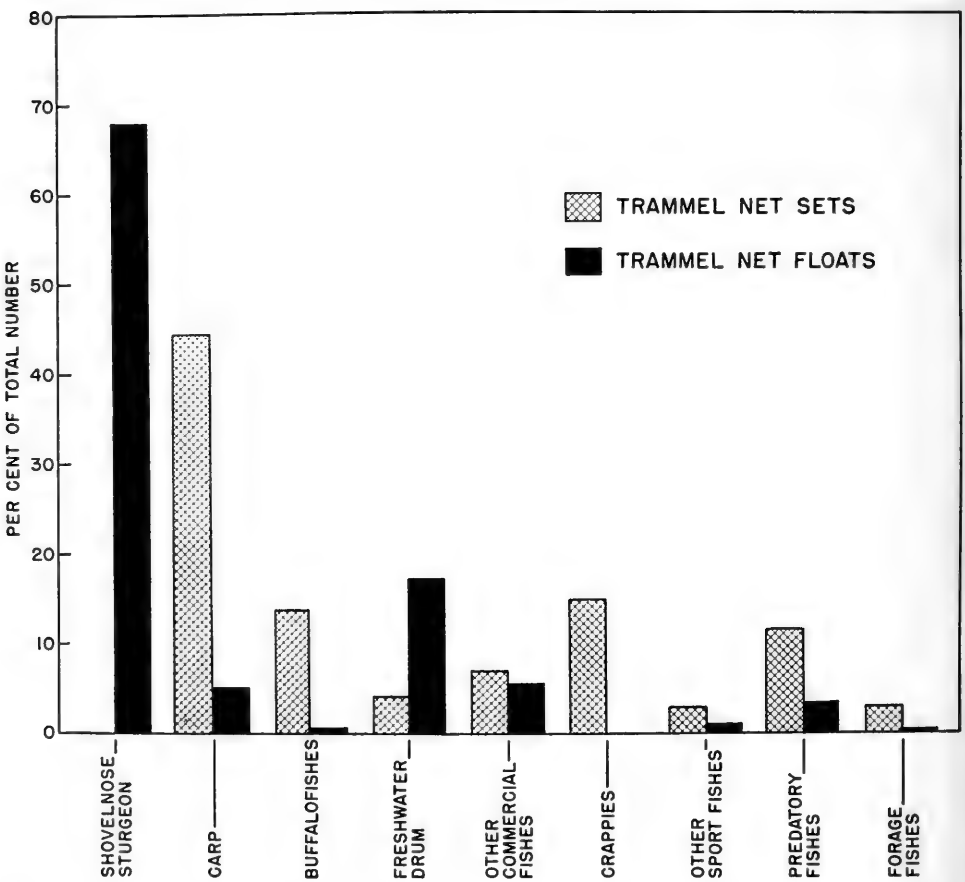

Fig. 17.—The relative numbers of commercial, sport, predator, and forage species of fish taken in trammel net sets and in trammel net floats on the Mississippi River between Grafton, Illinois, and Dubuque, Iowa, in 1944 and 1946. The graph is based on the total number of fish taken by each of the two methods of fishing, table 26.

Experimental Floats at Quincy.—An experiment with trammel net floats was conducted in the Mississippi River near Quincy, Illinois, in early November of 1944. The experimental net used was 100 yards in length and consisted of two sections, one 50-yard section with a 1½-inch-mesh inner net and the other 50-yard section with 2-inch-mesh inner net. The two sections were sewed together to form one continuous net.

In 33 floats, 197 fish were taken, table 29. The catches from these floats are included also in table 26. Shovelnose sturgeons comprised 51.3 per cent and freshwater drums 30.5 per cent of the number of fish in these catches. Other commercial fishes amounted to only 6.6 per cent of the number of individuals in these catches. Garfishes amounted to 8.6 per cent.

Five saugers were the only sport fishes taken in the 33 experimental floats. These fish were taken in the section of the net with the 1½-inch-mesh inner net. The float method of trammel netting, as demonstrated by the 33 experimental floats and the other 75 floats made during the 2-year survey, presents no problem relative to sport fishes.

The section of the experimental net with the 1½-inch-mesh inner net took 3.8 times as many shovelnose sturgeons as the section with the 2-inch-mesh inner net. The sturgeons taken in the 1½-inch mesh were smaller than those taken in the 2-inch mesh. The mean of the fork lengths* of shovelnose sturgeons was 25.5 inches for those taken in the 1½-inch mesh, and 26.8 inches for those taken in the 2-inch mesh. One 8.4-inch shovelnose sturgeon was taken in the 1½-inch mesh; the remainder taken in this mesh ranged from 22.5 to 31.2 inches fork length. In the section of the net with 2-inch mesh, the sturgeons caught ranged in fork length

* Fork length is the measurement from the tip of the snout to the base of the caudal filament.

Table 29.—Summary of the catches of fish taken in 33 floats with a 100-yard experimental trammel net (50 yards with 1½-inch-mesh inner net and 50 yards with 2-inch-mesh inner net) in the Mississippi River near Quincy, Illinois, November, 1944. Figures in parentheses indicate the numbers of fish gilled.

Kind of Fish	1½-Inch-Mesh Net		2-Inch-Mesh Net	
	Number Caught	Per Cent Gilled	Number Caught	Per Cent Gilled
COMMERCIAL				
Flathead catfish	4 (0)	0.0	1 (0)	0.0
Channel catfish	1 (0)	0.0	0 (0)	0.0
Carp	0 (0)	0.0	1 (0)	0.0
Freshwater drum	37 (1)	2.7	23 (1)	4.3
Smallmouth buffalo	0 (0)	0.0	1 (0)	0.0
Shovelnose sturgeon	80 (3)	3.8	21 (1)	4.8
Carpsuckers	2 (0)	0.0	0 (0)	0.0
Blue sucker	2 (0)	0.0	1 (0)	0.0
Subtotal	*126 (4)*	—	*48 (2)*	—
Average	—	**3.2**	—	**4.2**
SPORT				
Sauger	5 (0)	0.0	0 (0)	0.0
Subtotal	*5 (0)*	—	*0 (0)*	—
Average	—	**0.0**	—	**0.0**
PREDATORY				
Shortnose gar	4 (1)	25.0	1 (1)	100.0
Longnose gar	7 (1)	14.3	5 (0)	—
Subtotal	*11 (2)*	—	*6 (1)*	—
Average	—	**18.2**	—	**16.7**
FORAGE				
Goldeye	1 (0)	0.0	0 (0)	0.0
Subtotal	*1 (0)*	—	*0 (0)*	—
Average	—	**0.0**	—	**0.0**
Total	*143 (6)*	—	*54 (3)*	—
Average	—	**4.2**	—	**5.6**

from 23.0 to 30.6 inches. Of the sturgeons taken in this section of the net, 76.2 per cent were of commercial sizes (25 inches or more fork length); of those sturgeons taken in the section with 1½-inch mesh, 61.2 per cent were of commercial sizes.

The number and percentages of the fishes that were gilled in the experimental floats are listed in table 29. None of the five saugers taken during the experiment was gilled. In the section with the 1½-inch-mesh inner net, 4.2 per cent of the fish were gilled; in the section with the 2-inch-mesh inner net, 5.6 per cent were gilled.

Discussion

During the past 50 years, there have been increasing numbers of sport fishermen in Illinois and other states. Many of these fishermen view with suspicion the operations of commercial fishermen. Some even believe that commercial fishermen have been responsible for the decline of sport fish populations in certain localities. Their beliefs probably have developed as a result of hearsay, casual contact with the commercial fish industry, and lack of realization that many environmental changes have taken place in the past century and that some of these have had an effect on the fishery of the Mississippi River and other waters.

The effect of commercial fishing devices of illegal mesh size on certain sport fishes was demonstrated by Bennett (1948:411) in his study at Fork Lake, a small artificial lake of 1.38 acres stocked with bluegills and largemouth bass. After nearly 3½ years of being cropped heavily with small-mesh wing nets, Fork Lake still contained a large population of fish. If it was not possible in a 1.38-acre lake to reduce a sport fish population to a low level by concentrated effort with commercial gear of a mesh smaller than legal size, then it certainly does not appear logical that commercial fishermen, using nets of legal-size mesh, could remove enough sport fishes from the Mississippi River to affect the sport fishery, even if it were lawful to keep the sport fish taken in commercial devices.

It was demonstrated in the survey of 1944 and 1946 reported here that commercial fishing devices can be fished on a selective basis. Of the fishing devices tested in the survey, basket traps and floated trammel nets were found to be the ones most selective for commercial species. Other devices were found to be quite selective when fished for a particular species of fish. The type of fishing device, the mesh size, and the fishing site influenced the species composition of the catch.

Missouri statutes no longer specify minimum size limits for any commercial fish, except catfish. Illinois and Iowa still have minimum size limits on certain commercial species. Analysis of data from the Mississippi River survey of 1944 and 1946 indicates that, where minimum size limits of commercial fish are necessary, sizes of fish caught can be controlled by using nets of certain mesh sizes. The use of mesh size as a means of controlling the size of fish in the commercial catches reduces the labor of complying with the law by eliminating the necessity for measuring the fish in the catches.

Practices and policies of fish management for the Caruthersville-Dubuque section of the Mississippi River should not eliminate either sport fishing or commercial fishing. Prohibitive measures aimed at either kind of fishing affect the best use of the fishery. Too frequently, laws governing this dynamic river fishery tend to be static and thereby defeat their original purpose to benefit the fishery. Laws established to aid in the management of the river fishery should not be adopted with an attitude of permanency. These laws should be changed whenever scientific findings indicate they are no longer useful.

Summary

1. Data on fishing with various types of commercial fishing devices were collected during a fish survey of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa, in 1944 and 1946. Particular emphasis was placed on determining the selectivity and effectiveness of the commercial fishing devices of various mesh sizes used on the river.

2. During the survey, the following types of commercial fishing devices were used: seines, trammel nets, basket traps,

wing nets, hoop nets, trap nets, and trot lines.

3. Twenty-five seine hauls were made by the survey crew with 1-inch-mesh seines of 100-, 150-, and 200-yard lengths. Carp, buffalofishes, channel catfish, paddlefish, carpsuckers, and freshwater drum were the principal commercial species taken with seines. Shortnose gar was the principal predatory fish, gizzard shad the principal forage fish, and white crappie the principal sport fish. Sport fishes amounted to 11.7 per cent by number and 3.3 per cent by weight of the total catch with seines. Crappies comprised 82.1 per cent of the number of sport fishes taken with seines.

4. Of the fish taken in the survey with basket traps, 80.8 per cent were catfishes, 15.1 per cent were shortnose gars. No sport fish was taken in the basket traps.

5. One-inch-mesh wing nets with leads were found to be more efficient in taking crappies, bluegills, and buffalofishes than were nets of the same mesh fished without leads.

6. The number of commercial-sized channel catfish caught per net-day was larger in the 1-inch-mesh wing nets than in wing nets of larger mesh sizes.

7. The number of commercial-sized carp and buffalofishes caught per net-day was larger in the nets of large mesh sizes than in the nets of 1-inch mesh.

8. The efficiency of wing nets in taking sport fishes decreased as mesh size increased.

9. Wing nets took more sport fishes per net-day than did hoop nets.

10. The catch of freshwater drums of commercial sizes was larger per net-day in the 2½-inch-mesh hoop nets than in the 2½-inch-mesh wing nets. The catch of buffalofishes of commercial sizes was slightly larger in the 2½-inch-mesh wing nets than in the 2½-inch-mesh hoop nets. The 2½-inch-mesh hoop nets were the most effective entrapment devices used for flathead catfish of commercial sizes.

11. Three trammel net sets were made on a selective basis for carp and buffalofishes. Trammel nets having an inner net of 1½-inch mesh took a larger number of sport fishes than did trammel nets having inner nets with mesh sizes of 2 or 3 inches.

12. Trammel net float fishing was found to be selective for shovelnose sturgeons and freshwater drums. Only five sport fishes were taken by this method of trammel netting.

13. In 27 experimental trammel net sets at Grafton, 15.2 per cent of the fish taken in the section with an inner net of 1½-inch mesh were gilled; 19.7 per cent taken in the section with an inner net of 2-inch mesh, and 9.1 per cent taken in the section with an inner net of 3-inch mesh were gilled. No white crappie was gilled. In the section with the 1½-inch-mesh inner net, 15.1 per cent of the black crappies were gilled; in the section with the 2-inch-mesh net, 30.8 per cent of the black crappies were gilled. Of commercial species taken, buffalofishes had the greatest tendency to become gilled.

14. In 33 experimental trammel net floats made at Quincy, 4.2 per cent of the fish taken in the section of the net with a 1½-inch-mesh inner net were gilled; 5.6 per cent in the section with a 2-inch-mesh inner net were gilled.

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ILLINOIS NATURAL HISTORY SURVEY
HARLOW B. MILLS, *Chief*

Hill Prairies of Illinois

ROBERT A. EVERS

Printed by Authority of the
STATE OF ILLINOIS
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August 1955

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CONTENTS

Grassy strips on the steep upper slopes of bluffs of the Mississippi River along Illinois highway 96 in northwestern Calhoun County. Grasslands on steep slopes are hill prairies. The hill prairie on the bluff in the foreground is south of Howell Hollow; the distant one is on the Clendenny farm.

Hill Prairies of Illinois*

ROBERT A. EVERS

ON the sunny, windswept, upper slopes of some of the bluffs along the major Illinois streams are treeless areas distinctive enough to attract the attention of observing travelers. These areas are grassy strips or grassy openings on the otherwise forested slopes of the bluffs, frontispiece. Most of them have been little disturbed by man or domesticated animals. Those that are covered with prairie plants are prairies.

Prairies are grasslands. To many persons, prairies are flat grasslands. However, it is not topography but vegetation that distinguishes prairies and other plant communities. Forests occur on flat land or on slopes. So do prairies. Grasslands, or prairies, on pronounced slopes are *hill prairies*.

The term *hill prairies* was first used in 1943 by a University of Illinois botanist, Dr. Arthur G. Vestal, in his ecology classes and seminars to characterize prairies that occur on loess bluffs, on mounds, on steep, rocky slopes, on steep slopes of glacial drift, or on any other steep slopes. With few exceptions, the hill prairies of Illinois are not hill-top prairies; most of them occupy only the upper west- and southwest-facing slopes of elevations.

Most of the once extensive flatland prairies have disappeared from the Illinois landscape. There yet remain a few patches of these prairies on the till plains, but they have been very much disturbed by man or domesticated animals. The prairies of the bottomlands, the type studied by Turner (1934*a*, 1934*b*), now occur only in small scattered patches, usually in field borders or borders of roadside ditches in the Mississippi and Illinois river valleys. There are still sizable areas of sand prairies of the type studied by Gleason (1910), Gates (1912), Vestal (1913), and others, but the extent of these prairies is rapidly decreasing as a result of the activities of man in converting them to fields of watermelons or cantaloupes, or to another type of grassland, the cornfield.

There remain on the Illinois landscape numerous tracts of hill prairie and, as these prairie slopes were never plowed, they are now the least disturbed type of prairie in the state. Although rather complete studies of till plain, bottomland, and sand prairies of Illinois have been published, until this time no comparable study has been done for the hill prairies of this state.

Several studies have been published on the hill prairies of other states. The study by Bush (1895) on the mound flora of Atchison County, Missouri, and the work of Steyermark (1940) on succession in Ozark glades of the same state concerned, in part, prairie on pronounced slopes. Studies of Pammel (1896, 1899, 1902) and Shimek (1910*a*, 1910*b*, 1911, 1924) described the vegetation and enumerated the species of the loess bluff prairies in western Iowa or of the prairie openings or grassy meadows on the Iowa bluffs of the Mississippi River. Reports of Hanson (1922), of Costello (1931), and of Hopkins (1951) described prairies on loess bluffs along the Missouri River in Nebraska or prairies on loess hills in central Nebraska. A paper by Marks (1942) characterized what he termed the "goat prairies" of Wisconsin as prairies located on slopes "so steep that only the nimble goat could graze them." Sites described in these papers were prairies on steep slopes, or hill prairies.

Perhaps the earliest reference in the literature to Illinois grasslands on the upper slopes of bluffs is found in reports on the geology of Greene County and of Scott County by Worthen (1868). In these reports, Worthen described loess-capped bluffs with grass-covered knobs. These

*This article is based upon a thesis submitted by the writer to the Graduate College, University of Illinois, Urbana, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Botany.

grassy knobs were prairies on steep slopes, or hill prairies. It is surprising that no earlier descriptions of hill prairies are extant. Certainly the French settlers saw the grassy slopes and perhaps named the village of Prairie du Rocher (Prairie of the Rock) after the prairie above the cliffs. The capable botanist, André Michaux, who traveled from Kaskaskia to Cahokia and visited the village of Prairie du Rocher in 1795, apparently made no record, in that part of his journal included by Sargent (1889), of grasslands on the bluffs. Early gazetteers, as those of Peck (1834) and Ellsworth (1837), contain references to wet, dry, level, and undulating prairies, but apparently nothing about prairies on the bluffs. Short (1845) wrote a good description of the autumnal aspect of flatland prairies; his journey did not take him far enough to the west to include hill prairies.

Some references to hill prairies of Illinois have appeared in the past 50 years. Hus (1908) described the bluffs in the vicinity of Collinsville and mentioned open hillsides with grasses dominant and bluegrass the chief species. Vestal (1918) cited numerous prairie inclusions near Charleston, described their topography, and stated essential conditions for their presence. Woodard (1924) mentioned prairies on bluff-ridges. Vestal (1931) reported the occurrence of prairies on loess bluffs of the Mississippi River, and Vestal & Bartholomew (1941) briefly described some prairies on the loess bluffs of the Illinois River.

These authors were concerned only with local occurrences of hill prairies in Illinois. They did not report on the extent of hill prairies in the state, nor did they report in detail on the flora of the hill prairies, the characteristic plants, relative abundance, presence and space relations as determinable in plot studies, or the origin and history of hill prairies. In order to obtain the necessary information for a study of these characteristics of hill prairies and for a description of hill prairie vegetation in Illinois, the writer made numerous plant collections and plant identifications from 61 hill prairies, fig. 1, having a combined area of more than 200 acres. Detailed data pertaining to the vegetation were obtained from two prairies by use of plot studies, as explained in a later section of this paper.

The locations of some hill prairies were determined by the writer from the field notes made by Dr. Vestal during his travels in the state; of others, as the prairie southeast of Menominee Station in Jo Daviess County, from a study of aerial photographs. The majority, however, were found by field reconnaissance of the writer. During late autumn and early spring, hill prairies can easily be seen from the roads near or at the bases of the bluffs. Such roads, called bluff roads on some maps, are common in both the Mississippi and Illinois river valleys. In the Mississippi River valley, bluff roads were traveled by the author from Olive Branch in Alexander County northward to a point north and west of Glen Carbon in Madison County and from Hamburg in Calhoun County the 275-mile distance to the northwest corner of the state, except for short gaps in Hancock, Henderson, Mercer, Rock Island, and Jo Daviess counties. In the lower Illinois River valley, bluff roads were traveled from Grafton to Hennepin, except for a few gaps in Mason and Tazewell counties. The locations of prairie sites were marked on maps of sufficient scale to be used easily.

Not all hill prairies seen were visited, nor were bluffs of small streams examined for occurrences of hill prairies. Doubtless small prairie openings occur on the bluffs of small streams in the western part of the state. In eastern Illinois, Vestal (1918) observed several prairie openings along the Embarrass River near Charleston.

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It is indeed a pleasure to acknowledge the assistance given by Dr. A. G. Vestal, Department of Botany, University of Illinois, in the preparation of this study. I wish to thank him for his willingness to direct this investigation and for the many helpful suggestions he made during its progress.

Dr. L. R. Tehon, now deceased, and Dr. H. B. Mills, of the Natural History Survey, greatly facilitated the progress of

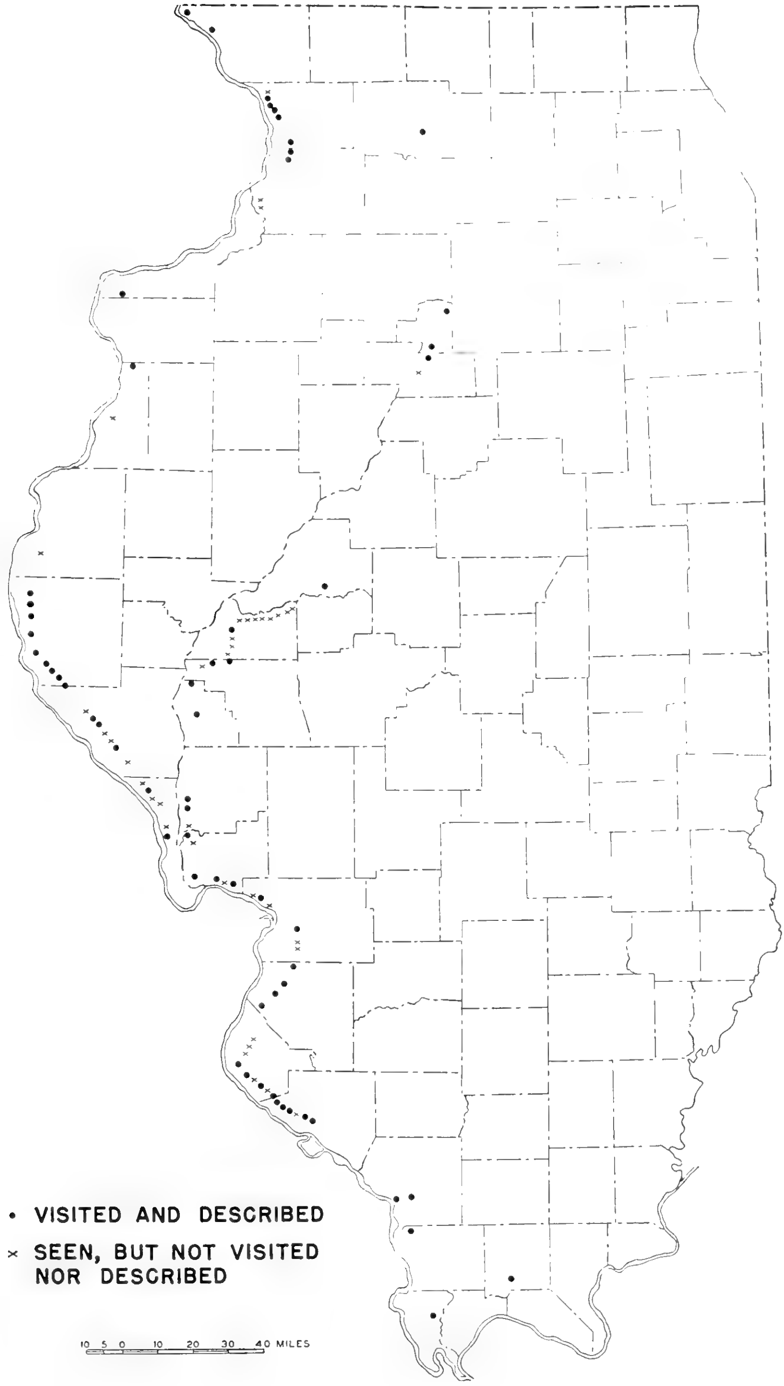

Fig. 1.—Location of the Illinois hill prairies which the author visited and of those which he saw only from a distance during the field work for this report. Hill prairies are most numerous on bluffs that trend northwest and southeast and have upper slopes facing the southwest. Bluffs of tributary streams were not examined for occurrences of hill prairies.

this study; for their help I am truly grateful.

Also, I wish to acknowledge here the assistance given by Mr. W. H. Phegley and Mr. J. J. Steibel of Prairie du Rocher, both of whom are now deceased. Some of the vegetation studies for this investigation were accomplished through their kind co-operation. I wish to thank Dr. G. W. White, Department of Geology, University of Illinois, and Dr. H. B. Willman and Dr. G. E. Ekblaw, Illinois State Geological Survey, for information concerning the geology of hill prairies; Mr. B. M. Woods, University Library Map Room, for his efforts to locate suitable aerial photographs; Mr. Julian Neill, East St. Louis, for assistance in the study of hill prairies in that region; Dr. J. L. Forsberg, Dr. P. F. Hoffman, Mr. J. W. Curfman, and Mr. R. E. Teegardin, while members of the Natural History Survey staff, for assistance with the statistics, the hydrogen-ion determinations, and the maps, diagrams, and drawings; and Mr. J. S. Ayars, also a Survey staff member, for his assistance with editorial problems.

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Mr. Dewey Clark, Quincy, took the pictures for the frontispiece and fig. 16. Mr. W. E. Clark, Natural History Survey staff, took the photographs used as figs. 3, 17, 18, 22, and 24. All other photographs were taken by the author.

The plant nomenclature used in this study is for the most part that of Hitchcock (1950) for grasses and Fernald (1950) for other plants. Where the nomenclature in this report does not conform to that in the manual of Hitchcock or that of Fernald, the manual name is included in brackets in the section on the flora of hill prairies. In instances in which a name of long standing has been changed in recent manuals, the former name, in brackets, also appears. Common names not from the above manuals are from Deam (1940) or Jones (1950).

ENVIRONMENT

The occurrence and distribution of plants, and consequently plant communities, is determined largely by climate and other environmental conditions, including the soil or substratum in which they grow. Some of the environmental conditions favoring the existence of hill prairies in Illinois are discussed in the following sections.

The climate in practically any part of Illinois permits growth of either prairie or forest. The circumstances (aside from those of accident and of history) which tip the balance and thus determine the details of local distribution of prairie and forest are chiefly the controls exerted by topography.

Climate

The following information on climatic conditions applies to the Mississippi River valley along the western border of Illinois, the region of the majority of hill prairies observed for this report. With few exceptions, the climatic data, taken from Page (1949), are from weather stations located along the Mississippi River. Exceptions are the data from the Mount Carroll, Carbondale, Anna, and Greenville weather stations; these stations are, respectively, about 9, 11, 12, and 33 miles from the nearest hill prairies.

Temperature.—The average January temperature along the western border of Illinois varies from 19.6 degrees Fahrenheit in northwestern Illinois (Dubuque, Iowa, weather station) to 36.2 in southern Illinois at Cairo. The average July temperature is 74.6 degrees in northwestern, 80.2 in west-central (Quincy weather station), and 79.8 in southwestern and southern Illinois (St. Louis, Missouri, and Carbondale, Illinois, weather stations). In Cairo, at the southernmost weather station in Illinois, the average July temperature is 79.5 degrees. The re-

Fig. 2.—An excavation in the toe or basal slope of a bluff southwest of Renault, Monroe County, which shows the characteristics of the rock fragments that form the basal slopes of many river bluffs. The fragments have spalled from the cliff above the slope.

corded extremes of temperature are –35 degrees at Mount Carroll (January 22, 1930) and 115 degrees at Greenville (July, 1936). The highest recorded temperature in that part of Illinois along the Mississippi River is 114 degrees, recorded at Quincy in July, 1936.

Precipitation.—The average annual precipitation along the western border of Illinois varies from 33.13 inches in northwestern Illinois (Dubuque, Iowa, weather station) to 41.39 at Cairo and 47.43 at Anna. Averages of snowfall, notably less than 10 per cent of the annual precipitation, are 9.9 inches at Cairo and 32.3 at Mount Carroll. The wettest month in northern and west-central Illinois is June. The wettest month in southern Illinois varies with location; May is the wettest month at Anna, March the wettest at Cairo. During the growing season, April through September, Cairo receives 49.41 per cent of its annual rainfall; Anna, 52.77 per cent; Quincy, 65.26 per cent; and northwestern Illinois (Dubuque, Iowa, weather station), 66.77 per cent.

Frost.—The average frost-free periods along the western border of Illinois are April 19 to October 16 in northwestern Illinois (Dubuque, Iowa, weather station), April 13 to October 20 at Quincy in west-central Illinois, April 9 to October 26 at Anna, and March 30 to October 29 at Cairo.

Wind.—The prevailing wind in winter along the western border of Illinois is from the northwest; in summer, it is from the southwest, often hot and dry.

Physiography and Geology

Steep slopes or bluffs abut the broad, deeply alluviated floodplains or bottomlands of many of the major stream valleys in Illinois. The continuity of the bluffs is broken by tributary streams that enter the main valleys. The underlying bedrock and the surficial material determine the form of the bluffs.

The bedrock of the bluffs on which hill prairies occur is limestone, dolomite, sandstone, shale, or combinations of these; the geological ages of the uppermost strata range from Middle Ordovician to Upper Pennsylvanian. In most places, the bedrock crops out to form a cliff as much as 200 feet above the valley floor. Frequently, a stony talus or toe slope is present at the base of the cliff, fig. 2, and, unless recently disturbed, supports a mixed forest. A mantle of surficial material covers the bedrock at the top and forms the brow or upper slope of the bluff. In some places, as in parts of Morgan and Madison counties, sandy loess and colluvium completely mantle and conceal the bedrock.

Surficial Material.—Surficial material, the unconsolidated material above the bedrock, may be residual or transported. Residual material, which supports both prairie and forest in Illinois, occurs south of the glaciated area, as, for instance, on the rocky slopes at Cave Creek prairie and the cherty ridge-top at Tamms. On most other prairie slopes the surficial material is transported—loess or glacial drift.

Loess, a windblown accumulation of silt with subordinate clay and minor amounts of fine sand, occurs over large areas of the Midwest. "One of the most important and best-known occurrences of loess in the world is in the Mississippi River Basin" (Leighton & Willman 1950). Loess mantles most of Illinois except the large stream valleys and areas of lake sediments and sand dunes.

The eolian hypothesis of the origin of loess deposits is the one accepted by most geologists who have studied this material extensively. Udden (1894) wrote, "From a dynamical point of view the wind-theory would appear to furnish an adequate explanation of the occurrence of the loess in the Mississippi valley, at least as to most of its phases." Shimek (1896) advocated the eolian hypothesis and based his conclusions in part upon the land snail shells he found in loess. Chamberlin (1897) presented the hypothesis that loess (of the Mississippi Valley) is a wind deposit and that the sources of the material were the floodplain deposits of the glacial rivers. The hypothesis of the origin of loess deposits from backswamp sediments (Russell 1944) does not seem tenable for Illinois.

The thickest loess deposits in Illinois

are found along the east bluffs of the Mississippi and Illinois rivers, where, in some places, they are more than 300 inches in depth. Such thick deposits occur in places where the valley changes from a northwest-southeast trend to one that is north-south or northeast-southwest, as in Carroll, Madison, and Jackson counties. Other deposits of great thickness occur just east of the wide portions of the main valleys, as east of the Illinois River valley from Mason County south into Morgan County. Away from the main river valleys the loess deposits become progressively thinner. Not only do the deposits of loess become thinner but also the mean particle size decreases with distance from the bluffs (Smith 1942). Loess on the bluffs in many places is somewhat sandy.

The hydrogen-ion concentration of loess, as determined with a Beckman pH meter in samples from 10 hill prairies in southern and central Illinois, ranges from 7.86 to 8.41. All samples, when treated with dilute hydrochloric acid, effervesced freely, showing the presence of calcium carbonate. Calcium carbonate is often found in the form of concretions, "loess kindchen," fig. 3, on prairie slopes.

In Illinois, soils derived from loess support both prairie and forest.

The only bluff prairie slopes that are mantled by glacial drift and that the writer examined for this report are in Putnam County. These bluffs were last covered by ice during the Tazewell substage of the Wisconsin glaciation, fig. 4. Soils derived from till support both prairie and forest in Illinois.

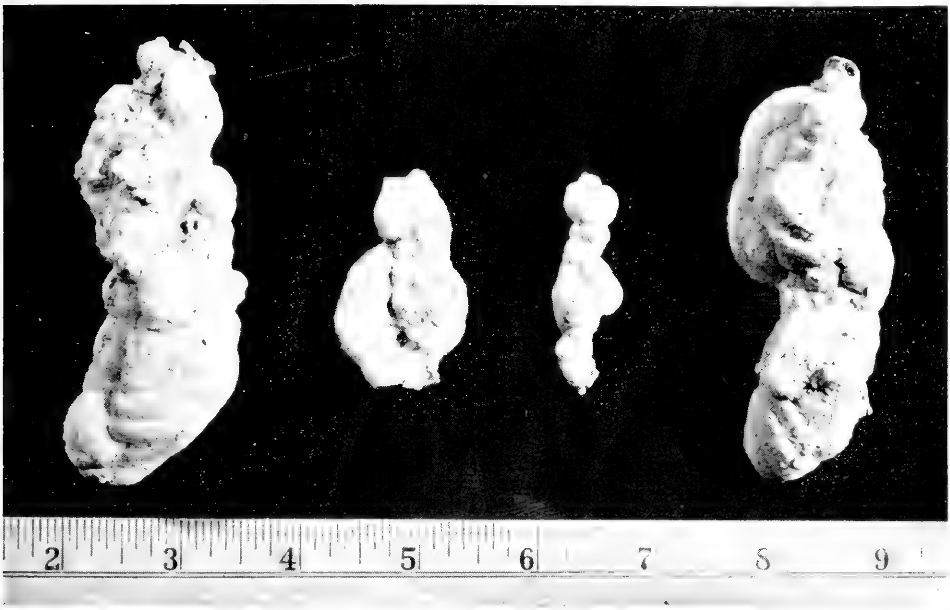

Fig. 3.—Calcareous concretions or "loess kindchen" from Phegley hill prairie near Prairie du Rocher, Randolph County. Such concretions are common on many prairie slopes in Illinois.

Exposure.—Hill prairies are most abundant on the northeast sides of the valleys, fig. 1, where the bluffs trend northwest-southeast, or on bluffs that border the wide, flat bottomlands or broad, flat terraces over which winds blow with little hindrance, or on bluffs that are high. Certain physiographic situations, direction and steepness of slopes, altitudes of bluffs, and width of adjacent bottomlands are very advantageous in bringing about high temperature and low humidity, two conditions that favor a high evaporation rate, which in turn favors prairie (Shimek 1911). Southwest- and west-facing bluff slopes receive more nearly at right angles the rays of the hot afternoon (2 o'clock) summer sun than do other slopes. Slopes that face these directions are subject to higher temperatures. Such slopes, especially those of high bluffs, are also directly exposed to the prevailing southwesterly winds of the growing season, which increase the water-loss both from plants and the surface soil. The upper bluff slopes are consequently extremely xeric and support prairie rather than forest.

STAGE	SUB-STAGE
WISCONSIN GLACIAL	MANKATO
	CARY
	TAZEWELL
	IOWAN
	FARMDALE (PRO-WIS.)
SANGAMON INTERGLACIAL	
ILLINOIAN GLACIAL	BUFFALO HART JACKSONVILLE PAYSON
	LOVELAND (PRO-ILL.)
YARMOUTH INTERGLACIAL	
KANSAN GLACIAL	
	PRO-KANSAN?
AFTONIAN INTERGLACIAL	
NEBRASKAN GLACIAL	

Fig. 4.—Classification of geologic time during the Pleistocene Period. (After Leighton & Willman 1950.)

Where the bottomlands are wide, wind movement is unimpeded for some disstance. Brow slopes of bluffs bordering such bottomlands are xeric. Accordingly, hill prairies are common in the northern part of the American Bottoms in Madison and St. Clair counties where the Missisipi River valley is wide. In northern Cass County, hill prairies are found on bluffs that trend almost east-west and that border a broad, flat, sandy terrace that extends to the Illinois River, which here flows southwestward. The xeric conditions on these brow slopes result in part from the movement of westerly winds over the broad, flat, sandy terrace and in part from the deep mantle of very sandy loess, which favors rapid loss of water by downward percolation.

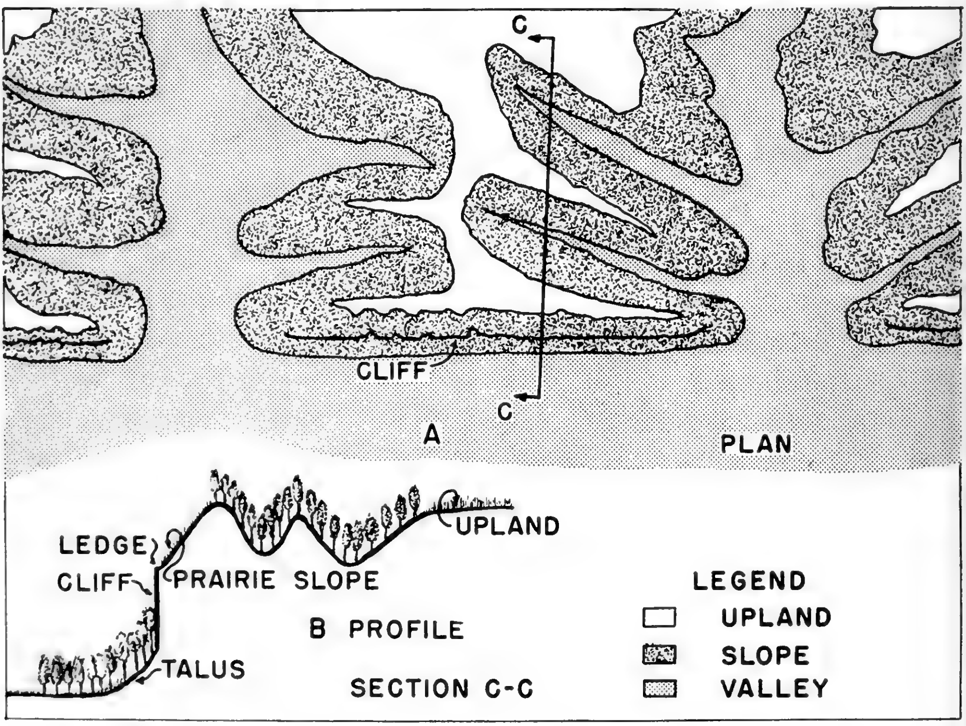

Fig. 5.—Schematic plan, *A*, and profile, *B*, of a bluff of type common along major stream valleys in Illinois. The steep valley wall between the two large tributary valleys in the plan is the bluff shown in the profile (section C-C). The bluff includes a talus or toe slope, a cliff, a rock ledge, and an upper or brow slope, which in the profile shows a cover of prairie.

Hill prairies are absent from the generally northeast-facing slopes of the bluffs on the southwest sides of valleys; these slopes are covered by forests except where they have been cleared and are now in cultivation.

Altitude.—A relationship apparently exists between height of the bluffs and occurrence of hill prairies. More prairie openings and prairie strips are found on the Mississippi River bluffs in Pike, Calhoun, Monroe, and Randolph counties where the bluffs are high than on those bluffs just north or south of Quincy in Adams County where the bluffs are low. At Clendenny prairie (Calhoun County), the bluff rises 220 feet above the bottomland; at Sessions (Pike County), 240 feet; at Fults (Monroe County), 340 feet; and at Phegley and Sampson (Randolph County), 310 feet. The bluffs north of Quincy are only slightly more than 100 feet and those south of Quincy are but 120 feet above the Mississippi River bottomland.

Parallel Tributary Valleys.—During the course of field work, the writer observed an interesting feature of the bluffs. In 34 of the 61 hill prairies visited, tributary valleys are found approximately parallel to and short distances back of the bluffs, fig. 5. In each of the 34 sites, the area between the major stream valley and the parallel valley, or valleys, is a narrow ridge that is joined to the upland beyond by another narrow ridge more or less at right angles to the bluff. Hill prairies grow on the upper slope of the ridge that faces the major stream valley, a slope referred to as the upper bluff slope or the brow slope. Narrow ridges of this type occur where streams have cut back into the valley wall and where, at approximately right angles to them, their tributaries have developed. The tributary valleys, mostly parallel to the bluffs, are V-shaped and forest covered.

Environmental Conclusions

As the climate and soils of Illinois permit the growth of both prairie and forest, it can be concluded that certain geomorphic conditions are accountable for the occurrence of hill prairies on the upper bluff slopes. Location, the place in reference to major stream valleys, and topography, largely the result of the geomorphic history of the region, exert strong influences, or controls, that are responsible for the presence of hill prairies. The growth of grassland rather than forest on the upper bluff slopes is attributed to priority of occupation by prairie species and to the xeric conditions that are produced by the combination of local exposure to the sun and to the wind (especially to wind moving unimpeded across wide floodplains), the height of the bluffs above the adjacent bottomlands, the steepness and direction of the upper slopes, and the permeability of the substratum. Thus, the hill prairie community is the result of a complex set of conditions, the effectiveness of which is determined by location and topography.

VEGETATION OF HILL PRAIRIES

The typical vegetation of hill prairies is the bunch-grass type. In most places, *Andropogon scoparius* is the dominant species. In some places, such bunch grasses as *Bouteloua curtipendula, A. gerardi,* and *Sorghastrum nutans* are locally dominant. In order to learn about the vegetation, its density, the ground space it occupies, the foliage area or crown cover, the available space per plant, and the frequency of occurrence of species in plots of several sizes, the writer made detailed studies of hill prairie vegetation by means of plot studies in two prairies. He also made studies of some characteristics of all stands from species lists and field notes.

Phegley and Sampson Prairies

From the 61 hill prairies that he visited, the writer chose Phegley and Sampson hill prairies for the detailed vegetational studies. These areas are on the same bluff ridge. In their surface features, Phegley and Sampson prairies are typical of hill prairies. There is a rock ledge and cliff at their base. A stony slope lies above the rock ledge, and loess caps the bluff. Each prairie area possesses spurs and coves. At the time this study was made, prairie covered both the stony

Fig. 6.—Steep spur front in unpastured Sampson hill prairie, north of Prairie du Rocher, Randolph County, showing some slumping of the loess.

Fig. 7.—Steep spur front in pastured Phegley hill prairie, north of Prairie du Rocher, Randolph County, showing considerable slumping of the loess.

and loess slopes. The Phegley prairie was pastured; the Sampson was not. Thus, it was possible to compare pastured and unpastured prairie slopes in the same locality.

Because Phegley and Sampson prairies were accessible to the writer by automobile, no laborious and time-consuming ascent from the bottomland, up the basal slopes and over the rock ledge, was necessary; steep climbs are necessary to attain the majority of hill prairies in Illinois.

Study Procedures.—For detailed vegetation studies in hill prairie, the upper slopes of spurs seemed to be the best sites because these slopes had a vegetation that was nearly "pure" prairie, and they had surfaces that showed little erosion. The steep spur fronts, figs. 6 and 7, contained species characteristic of prairie but showed

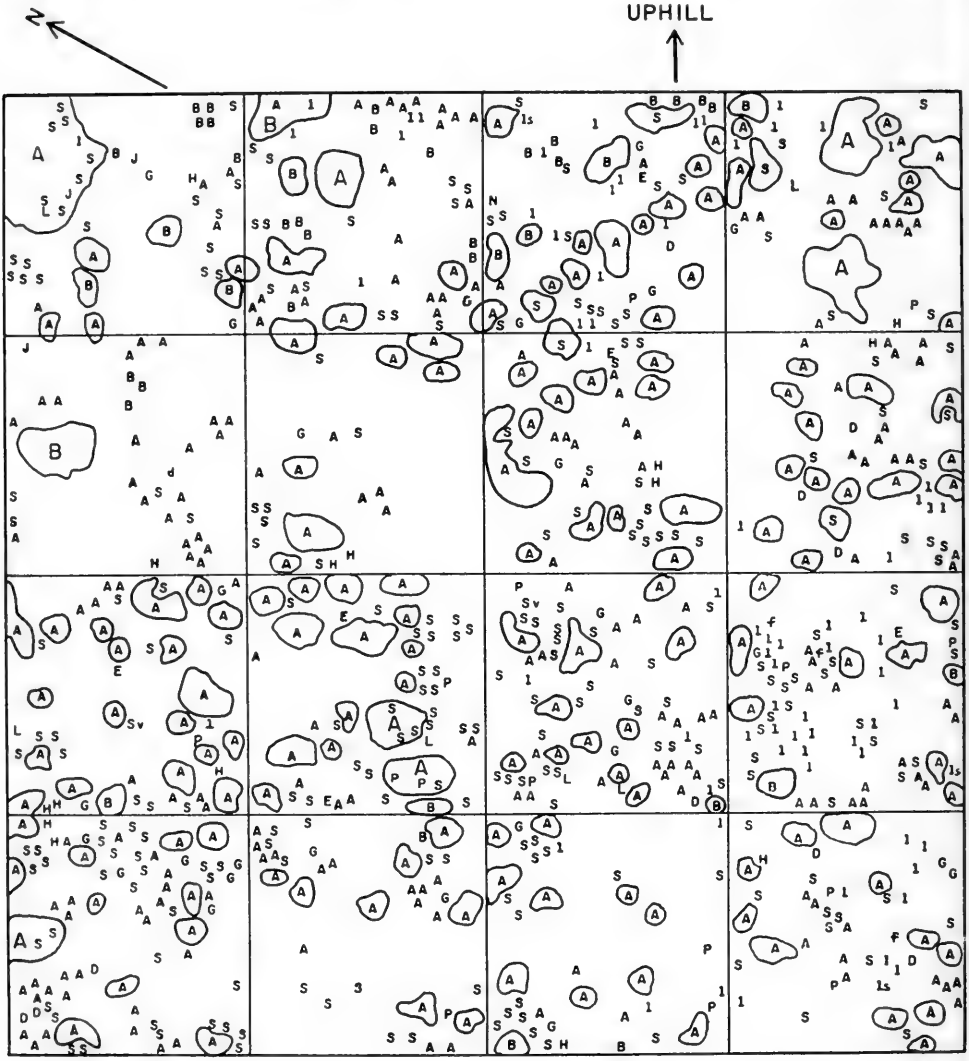

Fig. 8.—A 1-milacre quadrat in the pastured Phegley hill prairie, charted October 9 and 10, 1951, by A. G. Vestal and R. A. Evers. A, *Andropogon scoparius*; S, *Solidago nemoralis*; l, *Lespedeza stipulacea*; B, *Bouteloua curtipendula*; G, *Gerardia* sp.; P, *Petalostemum purpureum*; H, *Houstonia nigricans*; D, *Desmodium ciliare*; L, *Lespedeza capitata*; E, *Euphorbia corollata*; f, *Cassia fasciculata*; J, *Juniperus virginiana*; ls, *Linum sulcatum*; N, *Senecio plattensis*; v, *Polygala verticillata*; and d, *Hedeoma hispida*.

more or less slumping of loess and, as a consequence, possessed sizable areas without plant cover. The more gentle slopes near the bases of the prairies had less severely eroded surfaces, and consequently more plant cover, than the steep spur fronts, but they contained more species characteristic of rock ledges.

Sizes and Shapes of Study Plots.—A 9-milacre square was staked on the upper slope of a spur of each of the prairies, Phegley and Sampson. These plots were located at some distance from the crest of the bluff in an attempt to exclude forest plants and pasture weeds. Each 9-milacre square was then divided into nine 1-milacre quadrats (0.001 acre or 4.046 square meters). The central milacre of the 9-milacre grid was selected for mapping.

Each central milacre was divided into

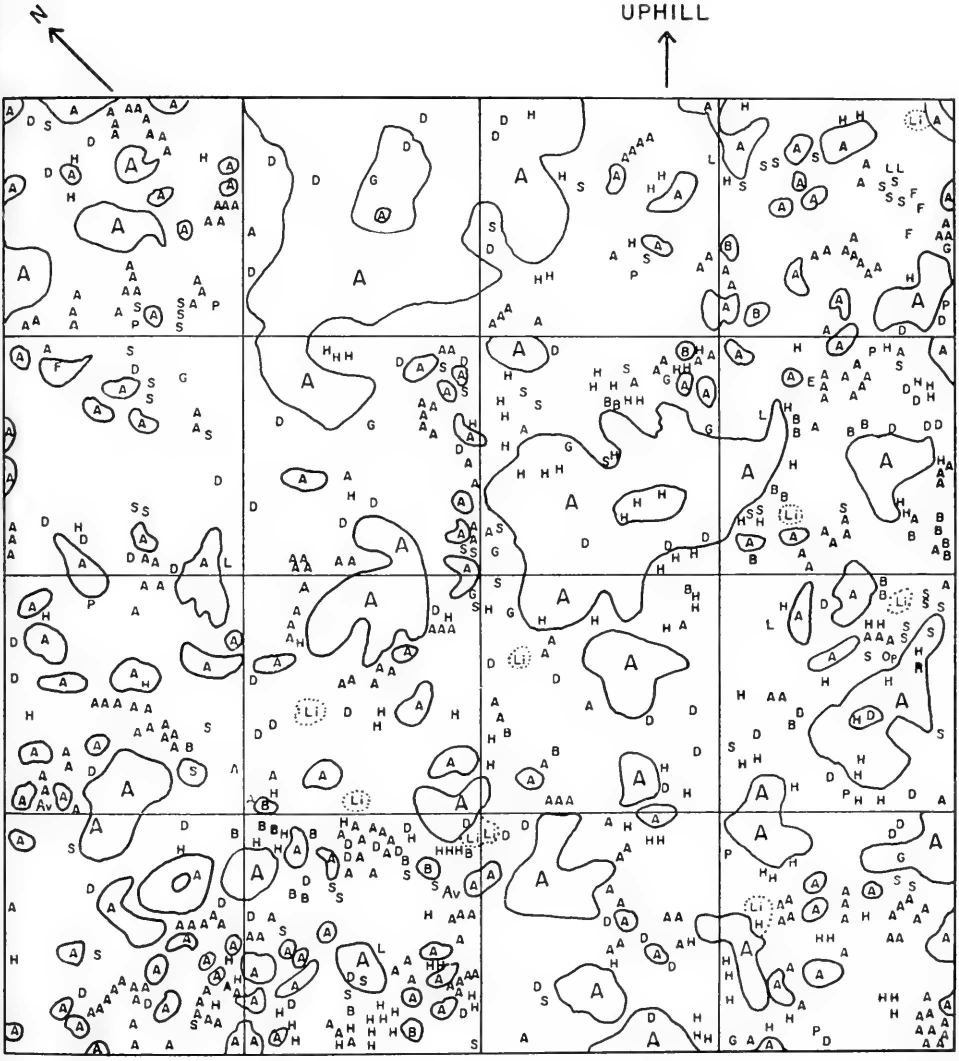

Fig. 9.—A 1-milacre quadrat in the unpastured Sampson hill prairie, charted October 15 and 16, 1951, by R. A. Evers. A, *Andropogon scoparius*; Li, *Lecidea* spp.; H, *Houstonia nigricans*; D, *Desmodium ciliare*; S, *Solidago nemoralis*; B, *Bouteloua curtipendula*; G, *Gerardia* sp.; P, *Petalostemum purpureum*; F, *Andropogon gerardi*; L, *Lespedeza capitata*; Av, *Agave virginica*; E, *Euphorbia corollata*; Op, *Opuntia rafinesquii.*

64 small squares of 1/64 milacre (approximately 6.25 square decimeters) to facilitate mapping. These small units were combined in working over the data to give 1/16-, 1/4-, and 1-milacre plots. The central milacre quadrat in the Phegley prairie was mapped, fig. 8, and the shoots in this milacre were counted on October 9 and 10, 1951, by the writer with the assistance of Dr. A. G. Vestal; the central milacre in Sampson prairie was mapped, fig. 9, and the shoots were counted on October 15 and 16, 1951, by the writer. In addition, a list of plant species was made for each 1/4 milacre in the other 8 milacres of each of the 9-milacre grids.

In order to find the increase in number of species with an increase in area, the writer staked a 25-milacre square and a 50-milacre rectangle in each of the two prairies, fig. 10. In Phegley, the 25-milacre square was downslope from the north half of the 50-milacre plot, the half that included the 9-milacre square. In Sampson, because of the proximity of woodland, the arrangement could not be made identical with the arrangement of plots in Phegley: the 9-milacre square was inside the 25-milacre square; the south half of the 50-milacre rectangle was downslope from the 25-milacre square. The staked 25- and 50-milacre plots were divided into strips 6.6 feet wide, making five strips each with an area of 5 milacres and five each of 10 milacres. Species lists were then compiled for the staked areas of each prairie by units of 1/64, 1/16, 1/4, 1, 3, 5, 9, 10, 25, 50, and 75 (303.5 square meters) milacres.

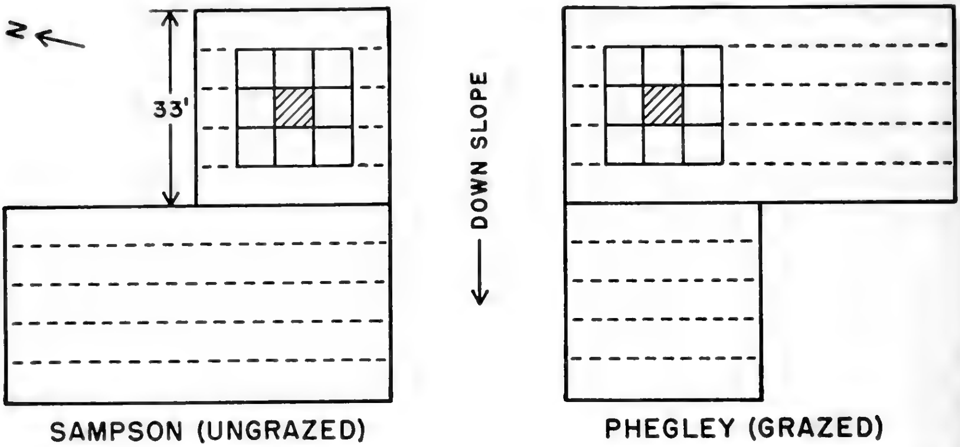

Fig. 10.—Arrangement of plots and strips in two hill prairies. Each shaded square represents the mapped central milacre of a 9-milacre grid.

From data obtained from the staked areas, it was possible to determine the number of plant species and number of shoots in plots of various sizes; for each species, the frequency of occurrence in plots; for each of the several grass species, the area covered or ground space of plants; and, for all species collectively, the estimated number of plants per unit of area and the available space per plant. Comparisons between pastured and unpastured hill prairie were made. From the data it was possible to construct a species-area curve and from the curve to find the sizes of certain reference areas, as will be explained later in this section.

Method of Counting Plant Units.—For plants other than grasses, each shoot that appeared above the ground surface and was without obvious connection to another shoot was counted as one unit, or individual. For example, each single rosette of *Solidago nemoralis* was counted as one individual; each shoot of *Houstonia nigricans, Petalostemum purpureum,* and *Desmodium ciliare* was counted as one individual unless connections with other shoots could be traced.

For the three bunch grasses, *Andropogon scoparius, A. gerardi,* and *Bouteloua curtipendula,* the shoots that grew as individuals or in small bunches were counted and recorded. In the Phegley prairie, the shoots were small and mostly distinct and separate. In the Sampson prairie, the shoots were mostly aggregated into "tufts," and these into bunches of varying sizes. In this prairie, *A. scoparius* occurred also in several large patches within the plots. The number of shoots in such patches was estimated as follows: the average number of shoots per square inch in the smaller bunches was determined by counts; this number was multiplied by the number of square inches in each of the larger patches.

During later stages of preparation of this report, it was evident that an estimate of numbers of grass-plant individuals per unit of area could be of great value in finding average plant densities in hill prairies. Other workers have made such estimates. Steiger (1930), in his study of high and low prairies of Nebraska, apparently counted each occurrence, whether a single shoot or a bunch, as a grass-plant individual. From the quadrat maps in his report, the bunches of grass appear not so large as those in hill prairies in Illinois. Korstian & Coile (1938), in a study of plant competition in forest stands, found the most densely covered forest-floor milacre had about 10 grass plants per 0.01 milacre. "Thus each 0.01 milacre occupied by a colony was regarded as fully stocked, even though it contained few or no individual plants." Neither Steiger's procedure nor the one followed by Korstian & Coile seemed adequate for Illinois hill prairies. The estimate of numbers of grass-plant individuals for these prairies was therefore made by a different method.

Two bunches of *Andropogon scoparius* were obtained, one from the Northeast Meredosia prairie, one from the basal slope at Reavis Spring prairie. Each bunch was taken from an unpastured prairie strip that was separated from the adjacent pastured prairie slopes by a fence. These bunches were carefully dissected to find how many shoots were connected by living stems in what might be considered as individual plants. For convenience, each aggregate of shoots considered to be an individual plant was called a tuft. Before separation, each bunch was mapped with a pantograph to show foliage area or crown cover, area at ground surface, location of solitary live shoots, and what *appeared* to be aggregates of shoots or "apparent tufts." (It was recognized that separation of a bunch into tufts might give very different results from those of the preliminary surface examination.) It was found that the average number of shoots per tuft of *A. scoparius* was 3.375 for the Northeast Meredosia sample and 3.793 for the one from Reavis Spring. The characteristic tuft (grass-plant individual) of *A. scoparius* was found to be an aggregate of 3 or 4 shoots, average 3.5.

The same method was used by H. A. Moore and A. G. Vestal to determine the number of shoots per plant individual for *Andropogon gerardi.* In a clump of big bluestem, collected by Moore from a railroad trackway east of Urbana, Moore and Vestal found by separation that the average number of shoots per tuft or grass plant was 1.739. The characteristic tuft (grass-plant individual) of big bluestem consisted of 1 or 2 shoots, average 1.75.

As a preliminary step in estimating the number of plants of *Bouteloua curtipendula,* the writer obtained a small sample from Mud Creek prairie and carefully dissected the bunches to determine the number of shoots per plant or tuft. It was found that the average number of shoots per tuft was 3.437; the individual plant of *B. curtipendula* was an aggregation of 3 or 4 shoots, average 3.5.

For each of the bunch-grass species, the estimated number of tufts in bunches was found by dividing the number of shoots in bunches by the average number of shoots per tuft, or by a factor based upon this average.

Density of Vegetation.—The measure of vegetation density in this study is the number of plants per milacre. The mapped central milacre of the Sampson and that of the Phegley prairie were used in determining density for this report.

Grasses.—In the central milacre of the Sampson prairie, 4,051 shoots of *Andropogon scoparius* grew in bunches and patches. The 4,051 shoots formed an estimated 1,157 grass-plant individuals or tufts. This estimate was reached by dividing the number of shoots in bunches and patches (4,051) by the number of shoots in a typical tuft (3 or 4, average 3.5). There were in addition 247 shoots not aggregated into tufts or bunches. These were considered individual plants, as it was impossible to determine any underground connections without digging and removing these shoots from the milacre. The estimated total number of individuals of *A. scoparius* was 1,404.

In the Phegley prairie, the shoots of *Andropogon scoparius* were mostly short and well separated, with very little lateral extension of the foliage. The open appearance of each bunch, the large proportion of bare ground, and the considerable ground area per shoot within the bunches were attributed to grazing and trampling by cows. Cows doubtless destroyed many shoots either by pulling them out or breaking them off and thus materially reduced the number of shoots per tuft.

In the samples taken from ungrazed hill prairie in two sites, Northeast Meredosia and Reavis Spring, the number of shoots per tuft averaged between 3 and 4. In the mapped central milacre of the pastured Phegley prairie, the number of shoots per tuft was not so large; it was conservative to place the number of shoots per tuft at one-half that of ungrazed prairie, that is, 1.5 or 2.0, average 1.75. The 1,143 shoots in bunches thus formed an estimated 653 tufts or grass-plant individuals. In addition, 196 isolated shoots, representing that many isolated plant individuals, were counted. The estimated total number of *A. scoparius* plants was 849.

In the mapped Sampson milacre, 22 shoots of *Andropogon gerardi* were found; 19 of these occurred in one bunch. These 19 shoots formed 11 plant individuals (estimated). With the 3 isolated plants added, the estimated number of *A. gerardi* individuals was 14. *A. gerardi* did not occur in the mapped milacre in the Phegley prairie.

In the central milacre of Sampson, 6 bunches of *Bouteloua curtipendula* with 43 shoots were mapped. These 6 bunches contained an estimated 12 plants. In addition, 32 isolated plants were counted. The estimated number of individuals of *B. curtipendula* was 44.

In the mapped Phegley milacre, 15 bunches of *Bouteloua curtipendula* with 108 shoots were charted. These 15 bunches contained an estimated 31 plants. In addition, 25 isolated plants were counted. The estimated number of individuals of *B. curtipendula* was 56.

The ungrazed Sampson prairie contained an estimated 1,462 grass plants in the central milacre; the grazed Phegley prairie 905 in the central milacre. Table 1 summarizes the above data.

Plants Other Than Grasses.—Of plants other than grasses in the central milacre of Sampson prairie, 487 plants of

Table 1.—Shoot counts and estimated numbers of bunch-grass plant individuals in the mapped central milacre of Sampson and of Phegley hill prairies.

Kind of Growth	Sampson Prairie				Phegley Prairie		
	Andropogon scoparius	*Andropogon gerardi*	*Bouteloua curtipendula*	Total	*Andropogon scoparius*	*Bouteloua curtipendula*	Total
Shoots aggregated in bunches	4,051	19	43	4,113	1,143	108	1,251
Isolated shoots	247	3	32	282	196	25	221
Total	*4,298*	*22*	*75*	*4,395*	*1,339*	*133*	*1,472*
Plants in bunches (estimated)	1,157	11	12	1,180	653	31	684
Isolated plants (estimated)	247	3	32	282	196	25	221
Total	*1,404*	*14*	*44*	*1,462*	*849*	*56*	*905*

Table 2.—Species and numbers of plant individuals in the central milacre of Sampson hill prairie.

SPECIES	NUMBER OF PLANT INDIVIDUALS
Andropogon scoparius	1,404*
Houstonia nigricans	141
Desmodium ciliare	80
Solidago nemoralis	64
Bouteloua curtipendula	44*
Andropogon gerardi	14*
Gerardia sp.†	11
Petalostemum purpureum	9
Lespedeza capitata	6
Agave virginica	2
Euphorbia corollata	1
Opuntia rafinesquii	1
Lecidea spp.	172*

* Estimated.
† Possibly *G. gattingeri.*

10 different species were mapped and counted; in the central milacre of Phegley prairie, 436 plants of 14 species. Table 2 shows density for both grass and nongrass species in the mapped Sampson milacre; table 3 gives similar information for species in the mapped Phegley milacre.

Total Densities.—In Sampson prairie, the density in the mapped central milacre was 1,949 plants; in Phegley, 1,341.

In both prairies, grass-plant individuals were more numerous than the nongrass plants. In Sampson, 75 per cent of the plant individuals were grasses and 25 per cent were not grasses; in Phegley, 67 per cent were grasses and 33 per cent were not. It is of interest that the nongrass species made up a higher percentage of the individual plants in grazed prairie than in ungrazed.

Ground Space of Plants.—Ground space of plants is considered here as the area occupied by the plants at ground surface. The writer determined the ground space for grasses, table 4, from the maps of the central milacre of Phegley and Sampson prairies by use of a planimeter.

Table 3.—Species and numbers of plant individuals in the central milacre of Phegley hill prairie.

SPECIES	NUMBER OF PLANT INDIVIDUALS
Andropogon scoparius	849*
Solidago nemoralis	270
Lespedeza stipulacea	71
Bouteloua curtipendula	56*
Gerardia sp.†	29
Petalostemum purpureum	15
Houstonia nigricans	13
Desmodium ciliare	11
Lespedeza capitata	8
Euphorbia corollata	6
Cassia fasciculata	4
Juniperus virginiana‡	3
Linum sulcatum	3
Senecio plattensis	1
Polygala verticillata	1
Hedeoma hispida	1

* Estimated.
† Possibly *G. gattingeri.*
‡ Small seedlings.

Phegley Prairie.—In the central milacre of this pastured prairie, *Andropogon scoparius* covered at ground level 1,107 square inches (71 square decimeters*), or 17.64 per cent of the milacre; *Bouteloua curtipendula* occupied 138.4 square inches (9 square decimeters), or 2.21 per cent of the milacre, tables 4 and 6. The two bunch grasses covered 1,245.4 square inches (80 square decimeters), or 19.85 per cent of the quadrat at ground level.

Most of the plants other than grasses, 437 individuals of 14 species, occurred in the spaces between the grass bunches. The

*Metric equivalents in this section on ground space are given to the nearest whole number.

Table 4.—Ground space or areas (square inches) occupied at ground surface by the bunch grasses in the central milacre of Sampson and of Phegley hill prairies.

TYPE OF PLANT GROWTH	SAMPSON PRAIRIE				PHEGLEY PRAIRIE		
	Andropogon scoparius	*Andropogon gerardi*	*Bouteloua curtipendula*	Total	*Andropogon scoparius*	*Bouteloua curtipendula*	Total
Bunches	1,678.0	8.7	18.8	1,705.5	945.0	112.4	1,057.4
Isolated shoots	103.0	1.3	10.5	114.8	162.0	26.0	188.0
Total	*1,781.0*	*10.0*	*29.3*	*1,820.3*	*1,107.0*	*138.4*	*1,245.4*

estimated ground space covered by these plants was 157.9 square inches, table 5, an estimation computed in the following manner. There were 29 rosettes of *Solidago nemoralis* that were clustered into five groups or patches. The five patches occupied 36.59 square inches in the central milacre. The remaining 241 rosettes of this species were small and covered about 0.5 square inch each, or a total of 120.5 square inches. The total ground space of *S. nemoralis* for the milacre was 157.09 square inches. The remaining 167 individuals of 13 species were small and averaged only 0.08 inch (2 mm.) in diameter, or 0.0049 square inch in area. The estimated ground space of these plants was 0.82 square inch (167 x 0.0049). The estimated ground space for all the nongrass species was 157.9 square inches (10 square decimeters), or 2.52 per cent of the quadrat, tables 5 and 6. The total ground space for all plants in the central milacre at Phegley prairie was 1,403.3 square inches (91 square decimeters), or 22.37 per cent of the quadrat. There remained 4,869.3 square inches, or 77.63 per cent of the quadrat, that was bare loess, tables 5 and 6.

Sampson Prairie.—In the central milacre of this unpastured prairie, *Andropogon scoparius* covered 1,781 square inches (115 square decimeters), or 28.39 per cent of the milacre; *Bouteloua curtipendula* and *A. gerardi* together occupied 39.3 square inches (3 square decimeters), or 0.63 per cent of the plot, tables 4 and 6. The three bunch grasses covered at ground level 1,820.3 square inches (117 square decimeters), or 29.02 per cent of the milacre.

The ground space for the remaining 487 plant individuals of 10 species was computed in the same manner as was the ground space for the plants in Phegley. *Lecidea,* which grows over the surface of the loess, occupied 29.6 square inches of the milacre as computed from the map by use of a planimeter. The *Agave* and *Opuntia* were each about 0.625 inch in diameter at the ground surface; the three plants occupied approximately a square inch. The 64 small rosettes of *Solidago nemoralis* covered 32.0 square inches (64 x 0.5). The remaining 248 plants, all small, covered 1.2 square inches. The nongrass species together occupied 63.8 square inches (4 square decimeters), or 1.02 per cent of the quadrat, tables 5 and 6. The total ground space for the plants in this milacre of ungrazed prairie was 1,884.1 square inches (122 square decimeters), or 30.04 per cent of the charted area. There remained 4,388.5 square inches or 69.96 per cent of the quadrat not occupied at ground level by plants.

Table 5.—Ground space or areas (square inches) occupied at ground surface by grass plants, plants other than grasses, and bare loess in the central milacre of Sampson and of Phegley prairies.

Type of Plant Growth	Sampson Prairie	Phegley Prairie
Bunch grasses	1,820.3	1,245.4
Plants other than grasses	63.8	157.9
All plants	1,884.1	1,403.3
Bare loess	*4,388.5*	*4,869.3*

Table 6.—Per cent of the central milacre of Sampson and of Phegley hill prairies occupied at ground surface by bunch grasses, plants other than grasses, and bare loess.

Species or Type of Plant Growth	Sampson Prairie	Phegley Prairie
Andropogon scoparius	28.39	17.64
Andropogon gerardi	0.16	0.00
Bouteloua curtipendula	0.47	2.21
All bunch grasses	29.02	19.85
Plants other than grasses	1.02	2.52
All plants	30.04	22.37
Bare loess	*69.96*	*77.63*

Foliage Area or Crown Cover.—Foliage area, crown area, or crown cover is considered here as the area that would be mapped if the crowns of the plants were projected on the ground surface directly below. Although foliage area was not mapped in the field, it was estimated in the following manner.

In the Sampson prairie, *Andropogon scoparius* had a large foliage area, fig. 11. The aspect of this grass in Sampson was similar to its aspect at Northeast Meredosia, where a sample was collected for separation. Foliage area of this sample was mapped. A factor of approximately 2.7 was derived when foliage area of the sample was divided by its ground space.

Fig. 11.—Upper spur slope in unpastured Sampson hill prairie. The foliage area of the plants is much greater here than in the pastured Phegley prairie. *Andropogon scoparius* is the dominant grass; *A. gerardi* also is present. The above view is to the left (northwest) of plots staked for vegetation studies of this report.

Fig. 12.—Upper spur slope in the pastured Phegley hill prairie. The foliage area of the plants is small. *Andropogon scoparius* is the dominant grass. To the right in the above view is a small part of some of the plots staked for the vegetation studies of this report.

Table 7.—Foliage area (square inches) for plants in the central milacre of Sampson and of Phegley hill prairies.

Species or Type of Plant Growth	Sampson Prairie	Phegley Prairie
Andropogon scoparius	4,809	1,994
Andropogon gerardi	27	0
Bouteloua curtipendula	60	285
All bunch grasses	4,896	2,279
Plants other than grasses	92	246
All plants	4,988	2,525

Table 8.—Foliage area (per cent of total area) for plants in the central milacre of Sampson and of Phegley hill prairies.

Species or Type of Plant Growth	Sampson Prairie	Phegley Prairie
Andropogon scoparius	76.66	31.79
Andropogon gerardi	0.43	0.00
Bouteloua curtipendula	0.96	4.54
All bunch grasses	78.05	36.33
Plants other than grasses	1.47	3.92
All plants	79.52	40.25

In order to estimate foliage area of *A. scoparius* in the central milacre of Sampson, the writer multiplied the ground-space value of this grass by 2.7. The same factor was used in order to estimate foliage area for *A. gerardi*. For *Bouteloua curtipendula,* a factor of 2.06 was used; this figure was indicated by separation of the sample from Mud Creek prairie. The estimated foliage area for all grass species in the central milacre of Sampson was 4,896 square inches, table 7. For *Solidago* rosettes, growing on the surface of the soil, foliage area was assumed to be the same as ground space. The lichens, *Lecidea,* are not included here as their thalli—simple plant bodies without true roots, stems, or leaves—grow under the foliage cover of other plants and thus do not contribute to foliage area. The estimated foliage area of *Agave* and *Opuntia* was 10.35 square inches. For the remaining 251 plants, mostly seedlings or small plants, the foliage area was estimated at 0.2 square inch per plant. The aggregate foliage area of plants other than grasses was estimated to be 92 square inches. The total estimated foliage area in the central milacre of the Sampson prairie was 4,988 square inches or 79.52 per cent of the milacre, tables 7 and 8.

In the Phegley prairie, both in the central milacre and in the prairie as a whole, *Andropogon scoparius* showed obvious reduction of cover, fig. 12, both at ground level and at foliage levels as compared with this species in the unpastured prairie. The leaves covered an area larger than the ground space, but not so large as the area covered by the leaves in the Sampson prairie. Foliage area for *A. scoparius* in the central milacre of the Phegley prairie was estimated at 1.8 times the ground space; this factor multiplied by the ground space gave an aggregate foliage area of 1,994 square inches, table 7. For *Bouteloua curtipendula,* the factor 2.06 was again used (as in Sampson), which gave for this species in Phegley an estimated foliage area of 285 square inches. Plants of *Lespedeza stipulacea,* with an estimated foliage area of 1.5 square inches per plant, had an estimated aggregate area of 106 square inches. For prostrate rosettes of *Solidago,* the foliage area was considered to be equivalent to ground space (as in Sampson). For the remaining plants, all small and mostly seedlings, foliage area was estimated at 0.2 square inch per plant. Plants other than grasses had an estimated aggregate foliage area of 246 square inches. The total estimated foliage area in the central milacre of the Phegley prairie was 2,525 square inches, or 40.25 per cent of the milacre, tables 7 and 8.

Available Space per Plant.—Available space per plant, the inverse of plant density, is another character that, like density, can be useful in descriptions and comparisons of vegetation. It is simply obtained by dividing the area of the measured sample by the number of plants in it.

Variables affecting available space per plant are size of plants, degree of crowding, and percentage of the measured area covered by plants. In those vegetations which show great disparity in sizes of plants of different species, as sagebrush with short-grass, average available space per plant should be separately found for each component or layer. In the Illinois hill prairies studied, individuals of the

Table 9.—Available space per plant in the central milacre of Sampson and of Phegley hill prairies.

Hill Prairie	Area of Milacre in Square Inches	Number of Plants	Available Space per Plant	
			Square Inches	Square Centimeters
Sampson	6,272.64	1,949	3.22	20.77
Phegley	6,272.64	1,341	4.68	30.19

three bunch-grass species are not so different in size from the plants of most other herb species (most of them dicotyledons) as to call for separate estimations of available space for grasses and for other herbs.

Available space per plant for Sampson and Phegley hill prairies is given in table 9.

Numbers of Plant Species for Various Plot Sizes.—From the species lists compiled for plot sizes ranging from 1/64 milacre to 75 milacres, it was possible to find the average number of plant species in plots of several sizes and also the increase in number of species with an increase in area.

Sampson Prairie.—In the central milacre of the Sampson prairie, for plots of 1/64-milacre size the average number of species was 3.79, the average number of individuals, 30.45. One of the plots of this size contained but one species, *Andropogon scoparius*; the plot with the greatest number of species contained seven, *Andropogon scoparius, Solidago nemoralis, Houstonia nigricans, Desmodium ciliare, Bouteloua curtipendula, Agave virginica,* and *Lecidea* sp.

Plots of 1/16-milacre size in the central milacre contained 3 to 10 species each and averaged 6.56 per plot; the number of plants averaged 121.81. Quadrats of 1/4-milacre size in this milacre contained 7 to 11 species each and averaged 9.5 per plot; the average number of plants was 487.25.

In the 9-milacre square, the species list compiled by 1/4-milacre units showed a range of 5 to 11 species and an average of 7.33 per unit; plots of the 1-milacre size had 9 to 13 species each and averaged 11.22. In the 9-milacre square, a total of 18 species was found. Species not found in the central milacre but found in one or more of the 8 milacres surrounding it were *Senecio plattensis, Carya* sp. (seedling), *Aster patens, Sisyrinchium albidum,* and an unidentified moss.

The 9-milacre plot formed a part of the staked 25-milacre square. Species lists were made for the 25-milacre quadrat by 5-milacre strips. Three species, *Juniperus virginiana, Kuhnia eupatorioides,* and *Helianthus divaricatus,* not found in the 9-milacre plot, were found in other parts of the 25-milacre quadrat, and brought the total to 21 species for the 25-milacre quadrat.

The 50-milacre rectangle, fig. 10, downslope from the 25-milacre quadrat, was checked by 10-milacre strips. Twenty species were found in this 50-milacre area. Three species, *Aster oblongifolius, Elymus canadensis,* and *Eupatorium altissimum,* found here were not found in the 25-milacre unit. However, the species of *Carya, Opuntia, Sisyrinchium,* and *Helianthus* found within the 25-milacre square were absent from the larger area. In the 75-milacre area, 24 species were present.

Phegley Prairie.—In the central milacre of the Phegley prairie, for plots of 1/64-milacre size the average number of species was 3.94, the average number of plants, 20.95. In one of the plots of this size only one species, *Andropogon scoparius,* with two individuals, was found; the plot with the greatest number of species contained eight, *A. scoparius, Solidago nemoralis, Houstonia nigricans, Gerardia* sp. (possibly *G. gattingeri*), *Lespedeza stipulacea, Bouteloua curtipendula, Euphorbia corollata,* and *L. capitata.*

Plots of 1/16-milacre size in the central milacre contained 4 to 11 species each and averaged 7.13 per plot. The number of plants in plots of this size averaged 83.81. Quadrats of 1/4-milacre size in this milacre contained 11 or 12 species each and averaged 11.5. The average number of plants was 335.25 in this size unit.

In the 9-milacre square, the species list compiled by 1/4-milacre units showed a range of 6 to 12 species and an average of 9.27 per unit. The 1-milacre plot size had a range of 11 to 16 species each and an average of 13.44. Ten species not found in the central milacre but found in the surrounding eight were *Andropogon gerardi*, *Lecidea* sp., *Aster patens*, *Eragrostis spectabilis*, *Rhus copallina*, *Kuhnia eupatorioides*, *Panicum scribnerianum*, *Poa pratensis*, *Ruellia humilis*, and a second species of *Gerardia* (possibly *G. aspera*). Twenty-six were found in the 9-milacre quadrat.

The 9-milacre plot formed a part of the staked 50-milacre rectangle, fig. 10, which was examined by 10-milacre strips. Six species not found in the 9-milacre square were found in other parts of the rectangle. These were *Aster oblongifolius*, *Opuntia rafinesquii*, *Tridens flavus*, *Melilotus alba*, *Rhus aromatica*, and *Erigeron strigosus*. The first four of these were found only in the 10-milacre strip nearest the improved pasture eastward from the crest of the ridge. This strip, because of its proximity to the pasture, probably should not be considered typical hill prairie. Two species not found in the 9-milacre plot were found in other parts of the four downslope 10-milacre strips and brought the total to 28 species.

The 25-milacre quadrat downslope from the 50-milacre rectangle yielded but one species that did not occur in the 50-milacre rectangle; this was *Asclepias viridiflora*. There were, however, seven species in the four downslope 10-milacre strips of the 50-milacre area that did not occur in the 25-milacre unit. These were *Rhus copallina*, *Kuhnia eupatorioides*, *Panicum scribnerianum*, *Poa pratensis*,

Table 10.—Frequency of occurrence of plant species in plots of five sizes, Sampson hill prairie.

Species	Size A (1/256 Milacre, 0.0156 Square Meter)		Size B (1/64 Milacre, 0.0625 Square Meter)		Size C (1/16 Milacre, 0.25 Square Meter)		Size D (1/4 Milacre, 1.01 Square Meters)		Size E (1 Milacre, 4.05 Square Meters)	
	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots
Andropogon scoparius	60	93.8	64	100.0	16	100.0	36	100.0	9	100.0
Houstonia nigricans	22	34.4	49	78.1	15	93.8	36	100.0	9	100.0
Desmodium ciliare	19	29.7	42	65.6	16	100.0	33	91.7	9	100.0
Solidago nemoralis	13	20.3	32	50.0	15	93.8	33	91.7	9	100.0
Lespedeza capitata	1	1.6	5	7.8	5	31.3	24	66.7	9	100.0
Gerardia gattingeri(?)	1	1.6	11	17.2	8	50.0	20	55.6	9	100.0
Bouteloua curtipendula	12	18.5	17	26.6	9	56.3	18	50.0	8	88.9
Lecidea spp.	4	6.3	8	12.5	8	50.0	15	41.7	7	77.8
Andropogon gerardi	—	—	3	4.7	2	12.5	14	38.9	6	66.7
Petalostemum purpureum	1	1.6	8	12.5	7	43.8	13	36.1	7	77.8
Senecio plattensis	—	—	—	—	—	—	7	19.4	4	44 4
Euphorbia corollata	—	—	1	1.6	1	6.3	7	19.4	5	55.6
Agave virginica	2	3.1	2	3.1	2	12.5	2	5.6	2	22.2
Opuntia rafinesquii	—	—	1	1.6	1	6.3	2	5.6	2	22.2
Aster patens	—	—	—	—	—	—	1	2.8	1	11.1
Carya sp.	—	—	—	—	—	—	1	2.8	1	11.1
Sisyrinchium albidum	—	—	—	—	—	—	1	2.8	1	11.1
Unidentified moss	—	—	—	—	—	—	1	2.8	1	11.1
	10 species 64 plots		*13 species* 64 plots		*13 species* 16 plots		*18 species* 36 plots		*18 species* 9 plots	

Hedeoma hispida, *R. aromatica*, and *Gerardia* (possibly *G. aspera*). The 75-milacre unit minus the 10-milacre border strip contained 29 species. The 75-milacre unit contained 33 species.

Frequency of Occurrence of Species.—The frequency, or repeated occurrence, of plant species in Phegley and Sampson prairies was determined from species lists of each of the following plot sizes: 1/256-, 1/64-, 1/16-, 1/4-, and 1-milacre. Although the 1/256-milacre unit was not marked in the field, data for plots of this size were obtained from maps of the mapped central milacre of both Sampson and Phegley prairies, figs. 8 and 9. On such maps the northwest quarter of the milacre was divided into 64 equal quadrats and, from these, species lists were compiled. The metric equivalent of this quadrat size is 0.0156 square meter. For any given plot size the frequency was expressed as a percentage computed by dividing the number of quadrats in which the species occurred by the total number of quadrats of that size employed.

Sampson Prairie.—Table 10 summarizes the data for the frequency study in unpastured Sampson prairie. It is evident that the 1/256-milacre size was too small for use in ecological studies of Illinois hill prairies; only one species, *Andropogon scoparius*, attained a high percentage of occurrence. The 1/64-milacre

Table 11.—Frequency of occurrence of plant species in plots of five sizes, Phegley hill prairie.

SPECIES	SIZE A (1/256 MILACRE, 0.0156 SQUARE METER)		SIZE B (1/64 MILACRE, 0.0625 SQUARE METER)		SIZE C (1/16 MILACRE, 0.25 SQUARE METER)		SIZE D (1/4 MILACRE, 1.01 SQUARE METERS)		SIZE E (1 MILACRE, 4.05 SQUARE METERS)	
	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots	Number of Plots	Per Cent of Plots
Andropogon scoparius	57	89.1	64	100.0	16	100.0	36	100.0	9	100.0
Solidago nemoralis	42	65.6	59	92.2	16	100.0	36	100.0	9	100.0
Desmodium ciliare	2	3.1	8	12.5	6	37.5	33	91.6	9	100.0
Bouteloua curtipendula	3	4.7	21	32.8	9	56.3	33	91.6	9	100.0
Lespedeza stipulacea	3	4.7	29	45.3	12	75.0	31	86.1	9	100.0
Gerardia gattingeri(?)	9	14.1	21	32.8	13	81.3	30	88.3	9	100.0
Petalostemum purpureum	3	4.7	13	20.3	10	62.5	29	80.6	9	100.0
Houstonia nigricans	3	4.7	11	17.2	10	62.5	27	75.0	9	100.0
Lespedeza capitata	1	1.6	7	10.9	6	37.5	18	50.0	7	77.8
Euphorbia corollata	3	4.7	6	9.4	5	31.3	11	30.6	5	55.6
Juniperus virginiana	—	—	3	4.7	2	12.5	10	27.8	6	66.7
Senecio plattensis	—	—	1	1.6	1	6.3	9	25.0	7	77.8
Cassia fasciculata	—	—	3	4.7	2	12.5	7	19.4	4	44.4
Polygala verticillata	1	1.6	2	3.1	2	12.5	4	11.1	3	33.3
Panicum scribnerianum	—	—	—	—	—	—	4	11.1	3	33.3
Linum sulcatum	—	—	3	4.7	3	19.4	3	8.5	2	22.2
Aster patens	—	—	—	—	—	—	3	8.5	2	22.2
Eragrostis spectabilis	—	—	—	—	—	—	2	5.6	2	22.2
Andropogon gerardi	—	—	—	—	—	—	1	2.8	1	11.1
Lecidea spp.	—	—	—	—	—	—	1	2.8	1	11.1
Rhus copallina	—	—	—	—	—	—	1	2.8	1	11.1
Kuhnia eupatorioides	—	—	—	—	—	—	1	2.8	1	11.1
Gerardia aspera(?)	—	—	—	—	—	—	1	2.8	1	11.1
Poa pratensis	—	—	—	—	—	—	1	2.8	1	11.1
Hedeoma hispida	—	—	—	—	—	—	1	2.8	1	11.1
Ruellia humilis	—	—	—	—	—	—	1	2.8	1	11.1
	11 species 64 plots		*15 species* 64 plots		*15 species* 16 plots		*26 species* 36 plots		*26 species* 9 plots	

size in Sampson was more nearly adequate than the 1/256-milacre size in this unpastured prairie; 4 species of the 13 found in the 64 plots of the 1/64-milacre size attained a percentage of 50 or more. These 4 species represented 30.77 per cent of the number of species found in the 64 plots. *A. scoparius* occurred in all the quadrats of the 1/64-milacre size. It is evident that the 1/16- and the 1/4-milacre plots (C and D in table 10) gave good distribution among species. In the one (C), with a small number of plots and 13 species, 7, or 53.85 per cent, attained a percentage of 50 or more; in the other (D), with a large number of plots and 18 species, 7, or 38.88 per cent attained a percentage of 50 or more. In Sampson prairie, the frequency study showed, plots of 1/64 to 1/4 milacre were of sufficient size to give a satisfactory distribution of species.

Phegley Prairie.—Table 11 summarizes the data for the frequency study in pastured Phegley prairie. As in Sampson, the 1/256-milacre size was much too small to give good distribution; only *Andropogon scoparius* attained a high frequency percentage. The 1/64-milacre size did not give good distribution of species; only two, *A. scoparius* and *Solidago nemoralis,* attained percentages of 50 or more. These species represented 13.33 per cent of the total found in the 64 plots of this size. In Phegley prairie, the frequency study showed, plots of 1/16 to 1/4 milacre were of sufficient size to give a satisfactory distribution of species.

Frequency Values for Combinations of Species.—In Sampson and Phegley prairies, certain species of plants occurred together in so many plots as to call attention to the combinations. In Sampson, the species in combination were *Andropogon scoparius, Solidago nemoralis, Houstonia nigricans,* and *Desmodium ciliare.* In Phegley, they were *Andropogon scoparius, Solidago nemoralis, Desmodium ciliare,* and *Bouteloua curtipendula.* The frequency values for these combinations of species are summarized in table 12. For the two larger plot sizes, 1/4 and 1 milacre, the sample was the 9-milacre square. For the 1/64- and 1/16-milacre sizes, the sample was the central milacre of the 9-milacre square. For the 1/256-milacre size, the sample was 1/4 milacre, the northwest quarter of the central milacre. If the 1/4-milacre size had been studied in only the central milacres, the percentage of occurrence of the characteristic combinations for both Sampson and Phegley would have been 100.

Wherever one or more combinations of species can be discerned in any particular type of vegetation, the combinations can serve as a criterion of adequacy of plot size. In Phegley prairie, the 1/16-milacre size was obviously too small to give a fairly high frequency of occurrence for the characteristic combination; in Sampson prairie, the 1/64-milacre size was too small.

Frequency of occurrence of characteristic combinations of species has been used as a test of the adequacy of size of sam-

Table 12.—Frequency of occurrence of characteristic combinations of plant species, Sampson and Phegley hill prairies.

Number of Quadrats	Size of Quadrats	Sampson Combination*		Phegley Combination†	
		Number of Occurrences	Per Cent of Occurrence	Number of Occurrences	Per Cent of Occurrence
9	1	9	100.0	9	100.0
36	1/4	31	79.5	30	83.3
16	1/16	15	93.8	2	12.5
64	1/64	19	29.7	1	1.7
64	1/256	2	3.2	0	0.0

* Combination in Sampson hill prairie: *Andropogon scoparius, Solidago nemoralis, Houstonia nigricans,* and *Desmodium ciliare.*

† Combination in Phegley hill prairie: *Andropogon scoparius, Solidago nemoralis, Desmodium ciliare,* and *Bouteloua curtipendula.*

ple in one study known to the writer: the forest study by Vestal & Heermans (1945).

Species-Area Curve.—A species-area curve can be constructed from data obtained from the species list for the various plot sizes. The maps of the central milacres, figs. 8 and 9, furnished the data for deriving average numbers of species in quadrats of 1/256-, 1/64-, and 1/16-milacre sizes. Species lists, compiled by 1/4-milacre units, for each of the 9-milacre squares furnished the data for computing the averages for quadrats of 1/4- and 1-milacre sizes. The total number of species found in the 9-, 25-, 40-, 50-, 65-, and 75-milacre areas provided the figures for the larger plot sizes. These data are shown in table 13.

When the data are plotted on semilogarithmic paper, the resulting curves are S-shaped, fig. 13. From this type of curve, certain reference areas can be determined with the method described by Vestal (1949). These are (1) the smallest representative area, (2) the minimum area for assignment to type, after this referred to briefly as minimum area, and (3) the area of fair-sized stand. The smallest representative area (Ar) is the smallest one-piece area having some claim to be representative. It is the effective plot-size of Vestal & Heermans (1945). The minimum area (Am), a plot-size that is large enough to include all the important

Table 13.—Numbers of plant species in plots of various sizes, Sampson and Phegley hill prairies.

Plot Size, Milacres	Number of Species*	
	Sampson Prairie	Phegley Prairie
1/256	2.11	1.98
1/64	3.79	3.94
1/16	6.56	7.13
1/4	7.33	9.27
1	11.22	13.44
9	18.0	26.0
25	21.0	20.0
40	—	28.0
50	20.0	—
65	—	29.0
75	24.0	—

* The average number of species per quadrat for plot sizes of 1 milacre and smaller; total number of species in larger quadrats.

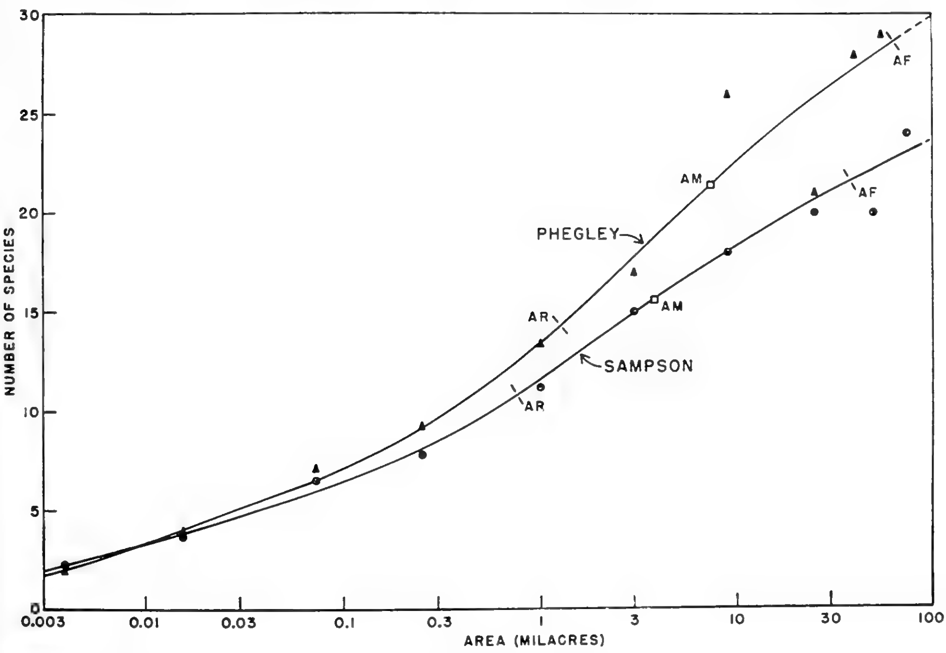

Fig. 13.—Species-area curves for Phegley (grazed) and Sampson (ungrazed) hill prairies. Ar, smallest representative area; Am, minimum area for assignment to type; Af, fair-sized stand.

and a moderate number of minor species, is an area 5 times as large as the smallest representative area and usually contains 1.44 to 1.5 times as many species. It is the smallest size to be used if a single one-piece sample is to be examined. The fair-sized stand (Af) is an area 50 times as large as the smallest representative area and contains twice as many species.

For Sampson prairie, the curve indicates the smallest representative area to be 0.76 milacre, with 10.8 species; the computed minimum area 3.80 milacres, with 15.6 species, or 1.444 times as many species as in the smallest representative area; the fair-sized stand 38.0 milacres, with 21.6 species.

For Phegley prairie, the curve indicates the smallest representative area to be 1.26 milacres, with 14.3 species; the computed minimum area 6.30 milacres, with 21.4 species, or 1.497 times the number in the smallest representative area; the fair-sized stand 63.0 milacres, with 28.6 species.

The 9-milacre square was larger than the smallest representative area and minimum area for both prairies. Both prairies were of more than sufficient size to qualify as fair-sized stands. The number of species in 1 acre was estimated to be 28.0 in Sampson and 35.2 in Phegley.

Summary of Pastured and Unpastured Prairies.—Some of the differences in vegetation of the pastured and the unpastured hill prairies are here summarized.

1. The number of species in a quadrat was larger in the pastured than in the unpastured hill prairie.
2. Plant density, based on the number of plants in a quadrat, was smaller in the pastured than in the unpastured prairie; the grass bunches were smaller, less vigorous, and not so tall.
3. Grasses constituted a smaller percentage of the total number of individual plants in the pastured prairie than in the unpastured.
4. The ground space occupied by grasses was smaller in the pastured prairie than in the unpastured.
5. Foliage area, or crown cover, was understandably much smaller in the pastured than in the unpastured prairie. Also, the ratio of crown cover to ground space was smaller in the pastured prairie than in the unpastured prairie.

Vegetation Characters From Other Stands

In the preceding section, some analytic characters of vegetation were described for two hill prairie stands, Sampson and Phegley prairies. Analytic characters of vegetation, according to some phytosociologists, are those traits which are studied in each stand. Synthetic characters of vegetation are those which are studied from comparisons of large numbers of stands. Presence, a synthetic character of vegetation, and seasonal aspect, also synthetic in that it was described from observations made on most of the stands of Illinois hill prairies, are here briefly presented.

Presence.—Presence, as used here, is defined as the more or less persistent occurrence of a species in the stands of a plant community. Used for this study were 36 stands of hill prairies that the writer visited at least twice during the field work. From species lists of the 36 stands, a table was devised which lists the species and the stands in which they occurred, table 14. Species of forests or thickets and those of foreign origin were not included in the table unless they occurred in 18 or more of the stands.

Three species were present in 90 per cent or more of the stands. They were *Andropogon scoparius, Erigeron strigosus,* and *Bouteloua curtipendula.* Six species were present in 80 to 89 per cent of the stands. They were *Petalostemum purpureum, Euphorbia corollata, Penstemon pallidus, A. gerardi, Verbena stricta,* and *Kuhnia eupatorioides.* These nine species were the "constants" of the association; they can be classed as "constantly present." The "commonly present" species, that is, those present in 60 to 79 per cent of the stands, were *Eupatorium altissimum, Rhus glabra, Oxalis violacea, Solidago nemoralis, Panicum scribnerianum, Aster oblongifolius,* and *Ruellia humilis.* Species in 50 to 59 per cent of the stands were *Linum sulcatum, Lithospermum incisum, Melilotus alba, Lespedeza capitata, Pycnanthemum pilosum, Poa pratensis, Psoralea tenuiflora, Cassia fascicu-*

lata, and *Sorghastrum nutans.* Thus, in 50 per cent or more of the hill prairies, there were 25 species present. All are natives of North America except one, possibly two. *Melilotus alba* is Eurasian. *Poa pratensis* is generally considered European by many authorities, but Gleason (1952) states, "In most of our range introduced from Europe; along our n. boundary and in Canada it may be native." It might prove difficult to determine whether Illinois plants of this species had their origin in Europe or Canada.

Species most characteristic of the hill prairie type are *Bouteloua curtipendula, Psoralea tenuiflora, Petalostemum candidum, Linum sulcatum,* and *Lithospermum incisum.* The presence of these species in other prairie types in Illinois is much lower than in hill prairie.

Seasonal Aspect.—The Illinois hill prairies studied in the years covered by this report showed certain seasonal aspects.

In winter, the brownish color of the grass cover predominated. On some ungrazed hill prairies, tall grass stems of the previous growing season bent over and trended downslope to form a fairly complete cover over the soil. Small purplish rosettes of *Solidago nemoralis* and green rosettes of *Senecio plattensis* were evident between the grass clumps in some of the prairies.

The prevernal aspect was mostly brown. In early April in some prairies, the small white flowers of *Draba reptans* were seen. By late April, the violet flowers of *Oxalis violacea,* the yellow-orange blossoms of *Lithospermum canescens,* and the yellowish flowers of *Salix humilus* and *Rhus aromatica* were evident among the grass bunches.

In the vernal phase, the dominant color changed from brown, through brownish-green, to green as the grasses began their growth. *Hedeoma hispida,* with very small bluish blossoms, was common in the interspaces in many prairies. *Erigeron strigosus,* taller than the grasses during the vernal phase, was very conspicuous with its white flowers, as was also *Penstemon pallidus. Tradescantia,* with purple blooms raised above the level of the grasses, was scattered in many prairies. The yellow rays of *Senecio plattensis* and *Coreopsis lanceolata* were conspicuous in some. Several grasses, *Panicum scribnerianum, Poa pratensis, Festuca octoflora,* and *Koeleria cristata,* flowered at this time.

In the aestival stage, the predominating color was green or purplish-green. *Echinacea pallida,* with purplish rays, was in bloom, and *Linum sulcatum,* with small yellow petals, began its flowering. In some prairies the small whitish flowers of *Houstonia nigricans* were frequent. The inflorescences and foliage of *Psoralea tenuiflora* gave some prairies a purplish-green hue, especially in early July. The purple-flowered *Buchnera americana* and *Petalostemum purpureum* and the white-flowered prairie-clover, *P. candidum,* were scattered in some prairies. In late June and early July, the green or purplish-green inflorescences of *Bouteloua curtipendula* appeared. In the latter part of July and early August, the bronze, green, or purplish-green inflorescences of *Andropogon scoparius* and *A. gerardi* were conspicuous. By late August, the yellow of *Solidago nemoralis* and the purple of *Liatris aspera* were evident.

In the autumnal phase, beginning in September, the dominant color changed from green to brownish hues. The yellow rays of *Solidago nemoralis* and the white or purple rays of several species of *Aster* were common. By October, very few plants, an occasional *Solidago* or a *Houstonia,* or, less often, a *Spiranthes,* were still in flower. By November the prairie was again dormant; the dominant grass cover was brown.

VEGETATIONAL HISTORY AND SUCCESSION

The vegetational history of Illinois, a state that is within the area of overlap of eastern prairie and forest, is deduced mainly from circumstantial evidence. The evidence is derived from the present flora and vegetation, especially from apparent relict colonies, from fossils in the loess, and from analyses of pollens and fossils in peat and lacustrine deposits. Deductions must conform not only to the facts of botany but also to the facts of meteorology and geology. In making deductions concerning plant succession and vegetational history of Illinois hill prairies, it is necessary to keep in mind some of the Pleistocene history of the area in which these prairies occur.

The strip of land along the present Mississippi River valley in western Illinois has had a vegetational cover since Kansan glacial times, fig. 4, except for the portion from southern Carroll County to northern Adams County, inclusive, which was covered by ice during part of Illinoian glacial time. Except for a strip between Fulton, Whiteside County, and Cordova, Rock Island County, which was covered during Tazewell glacial time (Shaffer 1954), the entire western border has supported a plant cover since Sangamon interglacial time. It was during Tazewell time that the present valley of the Mississippi from the Rock Island area south to Adams County was established. The eroding valley perhaps did not maintain a continuous plant cover but the adjacent uplands did; their cover was probably prairie.

The Illinois River valley south from the "Big Bend" at De Pue was established in pre-Pleistocene time and has been occupied by vegetation since Illinoian deglaciation except for the area from Peoria northward, which was glaciated again during Tazewell time. The Rock River hill prairie site included in this report was not covered by ice after Farmdale glacial time. The area along the valley of Sangamon River near its mouth was last glaciated during Illinoian time.

It seems entirely possible that during the Tazewell substage, when the ice-front was at the Shelbyville moraine, a fairly steep climatic gradient prevailed, with climatic conditions along the valleys in western Illinois not very different from those of the present. Loess deposition occurred during the time of advance, maximum extent, and recession of the glacial ice. The major deposition doubtless took place in the autumn and winter, which were then, as now, the dry seasons of the year. Loess deposits of Kansas contain fossil snails that point to a plant cover for that area at the time of deposition that consisted of shrubs and herbaceous species (Leonard 1952) and of a forest border near the Missouri River (Leonard & Frye 1954). As the Kansas deposits are of comparable age to those of Illinois, a similar plant cover may have existed in parts of Illinois. The vegetation in much of western Illinois west of the Tazewell ice-front may be imagined as that of a prairie or grassland (Gleason 1923). The floodplains were devoid of plant cover because of the constant shifting of the overloaded streams with their braided channels. During the dry autumnal and winter seasons, the floodplain served as a source of silt, which was transported to the uplands by the then, as now, prevailing northwest winds.

While separating bunch-grass clumps from Reavis Spring to expose individual plants (page 381), Vestal and the writer observed that vigorous upward growth of plants had kept pace with the deposition of additional sandy material. From such observations it can be concluded that, along the bluffs, deposition of loess favored rather than discouraged the growth of bunch grasses. The inverse also was true; a grass cover favored the catching and holding of windblown silts (Shimek 1903). As new areas were exposed by deglaciation (for instance in the Putnam County hill prairie locations), the prairie species, because of proximity and the rapidity with which many of them could become established, moved in and occupied the bluffs before woody plants could do so. Mosses and lichens were not the first plants to become established in areas of deglaciation. On present-day loess and till slopes in Illinois, these cryptogamic species are absent from sizable areas without vascular plants but are present in some interstices where grass plants give some protection. A similar situation probably prevailed during deglaciation. Prairie vegetation thus can be assumed to have long antedated tree cover on many of the bluffs of the larger rivers in Illinois. The advantage of priority of occupation is probably far more important in succession than is commonly realized.

Although subsequent history has perhaps been one of progressive encroachment by forest on many of the Illinois bluffs, especially those of low altitude, several stretches of bluff frontage, totaling 25 to 30 miles, remain hill prairie or are in part hill prairie. Possibly as much as three times this extent, 75 to 90 miles, or about one-eighth of the bluff frontage on the east sides of the major stream valleys, was prairie in the early nineteenth century, but was converted to pasture or otherwise disturbed by the activities of man. The bases for such an estimation are the few scattered prairie plants along stretches of bluffs now occupied principally by bluegrass and numerous pasture weeds. Such stretches of bluffs are common along the Mississippi River in Jo Daviess County. Doubtless these bluffs were prairie covered in the not distant past.

Hill prairies have been surprisingly successful in resisting destruction by the grazing of domestic animals and by some of the activities of man. There are no records to show how heavily these prairies were grazed by bison before the arrival of white men in Illinois. It is possible that bison grazed many hill prairies, but that they failed to reach some that were hidden by surrounding dense forest. Whether or not pastured hill prairies observed for this report are being reduced by overpasturing is not yet evident. Goat pasturing in one site along the bluffs of the Illinois River south of Rosedale caused complete destruction of the prairie, leaving only bare loess on the slope. The spread of residential and industrial areas has destroyed some of the hill prairies. On the other hand, it is evident that fire has not destroyed them; seemingly, it has permitted an earlier and more tender growth of grass.

What is the probability that hill prairies are now being invaded by forests? Some of the most typical hill prairies are located on brow slopes where the cliffs are so high that they extend above the trees that grow on the toe slopes; without the shade of the trees, the brow slopes, especially those facing southwest, are exposed to the heat of the sun and to the prevailing winds of summer and are thus too xeric for growth of mesophytic forest and will probably remain prairie. The bluff coves, which serve as drainageways on the slopes, are more mesic and, in places, support mixed forest. Such forested coves contain tree species that are found in the forests of the basal slopes, of the slopes of the tributary valleys parallel to the main valleys, or of the uplands. Where the bluffs are low, or in the few places where the ascent from floodplain to upland is continuously of low gradient, trees have long shaded the upper slopes and greatly reduced wind movement. In such situations, forests have been established over entire slopes.

In years of abundant rainfall, forest seedlings become established on prairie spurs, only to die in years of less abundant rainfall or in periods of successive dry years, as of the 1930's. Dwarfed trees, as well as dead sumacs and red cedars, are reminders of dry years and a contest between forest and prairie. It thus seems probable that a shifting equilibrium was long ago reached between prairie and forest, especially on bluffs with high cliffs. As long as the present topography and climate persist, such hill prairies will remain approximately as they are.

Delimitation and description of the actual stages of succession within hill prairie areas cannot be made now, but must await the advent of interested botanists of the future. In the interim, it is important that botanists continue the study of these sites and publish the results of their studies. From such studies, botanists will be able to trace actual, not hypothetical, paths of succession and also deduce with a greater amount of accuracy the past vegetational history.

ANNOTATED LIST OF HILL PRAIRIES

The following list of Illinois hill prairies includes only those prairies which the writer visited during the field work for this study. The name given to each of the prairies was derived from one of several sources—the name of the landowner, or of the tenant, or of the farm on which the prairie was found; the name of that stretch of bluff occupied by the prairie; or the name of some nearby landmark or community as applied locally or found on a quadrangle of the United States Geological Survey topographic map. Location of each prairie is given according to section, town, and range except for prairies within municipalities, state parks, or the old French land grants. These grants extended inland at right angles to the bank of the Mississippi River and were not surveyed according to the township system. In this hill prairie study, such grants were encountered in Monroe and Randolph counties.

For convenience in listing, the prairies are divided into three groups, (a) those along the Mississippi River from East Dubuque to Grafton, (b) those along the Rock, Sangamon, and Illinois rivers, and (c) those along the Mississippi River from Grafton to Cairo and elsewhere in southern Illinois. On the bluffs south of Warsaw, Hancock County, were several small openings which were seen but not examined for this study. Also, on the south side of the lower Sangamon River valley were a number of hill prairies, some with north- and northwest-facing slopes. Many of these prairie slopes served as pastureland and were much disturbed. Some of the slopes were completely converted to bluegrass pastureland. None of these slopes was visited. Fig. 1 shows the locations of these hill prairie sites. Not described, nor indicated in fig. 1, are several pastured grass slopes on the bluffs of the Mississippi River, west and south of Galena, Jo Daviess County, which were visited June 15–16, 1950. At that time they were covered with many weeds and they contained few prairie plants.

East Dubuque to Grafton

El Rancho.—This prairie, located on the bluff above the El Rancho Café in East Dubuque, Jo Daviess County, was visited July 16 and October 4, 1950; May 9 and June 14, 1951. Prairie, slightly over an acre in area, covered the stony part of the slope above the cliff, and also the loess on that part of the slope above the stony part. The uppermost part of the slope and the generally flat bluff-top, greatly disturbed by the WPA in constructing stone foundations for a fireplace and two shelters, had been much trampled and was weedy. Two Indian mounds crowned the spur nearest the café. A forested cove separated this spur from another to the south. Three Indian mounds occupied the crest of the southern spur. *Andropogon scoparius* was the dominant grass of both spurs; *Stipa spartea* grew in large patches on the south spur and was in smaller, scattered patches on the north spur.

Menominee Station.—This prairie, in the southwest quarter of section 17, T. 27 N., R. 1 W., on the bluffs of the Mississippi River, about one-half mile southeast of Menominee Station, Jo Daviess County, was visited October 4, 1950; May 9 and June 14, 1951. Prairie covered about 4 acres on parts of four southwest-facing spurs. Rock fragments covered the surface for a few yards above the rock ledge; loess capped the bluff. *Andropogon scoparius* was the dominant grass. The northeast-facing slope of the northernmost spur and the uplands adjoining the remaining spurs supported a mixed forest. *Rhus glabra* formed dense stands on three spur-tops, and it extended downslope on the north sides of these spurs. *Populus tremuloides* occupied a part of the crest of the northernmost spur of this prairie.

North Savanna.—Prairie covered the upper southwest- and west-facing slopes of the bluff-ridge in section 21, T. 25 N., R. 3 E., 3 miles north of Savanna, Carroll County, when the site was visited June 14, 1951. On the slopes above the rock ledge, *Bouteloua hirsuta* was abundant. Disturbed prairie covered the crest of the ridge. Northward along the ridge, the slope and top were occupied almost entirely by *Juniperus virginiana.*

Sunset Trail.—At the time this study was made, prairie occupied one northwest-facing spur, three west-facing spurs, and one south- to southwest-facing spur on the bluff north of the Administration Building in the Mississippi Palisades State Park, north of Savanna, Carroll County. A trail, Sunset Trail, crossed parts of this prairie. *Andropogon scoparius* and *Bouteloua curtipendula* were abundant grasses. Sandy loess covered the northwest- and west-facing slopes; the south-facing slope was stony. The stony slope was not so steep as the loess slopes. These spurs were visited October 4, 1950, and June 14, 1951.

Hill-Top.—This prairie opening, when examined October 5, 1950, occupied about 4.5 acres on the uppermost surface of the bluff, one ravine south from the main entrance to the Mississippi Palisades State Park. A mixed forest surrounded the prairie. *Sorghastrum nutans* was the dominant grass; *Panicum virgatum* was abundant. Several paths crossed the prairie. Here and for a short distance into the prairie, weeds were common.

South Palisades.—This prairie occupied about 0.2 acre of the generally stony southwest-facing ridge-slope north of the abandoned quarry near the southern boundary of the Mississippi Palisades State Park, when observations were made there on June 22 and October 5, 1951. *Andropogon scoparius* was the dominant grass.

Bielema.—Prairie occupied slightly more than an acre of the bluff on the Bielema farm in section 32, T. 23 N., R. 4 E., southeast of Thomson, Carroll County, in 1950. Stones strewed the lower slope; sandy loess comprised the upper. The base of the lower slope, much disturbed by pigs, was weedy. Prairie, with *Bouteloua curtipendula* and *Andropogon scoparius* as dominant grasses, covered the upper part of the rocky slope. *Andropogon scoparius* was the dominant grass on the sandy loess, except where shallow drainageways on both the stony and loess slopes were densely covered by *Artemisia caudata*. *Poa pratensis* was the dominant cover on the northern part of the bluff-top; *Bouteloua curtipendula* dominated the southern part of this surface. Bielema prairie was visited June 23 and October 6, 1950.

Balk.—In 1951, two conspicuous prairie openings, together about 1 acre, were observed on the upper west-facing slope of the bluff-ridge in section 5, T. 22 N., R. 4 E., in Whiteside County. The southern opening and the surrounding forest were frequented by pigs; the northern opening, which was separated from the southern by a fence, was unpastured. *Bouteloua hirsuta* and *Stipa spartea* occurred in these openings. This site was visited June 13, 1951.

Wiersma.—Hill prairie, about 0.5 acre in area, occupied the upper west-facing slope of the bluff-ridge on the Wiersma farm in section 8, T. 22 N., R. 4 E., Whiteside County, in 1950. *Bouteloua curtipendula* was apparently the dominant grass; *Andropogon scoparius* was locally abundant. The entire ridge was heavily pastured. Wiersma prairie was visited October 6, 1950.

Rock Island 31.—This site, located in section 31, T. 16 N., R. 5 W., Rock Island County, was visited September 9, 1949. The slope, heavily pastured, and covered with a mixture of prairie and forest, was stony below and capped with sandy loess. *Andropogon scoparius, A. gerardi, Sorghastrum nutans,* and *Bouteloua hirsuta* were some of the grasses on this slope.

Bald Bluff.—The name denotes the prominent, narrow, northwest-projecting arm of the Mississippi bluffs in section 18, T. 12 N., R. 4 W., Henderson County. Mantled with sandy loess, Bald Bluff supported both mixed forest and prairie when visited. This prairie, with an abundance of *Bouteloua hirsuta* and many weedy species, was heavily pastured. Prairie covered about 9 acres, 3 of which were examined on August 18, 1951.

Ursa.—When visited, this hill prairie occupied the southwest- and west-facing slopes on the north side of Ursa Creek valley where the creek enters the Mississippi River bottomland in section 13, T. 1 N., R. 9 W., Adams County. Prairie covered about 1 acre of the slopes. A stony levee and small spring-fed stream separated the road on the west from the bluff to the east. The stony east bank of the stream supported prairie. Small rock outcrops capped the stream bank. Above these outcrops the surface was almost level. A dense stand of *Juniperus virginiana* with scattered individuals of *Quercus muhlenbergii* and *Cornus drummondi* grew on the level surface near the limestone outcrops. Eastward there was a narrow belt of prairie and beyond that a thicket which included small oaks, basswood, and hop hornbeam. This thicket bordered the base of a steep loess spur which was covered by prairie up to the top of the bluff. Prairie covered the southwest-facing spurs, mixed forest the coves. The bluff-top was a mixture of prairie and sumac. Ursa prairie was visited August 11 and September 9, 1950; June 2 and July 14, 1951.

Rock Creek.—Located north of Rock Creek, in the northwest quarter of section 25, T. 1 N., R. 9 W., Adams County, this prairie when visited covered more than an acre of a ridge of sandy loess. *Andropogon scoparius* was the dominant grass; *A. gerardi* and *Bouteloua curtipendula* were present. *Asclepias stenophylla* and *Chenopodium leptophyllum* occurred in the interspaces. *Psoralea tenuiflora* was common on the gentle lower slope and the almost level top, but was infrequent on the steeper slopes. Rock Creek prairie was visited September 8, 1949; August 11, 1950; April 25, June 2, and July 14, 1951.

Homan.—This name, which is also the name of the creek to the east, here designates the small hill prairie that in 1951 occupied slightly more than an acre in section 11, T. 1 S., R. 9 W., about 3 miles north of Quincy. Prairie covered the west- and southwest-facing slopes of the southern tip of a ridge that ends at Homan Creek. The crest of the ridge was almost covered with *Rhus glabra, Psoralea tenuiflora, Petalostemum candidum,* and *Melilotus alba.* A few individuals of *Asclepias stenophylla* and *Delphinium carolinianum* occurred there as well as on the slopes. Vegetation of the east-facing slope was principally a mixture of prairie and sumac. *Andropogon scoparius* dominated the west- and southwest-facing slopes. *Bouteloua curtipendula* occurred in scattered patches. This site was visited on April 25, June 2, and July 16, 1951.

Parker Heights.—This small hill prairie, which occupied the south part of a ridge in Parker Heights, a park about a mile north of Quincy, Adams County, was visited May 28, 1950, and July 16, 1951. Disturbed prairie, much trampled by people, covered the west- and southwest-facing slopes above the exposed limestone bedrock.

Hidden Lake.—The pond within the quarry in the southeast quarter of section 23, T. 2 S., R. 9 W., about 2 miles south of Quincy, provided the name for this site. A wall of limestone which forms the north and east limits of the lake is covered with a thick mantle of loess to form the bluff. Above the bedrock, the mantle of loess forms an almost vertical cliff with heights to 15 feet, and above the loess cliff is the gentle west- and southwest-facing brow slope of the bluff. Hidden Lake prairie, when visited September 8, 1949, and May 28, July 2, August 13, and September 9, 1950, covered about 0.2 acre of this slope. The steep loess face was almost without vegetation except at its junction with bedrock. Small shrubs occupied this junction. The prairie had been much disturbed by human trampling, because the site attracted numerous boys from nearby Quincy. *Andropogon scoparius* was dominant on the slopes. A dense stand of *Rhus glabra, Melilotus alba,* and *A. scoparius* occupied the crest of the ridge. *Tridens flavus* was frequent.

Seehorn Cemetery.—This prairie, located on the uppermost slope of the bluff, in the southeast quarter of section 26, T. 3 S., R. 8 W., Adams County, was visited September 9, 1950. Prairie occupied the cemetery and some of the slope to the northwest and southeast. Downslope there was a mixed forest; upslope a bit of prairie was found between the cemetery and the cultivated upland. *Sorghastrum nutans* was the dominant grass. *Andropogon gerardi, Bouteloua curtipendula,* and *Psoralea tenuiflora* were common.

Fall Creek.—This prairie in 1950 occupied the bluff about one-quarter mile south of Seehorn Cemetery prairie. Mixed forest occupied the coves; forest, or a mixture of prairie and forest, covered the spurs. *Andropogon scoparius, A. gerardi,* and *Sorghastrum nutans* appeared equally abundant. Interspaces between the bunches of grass were small. This area was visited September 9, 1950.

North Pandarmie.—This name designates a group of spurs and coves on the bluffs in section 31, T. 3 S., R. 7 W., and section 36, T. 3 S., R. 8 W., north of Pandarmie Hollow, 2.5 miles southeast of Fall Creek, Adams County. When North Pandarmie was visited September 9, 1950, forest occupied the coves; a mixture of prairie and forest covered the spurs. *Andropogon gerardi* and *Sor-*

Fig. 14.—Housen hill prairie, north of Rockport, Pike County. The forest of the basal slope extends to the bluff top through the drainageway at the left of the prairie.

ghastrum nutans were abundant; *A. scoparius* was infrequent. At the top of the brow slope was a strip of woodland. Its northeast side had a dense border, 3 to 6 feet wide, of *Sorghastrum*. At the base of the spurs, *Mentzelia oligosperma* grew in the crevices of the interrupted rock ledge.

Seehorn-Payson.—The name of this hill prairie comes from a village in Pike County and a township in Adams County. In 1950, prairie occupied about an acre of slope; part of this area was in the southwest quarter of section 31, T. 3 S., R. 7 W., Adams County, and part in section 6, T. 4 S., R. 7 W., in Pike County. *Astragalus distortus* occurred on the loess and on the rock ledges. *Mentzelia oligosperma* grew on the rock ledges and the rocky slope above the ledges. The prairie was heavily pastured by cattle and sheep. *Poa pratensis* was the most abundant grass on the prairie slopes; *Andropogon scoparius* was infrequent. In September, 1950, very little of the herbaceous vegetation was more than 6 inches tall; the average was 3 to 4 inches, except for an occasional bunch of *Bouteloua curtipendula*. This prairie was visited May 28, July 2, and September 9, 1950.

Sessions.—In the 3 years this hill prairie was under observation, it occupied about 4.5 acres of the upper southwest- and south-facing slope of the bluff in section 5, T. 5 S., R. 6 W., on the Sessions farm between Kinderhook and New Canton in Pike County. Prairie covered seven spurs, mixed forest the intervening coves. Above the rock ledge was a stony slope covered with prairie. Loess mantled the bluff. There was a generally flat upland to the northeast of the slope. Prairie covered the almost flat spur-tops and some of the flat upland to the northeast. Much *Rhus glabra* grew on this flat surface and at the heads of the south-facing coves. *Andropogon scoparius* was the dominant grass. The entire site served as a pasture. Visits were made to Sessions hill prairie on September 7, 1949; May 28, July 2, September 8, 1950; and April 24, 1951.

South New Canton.—A small hill prairie, less than 1,000 square feet in area, in 1950 occupied the southwest-facing bluff slope southeast of Morey Cemetery, about a mile southward along the bluffs from New Canton, Pike County. A rocky slope lay above the rock ledge, and loess capped the bluff. *Andropogon scoparius* was the dominant grass. *Mentzelia oligosperma* grew abundantly in the crevices and recesses of the ledge and infrequently on the lower part of the loess slope. The entire bluff and the upland ridge to the northeast was pastured and much disturbed. Visits were made to this site on May 27, July 1, and September 8, 1950.

Housen.—When visited April 24, 1951, this hill prairie in the southeast quarter of section 7, T. 6 S., R. 5 W., on the Housen farm north of Rockport, Pike County, covered more than an acre of the uppermost southwest-facing slope of the ridge shown in fig. 14. *Andropogon scoparius* was the dominant grass; *A. gerardi* and *Bouteloua curtipendula* were present. The prairie and a part of the adjacent woodland on the slope to the northeast were burned during the autumn of 1950 by a fire that swept the bluffs from Rockport northward to a point beyond this prairie.

Clendenny.—When last seen, this hill prairie, located in the northwest quarter of section 12, T. 8 S., R. 4 W., about 2.3 miles north of Belleview, Calhoun County, covered about 7 acres of the uppermost southwest-facing slope of a bluff. This bluff, fig. 15, served as the pasture of the Clendenny farm. Prairie covered the rocky slope above the rock ledge except in a few coves where a mixed forest extended upslope. Loess capped the bluff. Prairie covered the spurs and most of the coves; small trees and shrubs grew in scattered clumps in some coves. On the crest of the ridge grew a mixture of prairie, woodland, cultivated plants, and weeds. Some of the plants growing in this site were *Lespedeza stipulacea, Symphoricarpos orbiculatus, Melilotus alba, Tridens flavus, Bouteloua curtipendula, Andropogon scoparius, A. gerardi, Verbena stricta,* and *Eragrostis cilianensis.* The inner, or northeast, slope of the ridge supported both forest and prairie: mixed forest on the northwest part and a mixture of prairie and forest on the southeast part. Clendenny prairie was visited April 15, May 27, and September 8, 1950; August 30 and September 27, 1951.

Fig. 15.—The Clendenny hill prairie, northwest of Belleview, Calhoun County. *Buchnera americana* was common in parts of this prairie.

Swarnes.—An inscription on the monument* at the crest of the bluff in the northeast quarter of section 35, T. 9 S., R. 3 W., at the north limits of Hamburg, Calhoun County, furnished the name for this hill prairie. When the site was last seen, prairie occupied about 2 acres of the west- and southwest-facing slope of the ridge. A fence located a few feet north

*The following inscription appears on this monument:
In Memory of
Capt. Lewis Swarnes
Born
May 23, 1821
Died
July 11, 1867.

Lewis Swarnes, according to several residents of Hamburg, was a riverboat captain. He became ill on one of his trips and requested that his body should be buried on the bluff overlooking the Mississippi River at Hamburg.

Fig. 16.—Part of the west-facing slope of Swarnes hill prairie at Hamburg, Calhoun County. *Echinacea, Melilotus,* and *Psoralea* were common on this slope.

of the monument divided the prairie almost equally into pastured and unpastured areas. The pastured segment occupied a west-facing slope, fig. 16, the unpastured a west- and southwest-facing slope. The unpastured surface that bordered the rock ledge was stony, level near the ledge, and gradually steepening upward from the ledge. *Bouteloua curtipendula* was there locally dominant. Interspaces contained many individuals of *Houstonia nigricans.* The unpastured prairie of the steeper slopes and the top of the loess-capped bluff were dominated by *Andropogon scoparius.* Scattered clumps of *Bouteloua curtipendula* and *A. gerardi* were present, and *Asclepias stenophylla* occurred occasionally in the interspaces. The pastured slope supported a prairie that was dominated by *A. scoparius.* Near the top of the bluff, as well as at the top, *Rhus glabra* was locally dominant. *Psoralea tenuiflora* was common in the pastured prairie area. Swarnes prairie was visited September 7, 1949; April 14, May 27, July 1, and August 12, 1950; and September 27, 1951.

Along Rock, Sangamon, and Illinois Rivers

Devil's Backbone.—The bluff-ridge that extends along the Rock River in the northeast quarter of section 16, T. 23 N., R. 10 E., south of Oregon, Ogle County, is given the name Devil's Backbone on the Dixon quadrangle of the United States Geological Survey topographic map. St. Peter sandstone underlies this ridge. When the ridge was last seen, one southeast- and two northeast-facing prairie openings occupied the upper stony and sandy slopes. Sandstone fragments were abundant on the northeast-facing slope. The openings on this slope were covered with prairie in which *Poa pratensis* was very abundant, *Andropogon scoparius* less abundant, and *Bouteloua curtipendula* scattered throughout. *Synthyris bullii* also grew there. The southeast-facing opening was a sand prairie on a slope. *A. scoparius* was there the dominant grass. *Selaginella rupestris,* together with mosses and *Androsace occidentalis,* grew in the interspaces. Devil's Backbone was visited on June 23 and October 3, 1950, and May 7, 1951.

Standard.—In 1951, prairie occupied about a half acre of the upper southwest-facing ravine slope in section 26, T. 33 N., R. 1 W., 1 mile west and 3 miles north of Standard, Putnam County. *Petalostemum purpureum, Amorpha canescens,* and *Coreopsis palmata* were some of the plants in this prairie. This site was visited July 7, 1951.

Magnolia.—When the prairie opening given this name was last visited, it occupied slightly less than an acre on the west- to south-facing upper slope of the bluff in the southwest quarter of section 34, T. 31 N., R. 2 W., about 7 miles west of Magnolia, Putnam County. The bluff is capped with till; loess, if present, apparently is very thin. Scattered shrubs of *Rhus glabra* occurred throughout the opening. *Cornus drummondi* and small elms grew on the south-facing slope, where also a few dead and scattered stems of honey locust were seen. *Andropogon scoparius* was the dominant grass. *Comandra umbellata* was very abundant, *Psoralea tenuiflora* common. Mixed forest surrounded this prairie opening. Magnolia prairie was visited on September 29, 1949; May 16 and August 4, 1950.

East Henry.—This name designates a group of five prairie openings on the southwest-facing bluff of Sandy Creek; the bluff is in the northwest quarter of section 3, T. 30 N., R. 2 W., and southeast of Henry, Marshall County. When the area was visited August 4, 1950, the westernmost opening was weedy and much disturbed. At the base of the bluff below this opening was a gravel pit. The next opening eastward supported prairie plants and also a thicket of *Rhus glabra, Cornus drummondi, Malus ioensis,* and *Ulmus* sp. This opening and the next one to the east were pastured. In the prairie areas, *Andropogon scoparius* was the dominant grass, *Bouteloua curtipendula, Psoralea tenuiflora,* and *Silphium laciniatum* were common. Weeds, *Chamaesyce maculata, Medicago lupulina, Poinsettia dentata,* and *Melilotus alba,* were frequently encountered in these areas. Prairie openings on the two easternmost spurs were not examined.

Reavis Spring.—This prairie, when visited, covered almost 19 acres of the sandy loess bluffs in parts of sections 25, 26, and 36, T. 20 N., R. 7 W., about 5 miles south of Easton, Mason County. The name Reavis Spring was that of a school house, abandoned and later removed, that once occupied a part of the lower slope of the bluff in section 26. A road, which followed the general southwest-facing bluff, was on the lower sandy slopes. Downslope to the southwest was a series of thickets and cultivated fields. Upslope to the northeast was the prairie, which occupied numerous spurs. Thicket covered the bases of some coves, shrubs or prairie the upper slopes. Prairie covered the crests of the spurs; mixed forest or prairie occupied the tops of the bluffs.

The bluffs at Reavis Spring prairie rise 256 feet above the Sangamon River bottomland and are higher than the dissected upland to the northeast. The valley overlooked by these bluffs is notable in several respects. It has a wide bottom trending generally east-west. The Sangamon River enters it from the south and joins a small, west-flowing stream, Salt Creek, in section 6, T. 19 N., R. 6 W., about 1 mile upstream from the Reavis Spring location. The valley is about as wide, rather surprisingly, above the junction of the Sangamon River with the small stream as below it. Salt Creek has a volume too small to account for so wide a valley. It is probable that through this valley a glacial torrent once drained a part of the Wisconsin ice-front, then some miles east of the Reavis Spring site, and brought down huge amounts of sand and silt. From these were derived the thick deposits of loess and fine sand on the bordering bluffs. Other sizable hill prairies occur or did occur on the bluffs for a few miles east of the junction of Salt Creek with the Sangamon River.

Reavis Spring prairie was visited September 15, 1949; July 6, 1950; May 18, 1951; and March 25, 1952. The dominant grass was *Andropogon scoparius.* Also growing in the prairie were *Agoseris cuspidata, Polytaenia nuttallii,* and the easily overlooked *Spiranthes cernua.* The prairie, which served as a cow pasture, contained a number of weeds, *Verbascum* *thapsus*, *Achillea millefolium*, and *Setaria viridis*. On the last visit it was found that the prairie had been burned a week before, fig. 17. From the tenant farmer it was learned that this prairie is burned in early spring each year to allow an earlier and more tender growth of grass than would normally occur.

Fig. 17.—Surface of Reavis Spring hill prairie after an early spring fire. The size of the clumps of *Andropogon scoparius* is evident by comparison with the 1-foot rule.

Bluff Springs.—Disturbed prairie, which covered about a half acre on the north part of a loess mound in the southwest quarter of section 21, T. 18 N., R. 11 W., 0.1 mile north of Bluff Springs, Cass County, was visited September 15, 1949; July 6, 1950; and May 18, 1951. The mound and the adjacent lower slopes were pastured. The lower slope on the west was occupied by a mesophytic disturbed prairie with *Poa pratensis* locally dominant. The steeper slopes of the mound were prairie, with *Andropogon scoparius* the dominant grass. *Bouteloua curtipendula* and several plants of *Spiranthes cernua* occurred on these slopes. The almost level top, which had been much disturbed by trampling, supported a mixture of prairie and weeds.

Mud Creek.—In the years of this study, prairie occupied much of the sandy loess ridge that separates the bottomland of the Illinois River from Mud Creek in the northeast quarter of section 1, T. 16 N., R. 11 W., Morgan County. A thicket bordered the road on the lower northwest-facing slope. This thicket extended into the coves and partly up the cove slopes. Prairie covered the spurs and ridge-top, fig. 18. The dominant grass was *Andropogon scoparius*. *Bouteloua curtipendula* and *B. hirsuta* grew in scattered clumps in the prairie, *Psoralea tenuiflora* was common, and *Sisyrinchium campestre* very abundant. All of this prairie and that part of the ridge that was covered with thicket, about 13 acres in area, served as a cow pasture. Visits were made to Mud Creek prairie on July 6, 1950; May 18, 1951; and March 25, 1952.

Northeast Meredosia.—When last seen, this prairie covered about 9 acres of the loess bluffs in section 9, T. 16 N., R. 12 W., about 6 miles northeast of Meredosia, Morgan County. *Andropogon sco-*

parius was the dominant grass. *Bouteloua curtipendula,* as well as *B. hirsuta,* was scattered throughout. *Polygala incarnata* grew on the bluff top, and *Artemisia caudata* grew as scattered individuals in the sandy loess. This prairie, which served as pastureland, was visited September 15, 1949; July 6, 1950; May 18, 1951; and March 25, 1952.

Northeast Meredosia was the first of those hill prairies along the Illinois River observed by A. G. Vestal, who visited it in the spring of 1931 in company with James M. Schopf and Herman B. Wascher. They were impressed by the persistence of native prairie vegetation and by the lack of serious erosion on the steep loess slopes, over which the continuous trampling of cattle had worn steplike cowpaths.

Bluffs.—When this site was visited July 6, 1950, a mixture of prairie and forest covered about 8 acres of the west-facing slope of the bluff in the southwest quarter of section 10, T. 15 N., R. 13 W., north of Bluffs, Scott County. Prairie species included *Lespedeza capitata, Psoralea tenuiflora, Onosmodium occidentale,* and *Ambrosia coronopifolia.*

Walnut Creek.—The site of this 2-acre prairie occupies one southwest- and two west-facing spurs of the bluff north of which Walnut Creek enters the Illinois River valley in the northwest quarter of section 26, T. 14 N., R. 13 W., about 4 miles west of Winchester, Scott County. When visited August 13, 1950, and April 24 and May 18, 1951, the base of the slope contained a mixture of prairie and shrubbery. The spur slopes contained prairie, with *Andropogon scoparius* the dominant grass. The coves between the spurs supported prairie and some woody plants. The top of the ridge was very weedy. Walnut Creek prairie was used as a horse pasture.

Fig. 18.—Spurs of Mud Creek hill prairie (center of picture) in northwest Morgan County. In the distance beyond the Mud Creek prairie are slopes, some of which support prairie.

North Eldred.—Located in section 16, T. 10 N., R. 13 W., 2 miles north of Eldred, Greene County, this prairie in 1949 and 1950 covered several spurs on the upper slope of the bluff. The spur directly above the cemetery at the base of the bluff was heavily pastured; the spurs to the south of this were also pastured but not so greatly disturbed. Stones strewed the slope in places just above the rock ledge; sandy loess and sand capped the bluff. This prairie was visited September 1, 1949; April 14, May 23, and July 25, 1950.

South Eldred.—In 1950, prairie covered about 4.5 acres of two southwest-facing slopes in the southwest quarter of section 4, T. 9 N., R. 13 W., 2 miles south of Eldred, Greene County. The prairie formed an inverted U with the prongs of the U extending downslope. *Andropogon scoparius* was the dominant grass; *Senecio plattensis* and *Lithospermum canescens* were common. This site was visited May 23, 1950.

Richwood.—When last visited, this prairie, in the southeast quarter of section 8, T. 8 N., R. 13 W., Richwood Township, Jersey County, occupied 4 acres of the long, curved ridge which extends from the rock ledge on the southwest up to the bluff-top. The abundant grasses were *Andropogon scoparius, A. gerardi,* and *Bouteloua curtipendula.* A small arm of the prairie stretched northwestward on a small branch of the ridge. A mixed forest covered the bluff slope to the west and the ravines on the east and north. Richwood was visited September 7, 1949, and May 23, 1950.

Pere Marquette.—At the time of this study, prairie vegetation occupied about 3.5 acres on the spurs of the southwest-facing bluffs, Pere Marquette State Park, west of Grafton, Jersey County. The prairie observed for this study was on the slopes west of the westernmost parking area that was located on the crest of the bluff. Mixed forest grew in the coves between the grass-covered spurs. A little below the top of the eastern and central spurs a firebreak crossed the prairie. Weeds, including *Ambrosia elatior* and *Erigeron canadensis,* grew among scattered plants of prairie species in this firebreak. The dominant grass of the prairie slope was *Andropogon scoparius. Desmanthus illinoensis* grew on the western spur and was very abundant on the central one. The western spur was disturbed by a bridle path which followed the crest of the spur and had cut 2 feet into the loess. The bluff-top was covered by a thicket of small trees and shrubs, including *Crataegus crus-galli, Cornus drummondi, Malus ioensis, Cercis canadensis,* and *Sassafras albidum.* Pere Marquette was visited July 8 and August 29, 1950; May 25 and November 29, 1951.

Grafton to Cairo and Elsewhere in Southern Illinois

Chautauqua.—A small village resort at the convergence of several ravines about 3 miles east of Grafton furnished the name for this prairie. The prairie, a part of section 13, T. 6 N., R. 12 W., in Jersey County, covered four south-facing spurs, mixed forest the coves. The base of each spur was a rock ledge at the top of the cliff which here closely parallels the Mississippi River. The spur slope above each ledge was covered with prairie; *Andropogon scoparius* was the dominant grass. *Melica nitens* occurred on the stony prairie slope above the ledge. Numerous weedy species such as *Setaria viridis, Achillea millefolium, Ambrosia elatior, Lappula echinata,* and *Geranium carolinianum* were present. Chautauqua hill prairie was visited July 8 and August 29, 1950; also May 25, 1951.

Principia.—A college furnished the name for this hill prairie, a part of the college campus. At this location in section 20, T. 6 N., R. 11 W., east of Elsah, Jersey County, the bluff of the Mississippi River has a high limestone cliff that is capped by a mantle of loess. The cliff is not a simple wall, but has sharp salients projecting well beyond the loess spurs above them, fig. 19. Prairie, with an area of 4 acres, predominated on the spurs in 1950 and 1951. *Andropogon scoparius* was the dominant grass; *Sporobolus asper* was locally abundant. Several paths used by students traversed the spurs and the crest of the ridge; elsewhere the prairie was undisturbed. The lower parts of coves supported mixed forest. Above this forest, tree seedlings and *Rhus glabra* occurred scatteringly to the top of the ridge, fig. 20. The north side of the ridge was well forested. Principia prairie was visited April 21, May 23, July 8, and August 29, 1950; July 5 and November 29, 1951.

Fig. 19.—Part of the cliff at Principia, near Elsah, Jersey County, with sharp rock salients that project beyond the spur fronts above.

Fig. 20.—An upper slope of a cove of Principia hill prairie with a mixture of prairie plants, *Rhus glabra,* and small oaks.

Oblate Fathers.—This name, taken from the mailbox at the entrance to the property on which the prairie is located, was adopted to designate a much-disturbed hill prairie situated in the northeast quarter of section 5, T. 5 N., R. 10 W., between Alton and Clifton Terrace, Madison County. When this site was visited on July 25, 1951, prairie with many weeds covered about 3 acres of the southwest-facing bluff slope that served as a pasture for horses.

Fig. 21.—Block House hill prairie, near Glen Carbon, Madison County. In the foreground is a cultivated field, beyond which are prairie spurs.

Block House.—Responsible for the name of this hill prairie was the shape of a small house on the bluff-top in the northeast quarter of section 32, T. 4 N., R. 8 W., west and north of Glen Carbon, Madison County, fig. 21. Block House was visited July 8 and August 29, 1950; also May 24, 1951. Here the bluff was seen to be deep loess, with no visible rock outcrops. The lower slope of the bluff bordering the highway was a cultivated field; the upper slope had prairie-covered spurs and thicket-covered coves. *Andropogon scoparius* was the dominant grass. The top of the bluff was a disturbed prairie.

Bunker.—A group of loess mounds in section 5, T. 2 N., R. 8 W., that form a ridge between Illinois highway 157 and the Collinsville road just north of Caseyville in St. Clair County was the site of this hill prairie. The name of this prairie was derived from the presence of abandoned concrete bunkers along the highway. The site was visited July 8 and August 29, 1950; also May 24, 1951. The east-facing slope of the ridge supported a mixed forest. On the west-facing slope of the ridge were prairie spurs, much disturbed by mules and cattle that grazed this land. The steep spur-fronts were prairie, the coves more or less wooded. One small cove contained much prairie vegetation, including *Silphium integrifolium, Vernonia missurica,* and *Cacalia atriplicifolia.* A thicket covered the base of the slope.

Edgemont.—This hill prairie, located in the southeast quarter of section 26, T. 2 N., R. 9 W., in Edgemont, a subdivision of East St. Louis, in 1940 occupied 4 acres of the bluff slope as determined by planimeter from aerial photographs. *Andropogon scoparius, A. gerardi,* and *Bouteloua curtipendula* were some of the prairie grasses on this slope when the prairie was visited on September 2, 1949. This prairie, because of its location, is rapidly

Fig. 22.—Valmeyer hill prairie, 3 miles south of Valmeyer, Monroe County.

being destroyed and replaced by homes and lawns.

Southwest Edgemont.—A very small hill prairie occupied a part of the bluff in section 4, T. 1 N., R. 9 W., southwest of Edgemont, when this area was visited September 2, 1949. *Andropogon scoparius* was found with other prairie plants on this bluff.

Sugar Loaf.—This name is on the Cahokia sheet of the topographic map for that part of the bluff 1 mile south of Dupo, St. Clair County, that was visited July 9, 1950. Prairie, with *Bouteloua*

Fig. 23.—Part of the eroded cliff at Valmeyer hill prairie; prairie visible at upper right.

curtipendula locally abundant, covered both the rocky lower slope and the loess which capped the bluff. The loess had been badly disturbed by earth-moving operations to provide level homesites.

Valmeyer.—When visited, this hill prairie occupied the southwest-facing slope of the ridge north of Monroe City Hollow about 3 miles south of Valmeyer, Monroe County, fig. 22. The site was visited September 2, 1949; April 22, May 24, July 9, and August 30, 1950. Prairie covered almost 9 acres of the upper slope between the cliff and the crest of the bluff. Above the eroded cliff, fig. 23, the slope was stony; the upper part was loess. The east-facing slope at the highest part of the ridge supported a mixed forest; farther south along the ridge, prairie covered the upper east-facing slope and a mixed forest occupied the basal part of the slope; at the southernmost part of the ridge only mixed forest occurred. In some places the rock outcrops were merely small vertical drops separated by steep rocky slopes on which much *Juniperus virginiana* grew. In the prairie above the rocky slopes, *Andropogon scoparius* was the dominant grass; *Psoralea tenuiflora* was common.

Chalfin Bridge.—Prairie openings occupied the bluffs southeast of Chalfin Bridge, Monroe County, when this area was visited. An open mixture of trees and shrubs, with much *Juniperus virginiana,* surrounded the prairie openings, fig. 24. South along the bluffs large spurs were completely covered by prairie. The entire loess slope, with no visible rock outcrops, served as pastureland. This site was visited August 30, 1950, and visited and photographed February 6, 1952.

Fig. 24.—Prairie openings at Chalfin Bridge, Monroe County. Prairie is visible on the parallel ridges between rows of red cedars which grow in the coves.

Fults.—This hill prairie located on the bluff south of Fults Creek, southeast of the village of Fults in Monroe County, was visited September 11, 1948; June 16 and August 30, 1950; also May 24, 1951. It occupied about 12 acres, extended 0.6 mile along the upper southwest-facing slope of the bluff-ridge, fig. 25. On the northwest part of the bluff-ridge, long prairie spurs descended from the bluff-top to a small rock outcrop with a vertical face 2 to 3 feet high, below which was a forest-covered rocky slope that formed the lower third of the bluff. The coves between the long prairie spurs supported a mixed woodland. On the southeast part there was a high limestone cliff, and above it prairie covered both spurs and coves, which were there very poorly defined. *Galium virgatum* and *Heliotropium tenellum,* rare in Illinois, grew on the limestone ledge.

Renault.—Located about 2 miles south of Renault, Monroe County, this prairie when last visited extended about 0.7 mile along the bluff-ridge and occupied almost 14 acres, of which 5 were studied. There was very little level area just above the rock ledge; the steep loess slope abruptly ended at the cliff. *Andropogon scoparius* was the dominant grass. Renault was visited July 30, 1950, and May 24, 1951.

Fig. 25.—Fults hill prairie, southeast of Fults, Monroe County.

Phegley.—The appellation for this prairie came from the name of the former tenant and caretaker, W. H. Phegley. In 1950 and 1951, the prairie occupied 6.33 acres of the southwest-facing slope of the bluff-ridge above the Columbia (Solvay) Quarry, 1.1 miles north of Prairie du Rocher, Randolph County.

The lower part of the brow slope above the limestone ledge at the top of the 200-foot cliff, fig. 26, was covered with fragments of limestone. Prairie occupied this almost level stony surface, which measured about 10 to 15 feet in width. Loess covered the bluff above this surface. This mantle of loess was dissected to form a series of spurs and coves, fig. 27. The spur fronts were steep, the upper slopes gently sloping upward from the fronts to the top of the bluff.

Prairie, with *Andropogon scoparius* as the dominant grass, covered the spurs; prairie, forest, or a mixture of both occupied the coves. *Juniperus virginiana, Quercus muhlenbergii,* and *Carya texana* grew on the narrow bluff-top ridge. The east-facing slope of the ridge was a fairly productive pasture, presumably once wooded. The prairie spurs were grazed, though apparently less closely than the main part of the pasture. The principal results of grazing on the prairie spurs were the thinning of the native cover and the introduction of a few weeds.

Plots were staked on this and the adjacent prairie toward the northwest to furnish data for vegetation studies of this report.

Phegley hill prairie was visited June 15, July 29, and September 19, 1950; May 23, September 18, October 9–10, and October 16–18, 1951.

Sampson.—The name applied to this prairie was that of the farmer on whose land the prairie occurred. Sampson hill prairie, 4.5 acres in area, was actually a continuation of the Phegley hill prairie, from which it was separated by two parallel wire fences, 3 feet apart, an effective barrier against grazing cattle. The Phegley prairie served as a pasture; the Sampson prairie was not grazed. Located to the north of Columbia Quarry, the Sampson prairie was similar in most features to the Phegley prairie. However,

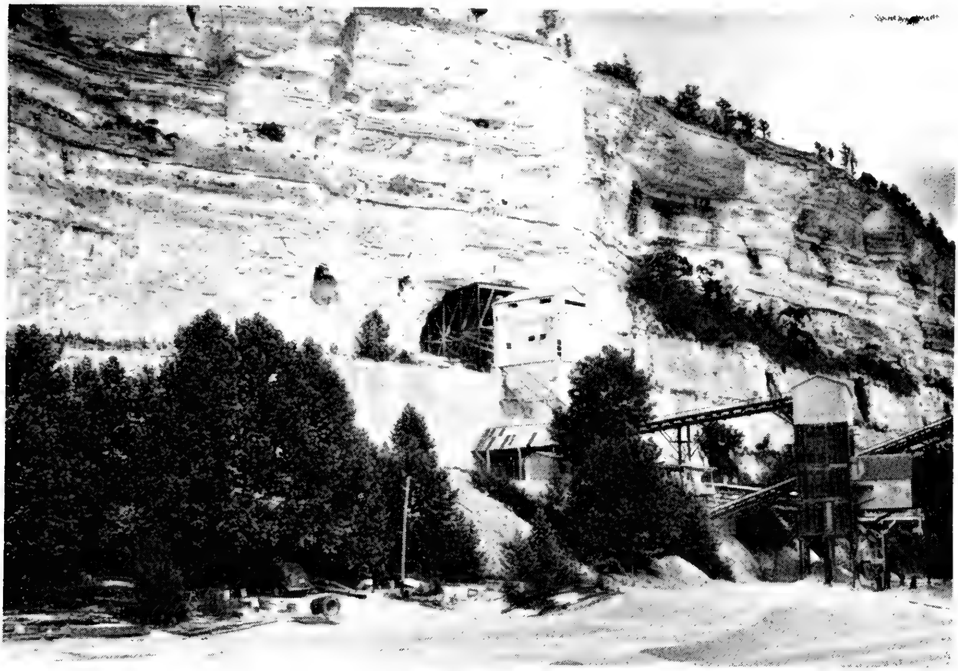

Fig. 26.—The cliff at the Columbia (Solvay) Quarry, north of Prairie du Rocher. The Phegley hill prairie occupies the slopes above this cliff. The spurs and coves shown in fig. 27 are located above the cliff near the right edge of the picture. Sampson prairie is to the north (left) of Phegley prairie.

Fig. 27.—A part of the Phegley hill prairie north of Prairie du Rocher. A small cove is visible in extreme lower left corner, a larger one near center of picture between two large spurs, which are plainly visible.

the bluff-top ridge and the east-facing slope of this ridge were forested, except for some cleared areas serving as fields for cultivated crops. This prairie was visited on the same dates as Phegley.

Stotz.—This hill prairie took its name from a quarry about a half mile north of Prairie du Rocher. Eight spurs of a bluff-ridge comprised the prairie, which covered about 6 acres in 1950; intervening ravines were wooded. The southernmost spur had been much trampled by humans, the others pastured. Native plants and weeds occurred on the pastured spurs in nearly equal proportions; the native plants persisted better on the nonpastured spur than on the others. *Andropogon scoparius* was the dominant grass of the prairie slopes. Patches of *Bouteloua curtipendula* grew throughout the prairie. The orchid *Hexalectris spicata* was found in the woodland border at the base of one spur. Stotz prairie was visited May 24 and July 30, 1950.

Allen Lake.—A small, crescent-shaped lake located near a loess-capped bluff-top supplied the name for this prairie, which was visited July 29, 1950. The prairie was west of the lake and 1.2 miles south of Prairie du Rocher. Prairie occupied 4.5 acres of the upper slope of the bluff. Limestone fragments covered the lower part of the slope. The dominant grass was *Andropogon scoparius.*

South Prairie du Rocher.—When visited June 16, 1950, this very small, pastured hill prairie occupied a part of the bluff 1.6 miles south of Prairie du Rocher. *Andropogon scoparius* was the dominant grass. *Cacalia tuberosa* was found growing in the loess.

Grand Canyon.—In 1949, this small prairie opening in section 2, T. 10 S., R. 3 W., 8 miles southwest of Murphysboro, Jackson County, occupied a west-facing slope at the north end of the bluff called Chalk Bluff, just south of the mouth of the valley known as Grand Canyon. *Andropogon scoparius* was the dominant grass. Small trees of hickory, sassafras, and white oak were scattered throughout. Grand Canyon prairie was visited October 28, 1949.

Fountain Bluff.—This hill prairie, observed in 1950 and 1951, took its name from the isolated upland known as Fountain Bluff, which has a dissected loess top and for the greatest part vertical sandstone walls and is situated between the Mississippi River and the broad bottoms of the Big Muddy River west of the main chain of bluffs in western Jackson County. This isolated upland extends 4 miles north and south, and is 1.8 miles across at the widest part. Prairie-covered slopes were observed in section 36, T. 9 S., R. 4 W., at the northern end of Fountain Bluff, a distance of about 1 mile west and a little south of Gorham.

The northern and northwestern side of Fountain Bluff is an almost vertical sandstone wall into which a sizable ravine has cut southeast and then eastward so that part of the ravine is almost parallel to the steep northwest wall. A sizable ridge lies between the ravine and the Mississippi River bottomland on the north. On this ridge were the prairie-covered slopes, described in detail below.

Above the vertical rock cliff which forms the northeast wall of the ravine are four rock-strewn spurs, which at the time of this study were covered with prairie plants; *Andropogon scoparius* was the dominant grass. These prairie-covered spurs were separated by three narrow belts of woodland in shallow drainageways. The three narrow belts of woodland were joined upslope to form another and larger belt of woodland, at right angles to the three; the larger belt covered a rock-strewn slope.

Upslope from the rock-strewn slope, the bluff is capped by loess. Three spurs on this highest exposure of the ridge were occupied by prairie, the intervening coves by small trees and shrubs. One spur faced almost westward, overlooking the Mississippi bottomland, the others southwestward. The westward-facing spur was separated from the others by a narrow belt of timber. At the ridge-top, the prairie areas of the two southwest-facing spurs were connected to form a U-shaped hill prairie with the prongs of the U extending downslope.

When visited June 14, August 17, and September 19, 1950, and April 19 and May 23, 1951, prairie occupied about 3 acres of these spurs.

Government Rock.—Located in the southeast quarter of section 9, T. 11 S., R. 3 W., 4.5 miles north of the village of Wolf Lake, Union County, this hill prairie, when visited, occupied one of the sizable spurs which extends from the summit downslope to the rock cliff in that portion of the Mississippi bluffs known as Pine Hills. The appellation here used—Government Rock—is the one applied to this spur on the Wolf Lake sheet of the topographic map.

Above the cliff at the base of the spur is a steep west- and southwest-facing slope strewn with chert stones. When last seen, the lower part of the slope was occupied by a thin stand of undersized trees. Above this was prairie, dominated by *Andropogon scoparius* and *Bouteloua curtipendula.* A few small trees of *Quercus muhlenbergii, Ostrya virginiana, Juniperus virginiana,* and *Virburnum rufidulum* occurred in several open groups within the prairie.

Upslope on the spur was a strip, about 20 feet wide, with fewer prairie plants and an abundance of *Tephrosia virginiana.* This strip was followed by a zone of mixed upland forest, which included *Quercus muhlenbergii, Q. stellata, Sassafras albidum, Juglans nigra, Carya* spp., *Cercis canadensis,* and some large trees as well as seedlings of *Pinus echinata. Vaccinium arboreum* and *Ceanothus americanus* were common shrubs.

The uppermost part of the spur, which was capped by loess, was occupied by prairie vegetation. The narrow ridge-top had been much disturbed by picnickers. The east-facing slope of the bluff-ridge was forested nearly to the ridge-top.

Government Rock was visited October 27, 1949; August 17 and October 16, 1950; April 19 and May 23, 1951.

Tamms.—This hill-top prairie opening, about a half acre in area and located on the crest of a cherty ridge in the southeast quarter of section 35, T. 14 S., R. 2 W., 1 mile west and 1 mile north of Tamms, Alexander County, was visited September 20, 1950. The prairie area, containing such plants as *Andropogon gerardi, Solidago nemoralis,* and *Helianthus divaricatus,* was surrounded by a woodland of xeric oaks, hickory, and some sassafras. One of the oaks on this ridge was *Quercus montana.*

Cave Creek.—When this area was last visited, a rock (limestone) hill prairie occupied part of the bluff on the east side of the confluence plain of Dutchman and Cave creeks, somewhat over a mile east of the Cache River, in the northeast quarter of section 28, T. 13 S., R. 3 E., about 5 miles south of Vienna and 1.5 miles northeast of Forman, Johnson County. The base of the bluff was wooded, but it had been much disturbed during the construction of a power line. The prairie opening above the disturbed wooded bluff base occupied about 1.5 acres of the south- and southwest-facing slope of the ridge. The prairie slope was strewn with rock fragments which had eroded from outcrops at various levels on the slope. In some places the slope was almost a rock pavement. Grasses and composites were the predominant vegetation; a few small trees of *Quercus muhlenbergii, Juniperus virginiana, Cornus florida,* and *Crataegus* spp. were found scattered throughout. The trees did not reach full size; after they had attained heights of 10 to 15 feet the tops lost vigor and the trees died.

Upslope from the prairie, the broadly rounded ridge was forested, but it had openings occupied chiefly by *Andropogon gerardi.* An interrupted limestone ledge traversed this forested surface. Much *Nothoscordum bivalve* grew in the crevices of this ledge.

Cave Creek prairie was visited June 10, August 17, and September 20, 1950; April 18 and May 22, 1951.

FLORA OF THE HILL PRAIRIES

As a means of determining what species of plants occur in Illinois hill prairies, numerous collections were made from early September, 1949, to the middle of October, 1951. Many of the plant species very common in Illinois were collected from only one prairie but their occurrence in other prairies was recorded in the field notes. Species less common were collected from each prairie site in which they were growing. More than

3,000 specimens were collected from the prairie areas; numerous others from the adjacent rock ledges, upland woods, wooded coves, and basal slopes of the bluffs. These specimens now form a part of the collections in the herbarium of the Illinois Natural History Survey at Urbana.

Collections and identification of hill prairie plants added several species to the known Illinois flora. *Rudbeckia missouriensis* was one of the rare plants reported (Evers 1951). The collections verified the present-day existence of certain species reported over a half century ago from Illinois but not collected in the state again until the field work for this study was undertaken. *Mentzelia oligosperma* is a notable example. The collections also increased the knowledge of the distribution of plants having somewhat restricted ranges in Illinois. Thus, it is now known that *Bouteloua curtipendula* ranges almost continuously, in suitable habitats, from northern to southern Illinois along the western border, that *Psoralea tenuiflora* ranges southward into Monroe County, and that *Houstonia nigricans* is quite common on loess slopes in southwestern Illinois.

The hill prairies contain prairie, woodland, cultivated, and introduced species. The woodland species are occasionally found in prairie just as the prairie species are found in woodland, especially in adjoining border areas. The cultivated plants usually are escapes that have become established in the hill prairies. Some, *Lespedeza stipulacea* for example, had been planted in certain prairies or in adjoining pastures by the landowners. Asia and Europe are the original homes of 30 of the species found, North America of the remainder.

Annotated List of Species

This list was compiled from collections made and notes taken on the Illinois hill prairies visited. Field notes were used to supplement the distribution record but no species is included in this list unless it was collected from at least one prairie. The list is not intended as a complete flora of the Illinois hill prairies. Such a compilation would require much additional time and many additional visits to these sites. In some cases, only the generic name of a plant is given. Thus, the four species of grapes are included in this list under the term *Vitis* spp. In most instances, both generic and specific epithets are used. Any pertinent synonym is placed within brackets following the scientific name. Brief notes on the occurrence of each plant or plant group follow its name. The name of each plant that is of foreign origin is preceded by an asterisk (*).

Table 14, which summarizes presence, as discussed on page 392, contains a partial enumeration of the annotated list of species. Species found only on rock ledges, in coves, or in woodland borders near, but not in, the prairie stands of any site listed in table 14 are not indicated for that site. Some species mentioned in the annotated list are not included in table 14 because they are not native to North America or are not regarded as characteristic prairie species.

Lecideaceae

Lecidea spp. Lichens of this genus were found in 14 hill prairies. Two samples were identified by Dr. C. W. Dodge of the Missouri Botanical Garden as *L. decipiens* and *L. demissa*. These plants grew between grass tufts under the shade of the grass foliage on either loess or fine rock fragments.

Marchantiaceae

Reboulia hemisphaerica (L.) Raddi. This was a frequently encountered liverwort on loess and rocks of hill prairies, where it grew in interspaces between bunches of grass.

Musci

An unidentified moss (or mosses) grew on loess of some hill prairies. All plants examined lacked sporophytes and accordingly remain unidentified.

Selaginellaceae

Selaginella rupestris (L.) Spring. The rock selaginella grew in the sandy hill prairie at Devil's Backbone. Although found on sandstone outcrops in southern

Illinois (Pope County), apparently it is absent from similar situations in the Fountain Bluff hill prairie.

EQUISETACEAE

Equisetum hyemale L. The tall scouring-rush was seen in three hill prairies, Rock Island 31, Bunker, and Southwest Edgemont, where it occurred in loess. It was not seen on rocky slopes.

Equisetum laevigatum A. Br. [*E. kansanum* Schaffn.] The smooth scouring-rush was observed in seven bluff prairies, all of them in northern or central Illinois.

POLYPODIACEAE

Cheilanthes lanosa (Michx.) D. C. Eaton. The woolly lip-fern was found in rock prairie at Cave Creek. It was more abundant, however, on rock outcrops than on prairie slopes.

Pellaea atropurpurea (L.) Link. Although the usual habitat for purple cliff-brake is calcareous rocks, it occurred on the loose stony slopes at Cave Creek and Government Rock.

PINACEAE

Juniperus virginiana L. Red cedar was found in both rock and loess hill prairies and was common on rock ledges at the bases of prairie slopes and in wooded coves. It was the only tree species on some of the prairie slopes. Steyermark (1940) noted its frequent occurrence in Missouri glades.

GRAMINEAE

Agrostis hiemalis (Walt.) B.S.P. Ticklegrass was encountered only in rock prairie at Fountain Bluff.

Andropogon gerardi Vitman. [*A. furcatus* Muhl.] The big bluestem is an abundant prairie grass in Illinois. It was observed in 37 hill prairies. It was found as a dominant only in scattered patches, and in this status in only a few hill prairies.

Andropogon scoparius Michx. Little bluestem was found to be the usual dominant and is the most important grass of the hill prairies of Illinois.

Andropogon virginicus L. Broomsedge, a common grass in open woods, old fields, and along roadsides in southern Illinois, was not found to be an important species of the hill prairies, having been seen in but one, Fountain Bluff, on the loess prairie slopes.

Aristida basiramea Engelm. ex Vasey. This plant was collected in only the Sunset Trail hill prairie.

Aristida intermedia Scribn. & Ball. This was observed only at Hill-Top and in the sandy prairie at Devil's Backbone.

Aristida longespica Poir. This three-awned grass was collected in prairie at Devil's Backbone and from a rock ledge at Cave Creek.

Aristida oligantha Michx. This weedy species was collected in only the Seehorn-Payson hill prairie.

Bouteloua curtipendula (Michx.) Torr. Side-oats grama was found in 48 of the hill prairies examined. In southern Illinois, it was found in Cave Creek and Government Rock prairies, but it was not observed at Tamms, Fountain Bluff, or Grand Canyon. It was seen at most of the sites examined from Allen Lake northward along the Mississippi and Illinois rivers. Vestal (1945) mentioned "hill prairie and sandstone cliff-tops" as common habitats of this species in Illinois. He observed in July, 1941, that this *Bouteloua* dominated several steep southwest slopes of prairies along the lower Illinois in Jersey County, sites not included in this study. Side-oats grama was the dominant grass just above the rock ledge at Swarnes; a few feet higher on the prairie slope, *Andropogon scoparius* was dominant.

Bouteloua hirsuta Lag. Hairy grama was observed in eight hill prairies, most of them in northern Illinois. It grew in the heavily pastured loess prairie at Bald Bluff and also along the bluffs of the Illinois River at Mud Creek and Northeast Meredosia in central Illinois.

**Bromus commutatus* Schrad. Hairy chess was found in loess and rock prairie at five sites and in crevices of rock ledges at two others.

**Bromus tectorum* L. Downy chess or cheat was found in situations similar to those of hairy chess. It was more abundant in crevices of rock ledges than in hill prairie.

Table 14.—Occurrence (indicated by +) of native prairie plants in 36 of the hill prairie stands studied in Illinois; also occurrence of native species of forests and thickets and of foreign species found in 18 or more stands. The heavy vertical rules divide the hill prairies into three principal groups: those along the Mississippi River from East Dubuque to Grafton, at the mouth of the Illinois River; those along the Rock, the Sangamon, and the Illinois rivers; those along the Mississippi River from Grafton to the mouth of the Ohio River and those elsewhere in southern Illinois.

Family and Species	El Rancho	Menominee Station	Sunset Trail	South Palisades	Bielema	Ursa	Rock Creek	Homan	Hidden Lake	Seehorn-Payson	Sessions	South New Canton	Clendenny	Swarnes	Devil's Backbone	Magnolia	Reavis Spring	Bluff Springs	Mud Creek	Northeast Meredosia	Walnut Creek	North Eldred	Pere Marquette	Chautauqua	Principia	Block House	Bunker	Valmeyer	Fults	Renault	Sampson	Phegley	Stotz	Fountain Bluff	Government Rock	Cave Creek	Total
LECIDEACEAE																																					
Lecidea spp.		+				+	+	+					+		+		+		+	+						+				+	+	+		+			14
MARCHANTIACEAE																																					
Reboulia hemisphaerica		+				+			+		+	+			+	+								+										+			9
SELAGINELLACEAE																																					
Selaginella rupestris															+																						1
EQUISETACEAE																																					
Equisetum hyemale																											+										1
Equisetum laevigatum					+		+										+		+	+																	5
POLYPODIACEAE																																					
Cheilanthes lanosa																																				+	1
Pellaea atropurpurea																																			+	+	2
GRAMINEAE																																					
Agrostis hiemalis																																		+			1
Andropogon gerardi	+	+	+		+	+	+		+		+	+	+	+	+	+	+			+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	30
Andropogon scoparius	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	36
Andropogon virginicus																																		+			1
Aristida basiramea			+																																		1
Aristida intermedia															+																						1
Aristida longespica															+																						1
Aristida oligantha										+																											1
Bouteloua curtipendula	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+		+	+	33
Bouteloua hirsuta	+				+														+	+																	4
Elymus canadensis	+	+				+				+	+	+										+		+	+			+	+		+	+		+			14
Elymus virginicus											+																							+		+	3

Eragrostis capillaris																																		+			1
Eragrostis spectabilis			+				+				+		+				+			+			+		+			+	+			+					11
Festuca octoflora												+		+											+							+		+			5
Hordeum pusillum																																+					1
Koeleria cristata			+	+	+								+		+		+				+			+				+	+	+			+	+			13
Leptoloma cognatum									+						+																						2
Melica nitens																								+													1
Muhlenbergia cuspidata																		+																			1
Muhlenbergia racemosa	+																																				1
Panicum capillare																		+																			1
Panicum dichotomum																																		+			1
Panicum huachucae			+																															+			2
Panicum linearifolium																																		+	+		2
Panicum scribnerianum	+	+	+		+	+		+			+			+	+				+	+	+	+	+	+	+	+	+	+	+	+	+	+					23
Panicum sphaerocarpon																																+					1
Panicum tennesseense		+																																			1
Panicum virgatum				+																																	1
Paspalum stramineum										+								+				+	+			+											5
Poa pratensis	+	+	+		+	+		+		+				+	+		+	+	+	+	+			+	+	+	+		+			+					20
Sorghastrum nutans			+				+			+	+		+	+	+	+		+		+								+	+	+	+	+		+	+	+	18
Sphenopholis obtusata													+																								1
Sporobolus asper	+		+										+						+	+	+	+			+				+			+					10
Sporobolus cryptandrus					+					+														+													3
Sporobolus heterolepis	+															+				+																	3
Sporobolus neglectus					+								+																								2
Sporobolus vaginiflorus					+									+																				+			3
Stipa spartea	+																			+																	2
Tridens flavus									+		+		+									+										+		+			6
CYPERACEAE																																					
Carex brevior	+	+	+		+	+	+	+	+																												8
Carex glaucodea																																		+			1
Carex gravida																		+																			1
Carex gravida var. *lunelliana*							+																														1
Carex meadii																																				+	1
Carex muhlenbergii																								+										+			2
Carex pennsylvanica															+					+																	2
Cyperus filiculmis							+	+	+	+	+		+		+		+	+							+			+						+			12
COMMELINACEAE																																					
Tradescantia ohiensis	+	+	+				+		+						+									+	+		+	+	+	+	+	+					14
Tradescantia virginiana																																		+	+		2

Table 14.—*Continued*

Family and Species	El Rancho	Menominee Station	Sunset Trail	South Palisades	Bielema	Ursa	Rock Creek	Homan	Hidden Lake	Seehorn-Payson	Sessions	South New Canton	Clendenny	Swarnes	Devil's Backbone	Magnolia	Reavis Spring	Bluff Springs	Mud Creek	Northeast Meredosia	Walnut Creek	North Eldred	Pere Marquette	Chautauqua	Principia	Block House	Bunker	Valmeyer	Fults	Renault	Sampson	Phegley	Stotz	Fountain Bluff	Government Rock	Cave Creek	Total
JUNCACEAE																																					
Juncus dudleyi																								+										+			2
Juncus interior			+																																		1
LILIACEAE																																					
Allium stellatum																													+		+	+			+		4
Camassia scilloides																								+													1
Nothoscordum bivalve																																			+	+	2
AMARYLLIDACEAE																																					
Agave virginica																													+		+	+				+	4
IRIDACEAE																																					
Sisyrinchium albidum																+									+		+	+	+	+	+	+	+	+		+	11
Sisyrinchium campestre	+	+	+		+						+		+	+	+		+	+	+	+	+					+											14
ORCHIDACEAE																																					
Spiranthes cernua													+				+	+														+					4
SALICACEAE																																					
Salix humilis		+											+									+				+	+										5
SANTALACEAE																																					
Comandra umbellata	+	+	+	+	+	+							+		+	+	+					+		+		+				+							14
POLYGONACEAE																																					
Polygonum tenue																																		+			1
CHENOPODIACEAE																																					
Chenopodium leptophyllum							+																														1
NYCTAGINACEAE																																					
Mirabilis nyctaginea															+																						1
CARYOPHYLLACEAE																																					
Cerastium nutans																												+						+			2
Silene antirrhina									+															+				+		+		+		+			6
RANUNCULACEAE																																					
Anemone cylindrica			+	+	+								+		+		+		+	+																	8

Anemone virginiana							+																												+		2
Delphinium carolinianum var. *crispum*								+	+		+																										3
Ranunculus fascicularis															+																						1
FUMARIACEAE																																					
Corydalis montana																												+									1
CRUCIFERAE																																					
Draba reptans		+							+						+					+								+					+				6
Lepidium virginicum																		+											+								2
SAXIFRAGACEAE																																					
Heuchera richardsonii	+	+	+										+											+		+	+	+		+	+			+	+		12
ROSACEAE																																					
Fragaria virginiana																		+	+	+																	3
Potentilla arguta	+	+	+	+	+										+																						6
Potentilla simplex			+																																		1
Rosa carolina	+		+			+	+								+					+	+		+												+	+	10
Rosa suffulta															+		+											+									3
LEGUMINOSAE																																					
Amorpha canescens	+	+	+	+		+				+			+		+	+	+					+	+	+	+			+									15
Astragalus canadensis																									+			+									2
Astragalus distortus										+																											1
Cassia fasciculata		+				+							+	+							+		+	+	+		+	+	+	+	+	+	+	+	+	+	18
Cassia nictitans																																+		+			2
Crotalaria sagittalis													+												+												2
Desmanthus illinoensis																							+		+												2
Desmodium canadense	+																																				1
Desmodium ciliare													+										+					+	+	+	+	+	+		+	+	10
Desmodium dillenii									+				+										+					+	+					+			6
Desmodium illinoense													+						+				+														3
Desmodium sessilifolium									+		+		+	+							+		+		+	+	+	+		+	+	+	+		+	+	16
Galactia volubilis																																			+	+	2
Lespedeza capitata		+	+				+						+	+	+		+				+	+		+	+	+		+	+	+	+	+	+			+	19
Lespedeza intermedia																															+			+	+	+	4
Lespedeza simulata																													+	+							2
Lespedeza virginica													+										+	+	+			+	+	+	+	+	+	+	+	+	13
Melilotus alba	+	+				+	+	+	+		+	+	+	+		+		+	+	+	+		+			+	+		+				+				20
Petalostemum candidum		+		+				+	+		+		+				+				+	+	+	+	+			+	+	+					+		16
Petalostemum purpureum	+	+	+	+	+	+	+			+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		31
Psoralea tenuiflora						+	+	+		+	+	+		+		+	+	+	+	+	+		+	+	+		+	+									18
Stylosanthes biflora																															+			+			2
Tephrosia virginiana																												+		+					+		3
LINACEAE																																					
Linum sulcatum					+	+	+	+			+		+	+		+	+	+		+	+		+			+	+	+	+	+	+	+	+				21

Table 14.—*Continued*

Family and Species	El Rancho	Menominee Station	Sunset Trail	South Palisades	Bielema	Ursa	Rock Creek	Homan	Hidden Lake	Seehorn-Payson	Sessions	South New Canton	Clendenny	Swarnes	Devil's Backbone	Magnolia	Reavis Spring	Bluff Springs	Mud Creek	Northeast Meredosia	Walnut Creek	North Eldred	Pere Marquette	Chautauqua	Principia	Block House	Bunker	Valmeyer	Fults	Renault	Sampson	Phegley	Stotz	Fountain Bluff	Government Rock	Cave Creek	Total
OXALIDACEAE																																					
Oxalis stricta			+							+		+	+											+			+						+	+			8
Oxalis violacea	+	+			+		+				+		+	+	+	+	+		+	+	+	+		+	+			+	+	+	+	+		+	+		23
GERANIACEAE																																					
Geranium carolinianum													+											+			+						+				4
POLYGALACEAE																																					
Polygala incarnata																				+																	1
Polygala verticillata					+								+	+	+					+						+						+		+			8
EUPHORBIACEAE																																					
Acalypha gracilens																																		+			1
Chamaesyce glyptosperma															+																						1
Chamaesyce maculata						+				+			+				+	+			+	+		+		+						+			+	+	12
Chamaesyce supina			+							+			+		+																			+			5
Croton capitatus																									+												1
Croton glandulosus																		+								+											2
Croton monanthogynus						+				+	+	+	+	+									+	+	+	+		+	+			+	+	+			15
Euphorbia corollata	+	+		+	+	+	+	+	+				+	+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	30
Poinsettia dentata		+				+				+	+	+	+	+			+	+								+											10
ANACARDIACEAE																																					
Rhus aromatica				+									+									+	+	+	+							+	+	+	+	+	11
Rhus aromatica var. *arenaria*				+	+																																2
Rhus copallina																													+			+					2
Rhus glabra	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+		+	+			+	+	+	+	+	+				+		+	+		26
RHAMNACEAE																																					
Ceanothus americanus			+																			+				+	+	+	+	+	+		+	+	+	+	12
HYPERICACEAE																																					
Hypericum punctatum																									+							+		+			3
Hypericum sphaerocarpum		+																						+												+	3
CISTACEAE																																					
Helianthemum bicknellii		+	+																																		2
Lechea stricta																												+									1

VIOLACEAE																																					
Viola pedata															+																				+		2
Viola rafinesquii												+										+						+	+				+				5
LOASACEAE																																					
Mentzelia oligosperma										+	+	+		+														+									5
CACTACEAE																																					
Opuntia rafinesquii											+													+	+				+		+	+					6
ONAGRACEAE																																					
Gaura biennis										+							+	+										+	+								5
Oenothera biennis					+	+	+		+				+								+		+														7
Oenothera laciniata												+	+										+		+	+	+	+				+	+	+			10
UMBELLIFERAE																																					
Polytaenia nuttallii																	+							+				+	+								4
Spermolepis inermis										+																											1
Taenidia integerrima																																				+	1
Zizia aurea																																				+	1
PRIMULACEAE																																					
Androsace occidentalis															+																						1
Dodecatheon meadia																	+																				1
GENTIANACEAE																																					
Sabatia angularis											+																										1
APOCYNACEAE																																					
Apocynum cannabinum																									+									+			2
Apocynum sibiricum						+				+																											2
ASCLEPIADACEAE																																					
Asclepias amplexicaulis		+							+							+										+	+			+	+						7
Asclepias stenophylla						+	+	+	+	+	+			+																							7
Asclepias tuberosa																																			+		1
Asclepias verticillata	+	+	+		+	+		+							+	+		+	+	+						+										+	13
Asclepias viridiflora					+			+					+		+		+							+		+	+	+	+	+	+	+	+		+	+	16
POLEMONIACEAE																																					
Phlox bifida																	+	+	+		+								+			+	+	+	+		9
Phlox pilosa																						+				+		+		+						+	5
BORAGINACEAE																																					
Lithospermum canescens			+											+		+	+			+	+	+				+		+			+	+			+	+	13
Lithospermum croceum										+												+															2
Lithospermum incisum					+		+			+	+		+	+	+	+	+	+	+	+	+	+	+		+		+		+	+		+					20
Myosotis verna																																		+			1
Onosmodium occidentale	+																+										+									+	4
VERBENACEAE																																					
Verbena canadensis																													+	+					+		3
Verbena simplex												+		+								+		+				+	+		+						7
Verbena stricta	+		+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+				29
LABIATAE																																					
Hedeoma hispida		+			+					+			+		+			+		+									+	+		+	+				11
Isanthus brachiatus										+	+		+	+		+						+												+		+	8

Table 14.—*Continued*

Family and Species	El Rancho	Menominee Station	Sunset Trail	South Palisades	Bielema	Ursa	Rock Creek	Homan	Hidden Lake	Seehorn-Payson	Sessions	South New Canton	Clendenny	Swarnes	Devil's Backbone	Magnolia	Reavis Spring	Bluff Springs	Mud Creek	Northeast Meredosia	Walnut Creek	North Eldred	Pere Marquette	Chautauqua	Principia	Block House	Bunker	Valmeyer	Fults	Renault	Sampson	Phegley	Stotz	Fountain Bluff	Government Rock	Cave Creek	Total
Labiatae (*continued*)																																					
Monarda bradburiana																									+			+						+	+	+	5
Monarda fistulosa	+				+				+		+		+				+			+	+	+		+						+				+			12
Monarda punctata																					+																1
Physostegia virginiana											+		+				+	+	+	+		+			+	+	+				+	+		+	+	+	15
Pycnanthemum pilosum			+			+	+			+	+		+				+	+	+	+	+	+			+		+	+		+	+	+	+				19
Salvia pitcheri																																				+	1
Scutellaria leonardi	+		+		+	+				+																										+	6
Scutellaria ovata																												+									1
Scutellaria parvula												+			+	+													+	+	+	+				+	8
Solanaceae																																					
Physalis heterophylla							+		+				+		+					+	+						+										7
Physalis pubescens																		+																			1
Physalis virginiana		+	+					+		+								+																			5
Scrophulariaceae																																					
Buchnera americana													+															+	+	+	+	+					6
Gerardia aspera					+					+		+	+	+			+	+		+		+			+	+	+		+								13
Gerardia gattingeri													+														+	+	+		+	+					6
Gerardia skinneriana										+	+									+																	3
Penstemon pallidus					+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	30
Synthyris bullii					+										+																						2
Veronica peregrina																																		+			1
Veronicastrum virginicum													+								+	+												+			4
Acanthaceae																																					
Ruellia humilis						+	+	+	+		+		+	+			+	+	+		+		+	+	+			+	+	+	+	+	+		+	+	22
Plantaginaceae																																					
Plantago aristata																		+					+						+								3
Plantago purshii					+													+																			2

Plantago rugelii																									+												1
Plantago virginica									+	+		+	+	+				+		+	+			+			+	+	+	+	+	+	+	+			17
RUBIACEAE																																					
Diodia teres																																	+				1
Houstonia lanceolata																										+										+	2
Houstonia longifolia																												+						+			2
Houstonia nigricans														+								+	+	+	+		+	+	+	+	+	+	+				12
CAMPANULACEAE																																					
Campanula rotundifolia					+																																1
Specularia perfoliata	+												+		+													+	+	+				+			7
LOBELIACEAE																																					
Lobelia spicata	+		+		+								+						+	+	+	+															8
Lobelia spicata var. *leptostachys*																		+		+		+				+	+					+					6
COMPOSITAE																																					
Agoseris cuspidata																	+																				1
Ambrosia coronopifolia											+						+			+	+	+															5
Ambrosia elatior	+						+		+													+	+	+			+							+			8
Ambrosia trifida																								+													1
Antennaria neglecta		+															+			+	+	+															5
Artemisia caudata		+	+		+										+	+	+			+																	8
Aster azureus		+	+		+								+				+	+		+	+		+			+	+								+		12
Aster ericoides	+	+	+		+				+		+		+	+							+		+			+	+		+	+					+		15
Aster linariifolius																				+							+										2
Aster oblongifolius	+	+	+	+	+	+				+	+	+	+	+		+		+		+				+	+		+	+			+	+			+	+	22
Aster parviceps										+	+													+													3
Aster patens													+												+			+	+	+	+	+		+	+	+	10
Aster pilosus					+	+				+	+	+			+					+	+		+		+						+	+			+		13
Aster sericeus					+								+				+			+		+					+	+	+	+							9
Aster turbinellus																																		+			1
Cacalia tuberosa					+									+																	+						3
Chrysopsis villosa																	+	+	+	+						+				+							6
Coreopsis lanceolata																	+											+	+								3
Coreopsis lanceolata var. *villosa*																												+	+								2
Coreopsis palmata			+	+										+		+	+											+		+							7
Echinacea pallida					+									+		+	+			+		+		+	+	+	+	+	+	+						+	14
Erigeron annuus																								+													1
Erigeron canadensis									+	+		+	+								+		+		+				+			+			+		10
Erigeron divaricatus										+																											1
Erigeron strigosus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		34
Eupatorium altissimum			+	+		+		+	+	+	+		+	+		+	+	+		+		+		+	+	+	+	+	+	+	+	+		+	+	+	26
Gnaphalium obtusifolium			+							+		+	+				+					+		+				+				+		+	+		11

Table 14.—*Concluded*

FAMILY AND SPECIES	EL RANCHO	MENOMINEE STATION	SUNSET TRAIL	SOUTH PALISADES	BIELEMA	URSA	ROCK CREEK	HOMAN	HIDDEN LAKE	SEEHORN-PAYSON	SESSIONS	SOUTH NEW CANTON	CLENDENNY	SWARNES	DEVIL'S BACKBONE	MAGNOLIA	REAVIS SPRING	BLUFF SPRINGS	MUD CREEK	NORTHEAST MEREDOSIA	WALNUT CREEK	NORTH ELDRED	PERE MARQUETTE	CHAUTAUQUA	PRINCIPIA	BLOCK HOUSE	BUNKER	VALMEYER	FULTS	RENAULT	SAMPSON	PHEGLEY	STOTZ	FOUNTAIN BLUFF	GOVERNMENT ROCK	CAVE CREEK	TOTAL
COMPOSITAE (*continued*)																																					
Helianthus mollis													+																								1
Helianthus occidentalis																											+										1
Helianthus rigidus														+										+		+		+		+							5
Helianthus strumosus																												+		+							2
Heliopsis helianthoides var. *scabra*																										+											1
Kuhnia eupatorioides	+	+	+		+	+	+			+	+		+	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	29
Lactuca canadensis																					+					+	+				+						4
Liatris aspera			+	+										+	+	+	+					+						+									8
Liatris cylindracea																						+		+	+	+		+	+		+						7
Liatris scabra																																		+		+	2
Ratibida pinnata			+	+		+								+								+						+		+						+	8
Rudbeckia missouriensis																												+	+		+	+					4
Rudbeckia serotina			+		+		+	+										+	+	+	+						+							+			10
Senecio pauperculus			+																																		1
Senecio plattensis													+	+			+	+	+	+		+	+		+	+	+	+	+	+	+	+	+				17
Silphium integrifolium																						+		+			+	+		+		+	+	+	+	+	10
Silphium laciniatum														+			+					+															3
Silphium terebinthinaceum																												+								+	2
Solidago altissima											+			+													+	+			+			+			6
Solidago canadensis	+		+																																		2
Solidago drummondii																						+		+								+		+			4
Solidago missouriensis																									+												1
Solidago nemoralis		+	+	+	+	+					+		+		+	+	+	+		+	+		+		+	+	+	+	+		+	+		+	+		23
Solidago radula											+	+	+	+								+		+			+	+	+	+	+	+	+	+	+		15
Solidago rigida	+																+									+		+		+					+		6
Solidago speciosa			+												+													+									3
Vernonia baldwini											+		+	+								+									+						5
Vernonia missurica							+							+							+		+		+		+		+			+					8

Danthonia spicata (L.) Beauv. ex Roem. & Schult. Poverty oat-grass was observed in rock prairie at Devil's Backbone. It is usually found in dry woodlands.

Elymus canadensis L. Canada wildrye was found in 16 of the 61 hill prairies visited.

Elymus virginicus L. Virginia wildrye was found in three hill prairies. It was more common in the adjacent woodlands than in prairie areas.

Eragrostis capillaris (L.) Nees. Lacegrass, a species of fields, clearings, rock ledges, and glades, was collected from hill prairie areas only on the rocky slope at Fountain Bluff.

**Eragrostis cilianensis* (All.) Lutati. Stinkgrass was found only on the disturbed crest of the bluff-ridge at Clendenny.

Eragrostis spectabilis (Pursh) Steud. Purple lovegrass was found scattered in 17 loess prairies.

Festuca octoflora Walt. Six-weeks fescue (including the variety *tenella*) was observed in six hill prairies, either on rocky or loess slopes. It was seen also on limestone ledges at three prairie sites.

Hordeum pusillum Nutt. Little barley was found only at Phegley hill prairie.

Koeleria cristata (L.) Pers. Junegrass occurred in scattered patches in 14 hill prairies, but it was never abundant.

Leptoloma cognatum (Schult.) Chase. Fall witchgrass, more frequent in sand prairie than in hill prairie, was observed at only two sites, Hidden Lake and Devil's Backbone.

Melica nitens (Scribn.) Nutt. ex Piper. Three-flower melic, a plant of rocky woods, bluffs, and glades, was found growing at Chautauqua on stony prairie slopes, at Valmeyer and Fults on the rock ledges.

Muhlenbergia capillaris (Lam.) Trin. This muhly of rocky or sandy woodlands was found only in rock prairie at Government Rock.

Muhlenbergia cuspidata (Torr.) Rydb. Plains muhly, a plant of rocky bluffs, sandy woods, and loess hills, was found only in loess at Bluff Springs.

Muhlenbergia racemosa (Michx.) B.S.P. This species occurred on loess slopes at Wiersma, on rock-strewn slopes of El Rancho, and on rock ledges at Fountain Bluff and Sampson.

Panicum capillare L. Witchgrass was observed in two hill prairies, Bluff Springs and Richwood.

Panicum dichotomum L. This panic grass was collected on the stony slopes at Fountain Bluff.

Panicum huachucae Ashe. [*P. lanuginosum* var. *fasciculatum* (Torr.) Fern.] This prairie species of panic grass was found in five hill prairies on the bluffs of the Mississippi River.

Panicum linearifolium Scribn. This species, usually of dry woods, was found on stony slopes of Fountain Bluff and Government Rock.

Panicum scribnerianum Nash. [*P. oligosanthes* var. *scribnerianum* (Nash) Fern.] This species was seen in 27 hill prairies, mostly on loess but occasionally on rocky slopes.

Panicum sphaerocarpon Ell. This panicum of sandy soil was collected at Phegley hill prairie in loess.

Panicum tennesseense Ashe. [*P. lanuginosum* var. *fasciculatum* (Torr.) Fern.] This plant grew in loess at Menominee Station and on stony slopes at Standard.

Panicum virgatum L. Switchgrass, common throughout most types of prairie in Illinois, was observed in hill prairie only at South Palisades and Hill-Top.

Paspalum stramineum Nash. This species was found in loess of five hill prairies.

**Poa compressa* L. Canada bluegrass occurred on two loess slopes and also two stony slopes.

Poa pratensis L. Kentucky bluegrass was found in more than 20 hill prairies. In some it was locally dominant but more often occurred scattered throughout the prairie area. It becomes dominant in pastures, and spreads from them.

**Setaria lutescens* (Weigel) Hubb. [*S. glauca* (L.) Beauv.] Yellow bristlegrass, or yellow foxtail, was found at Hidden Lake in loess and on the rock ledges at Valmeyer.

**Setaria viridis* (L.) Beauv. Green bristlegrass, or green foxtail, was seen on three prairie slopes. It was more common on rock ledges than in hill prairie.

Sorghastrum nutans (L.) Nash. Indian grass was observed in 23 hill prairies, usually in loess but occasionally on rocky slopes. It was the dominant grass in prairie at Hill-Top and also in the woodland border at North Pandarmie.

Sphenopholis obtusata (Michx.) Scribn. Prairie wedgegrass occurred in loess at Clendenny. It was seen in woodlands adjoining other prairies.

Sporobolus asper (Michx.) Kunth. This dropseed was observed in 10 hill prairies. It was frequent in loess at Principia.

Sporobolus cryptandrus (Torr.) A. Gray. Sand dropseed was seen in loess at Bielema, Seehorn-Payson, and Chautauqua prairies.

Sporobolus heterolepis (A. Gray) A. Gray. Prairie dropseed was not common in hill prairie. It was observed on stony slopes at El Rancho and Magnolia and on loess at Northeast Meredosia.

Sporobolus neglectus Nash. This annual dropseed grew on rocky slopes at Bielema and Clendenny hill prairies. At Clendenny it grew also on limestone ledges and in the border between prairie and wooded coves.

Sporobolus vaginiflorus (Torr.) Wood. This species occurred in loess at Bielema, Wiersma, and Swarnes, on rocky slopes and sandstone ledges at Fountain Bluff, and on limestone ledges at Phegley and Sampson.

Stipa spartea Trin. Porcupine grass, of infrequent occurrence in hill prairie, was observed at El Rancho, Balk, and Northeast Meredosia. It is commonly observed in flatland prairie.

Tridens flavus (L.) Hitchc. [*Triodia flava* (L.) Smyth.] Purpletop was found growing in loess at eight hill prairies in central and southern Illinois.

Uniola latifolia Michx. Broadleaf uniola, or spike grass, common in open woods in southern Illinois, was found in the disturbed loess prairie at Government Rock.

Cyperaceae

Carex brevior (Dewey) Mack. A sedge of dry, rocky ground, this plant was collected from 10 hill prairies in northern and central Illinois.

Carex glaucodea Tuckerm. [*C. flaccosperma* var. *glaucodea* (Tuckerm.) Kükenth.] This sedge was collected from rock prairie at Fountain Bluff.

Carex gravida Bailey. This common sedge was observed only at Bluff Springs, on the loess slope.

Carex gravida var. *lunelliana* (Mack.) E. J. Hermann. This variety was collected only at Rock Creek, from loess.

Carex meadii Dewey. This sedge was collected on stony slopes at Cave Creek.

Carex muhlenbergii Schk. This sedge, common in sand prairie, was observed in only four hill prairies, Balk, Standard, Chautauqua, and Fountain Bluff.

Carex pennsylvanica Lam. A sedge of sterile soil and open woods, this species was collected at Devil's Backbone and Northeast Meredosia.

Cyperus filiculmis Vahl. The slender cyperus (including the variety *macilentus*), a plant of dry sandy soil, was seen in 16 hill prairies; its southernmost station was Fountain Bluff.

Commelinaceae

Tradescantia ohiensis Raf. [*T. canaliculata* Raf.] This spiderwort was seen in 16 hill prairies, growing on loess or stony slopes. Also, it was observed in crevices of limestone ledges at Stotz and South Prairie du Rocher.

Tradescantia virginiana L. This species, which occurs mostly in woods, thickets, and meadows, was found on the rocky slopes of Fountain Bluff and Government Rock.

Juncaceae

Juncus dudleyi Wieg. This rush was observed in loess prairie at Chautauqua and Fountain Bluff.

Juncus interior Wieg. This species was seen growing on loess slopes at Sunset Trail and on rocky slopes at Standard.

Juncus tenuis Willd. [*J. macer* S. F. Gray.] This common rush of woodlands was observed only at Oblate Fathers, in loess.

Liliaceae

Allium canadense L. Wild garlic was seen in loess at Oblate Fathers and Allen Lake.

Allium stellatum Ker. This wild onion was found on rocky slopes at Government Rock and on loess slopes at Fults, Sampson, and Phegley. Its occurrence on loess and stony slopes was nowhere so abundant as on rock ledges at the bases of these slopes.

**Allium vineale* L. Field garlic was found in two prairies, Sugar Loaf and Phegley.

**Asparagus officinalis* L. Asparagus was seen at Principia and Oblate Fathers prairies.

Camassia scilloides (Raf.) Cory. Locally abundant in some upland prairies of Illinois, wild hyacinth was found in hill prairie at Chautauqua.

Nothoscordum bivalve (L.) Britt. False garlic, one of the most frequent plants in thin soil of cliff-tops in the Shawnee Hills of southern Illinois, was observed on rocky slopes at Cave Creek and Government Rock.

Smilax bona-nox L. Fringed greenbrier, a dry-woodland species, occurred in prairie at Fountain Bluff and Cave Creek.

Smilax hispida Muhl. [*S. tamnoides* var. *hispida* (Muhl.) Fern.] Common greenbrier was found in Hidden Lake and Phegley prairies.

Smilax rotundifolia L. This woodland species was seen in Phegley, Government Rock, and Cave Creek prairies.

Amaryllidaceae

Agave virginica L. American aloe was seen on stony slopes at Allen Lake and Cave Creek, and on loess slopes at Fults, Sampson, and Phegley. It was observed also on rock ledges at South Prairie du Rocher and Stotz. The mature plants seem to flower every year. In thin soil on rock, the plants have short vertical stems and leaf-bases that vary in length with the depth of the soil. The fleshy roots radiate horizontally over the rock surface. In places, chiefly on rock ledges, the rosettes form fair-sized patches.

Iridaceae

**Belamcanda chinensis* (L.) DC. Blackberry-lily, an Asiatic species that is very common on open wooded slopes in Pike and Greene counties, where it forms dense stands on the basal slopes of the bluffs, was found in loess at Walnut Creek and in the woodland border at Swarnes.

Sisyrinchium albidum Raf. This blue-eyed grass was found growing in loess in 11 hill prairies, most of them in southern Illinois.

Sisyrinchium campestre Bickn. This species occurred in 14 hill prairies in central and northern Illinois, from El Rancho south to Block House.

Orchidaceae

Spiranthes cernua (L.) Rich. Nodding ladies'-tresses were seen at Clendenny, Reavis Spring, Bluff Springs, and Phegley, in each case in loess. They were fairly frequent at Reavis Spring.

Salicaceae

Populus deltoides Marsh. A few individuals of eastern cottonwood were found in Ursa and Homan hill prairies.

Populus grandidentata Michx. The large-toothed aspen, usually found on wooded bluffs, occurred as small trees in Menominee Station, Hill-Top, and South Palisades hill prairies.

Populus tremuloides Michx. Quaking aspen was observed in the prairie at Menominee Station, North Savanna, and Balk. It and the large-toothed aspen were "in" but not "of" hill prairie.

Salix humilis Marsh. Prairie willow was collected from six hill prairies.

Juglandaceae

Carya texana Buckl. Buckley's or black hickory (including varieties) is a tree of dry upland woods. Seedlings occasionally were found growing on the upper prairie slopes at Valmeyer, Sampson, and Phegley. Here it was found also at the bluff-top in the woodland border.

Juglans nigra L. Small individuals of black walnut were seen in North Savanna, Homan, Fall Creek, Walnut Creek, and North Eldred prairies. Large specimens were never found in prairie, only in the adjacent coves and bluff woods.

Betulaceae

Corylus americana Walt. American hazel, a species of woods and thickets, was seen in hill prairie at Sunset Trail and Ursa.

Ostrya virginiana (Mill.) K. Koch. American hop-hornbeam was found on four rocky prairie slopes and also on one loess slope. It was usually one of the trees found in wooded coves.

Fagaceae

Quercus alba L. White oak saplings or small trees were observed in loess prairie at Sunset Trail, Hill-Top, and Fountain Bluff.

Quercus macrocarpa Michx. At Devil's Backbone and Ursa a few saplings of bur oak were found in the prairie. There and at other sites it was found also in the coves.

Quercus marilandica Muenchh. Black jack was represented by a few stunted individuals in the rock prairie at Government Rock.

Quercus muhlenbergii Engelm. Yellow or chinquapin oak occurred in 10 prairies. It was more abundant in clefts of limestone ledges, in coves, and on lower bluff slopes than in prairies.

Quercus stellata Wangh. Post oak occurred as scattered individuals in seven prairies. It was common in woodland borders in southwestern Illinois.

Quercus velutina Lam. Black oak, like other oaks a woodland species, was found in seven prairies, usually in the borders between prairie areas and upland woods, and occasionally as small solitary trees on the prairie slopes.

Ulmaceae

Celtis laevigata Willd. Sugarberry, a southern tree, most frequent in bottomlands, was represented by one specimen in rock prairie at Government Rock.

Ulmus alata Michx. Winged elm was found on the stony prairie slopes at Fountain Bluff, Government Rock, and Cave Creek.

Ulmus rubra Muhl. Very small individuals of slippery elm were found in eight hill prairies.

Moraceae

Maclura pomifera (Raf.) Schneid. Osage orange was observed in the pastured loess prairie at Walnut Creek and also in the prairie near woodland at Principia. In some other localities it was abundant in pastured woods on the basal slopes of bluffs.

Cannabinaceae

**Cannabis sativa* L. Common hemp, abundant in some pastured sand areas of Illinois, was seen at South New Canton, a pastured hill prairie.

Santalaceae

Comandra umbellata (L.) Nutt. [*C. richardsiana* Fern.] Bastard-toadflax was found on 13 loess and 7 rocky prairie slopes from El Rancho and Devil's Backbone south to Renault.

Polygonaceae

Polygonum tenue Michx. Slender knotweed was collected from the rocky prairie slopes and the sandstone ledges at Fountain Bluff.

Chenopodiaceae

Chenopodium leptophyllum Nutt. [*C. pratericola* Rydb.] The narrow-leaved goosefoot was found in sandy loess at Balk and Rock Creek.

Nyctaginaceae

Mirabilis nyctaginea (Michx.) MacM. Umbrella-wort was found in only one hill prairie, Devil's Backbone.

Caryophyllaceae

Cerastium nutans Raf. Nodding mouse-ear chickweed occurred in Valmeyer and Fountain Bluff prairies.

**Cerastium vulgatum* L. Common mouse-ear chickweed was found in loess at Seehorn-Payson.

**Saponaria officinalis* L. Bouncing-bet was found in loess at Homan.

Silene antirrhina L. Sleepy catchfly was observed in nine rock or loess prairies and in crevices of rock ledges at the bases of four prairies.

Ranunculaceae

Anemone canadensis L. Meadow anemone was found in Bielema hill prairie.

Anemone cylindrica Gray. The long-fruited anemone occurred in 14 hill prairies, mostly in loess.

Anemone virginiana L. Tall anemone, or thimbleweed, was seen on three loess prairie slopes.

Aquilegia canadensis L. Wild columbine was found under a red cedar growing in loess at North Savanna. It was frequent on some rock ledges and in adjacent rocky woods.

Delphinium carolinianum var. *crispum* Perry. Blue larkspur was collected at Homan, Hidden Lake, and Sessions, where it was growing in loess.

Ranunculus fascicularis Muhl. Tufted or early buttercup was found in Balk and Devil's Backbone prairies.

LAURACEAE

Sassafras albidum (Nutt.) Nees. Sassafras occurred as small individuals on four prairie slopes.

FUMARIACEAE

Corydalis montana Engelm. [*C. aurea* var. *occidentalis* Engelm.] This corydalis of rocky woods, prairies, and glades (Palmer & Steyermark 1935) was found in the Valmeyer prairie.

CRUCIFERAE

Arabis lyrata L. This species of rockcress occurred in loess at North Savanna and Balk, and on rock ledges at Menominee Station and Sunset Trail.

Draba reptans (Lam.) Fern. This small, inconspicuous species of whitlowcress grew in interstices at eight hill prairie stations.

**Lepidium campestre* (L.) R. Br. Field peppergrass, or cow-cress, was seen in hill prairie only at Devil's Backbone.

**Lepidium densiflorum* Schrad. This introduced weed was seen in five of the hill prairies visited.

Lepidium virginicum L. Common peppergrass, a weedy crucifer, was found in three hill prairies. It was in places more abundant in crevices of rock ledges at the base of a prairie slope than in the prairie itself.

SAXIFRAGACEAE

Heuchera richardsonii R. Br. Alumroot was found in loess and on rocky slopes of 13 hill prairies from El Rancho to Cave Creek.

Ribes missouriense Nutt. This common gooseberry, usually of woods and thickets, occurred on the disturbed rocky slope of Bielema prairie.

ROSACEAE

Agrimonia rostellata Wallr. Agrimony was collected only at Chalfin Bridge near the woodland border of one of the prairie openings there. It is a plant that is usually found in woodlands.

Amelanchier arborea (Michx. f.) Fern. Serviceberry, usually of wooded hillsides, was observed on the rock-strewn slopes at Government Rock and Fountain Bluff. It was seen in crevices and clefts in rock ledges near other hill prairies.

Crataegus crus-galli L. Cockspur-thorn was found on stony slopes at Cave Creek and in loess at Mud Creek and Pere Marquette. In these localities and in others it was found also in the woodland borders.

Crataegus engelmanni Sarg. This hawthorn grew on the rock slopes at Cave Creek.

Crataegus mollis (T. & G.) Scheele. Red haw, usually a small tree of thickets and woodland borders, occurred in Cave Creek prairie.

Fragaria virginiana Duch. Strawberry was collected in loess at Bluff Springs, Mud Creek, and Northeast Meredosia.

Malus ioensis (Wood) Britt. [*Pyrus ioensis* (Wood) Bailey.] Wild crab, or Iowa crabapple, was found as seedlings in six hill prairies. In the coves it was more frequent and the plants were larger than in the prairie areas.

Potentilla arguta Pursh. The tall cinquefoil grew on stony or loess slopes of nine hill prairies in northern Illinois.

Potentilla simplex Michx. Common or old-field cinquefoil was found only at Sunset Trail, in loess.

Prunus lanata (Sudw.) Mack. & Bush. [*P. americana* var. *lanata* Sudw.] This wild plum was found in rock prairie at Cave Creek. At other sites, if present, it occurred in the woodland border.

Rosa carolina L. The pasture rose was found in rock prairie or in loess prairie at 12 sites. It was not common there. It is probably more common in flatland prairie.

Rosa setigera Michx. One plant of the climbing rose was observed at Phegley; it was not seen in other hill prairies. This rose is common in woodland borders.

Rosa suffulta Greene. [*R. arkansana* var. *suffulta* (Greene) Cockerell.] This rose was infrequent on loess slopes in four hill prairies.

Rubus flagellaris Willd. The dewberry was found in one loess prairie, Phegley, near a thicket-covered cove.

Rubus frondosus Bigel. This blackberry was seen on the rocky slopes at Chautauqua prairie.

Rubus occidentalis L. Black raspberry was found in the rock prairie at Menominee Station.

LEGUMINOSAE

Amorpha canescens Pursh. Leadplant grew in scattered patches in 23 rock or loess prairies from El Rancho and Devil's Backbone south to Valmeyer.

Astragalus canadensis L. This milk-vetch occurred infrequently in loess at North Pandarmie, Principia, and Valmeyer. At Housen it was abundant in the woodland border at the crest of the ridge.

Astragalus distortus T. & G. This small milk-vetch was seen in loess, on rocky slopes, and in crevices of the rock ledge, at only one site, the Seehorn-Payson prairie.

Baptisia leucantha T. & G. Wild indigo, or prairie false-indigo, common in many of the upland prairies and in open woods of Illinois, was found in only one hill prairie, Hill-Top.

Cassia fasciculata Michx. Partridge-pea, common in hill prairies of southern Illinois, less frequent in those of northern Illinois and along the Illinois River, was found in 20 prairies.

Cassia nictitans L. This cassia was found in the cherty ridge-top prairie at Tamms, the stony and loess prairies at Fountain Bluff, and the loess prairie at Phegley.

Cercis canadensis L. Redbud, usually found on forested rocky slopes of bluffs, also was found in coves of hill prairies. Seedlings or very small trees were found occasionally on loess or rock prairie slopes.

Crotalaria sagittalis L. Rattlebox was observed in loess at Hill-Top, Clendenny, and Principia.

Desmanthus illinoensis (Michx.) MacM. Illinois- or prairie-mimosa, was found growing in loess of two hill prairies, Pere Marquette and Principia. In both sites it was locally abundant.

Desmodium canadense (L.) DC. This tick-clover was found only in the rock prairie at El Rancho.

Desmodium ciliare (Muhl.) DC. This species was collected at 12 stations from Clendenny south to Cave Creek. At Phegley and Sampson it grew also in the woodland.

Desmodium dillenii Darl.* This species was found in six hill prairies, Hidden Lake, Clendenny, Pere Marquette, Valmeyer, Fults, and Fountain Bluff.

Desmodium illinoense Gray. The Illinois tick-clover was collected in five hill prairies in central Illinois; all specimens collected were from loess slopes.

Desmodium paniculatum (L.) DC. This species, predominantly of open woods and thickets, was encountered in loess prairie at nine sites.

Desmodium sessilifolium (Torr.) T. & G. The sessile-leaved tick-clover was found at 22 sites, usually in loess prairie but occasionally on the rock-strewn slopes.

Galactia volubilis (L.) Britt. Milk-pea was collected from rock prairie at Cave Creek and Government Rock.

Gleditsia triacanthos L. Honey locust grew in scattered groups in four hill prairies.

Lespedeza capitata Michx. This bush-clover was a common plant on loess and occasionally on rocky prairie slopes. It was present in 27 of the 61 sites studied.

Lespedeza hirta (L.) Hornem. This lespedeza was collected from the cherty prairie at Tamms and was observed in the woodland border at Government Rock.

Lespedeza intermedia (S. Wats.) Britt. This species was found in loess at five prairie sites in southern Illinois.

Lespedeza procumbens Michx. Trailing bush-clover, a species of rocky woods,

*In the treatment of this genus in *Gray's Manual*, edition 8, this entity has been segregated into two species, *Desmodium perplexum* and *D. glabellum*.

was encountered in five prairies, where it grew also in the wooded coves.

Lespedeza repens (L.) Bart. A few plants of creeping bush-clover were found in Sampson and Ursa hill prairies.

X *Lespedeza simulata* Mack. & Bush. This species was collected from loess prairie at Renault and Fults, also on rocky prairie slopes of the latter.

**Lespedeza stipulacea* Maxim. Korean clover or lespedeza was seen in 13 hill prairies. At Rock Creek it had been planted; elsewhere it apparently was an escape from the nearby pasturelands.

Lespedeza violacea (L.) Pers. Although usually found only in thickets and rocky woods, this lespedeza was seen in five prairies. It was more common, however, in the nearby wooded coves than on the prairie slopes.

Lespedeza virginica (L.) Britt. Slender bush-clover, a plant of woods, thickets, prairies, and glades, was seen growing in 18 prairie sites, from Clendenny and Richwood south to Government Rock and Cave Creek.

**Medicago lupulina* L. Black medic, a European species, was observed in East Henry and Mud Creek prairies.

**Melilotus alba* Desr. White sweet clover was seen in 25 hill prairies. It appeared to have been planted at Clendenny. It formed a very dense stand at Hidden Lake.

**Melilotus officinalis* (L.) Lam. Yellow sweet clover was less frequent than white sweet clover; it was found at five prairie sites.

Petalostemum candidum (Willd.) Michx. White prairie-clover was collected or observed at 19 prairie sites from Government Rock northward. It occurred abundantly in loess prairie at Homan, but at Phegley it was restricted to rocky wooded coves.

Petalostemum purpureum (Vent.) Rydb. Purple prairie-clover occurred in 43 prairies from El Rancho and Devil's Backbone south to Government Rock.

Psoralea tenuiflora Pursh. The many-flowered psoralea occurred in 27 hill prairies from Valmeyer north to Ursa and Standard. In some sites it was the most conspicuous species in early summer. It is a distinctly western species and is very infrequent in Illinois other than in hill prairie.

Robinia pseudo-acacia L. Black locust, not native in Illinois, has spread from numerous plantations and was seen in four loess prairies.

Strophostyles helvola (L.) Ell. This wild bean of sand, rocky woods, or thickets was observed infrequently in seven hill prairies.

Strophostyles leiosperma (T. & G.) Piper. This species was observed in two places, at Hill-Top and Rock Island 31.

Stylosanthes biflora (L.) B.S.P. Pencil-flower, a plant of rocky woods and also glades, was collected at Fountain Bluff on both rocky and loess prairie slopes and at Sampson in loess prairie near a cove.

Tephrosia virginiana (L.) Pers. Goat's-rue, very common in the sand areas of Illinois, and occasional in dry, open woods with varying soil textures, was collected in a rock prairie at Government Rock, where it was abundant also in the woodland border, and in loess prairie at Oblate Fathers, Valmeyer, and Renault.

LINACEAE

Linum sulcatum Riddell. This annual flax was observed in loess and occasionally in stony soil in 28 hill prairies from Bielema and Magnolia south to Allen Lake.

OXALIDACEAE

Oxalis stricta L. Upright yellow wood-sorrel grew on rocky and loess prairie slopes at nine sites. It was found in crevices of ledges at two additional places.

Oxalis violacea L. Violet wood-sorrel was found at 25 sites. In some places it blossomed in spring and again in early autumn.

GERANIACEAE

Geranium carolinianum L. This weedy cranesbill was seen in four hill prairies in southwestern Illinois.

RUTACEAE

Ptelea trifoliata L. Scattered small individuals of wafer-ash grew in 11 hill prairies. This plant was more abundant in coves or on basal slopes of the bluffs than in the prairies.

Xanthoxylum americanum Mill. Prickly ash was seen in Balk prairie, where it was growing in loess. The woodlands adjoining many other prairies contained this species; only at Balk had it strayed into the prairie.

Polygalaceae

Polygala incarnata L. This milkwort was found in loess on the crest of the ridge at Northeast Meredosia.

Polygala verticillata L. This species, easily overlooked in its location between tufts of grass, was observed in nine prairies from Fountain Bluff northward.

Euphorbiaceae

Acalypha gracilens Gray. This three-seeded mercury grew on the rocky prairie slopes and sandstone ledges at Fountain Bluff.

Chamaesyce glyptosperma (Engelm.) Small. [*Euphorbia glyptosperma* Engelm.] This plant was found in rock prairie at Devil's Backbone.

Chamaesyce maculata (L.) Small. [*Euphorbia maculata* L.] Nodding spurge was seen in 14 hill prairies; in none of them was it abundant.

Chamaesyce supina (Raf.) Moldenke. [*Euphorbia supina* Raf.] Milk-purslane was found between the bunches of grass in six hill prairies. It was observed also in crevices of ledges.

Croton capitatus Michx. Hogwort was found only at Principia and Edgemont.

Croton glandulosus var. *septentrionalis* Muell. Arg. Sand croton was found only at Bluff Springs and Block House.

Croton monanthogynus Michx. Prairie-tea, a frequently encountered plant in hill prairie, was observed at 19 sites in central and southern Illinois.

Euphorbia corollata L. Flowering spurge, a common plant in prairies, glades, and rocky ground, was found in 36 hill prairies, where it grew in loess and rocky soil. It was found also in some adjacent woodlands.

**Euphorbia cyparissias* L. Cypress-spurge, or cemetery cypress, was found in the Seehorn-Payson prairie as an escape from a nearby cemetery.

Euphorbia obtusata Pursh. This species was collected at Fults.

Poinsettia dentata (Michx.) Small. [*Euphorbia dentata* Michx.] This weedy species was found in 15 hill prairies.

Anacardiaceae

Rhus aromatica Ait. Fragrant sumac was seen in 15 hill prairies, either in loess or rocky soil. It was encountered also in some wooded coves as well as in bluff-top woods.

Rhus aromatica var. *arenaria* (Greene) Fern. This variety of the fragrant sumac was found in sandy loess at Bald Bluff, Balk, Bielema, and South Palisades.

Rhus copallina L. Shining or dwarf sumac was found in loess at Southwest Edgemont, Chalfin Bridge, Fults, and Phegley.

Rhus glabra L. Smooth sumac was a very frequent plant in the hill prairies studied. It was observed on 33 rock and loess prairie slopes. It grew in coves and extended out on the spurs, or it grew in the borders of the bluff-top woods and out in the prairies as isolated individuals. In some places it was very dense and formed a thicket. In a few other places most of the individuals in open groups were dead or dying, a result possibly of fire, or of competition by grasses, competition intensified by summer drought.

Rhus radicans L. Poison ivy, erroneously called poison oak, was very abundant in woodlands adjacent to most of the hill prairies. It was found at Principia in loess and rock prairie.

Aquifoliaceae

Ilex decidua Walt. Possumhaw or swamp holly, normally found in bottomland woods or on basal slopes of bluffs, infrequently on shaded cliffs, was observed in a cove at Phegley, 200 feet above the adjacent bottomland.

Celastraceae

Celastrus scandens L. Bittersweet occurred in eight hill prairies that adjoined woods. It occurred also in wooded coves near prairie.

Rhamnaceae

Ceanothus americanus L. New Jersey tea, a plant of rocky woods, forest borders, and glades, was observed in 12 loess and in 2 rock prairies. It was found also in wooded coves nearby.

VITACEAE

Vitis spp. Stunted individuals of probably four species of grape were found in a number of hill prairies. No fruiting vines were found in these hill prairies.

HYPERICACEAE

**Hypericum perforatum* L. Common St. John's-wort was found in two loess prairies, Sunset Trail and Bluffs.

Hypericum punctatum Lam. Spotted St. John's-wort was observed in five hill prairies in central and southern Illinois.

Hypericum sphaerocarpum Michx. Round-fruited St. John's-wort was seen in five prairies.

CISTACEAE

Helianthemum bicknellii Fern. Frostweed, a plant of sand prairie, rocky prairie, and glade, was found in sandy loess at Menominee Station and Sunset Trail.

Lechea leggettii Britt. & Hollick. This pinweed was observed in loess at Menominee Station.

Lechea stricta Leggett. It was seen in hill prairie only at Valmeyer.

Lechea villosa Ell. This species was encountered at Principia.

VIOLACEAE

Viola pedata L. Bird-foot violet was not found frequently. It grew on rocky slopes at Government Rock and in loess at Balk and Devil's Backbone.

Viola rafinesquii Greene. [*V. kitaibeliana* var. *rafinesquii* (Greene) Fern.] Field or wild pansy, a plant of prairies, roadsides, glades, and waste places, occurred in five hill prairies.

LOASACEAE

Mentzelia oligosperma Nutt. Stickleaf, or few-seeded mentzelia, fig. 28, grew chiefly in crevices of rock ledges; it grew also on rocky slopes above the ledges. It was collected on ledges at North Pandarmie, Fults, and Phegley; on rock prairie, as well as ledges, at Seehorn-Payson, Sessions, South New Canton, Swarnes, and Valmeyer. It was not observed in the hill prairies between Swarnes and Valmeyer, nor north along the bluffs east of the Bluff Hall railroad siding in Adams County. In Illinois it is apparently restricted to unglaciated bluffs or to those not glaciated since Kansan time. This genus is one of those of chiefly western distribution which reaches its eastern limit in exposed xeric habitats in western Illinois.

CACTACEAE

Opuntia rafinesquii Engelm. [*O. humifusa* Raf.] The prickly pear was observed at 10 sites from Seehorn-Payson south to Phegley. It was found on rock ledges at Seehorn-Payson, Valmeyer, and Stotz; on rocky and loess slopes at Sessions, Housen, Chautauqua, Principia, Fults, Sampson, and Phegley.

ONAGRACEAE

Gaura biennis L. Biennial gaura, a plant of prairies, roadsides, and waste places, was collected in Seehorn-Payson, Reavis Spring, Bluff Springs, Valmeyer, and Fults prairies.

Oenothera biennis L. Common evening primrose was seen infrequently in eight hill prairies.

Oenothera laciniata Hill. This evening primrose was found in 11 hill prairies in central and southern Illinois.

UMBELLIFERAE

Chaerophyllum sp. An unidentified species of this genus was found at Clendenny.

**Daucus carota* L. Wild carrot was collected only at Phegley, where but few plants were found.

Polytaenia nuttallii DC. Prairie-parsley was found growing in loess prairie and also at the border between prairie and rock ledges. It was collected at Reavis Spring, Chautauqua, Valmeyer, and Fults.

Spermolepis inermis (Nutt.) Math. & Const. This umbellifer was found in loess prairie and on rock ledges at Seehorn-Payson.

Taenidia integerrima (L.) Drude. Taenidia, or yellow pimpernel, was found on rocky slopes at Cave Creek. It was restricted principally to slopes with sparse cover, or to comparatively bare

Fig. 28.—*Mentzelia oligosperma* growing in thin loess just above a limestone cliff, south of New Canton, Pike County.

spaces just above or just below slopes. Presumably it cannot compete with vigorous species.

**Torilis japonica* (Houtt.) DC. Hedge-parsley was found in hill prairie only at Chautauqua. This species seemingly is becoming widespread in Illinois.

Zizia aurea (L.) Koch. Golden alexanders, a plant of both prairie and forest, grew in the rock prairie at Cave Creek.

CORNACEAE

Cornus drummondi Meyer. This dogwood, common in thickets and in woodland borders, was observed growing singly or in small thickets in loess prairie at 19 sites. It was common also in the adjoining coves.

Cornus florida L. Scattered individuals of flowering dogwood, a very attractive plant in springtime, were seen in Swarnes and Cave Creek prairies.

ERICACEAE

Vaccinium arboreum Marsh. Farkleberry, or tree huckleberry, a plant of rocky woods, was collected in rock prairie at Government Rock.

Vaccinium vacillans Torr. Hill or low blueberry, a species of rocky woods, bluffs, and glades, grew on the sandstone ledges and in rock prairie at Fountain Bluff.

PRIMULACEAE

Androsace occidentalis Pursh. This species was encountered on the rock ledges at Valmeyer and in the rock prairie at Devil's Backbone.

Dodecatheon meadia L. This shooting star, occurring in both prairie and forest in Illinois, was found in loess prairie at Reavis Spring and in the border of prairie and rock ledge at Valmeyer.

EBENACEAE

Diospyros virginiana L. Persimmon occasionally was found growing as scattered individuals in the hill prairies of southern Illinois.

OLEACEAE

Fraxinus americana L. White ash, common in wooded coves, was found in a few hill prairies.

Fraxinus nigra Marsh. Black ash was observed in the border between the rock ledge and rock prairie at Principia. It was observed in no other prairie.

GENTIANACEAE

Gentiana quinquefolia L. Stiff gentian was collected in loess at Wiersma.

Sabatia angularis (L.) Pursh. Rose gentian, or rose-pink, was collected from rock prairie at Sessions.

APOCYNACEAE

Apocynum cannabinum L. Hemp dogbane, or Indian hemp, chiefly of open woods, glades, prairies, and roadsides, was collected at Principia and Fountain Bluff.

Apocynum sibiricum Jacq. This dogbane was found in two prairies, Seehorn-Payson and Ursa.

ASCLEPIADACEAE

Asclepias amplexicaulis Sm. This milkweed was collected from eight loess prairies.

Asclepias hirtella (Pennell) Woodson. [*Acerates hirtella* Pennell.] Although common in upland prairie in Illinois, it was collected in hill prairie only at Edgemont.

Asclepias quadrifolia Jacq. This woodland milkweed was seen in rock prairie at Government Rock.

Asclepias stenophylla Gray. [*Acerates angustifolia* (Nutt.) Dcne.] This species of green milkweed was collected from eight hill prairies in Adams, Pike, and Calhoun counties. In Illinois, it is apparently restricted to hill prairies.

Asclepias tuberosa L. Butterfly-weed, common in some upland prairies in Illinois, was found in but one hill prairie, Government Rock. It is one of the most attractive prairie plants. It can be successfully transplanted to home gardens.

Asclepias verticillata L. Horsetail or whorled milkweed, poisonous to livestock, was found in 18 hill prairies, most of them in northern and central Illinois.

Asclepias viridiflora Raf. [*Acerates viridiflora* (Raf.) Eaton.] This green milkweed was common in hill prairies; it was observed in 20 of them.

POLEMONIACEAE

Phlox bifida Beck. Sand phlox was found in five rocky prairies in southern Illinois, and in five sandy loess prairies in the Illinois River valley.

Phlox pilosa L. Downy phlox was found in five hill prairies, on either rocky or loess slopes.

BORAGINACEAE

**Lappula echinata* Gilib. European stickseed was collected at Chautauqua in rock prairie.

Lithospermum canescens (Michx.) Lehm. This gromwell occurred on 2 rock and 14 loess prairie slopes.

Lithospermum croceum Fern. Although common in sand prairie in Illinois, this species was collected in only two hill prairies, Seehorn-Payson and North Eldred.

Lithospermum incisum Lehm. This narrow-leaved gromwell was very common in hill prairie from Bielema and Devil's Backbone south to Allen Lake. It was observed in 27 prairies.

Myosotis verna Nutt. This forget-me-not was found in the Fountain Bluff prairie.

Onosmodium occidentale Mack. False gromwell or marbleseed was seen in seven hill prairies from El Rancho and Reavis Spring to Cave Creek.

Verbenaceae

Verbena bracteata Lag. & Rodr. This vervain, abundant along roadsides, was observed in hill prairie only at Balk.

Verbena canadensis (L.) Britt. This attractive vervain, common on rocky bluffs in Monroe County, was collected at Fults and Renault in that county and at Government Rock in Union County.

Verbena simplex Lehm. The narrow-leaved vervain was found growing in seven hill prairies, in either rocky soil or loess.

Verbena stricta Vent. Hoary vervain was present in 42 hill prairies from El Rancho and Magnolia to Allen Lake.

Labiatae

Blephilia ciliata (L.) Benth. Wood mint was collected on the rocky prairie slope at Devil's Backbone.

Cunila origanoides (L.) Britt. Stone mint was found in the rock prairie and on sandstone ledges at Fountain Bluff, and on a rock outcrop at Government Rock. It was more abundant in adjacent open woods than in prairie areas.

Hedeoma hispida Pursh. Rough pennyroyal was present in many hill prairies and adjoining rock ledges from Menominee Station and Devil's Backbone south to South Prairie du Rocher.

Hedeoma pulegioides (L.) Pers. American pennyroyal, common in woodlands, was found in rock prairie at Ursa and in loess prairie at Wiersma.

Isanthus brachiatus (L.) B.S.P. False pennyroyal grew in 10 rock and loess prairies and on 7 rock ledges from Fall Creek and Magnolia south to Cave Creek.

Monarda bradburiana Beck. [*M. russeliana* Nutt. (?)] This species of bergamot was observed in three rock and three loess prairies in southern Illinois. It was commonly found also in open woods and thickets near hill prairies.

Monarda fistulosa L. Wild bergamot, common in prairie vegetation along roadsides and railroads, was seen in 16 hill prairies.

Monarda punctata L. Spotted bergamot, locally abundant in sand prairies and barrens of Illinois, was found in sandy loess at Walnut Creek.

**Nepeta cataria* L. Catnip was found in hill prairie at South New Canton and Chautauqua.

Physostegia virginiana (L.) Benth. [*P. angustifolia* Fern. (?)] False dragonhead was found in 16 hill prairies from Sessions and Reavis Spring south to Cave Creek. It was seen in loess and rock prairie and occasionally in crevices of rock ledges.

Prunella vulgaris L. Selfheal, a common plant of woods, fallow fields, and thickets, was observed growing in loess at Sunset Trail.

Pycnanthemum flexuosum (Walt.) B.S.P. This mint of open rocky woods, thickets, and fields was seen in loess at Oblate Fathers.

Pycnanthemum pilosum Nutt. This was the common mountain mint in 29 loess prairies from Sunset Trail and Reavis Spring south to Allen Lake.

Pycnanthemum virginianum (L.) Dur. & Jacks. This species was collected at El Rancho, Ursa, and Block House.

Salvia pitcheri Torr. [*S. azurea* var. *grandiflora* Benth.] Blue sage was collected from rock prairie at Cave Creek. This sage is a western species, with the eastern extent of its range from Minnesota to Kentucky coming through Illinois.

Scutellaria leonardi Epling. [*S. parvula* var. *leonardi* (Epling) Fern.] This small skullcap grew in 10 hill prairies, most of them in northern and central Illinois.

Scutellaria ovata Hill. This skullcap was found in loess prairie at Valmeyer.

Scutellaria parvula Michx. This small glandular-pubescent skullcap was seen in 10 rock and loess prairies and in crevices of 7 rock-ledge locations.

Teucrium canadense L. This woodsage was found in small numbers in six loess prairies.

Solanaceae

Physalis heterophylla Nees. This ground-cherry was seen in seven hill prairies.

Physalis pubescens L. This pubescent annual ground-cherry was seen at Bluff Springs.

Physalis virginiana Mill. Virginia ground-cherry was collected from six loess prairies in central and northern Illinois.

Solanum carolinense L. Horse-nettle was seen only in pastured loess prairie at Walnut Creek.

SCROPHULARIACEAE

Aureolaria grandiflora (Benth.) Pennell. [*Gerardia grandiflora* Benth.] False foxglove, a species of woods, openings, and thickets, was observed in loess at Sunset Trail and Magnolia.

Buchnera americana L. Blue hearts, previously reported in Illinois only from Cook and Menard counties, was found in six hill prairies in Calhoun, Monroe, and Randolph counties.

Dasistoma macrophylla (Nutt.) Raf. [*Seymeria macrophylla* Nutt.] Mullein foxglove, commonly found in open woods and thickets, was found growing in loess at Swarnes hill prairie.

Gerardia aspera Dougl. This gerardia was seen in at least 17 hill prairies from northern to southern Illinois.

Gerardia gattingeri Small. This plant was seen in at least six hill prairies in south-central Illinois.

Gerardia skinneriana Wood. This plant of bluffs, sands, and barrens was found in four loess prairies.

Gerardia tenuifolia Vahl. This gerardia of wooded slopes was found in three hill prairies.

Pedicularis canadensis L. Wood-betony or common lousewort was found in loess prairie at North Eldred, where also it was very common in the wooded coves.

Penstemon pallidus Small. This pale penstemon was collected from 36 loess and rock prairie slopes and 14 rock ledges in 40 sites from Bielema and Devil's Backbone to Cave Creek. It was moderately abundant in many of these sites.

Scrophularia marilandica L. Usually found in thickets and woodland borders, this figwort was collected from loess prairie at Balk.

Synthyris bullii (Eaton) Heller. [*Wulfenia* Barnh.; *Besseya* Eaton.] This plant of sandy soil was collected from hill prairie at Bielema and Devil's Backbone, both sites near the margin of the Wisconsin glaciation.

**Verbascum thapsus* L. Common mullein was observed in loess or rock prairie, or in crevices of rock ledges, in 17 hill prairies.

**Veronica arvensis* L. Corn-speedwell, a common European weed, was found infrequently in eight hill prairies.

Veronica peregrina L. Purslane-speedwell, another weedy species, was collected from rock prairie at Fountain Bluff.

Veronicastrum virginicum (L.) Farw. Culver's-root, a plant of woods, thickets, and prairies, was observed in seven hill prairies. In none of these was it so common as in flatland prairie.

BIGNONIACEAE

Bignonia capreolata L. Cross-vine, a southern species, was found as a stray at Cave Creek.

Campsis radicans (L.) Seem. Trumpet-creeper, common in woods, thickets, and fields in southern Illinois, was found in four hill prairies.

ACANTHACEAE

Ruellia humilis Nutt. Hairy ruellia was found in 30 hill prairies (also occasionally in crevices of rock ledges) from Bald Bluff and Devil's Backbone to Cave Creek.

PLANTAGINACEAE

Plantago aristata Michx. The bracted plantain, a common roadside and open-field weed in compact soils of southern Illinois, was collected from five hill prairies, in loess and in rocky soil.

Plantago purshii R. & S. This western species of plantain, locally abundant in some sand prairies of the state, was found in sandy loess at Bielema and Bluff Springs.

Plantago rugelii Dcne. This plantain was seen in loess prairie at Principia and Hill-Top. In both sites it grew in the disturbed portions.

Plantago virginica L. Hoary plantain, common in fields and rocky waste places, was found in 20 hill prairies.

RUBIACEAE

Diodia teres Walt. Rough buttonweed was collected from one loess prairie, Stotz.

Galium aparine L. Cleavers was found in nine hill prairies. It was nowhere very abundant in the prairies, but was common in the adjacent woodlands.

Galium circaezans Michx. Wild licorice, a plant of thickets and rocky woods, was found growing in three hill prairies. Also, it was seen in wooded coves.

Galium pilosum Ait. This bedstraw, a plant of thickets and rocky woods, was seen in three loess prairies and one rock prairie in southern Illinois. It was found in wooded coves also.

Houstonia lanceolata (Poir.) Britt. This species of bluets was found at Cave Creek and Block House.

Houstonia longifolia Gaertn. This species was encountered in rock prairie at Fountain Bluff and in loess prairie at Valmeyer.

Houstonia nigricans (Lam.) Fern. This narrow-leaved species of bluets was found growing abundantly in hill prairie from Swarnes to South Prairie du Rocher, except at Block House, South Edgemont, Sugar Loaf, and Chalfin Bridge. It was present also at North Eldred, Richwood, and Pere Marquette.

Caprifoliaceae

Symphoricarpos orbiculatus Moench. Buckbrush, a plant of thickets, pastures, and open woods, was seen in 16 loess hill prairies. It was frequent in the coves; in places it formed open pure stands and was the only shrubby species present.

Triosteum perfoliatum L. Horse-gentian, or wild coffee, a species of open woods and thickets, was observed in loess prairie at Fall Creek, Reavis Spring, Walnut Creek, and Block House.

Viburnum rufidulum Raf. Southern blackhaw, a small tree or shrub of rocky woods, thickets, and glades, was found in rock prairie at Government Rock and Fountain Bluff. It was found in coves at Phegley and on the rock ledges at Renault, Chautauqua, and Clendenny.

Campanulaceae

Campanula rotundifolia L. [*C. intercedens* Witasek.] This bellflower was collected from rock prairie at Bielema. It was also seen on the cliffs at Balk and on sandstone at Fountain Bluff.

Specularia perfoliata (L.) A. DC. Venus's looking-glass, a plant of fallow fields, prairies, and waste places, was found growing in eight hill prairies.

Lobeliaceae

Lobelia spicata Lam. Spiked or pale-spike lobelia was observed in 11 loess hill prairies.

Lobelia spicata var. *leptostachys* (A. DC.) Mack. & Bush. [*L. leptostachys* A. DC.] This variety was found in six loess hill prairies, in two of these prairies with the typical form of the species.

Compositae

**Achillea millefolium* L. Yarrow, common in pastures, waste places, along roadsides, and similar places, was found infrequently in five hill prairies.

Agoseris cuspidata (Pursh) Raf. This plant was found in loess prairie at Reavis Spring.

Ambrosia coronopifolia T. & G. [*A. psilostachya* var. *coronopifolia* (T. & G.) Farw.] Western ragweed was found in central Illinois hill prairies at Sessions, Reavis Spring, Northeast Meredosia, Bluffs, Walnut Creek, and North Eldred. It is abundant in the sand prairies of Illinois.

Ambrosia elatior L. [*A. artemisiifolia* var. *elatior* (L.) Descourtils.] The common ragweed was found in 12 loess hill prairies.

Ambrosia trifida L. Giant ragweed was found in hill prairie only at Chautauqua. It was observed in a disturbed part of the rock prairie and was only about 2 feet tall.

Antennaria neglecta Greene. This small pussytoes was found between the bunches of grass at Menominee Station, Reavis Spring, Northeast Meredosia, Bluffs, Walnut Creek, and North Eldred.

Antennaria plantaginifolia (L.) Hook. This species was seen in seven hill prairies. It was more abundant in the adjacent rocky open woods than in the prairie areas.

Artemisia caudata Michx. This wormwood, frequently encountered in sand prairies, was observed in rocky and sandy loess hill prairies at seven sites in northern and central Illinois.

Aster anomalus Engelm. This aster, a plant of rocky wooded bluffs, was found in hill prairie at Sessions and Fountain Bluff.

Aster azureus Lindl. The bright blue aster was found in 16 hill prairies from Menominee Station and Reavis Spring south to Chalfin Bridge.

Aster ericoides L. (including *A. exiguus* Rydb.). This weedy aster was seen in 18 hill prairies.

Aster linariifolius L. Abundant in sand prairie, this aster was collected from loess prairie at Northeast Meredosia and Bunker.

Aster oblongifolius Nutt. The oblong-leaf aster, frequently seen on rocky bluffs, was collected from 36 sites in loess and rock prairies; also it was observed in crevices of rock ledges, in recesses on small cliffs, and on rocky wooded slopes. It ranged from El Rancho and Devil's Backbone south to Cave Creek.

Aster parviceps (Burgess) Mack. & Bush. An aster, possibly this species, was collected from rock prairie at Chautauqua and from loess prairie at Fall Creek, Seehorn-Payson, and Sessions.

Aster patens Ait. The spreading aster was seen in 13 hill prairies from Clendenny to Cave Creek.

Aster pilosus Willd. Heath aster, a weedy species, was present in 16 hill prairies. It was not so common there as in flatland prairies.

Aster ptarmicoides (Nees) T. & G. White upland aster was found at Wiersma and Rock Island 31 prairies.

Aster sagittifolius Wedem. The arrow aster, usually found in open woods, occurred in the rocky prairie at Government Rock and in loess prairie at Clendenny.

Aster sericeus Vent. Silky aster was collected from 10 loess hill prairies from Bielema and Reavis Spring south to Renault. It was not very abundant at these sites.

Aster turbinellus Lindl. This aster was found in loess and rock prairie at Fountain Bluff. At Government Rock it grew in crevices of rocks, and also in the woodland border, but not in the prairie.

Cacalia atriplicifolia L. Pale Indian-plantain, which grows in a variety of habitats, open woods, thickets, and prairies, was encountered in loess prairie at four sites and also in coves at two of these places.

Cacalia tuberosa Nutt. This species was seen in loess prairie at Bielema, Balk, Bald Bluff, Swarnes, Sampson, and South Prairie du Rocher.

Chrysopsis villosa (Pursh) Nutt. [*C. camporum* Greene.] Golden aster was found in loess at three sites along the Mississippi and at five along the Illinois River.

Coreopsis lanceolata L. Lance coreopsis was found in rocky soil at Fults; in loess at Reavis Spring, Valmeyer, and Fults; and on rock ledges at Fults and Stotz.

Coreopsis lanceolata var. *villosa* Michx. [*C. crassifolia* Ait.] This variety was found in loess prairie at Valmeyer, Fults, and South Prairie du Rocher.

Coreopsis palmata Nutt. Finger coreopsis occurred in more prairies than the preceding species and variety. It was seen in 11 prairies from Sunset Trail and Standard south to Renault.

Coreopsis tripteris L. Tall coreopsis was seen in loess prairie at Fountain Bluff.

Echinacea pallida (Nutt.) Nutt. Pale coneflower was observed in 18 hill prairies from Bielema and Magnolia south to Cave Creek.

Erigeron annuus (L.) Pers. White-top, or daisy-fleabane, common in fallow fields, prairies, and waste places, was observed in only two hill prairies, Chautauqua and Oblate Fathers.

Erigeron canadensis L. Horse-weed or mule tail, a common weed, was observed in 16 hill prairies.

Erigeron divaricatus Michx. Spreading fleabane was found in a pastured hill prairie, Seehorn-Payson.

Erigeron strigosus Muhl. This fleabane was observed in 40 hill prairies. Possibly it occurred in some of the other prairies that were visited but once during this study.

Eupatorium altissimum L. Tall thoroughwort, common in pastures, rocky hills, thickets, and along roadsides, was observed at 35 sites from Sunset Trail and Magnolia to Cave Creek.

Gnaphalium obtusifolium L. Catfoot, old-field balsam, or sweet everlasting, was observed in 15 hill prairies.

Helianthus divaricatus L. This sunflower of dry woods and thickets was seen in 13 hill prairies, often on the upper slopes toward the crests of the ridges.

Helianthus mollis Lam. Ashy sunflower, common in some upland prairies, was collected from loess hill prairie and the woodland border at Clendenny.

Helianthus occidentalis Riddell. This sunflower was found growing in loess at East Henry and Bunker.

Helianthus rigidus (Cass.) Desf. [*H. laetiflorus* var. *rigidus* (Cass.) Fern.] Prairie sunflower was seen in five hill prairies from Swarnes to Renault.

Helianthus strumosus L. This sunflower was encountered in loess at Southwest Edgemont, Valmeyer, and Renault. At Fults and Fountain Bluff it was found in wooded coves.

Heliopsis helianthoides (L.) Sweet. The scabrous form [var. *scabra* (Dunal) Fern.] of sunflower heliopsis was found in loess at Block House.

Kuhnia eupatorioides L. False boneset was a common species in hill prairie. It was seen in rock and loess prairies from El Rancho and Devil's Backbone to Cave Creek.

Lactuca canadensis L. This wild lettuce was found in loess at four hill prairies. Only a few isolated plants were present at each of these sites.

**Lactuca scariola* L. Prickly lettuce was seen only in the pastured Walnut Creek prairie.

Liatris aspera Michx. This blazing-star or gay-feather was observed in 12 hill prairies from Sunset Trail and Devil's Backbone to Grand Canyon.

Liatris cylindracea Michx. The cylindric blazing-star was collected from loess prairie at North Eldred, Chautauqua, Principia, Block House, Valmeyer, Fults, and Sampson; at Sunset Trail it was observed in crevices of rock ledges.

Liatris scabra (Greene) K. Schum. This species was collected in rock prairie at Cave Creek and Fountain Bluff, where it occurred also in loess prairie and in crevices of the sandstone ledges. At Government Rock (in the type locality for this species) it was collected in rocky woodlands.

Ratibida pinnata (Vent.) Barnh. Prairie coneflower, common in upland prairie, was found in nine scattered hill prairies.

Rudbeckia missouriensis Engelm. This coneflower apparently is restricted in its range in Illinois to Monroe and Randolph counties, where it was found in four hill prairies, Valmeyer, Fults, Sampson, and Phegley (Evers 1951).

Rudbeckia serotina Nutt.* Black-eyed Susan was found in 12 hill prairies. It was not common at any of these sites.

Senecio pauperculus Michx. This ragwort was found in loess at Sunset Trail.

Senecio plattensis Nutt. Prairie ragweed was found in scattered hill prairies from North Savanna and Reavis Spring to Stotz.

Silphium integrifolium Michx. Rosinweed was found in scattered hill prairies from Fall Creek and East Henry to Cave Creek.

Silphium laciniatum L. Compass-plant was collected in four loess hill prairies, Swarnes, East Henry, Reavis Spring, and North Eldred.

Silphium terebinthinaceum Jacq. This species was found at Valmeyer and Cave Creek. Scattered individuals at Cave Creek can be referred to the variety *pinnatifidum* (Ell.) Gray.

Solidago altissima L. Tall goldenrod was found in eight hill prairies from Wiersma to Tamms.

Solidago canadensis L. This species was found in loess at El Rancho, Sunset Trail, and Wiersma.

Solidago drummondii T. & G. Drummond's goldenrod was found in hill prairie at North Eldred, Chautauqua, Phegley, and Fountain Bluff. It was collected also from crevices in rock ledges at Richwood, Valmeyer, Fountain Bluff, and Government Rock.

Solidago missouriensis var. *fasciculata* Holz. [*S. glaberrima* Martens.] Prairie goldenrod was seen at Principia and Tamms.

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*This name was applied by Fernald (1950) to our common black-eyed Susan. He separated it from *R. hirta* L. on the shape of the basal and cauline leaves. The specific name *serotina* is used in this paper although further study of the plant in the field and of herbarium specimens may show it not specifically distinct from *R. hirta* L.

Solidago nemoralis Ait. Field goldenrod was found to be the most abundant goldenrod of the hill prairies. It was observed in 33 loess and rock prairies in Illinois.

Solidago petiolaris Ait. This species was found in cherty prairie at Tamms.

Solidago radula Nutt. Rough goldenrod was found in 15 hill prairies from North Pandarmie and North Eldred south to Government Rock.

Solidago rigida L. Rigid goldenrod, common in flatland prairie remnants, was seen in hill prairie at El Rancho, Reavis Spring, Block House, Valmeyer, Renault, and Government Rock.

Solidago speciosa Nutt. Showy goldenrod was collected from loess prairie at Sunset Trail, Devil's Backbone, and Valmeyer.

Solidago ulmifolia Muhl. Elm-leaved goldenrod, a plant of thickets and open woods, was found in six hill prairies, chiefly in stony soil.

**Tragopogon major* Jacq. [*T. dubius* Scop.] This European species was found in the rock prairie at Devil's Backbone.

**Tragopogon pratensis* L. Goat's-beard was found in loess prairie at Sunset Trail and Oblate Fathers.

Verbesina helianthoides Michx. This crownbeard, usually found growing in dry woods and thickets, was seen in rock prairie at Fountain Bluff and Cave Creek and in loess at Chautauqua and Fountain Bluff.

Verbesina virginica L. White crownbeard, or tickweed, was collected from rock prairie and woodland borders at Cave Creek.

Vernonia baldwini Torr. This ironweed was found in loess at six hill prairies from Sessions and North Eldred south to Sampson.

Vernonia missurica Raf. More generally present in hill prairie than the preceding species, this ironweed was found in 11 loess hill prairies and in some of the adjoining wooded coves.

Three hundred ninety-four species and varieties of plants were found by the writer in the hill prairies of Illinois. Of these, 390 were vascular plants distributed among 209 genera and 70 families. The family represented by the greatest numbers of species and genera was the Compositae, 71 species and varieties in 26 genera. *Aster* was the largest genus; 12 species were represented. The four species of nonvascular plants included two species of the lichen *Lecidea,* a liverwort, and a moss.

Geographical Relations of the Hill Prairie Flora

The majority of plant species in Illinois hill prairies are presumably of southeastern origin. Three of the important grass species, *Andropogon scoparius, A. gerardi,* and *Sorghastrum nutans,* came from southeastern United States.

There are, however, numbers of species characteristic of the western plains and of the Ozark plateau. These are *Bouteloua hirsuta, Psoralea tenuiflora, Polytaenia nuttallii, Asclepias stenophylla, Mentzelia oligosperma, Salvia pitcheri, Plantago purshii, Agoseris cuspidata, Ambrosia coronopifolia, Solidago drummondii, Aster anomalus,* and *Rudbeckia missouriensis.* The last three possibly are from the Ozark plateau. In addition to the plants enumerated above, *Synthyris bullii* may be mentioned as a species, possibly from the Rocky Mountains, that migrated eastward along glacial moraines (Pennell 1935).

SUMMARY

1. Hill prairies are grasslands on pronounced slopes. *Prairies* is here used as a vegetational term rather than a locational or topographic term for an expansive flat.

2. Of the many hill prairies in Illinois, 61, with a combined area of more than 200 acres, were visited by the writer in the course of this study.

3. In Illinois, hill prairies occur on the exposed upper or brow slopes of the generally southwest- and west-facing bluffs east of the Mississippi River for most of the length of the state and on similar slopes along the Illinois River from Putnam County southward into Jersey County, where the valley of the Illinois enters the Mississippi valley. Hill prairies are present also along the Sangamon and Rock rivers.

4. Location and topography exert the strongest controls, or place influences, that

determine the occurrence of prairie on the upper slope of a bluff. The west- to southwest-facing position of the slope, which exposes the slope directly to the hot rays of the afternoon sun and to prevailing southwest summer winds, and the altitude of the bluff and width of the adjacent bottomlands help to provide the extremely xeric conditions under which this type of prairie thrives. Rapid and excessive drainage, due both to slope and to permeable loess substratum, is a reinforcing condition.

5. The vegetation of Illinois hill prairies is the bunch-grass type, with *Andropogon scoparius* the dominant species in most stands. *Bouteloua curtipendula* is usually present, in a few prairies dominant. In a few hill prairies, *Sorghastrum nutans* and a few other bunch grasses occur frequently and may dominate small areas within the prairie, or, rarely, the entire stand.

6. For detailed studies of the vegetation, plots were staked in unpastured and in pastured variants of the same prairie slope. Data were obtained from plot sizes ranging from 1/256 milacre to 9 milacres. The smallest size found to be effective was 1/64 milacre. The largest area staked in each prairie was 75 milacres. One milacre in each prairie—pastured and unpastured—was mapped. All plant individuals were charted and counted in each of these milacres. Species lists were compiled for plots of the several sizes.

7. In the mapped milacre of the unpastured prairie, the estimated number of plants was 1,949; 1,404 of these were *Andropogon scoparius.* In the mapped milacre of the pastured prairie, the estimated number of plants was 1,341; 849 of these were *A. scoparius.*

8. The ground space occupied by plants in the mapped milacre of the unpastured prairie was 1,884.1 square inches, of which 1,781.0 square inches were occupied by *Andropogon scoparius.* In the mapped milacre of the pastured prairie the ground space occupied by plants was found to be 1,403.3 square inches, of which 1,107.0 square inches were occupied by *A. scoparius.* In the unpastured prairie, at ground surface, 69.96 per cent of the mapped milacre was bare loess; in the pastured prairie, 77.63 per cent.

9. In the mapped milacre of the unpastured prairie, foliage covered 4,988 square inches, approximately 80 per cent of the milacre. In the mapped milacre of the pastured prairie, foliage covered 2,525 square inches, about 40 per cent of the milacre. In both pastured and unpastured prairie, *Andropogon scoparius* was the species with the largest foliage area. In the unpastured milacre, approximately 20 per cent of the ground was not covered by foliage; in the pastured milacre, about 60 per cent.

10. The available space per plant in the unpastured milacre was found to be 3.22 square inches; in the pastured milacre it was 4.68 square inches.

11. For the study of frequency of occurrence of species in plots within hill prairie, a good distribution of species was obtained with quadrat sizes of 1/64 to 1/4 milacre in unpastured prairie; 1/16 to 1/4 milacre in pastured prairie.

12. From species-area curves, the smallest representative area—the smallest one-piece area having some claim to be representative—was determined for the unpastured prairie as 0.76 milacre, and, for the pastured, 1.26 milacres. The minimum area for assignment to type—an area that is large enough to include all the important and a moderate number of minor species—was determined as 3.80 milacres for the unpastured and 6.30 milacres for the pastured prairie. The fair-sized stand—an area that is 50 times as large as the smallest representative area and contains twice as many species—was 38.0 milacres for the unpastured and 63.0 milacres for the pastured hill prairie.

13. The flora of 36 hill prairies was used as a basis for presence studies. The "constants" (species in 29, 80 per cent, or more of the 36 locations) of this type of prairie in Illinois were *Andropogon scoparius, Erigeron strigosus, Bouteloua curtipendula, Petalostemum purpureum, Euphorbia corollata, Penstemon pallidus, A. gerardi, Verbena stricta,* and *Kuhnia eupatorioides.* Twenty-five species were found in 18 or more of the 36 prairies used in this study of presence. Species most characteristic of the hill prairie type

(i.e., of much lower presence in other prairie types in Illinois) were *Bouteloua curtipendula, Psoralea tenuiflora, Petalostemum candidum, Linum sulcatum,* and *Lithospermum incisum.*

14. Prairie stands possibly existed on the bluffs that now support prairie from Wisconsin or pre-Wisconsin time to the present. This vegetation will presumably continue to grow on these sites until a change in climate occurs which will provide more mesic conditions, or until advanced erosion of the bluffs forms a continuously gentle slope, or until high cliffs are reduced.

15. The observed flora of Illinois hill prairie was 394 species and varieties. Of these, 390 were vascular plants distributed in 209 genera and 70 families. The largest family was Compositae, with 26 genera and 71 species and varieties. *Aster* was the largest genus, with 12 species. Thirty species were of foreign origin.

16. Although most species of Illinois hill prairie plants are of southeastern origin, nine species are distinctly western or southwestern, and three are from the Ozark plateau. Of these 12 species, *Mentzelia oligosperma, Asclepias stenophylla,* and *Rudbeckia missouriensis* are seemingly restricted to hill prairie and adjacent rock ledges.

17. Some prairie slopes are grazed, and some are annually or less frequently burned, yet the prairie persists. As these steep slopes have never been plowed, they represent one of the least disturbed types of prairie in Illinois, and some of them should be preserved.

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Volume 26, Article 6 Urbana, Illinois September 1955

BULLETIN
of the
ILLINOIS NATURAL HISTORY SURVEY
HARLOW B. MILLS, *Chief*

Fusarium Disease of Gladiolus:
Its Causal Agent

JUNIUS L. FORSBERG

Printed by Authority of the
STATE OF ILLINOIS
WILLIAM G. STRATTON, *Governor*

DEPARTMENT OF REGISTRATION AND EDUCATION
VERA M. BINKS, *Director*

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NATURAL HISTORY SURVEY DIVISION
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URBANA, ILLINOIS

September 1955

This paper is a contribution from the Section of Applied Botany and Plant Pathology.

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Examining gladiolus corms for disease symptoms preparatory to making laboratory cultures. The gladiolus *Fusarium* grows well on most of the common laboratory media.

Fusarium Disease of Gladiolus: *Its Causal Agent*

JUNIUS L. FORSBERG

THE Fusarium disease of gladiolus is one of the most destructive maladies known to affect flower crops. At a conference held in January, 1953, at Cleveland, Ohio, under the auspices of the Joint Research Committee of the North American Gladiolus Council and the North American Commercial Gladiolus Growers, the concensus of those present was that the Fusarium disease is the most important gladiolus disease in the United States (Ryan 1953). The disease causes large losses to commercial gladiolus growers in Illinois, Indiana, Michigan, California, eastern Washington, and all of Oregon except the northern part. It causes an estimated loss of 1½ to 2 million dollars per year in Florida alone. Because the Fusarium disease is corm-borne and because many of the corms grown in Illinois are shipped to Florida and planted there for winter flower production, the fate of the crop in Florida is of importance to growers in Illinois as well as to growers in Florida. Only one commercial gladiolus-growing area in the United States is not seriously troubled with the Fusarium disease. This is the cool region in western Washington where, according to Gould (1949), Fusarium rot is uncommon except on recently introduced stocks.

ACKNOWLEDGMENTS

The writer wishes to express his sincere appreciation to all who have assisted in any way during the course of this investigation, the greater part of which was presented as a thesis submitted to the Graduate College, University of Illinois, Urbana, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Plant Pathology. He is especially grateful to the late Dr. Leo R. Tehon, for many years head of the Section of Applied Botany and Plant Pathology at the Natural History Survey, for his guidance and many helpful suggestions during the course of the investigation and the preparation of the manuscript. Helpful suggestions were made by Dr. Wayne M. Bever, Professor of Plant Pathology, University of Illinois, and Agent, United States Department of Agriculture. The photographic work was done by Mr. William E. Clark, Assistant Technical Photographer of the Natural History Survey, and by Mr. Ray R. Hamm, Manager of the University of Illinois Photographic Laboratory. Several present or former members of the Natural History Survey staff made valuable contributions. Mr. James W. Curfman drew the graphs. Mrs. Rovenia Fitz-Gerald and Mrs. Virginia Lee Johnstone assisted in preparation of the manuscript. Mr. James S. Ayars and Mrs. Blanche P. Young read all or parts of the manuscript. Each offered valuable criticism. The author is especially grateful to his wife, Edith L. Forsberg, for her encouragement and help in many ways during the course of this work.

HISTORY OF THE DISEASE

The disease of gladiolus which is called herein the Fusarium disease is a much misunderstood malady which exists in three forms. These forms have been designated as the vascular, the brown rot, and the basal dry rot types, each of which has been described as a distinct disease by various workers. The disease was first recognized in the early 1920's but it probably existed prior to that time. W. A. Pryal (1909), a California grower, published a note in which he described an interior corm rot and leaf yellowing of gladiolus, but no proof was presented that the disease was caused by a fungus of the genus *Fusarium.*

McCulloch (1944) reported that in 1923 she received from two localities in California a large number of gladiolus corms which, although normal in external appearance, showed, when cut, 90 per cent of the interior rotted. The rot varied from a slight discoloration in the basal scar to browning of the entire core and radiating fibrovascular strands. From these corms was isolated a *Fusarium* that proved capable of causing the disease.

McCulloch (1944) reported further that in 1925 and 1926 she received similar specimens from states as widely separated as North Dakota, Mississippi, and New Jersey. The progress of the disease seemed definitely from west to east, with prevalence increasing each season. In 1926 and 1927, McCulloch found the disease in shipments of corms from Holland. The usual *Fusarium* was isolated from all these specimens.

According to McCulloch (1944), N. van Poeteren "reported the vascular disease as present in Holland as early as 1925." A dry rot of gladiolus caused by *Fusarium* was mentioned in an Annual Report of the Experimental and Research Station, Cheshunt, Hertfordshire, England (Anonymous 1927). Moore (1939) reported a vascular Fusarium disease from the same country. Bellard (1933), Dimock (1941, 1945), and Nelson (1937*a*, 1938*a*, 1938*b*, 1948) published brief accounts of the vascular form of the disease. McCulloch (1944) published an extensive account of this form.

Massey (1922) published a brief note and, later (1926), a more extensive description of a corm rot which he considered primarily a disease of stored corms, although infections occurred in the field. McCulloch (1944) considered "the vascular disease" entirely distinct from the corm rot described by Massey.

Nelson (1937*b*, 1948) described a Fusarium disease of gladiolus which he thought distinct from the diseases described by Massey and McCulloch.

McClellan (1947) included as symptom expressions of one disease the symptoms of the two diseases described by Massey and McCulloch. McClellan recognized, however, that there are differences of opinion among those who have worked with Fusarium disease of gladiolus as to whether the two types are distinct diseases or merely forms of the same disease.

NAMES OF THE DISEASE

The use of various names in the literature to designate the forms of the Fusarium disease of gladiolus has created much confusion in the minds of readers and research workers. McCulloch (1944) used the names yellows, wilt, and core rot for the vascular type of the disease. Massey (1922, 1926) designated the disease described by him merely as Fusarium rot.

Creager (1944) used the name brown rot for the type of corm rot commonly associated with the Picardy variety. He stated, "Fusarium brown rot is not the same as Fusarium yellows or core rot; they are two distinct diseases." The symptoms commonly found on Picardy, however, seem to be the same as those described by Massey (1926) on other varieties. Picardy was not introduced until 1931, 5 years after Massey's work was published.

Dimock (1945) used only the name yellows and listed Picardy as one of the susceptible varieties.

Nelson (1948) used the names Fusarium dry rot and brown rot for the disease originally described by Massey. He stated that this disease "has sometimes been confused with Fusarium yellows, an entirely different malady. The chief resemblance between the diseases is that both cause a brown, dry rot of the corm. The best evidence of dissimilarity is demonstrated by the high resistance of the variety Picardy to Fusarium yellows and its equally great susceptibility to Fusarium dry rot."

The third type of disease described by Nelson (1937*b*, 1948) was designated by him as basal dry rot.

McClellan (1947) stated, "At least two diseases of gladiolus have been described as being caused by fungi of the Fusarium group. One of these is a corm rot that is principally a storage disease; the other is the yellows disease that occurs in the field. Yellows has been subdivided further into (1) a core rot type, a type confined to the water-conducting system; and (2) a basal rot type." He then followed with a description of the several kinds of symptoms and considered them as expressions of the same disease.

Magie & Miller (1948) referred to the Fusarium corm rot and yellows disease. In a later article the same authors (1949) used the name Fusarium brown rot. Magie (1950) used the names Fusarium yellows and Fusarium corm rot but referred to them as designating a single disease. He applied the term "yellows symptoms" to the leaf symptoms and vascular discoloraton but not to the corm rot phase of the disease.

SYMPTOMATOLOGY

Symptoms of the Fusarium disease are produced on foliage, corms, and roots. Detailed descriptions of symptoms associated

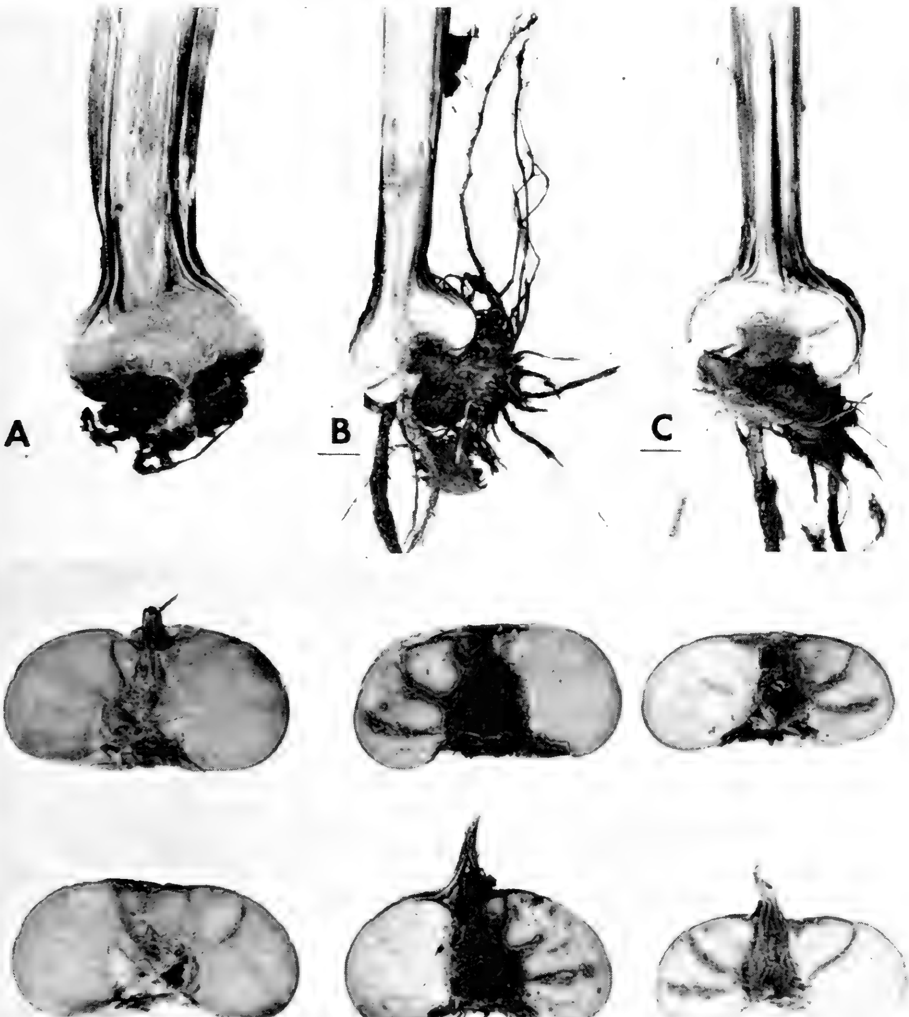

Fig. 1.—Above: lengthwise sections of gladiolus corms showing, *A*, how the brown rot form of the Fusarium disease progresses from the mother corm to the daughter corm; *B* and *C*, how the vascular form progresses from the mother corms into the core and vascular tissues of the daughter corms. Below: sections of six older corms showing rotted cores and discolored vascular streaks associated with the vascular form of the disease.

with the three forms of the disease, vascular, brown rot, and basal dry rot, have been published by McCulloch (1944), Massey (1926), Nelson (1948), and McClellan (1947). The symptoms common to all three forms of the disease are a brownish to black dry rot of the corm tissues; yellowing, browning, and death of the foliage; and browning and destruction of the roots.

The three forms of the disease have been distinguished mainly by effects on the corms. In the vascular form of the disease a sectioned corm will reveal a brown discoloration of the core and dark-colored vascular bundles extended laterally into the flesh, fig. 1*B* and *C*. In an advanced stage of the disease, the infected strands reach the surface of the corm at the nodes, and brown lesions develop at these points.

In the brown rot form of the disease, tan, brown, or blackish lesions may occur anywhere on the corm but most commonly near the base, fig. 2. The rotted tissue is often quite thick and may extend all the way through the corm, fig. 2, bottom row. Vascular discoloration is not associated with this form of the disease.

The basal dry rot form of the disease differs from the brown rot form mainly in the thickness and position of the lesions. Basal dry rot lesions occur only on the bases of the corms and are usually restricted to the first and second internodes, fig. 3. The lesions are visible when the corms are dug and, under favorable curing conditions, they do not enlarge after harvest. They rarely, if ever, extend deeper than 2 to 4 millimeters into the flesh. The diseased tissue is dark brown to black,

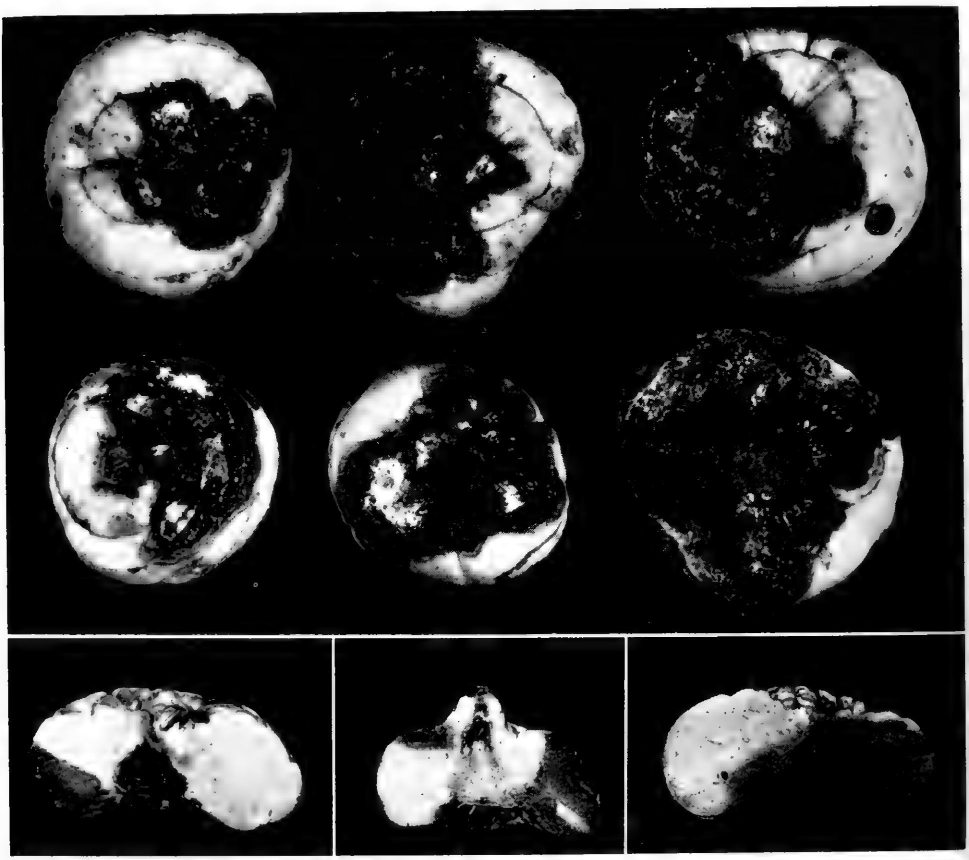

Fig. 2.—Picardy gladiolus corms affected with the brown rot form of the Fusarium disease. Above: bottom views of six corms with lesions of various sizes. Below: sections of three corms showing thickness of rotted tissues.

hard, rough, and usually somewhat scaly after the corms are dry. The affected area is sunken, and there is a sharp line of demarcation between diseased and healthy tissues.

While the majority of diseased corms in any given lot usually have symptoms characteristic of only one of the disease forms, it is not uncommon to find corms that have symptoms of two of the disease forms or symptoms intermediate between them, fig. 4. Bald (1953) stated, "In any large collection of gladiolus varieties infected with Fusarium diseases it has not been found possible to maintain on a symptomological basis the division between Fusarium basal rot and Fusarium yellows. On different varieties a gradation was found between the 2 symptom types."

ETIOLOGY

The etiology of the Fusarium disease of gladiolus is quite typical for that of plant diseases caused by fungi of the genus *Fusarium*. The occurrence of the disease in more than one form and the great variability commonly found in species of *Fusarium* have contributed to the confusion regarding the cause of this disease.

Previous Accounts

A report by Massey (1922) was the first published account of a gladiolus disease in which a fungus of the genus *Fusarium* was established as the cause. A more extensive description of this disease and its causal agent was later published by

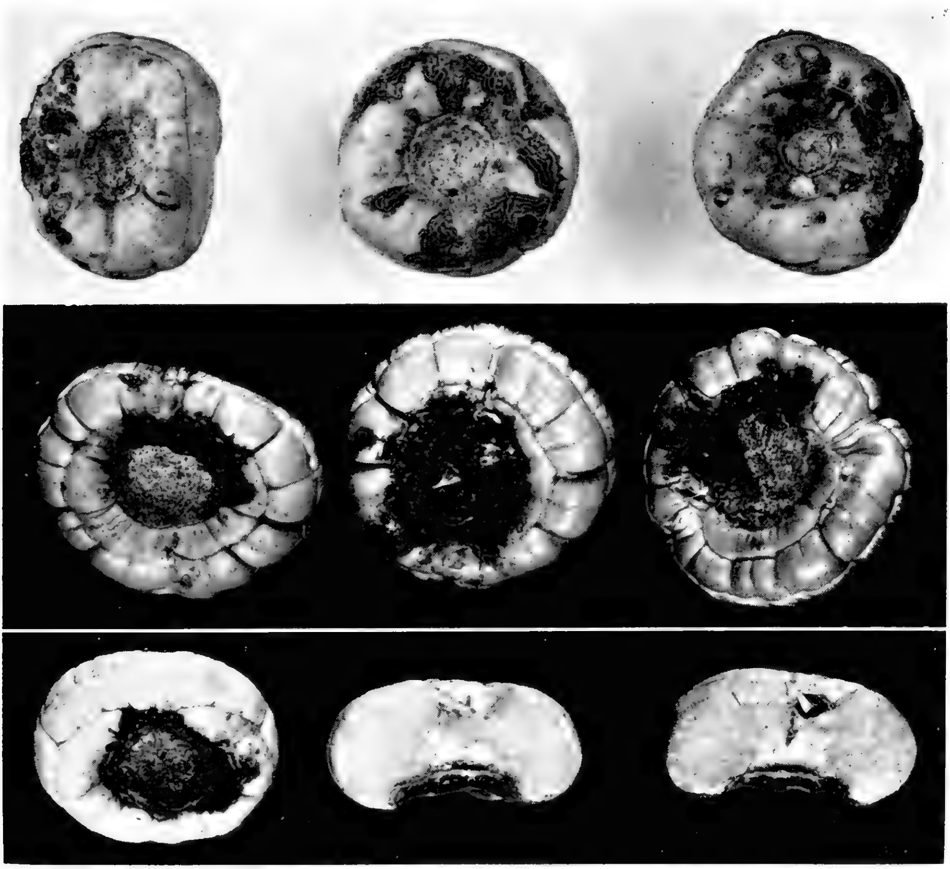

Fig. 3.—Corms of three gladiolus varieties affected with the basal dry rot form of the Fusarium disease: top row, variety Gold Eagle; middle row, Lake Placid; bottom row, Spotlight. The two sectioned Spotlight corms show the extreme thinness of the rotted tissue.

the same worker (1926). Massey classified the organism as *Fusarium oxysporum* Schlecht. emend. Wr. var. *gladioli* n. var.

McCulloch (1944) considered the *Fusarium* she found associated with the vascular form of the disease to be sufficiently distinct from *Fusarium oxysporum* var. *gladioli*, described by Massey, to warrant putting it in another species. She classified it as *Fusarium orthoceras* App. et Wr. var. *gladioli*. In comparing the two organisms she stated, "In culture the bulb-rot organism has, in most tests and examinations, shown less abundant aerial growth, less pigment, and wider macrospores than the yellows organism. . . . The most distinctive characteristics of these two Fusaria of gladiolus are the effects on the host."

Other workers have been inconsistent in their use of names for the causal agents of the different forms of the disease. McClellan (1945) used the name *Fusarium orthoceras* App. & Wr. var. *gladioli* McCulloch for the vascular *Fusarium* of gladiolus. In a later article the same writer (1947) listed *F. oxysporum* f. *gladioli* Sny. & Hans. as the causal agent for yellows and rot. He described the other forms of the disease but did not name the causal agents. McClellan & Stuart (1947) used the name *F. oxysporum* f. *gladioli* (Massey) Sny. & Hans. for the causal agent of gladiolus "yellows, or corm rot." McClellan (1948) used both names, *F. oxysporum* var. *gladioli* Massey and *F. orthoceras* var. *gladioli* McCulloch. Nelson (1948) listed *F. orthoceras* Woll. var. *gladioli* McCull. as the cause of yellows,

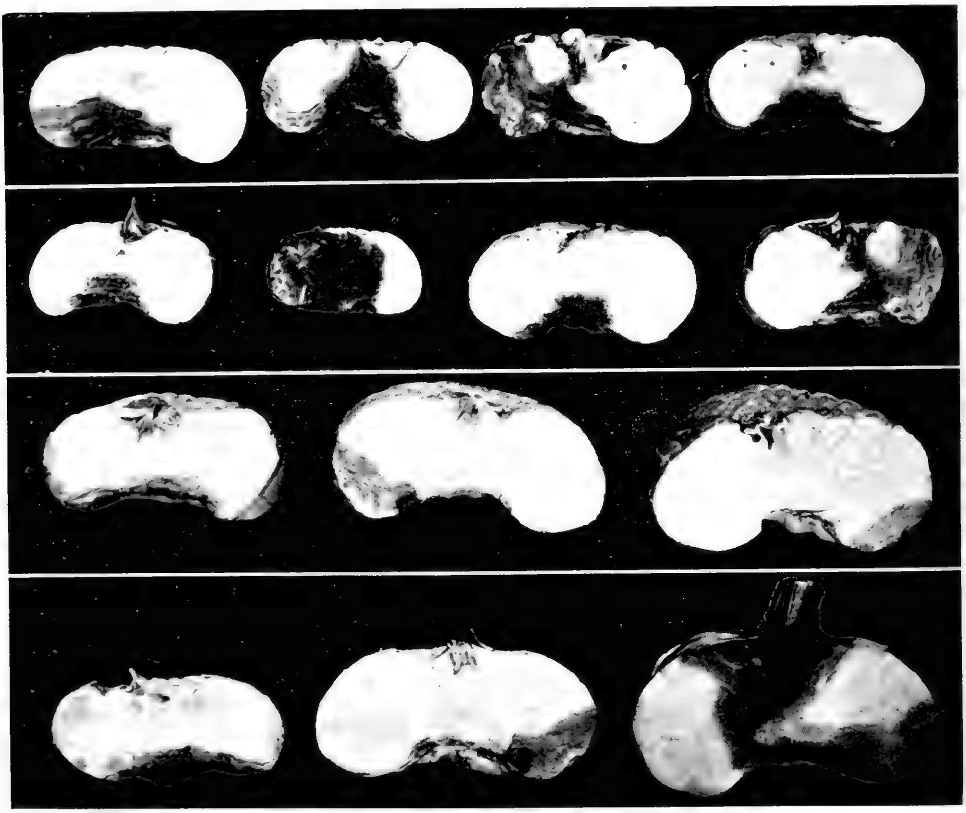

Fig. 4.—Sectioned corms of gladiolus variety Dieppe, in upper two rows, and Golden Arrow, in lower two rows, showing symptoms of all three forms of the Fusarium disease. The second corm from the left in the top row shows core rot and vascular discoloration. The first and third corms in the second row and the fourth corm in the top row show symptoms intermediate between basal dry rot and core rot. The first corms in the third and fourth rows have basal dry rot. The other corms show the brown rot form of the Fusarium disease.

F. oxysporum Schlecht. var. *gladioli* Massey as the cause of brown rot, and merely *Fusarium* sp. as the cause of basal dry rot. Gould (1949) called *F. oxysporum* f. *gladioli* the cause of Fusarium rot. Miller & Magie (1950) listed *F. oxysporum* f. *gladioli* as the cause of Fusarium storage rot of gladiolus corms. Magie (1950) referred to the causal agent of Fusarium yellows and Fusarium corm rot as *F. oxysporum* f. *gladioli.*

Bald (1953) stated, "Typical single spore cultures from basal rot, yellows, and intermediate infections were submitted to Dr. W. C. Snyder for identification. He placed all the cultures in the species *Fusarium oxysporum* Schl. As these Fusaria were obtained from active lesions, and some similar isolates were shown by inoculation tests to be pathogenic on gladiolus corms, the strains causing basal rot, yellows, and intermediate symptoms on gladioli in southern California have been provisionally grouped under the name *F. oxysporum* f. *gladioli* (Massey) Sny. and Hans."

Difficulties in Classifying Fusaria

A review of the literature indicates that the difficulties encountered by plant pathologists in classifying strains of the gladiolus *Fusarium* have been great and are similar to the experiences of many other workers faced with the task of determining the relationship and specific name to be applied to a pathogenic *Fusarium.*

Some of the confusion is a result of the use of two different systems of nomenclature and taxonomy now available for naming and classifying isolates of *Fusarium.* These are the detailed system of Wollenweber & Reinking (1935) and the simplified system of Snyder & Hansen (1940, 1941, 1945).

In the system of Wollenweber & Reinking (1935), the genus *Fusarium* is divided into 16 named sections in which a total of 65 species, 55 varieties, and 22 forms are differentiated. This system is based largely on recommendations made at a conference held in Madison, Wisconsin, in 1924 (Wollenweber *et al.* 1925). According to these recommendations, species and varieties must be distinguished by morphological characters only. Each species includes groups of individuals that can be distinguished by morphological characters which must be "of such a nature as to be applicable and usable by mycologists in general and which will be most serviceable for practical purposes." Each variety is distinguished by morphological characters of less importance than those used for specific segregation. Groups of individuals differing from the species and the variety only in certain physiological characters are separated as forms. This system failed to meet with unqualified approval because of difficulties that still were encountered by workers in attempting to classify specific isolates of *Fusarium.*

The simplified system of nomenclature and taxonomy proposed by Snyder & Hansen (1940, 1941, 1945) was based on their extensive investigations of the variability shown in culture by species, varieties, and forms of *Fusarium.* Section Elegans was the first to be revised according to their concept of species. Simplification was achieved by emending the description of one species, *Fusarium oxysporum* Schl., to agree with the description of section Elegans given by Wollenweber (1913). The 10 species, 18 varieties, and 12 forms comprising section Elegans of Wollenweber & Reinking (1935) were placed in one species, *Fusarium oxysporum,* on the sole basis of morphology. Twenty-five parasites of the section were made forms of this common species on the basis of pathogenicity alone. Revision of the other sections followed. As a result of the complete revision of the genus, the 16 sections, 65 species, 55 varieties, and 22 forms of *Fusarium* of Wollenweber & Reinking were reduced to 8 species and 34 forms. No varieties were recognized in the system of Snyder & Hansen.

Massey (1926), McCulloch (1944), and Nelson (1948) used the system of Wollenweber & Reinking to designate species names for the gladiolus *Fusarium.* Gould (1949), Miller & Magie (1950), Magie (1950), and Bald (1953) used the system of Snyder & Hansen. McClellan (1945, 1947, 1948) used both systems. Wollenweber's classification was the only one in existence at the time Massey published the results of his investigations.

Both systems were available to workers after 1940.

PURPOSE OF PRESENT INVESTIGATION

This study was undertaken to rectify the confusion appearing in the literature regarding the relationship between the causal agent or agents of the different forms of the Fusarium disease on gladiolus and the symptoms produced. The main object of the investigation was to determine if different strains of *Fusarium* produced the different symptoms and if these strains could be fitted into well-defined groups on the basis of their pathogenicity and physiological characters.

METHODS

Several hundred isolates of *Fusarium* were cultured by the writer from diseased gladiolus corms in the years 1945 through 1950. Thirty-three of these isolates together with six isolates received from Ray Nelson of Michigan State College and one isolate from Robert O. Magie of the University of Florida Gulf Coast Experiment Station (a total of 40 isolates)

Table 1.—Sources of the 40 isolates of the gladiolus *Fusarium* used in the infection experiments and physiological studies reported in this study.

Isolate	Date of Isolation	Disease Form	Gladiolus Variety	Locality
45-73	Dec. 10, 1945	Vascular	Dr. F. E. Bennett	Wichert, Ill.
45-80	Dec. 10, 1945	Vascular	Dr. F. E. Bennett	Wichert, Ill.
46-3	Dec. 13, 1946	Vascular	Phyllis McQuiston	Wichert, Ill.
46-5	Dec. 14, 1946	Vascular	Phyllis McQuiston	Wichert, Ill.
46-9	Dec. 17, 1946	Vascular	Bit o' Heaven	Wichert, Ill.
46-14	Nov. 1, 1946	Vascular	Unknown	Cairo, Ill.
47-6	Jan. 24, 1947	Vascular	Beacon	Wichert, Ill.
47-10	Feb. 5, 1947	Vascular	Dr. F. E. Bennett	Wichert, Ill.
49-4	Jan. 14, 1949	Vascular	Margaret Beaton	Wichert, Ill.
49-15	Jan. 19, 1949	Vascular	Lantana	Champaign, Ill.
49-23	Jan. 21, 1949	Vascular	Myrna	Wichert, Ill.
49-30	Jan. 21, 1949	Vascular	Dream of Beauty	Wichert, Ill.
49-31	Jan. 21, 1949	Vascular	Mother Kadel	Wichert, Ill.
50-6	Feb. 15, 1950	Vascular	Yellow Herald	Wichert, Ill.
50-24*	April 2, 1945	Vascular	Unknown	East Lansing, Mich.
50-27*	Nov. 4, 1949	Vascular	Corona	Oregon
50-28*	April 14, 1950	Vascular	Unknown	California
45-8	Feb. 5, 1945	Brown rot	Picardy	Wichert, Ill.
45-74	Dec. 14, 1945	Brown rot	Picardy	Wichert, Ill.
45-75	Dec. 14, 1945	Brown rot	Picardy	Wichert, Ill.
45-78	Dec. 10, 1945	Brown rot	Dr. F. E. Bennett	Wichert, Ill.
46-4	Dec. 14, 1945	Brown rot	Phyllis McQuiston	Wichert, Ill.
46-12	Dec. 16, 1946	Basal dry rot	Aladdin	Wichert, Ill.
47-1	Jan. 23, 1947	Brown rot	Picardy	Wichert, Ill.
47-8	Jan. 24, 1947	Basal dry rot	Beacon	Wichert, Ill.
47-12	Feb. 5, 1947	Brown rot	Corona	Wichert, Ill.
47-19	Feb. 13, 1947	Brown rot	Picardy	Fort Collins, Colo.
47-32	Sept. 27, 1947	Brown rot	Unknown	Cocoa, Fla.
49-1	Jan. 14, 1949	Brown rot	Margaret Beaton	Wichert, Ill.
49-17	Jan. 19, 1949	Brown rot	Abu Hassan	Wichert, Ill.
49-19	Jan. 19, 1949	Brown rot	Wings of Song	Wichert, Ill.
50-7	Feb. 15, 1950	Brown rot	Ohio Nonpareil	Champaign, Ill.
50-22†	1950	Brown rot	Spic and Span	Bradenton, Fla.
50-25*	Sept. 3, 1948	Brown rot	Picardy	East Lansing, Mich.
47-2	Jan. 23, 1947	Basal dry rot	Picardy	Wichert, Ill.
47-3	Jan. 24, 1947	Basal dry rot	Picardy	Wichert, Ill.
49-8	Jan. 14, 1949	Brown rot	Valeria	Wichert, Ill.
49-20	Jan. 19, 1949	Basal dry rot	Wings of Song	Wichert, Ill.
50-23*	Nov. 25, 1936	Basal dry rot	Souvenir	East Lansing, Mich.
50-26*	Dec. 23, 1948	Basal dry rot	Souvenir	East Lansing, Mich.

*Isolated by Ray Nelson, Michigan State College, East Lansing.
†Isolated by Robert O. Magie, University of Florida Gulf Coast Experiment Station, Bradenton.

Table 2.—Growth of six isolates of the gladiolus *Fusarium* on Coons's agar at various temperatures. Incubation period 160 hours.

Temperature, Degrees C.	Mean of Diameters (Millimeters) of Two Colonies					
	Brown Rot Isolates		Vascular Isolates		Basal Dry Rot Isolates	
	45-75	50-22	45-73	50-24	47-3	50-23
1–3	0.0	0.0	0.0	0.0	0.0	0.0
5	0.0*	0.0	0.0	0.0*	0.0	0.0
20–22	52.0	63.0	66.0	50.0	58.0	51.5
24	67.0	78.0	83.0	63.0	64.0	63.0
26	78.0	85.0	90.0	68.0	73.0	74.0
27–28	74.0	87.0	90.0	71.0	75.0	75.0
30–31	43.5	49.0	57.0	50.0	49.0	49.0
32	39.5	48.0	54.0	47.0	48.0	47.0
36	5.5	8.5	7.0	11.5	6.0	6.0
37	2.5	3.5	3.0	5.5	4.0	3.0
39	0.0	0.0	0.0*	0.0	0.0	0.0*
40	0.0	0.0	0.0	0.0	0.0	0.0

*A trace of growth insufficient for measurement appeared in these plates.

were selected for comparison in pathogenicity tests and physiological studies. Seventeen of these isolates were obtained from corms with the vascular, 16 from corms with the brown rot, and 7 from corms with the basal dry rot form of the disease. They will be referred to hereafter as vascular, brown rot, and basal dry rot or basal rot isolates.

The original isolations were made on *Difco* potato dextrose agar. Single-spore isolates were obtained from spore suspensions in sterile water blanks; each suspension was diluted until a desired spore concentration was reached, and then the diluted suspension was poured over the surface of a thin film of 2 per cent water agar in a Petri dish. After a few seconds the excess suspension was poured off and the plate was allowed to stand for 15 to 16 hours. The Petri dish was then placed on the stage of a dissecting microscope, and germinated spores were picked off singly on the tip of a needle and transferred to potato dextrose agar slants. Progenies from these single-spore isolates were used in the infection experiments and physiological studies. The sources of all isolates are listed in table 1.

Comparisons of isolates from the three forms of the disease were made on the following bases: reactions to temperature, reactions to aniline dyes, reactions to copper salts, reactions to mercuric chloride, color reactions on steamed rice, growth types on Wellman's differential medium, pH changes produced in liquid media, spore measurements, inoculation tests in the laboratory, and inoculation tests in the greenhouse.

PHYSIOLOGICAL STUDIES

Physiological studies of the gladiolus *Fusarium* were made by the writer in an effort to determine if isolates from the three forms of the disease could be distinguished by their physiological characters.

Influence of Temperature on Growth Rates

Massey (1926) reported that the gladiolus *Fusarium* studied by him grew in culture at temperatures ranging from 5 degrees to 35 degrees C.; the optimum was 27.5 degrees. McCulloch (1944) reported that the *Fusarium* she studied grew at temperatures ranging from less than 3 degrees to about 34–36 degrees C.; the optimum temperature range was 23–26 degrees C.

In the present investigation, the influence of temperature on the growth rates of the gladiolus *Fusarium* was studied on two isolates grown from each disease type on Coons's agar in Petri dishes through a series of 12 temperatures. The inoculum for the Petri dishes was prepared in the following manner to obviate erratic behavior traceable to size or character of inoculum: coarse white cotton thread was cut in pieces about 1½ inches long and autoclaved in distilled water. These pieces were laid on an agar slant, which was then inoculated from the isolate to be tested. About a week after fungus growth had overrun the cotton threads, the threads were lifted from the culture, scraped clean of adhering agar, and cut with sterile scissors into sections, each about 2 millimeters long. One piece of *Fusarium*-infested thread was placed in the center of each dish. Immediately after inoculation the dishes were placed in electrically controlled incubators kept at temperatures shown in table 2 and left for 160 hours. At the end of the incubation period the diameters of the colonies were measured, table 2. Two dishes of each isolate were used for each temperature. Relative sizes of the colonies grown at different temperatures are shown in figs. 5, 6, 7, and 8.

None of the isolates grew at the 1–3 degree C. temperature range, table 2, and only brown rot isolate 45-75 and vascular isolate 50-24 showed traces of growth at 5 degrees C. Since the next higher tempera-

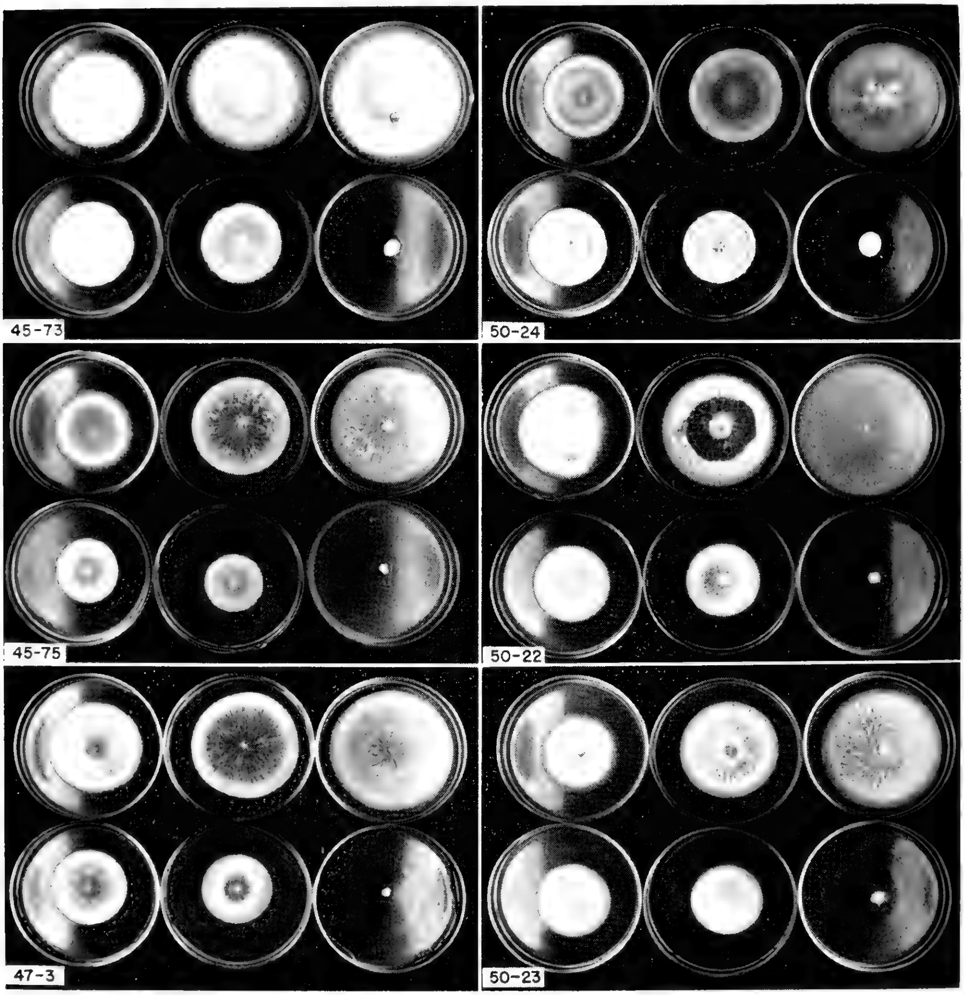

Fig. 5.—Six isolates of *Fusarium* grown on Coons's agar for 160 hours at the following temperatures: 20–22, 24, 27–28 degrees C. (top row in each set of six dishes, left to right); 30, 32, and 36 degrees C. (bottom row in each set, left to right). Isolates 45-73 and 50-24 are vascular isolates, 45-75 and 50-22 are brown rot isolates, 47-3 and 50-23 are basal dry rot isolates.

ture range used was 20–22 degrees C., the minimum temperature for growth of these isolates was not determined. The range of temperatures for optimum growth of all six isolates was 26–28 degrees C. All isolates grew at 37 degrees C., but only vascular isolate 45-73 and basal dry rot isolate 50-23 showed traces of growth at 39 degrees C. None of the isolates grew at 40 degrees C. After the test period, all Petri dishes that had been incubated at 40 degrees were kept at room temperature for

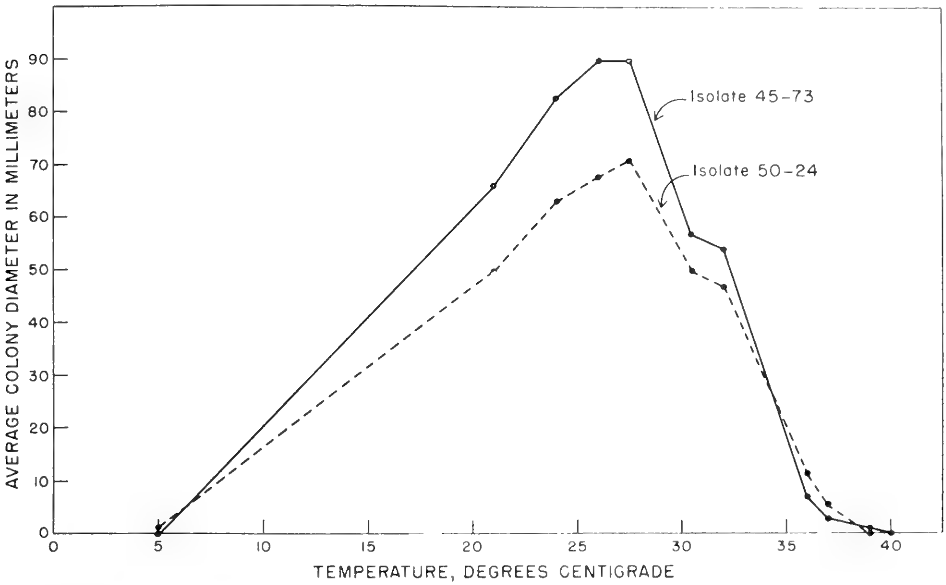

Fig. 6.—Effect of temperature on the colony size of two vascular isolates of *Fusarium* grown 160 hours on Coons's agar.

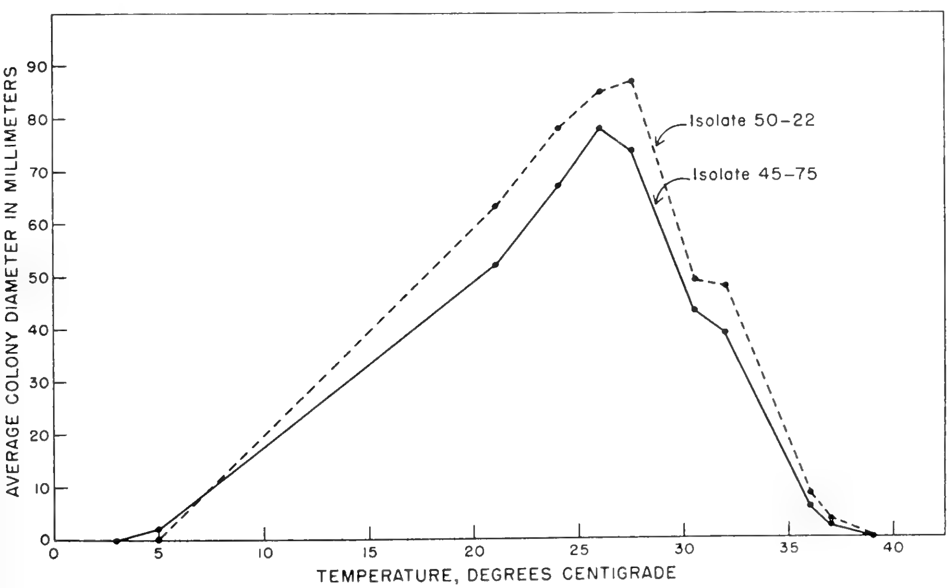

Fig. 7.—Effect of temperature on the colony size of two brown rot isolates of *Fusarium* grown 160 hours on Coons's agar.

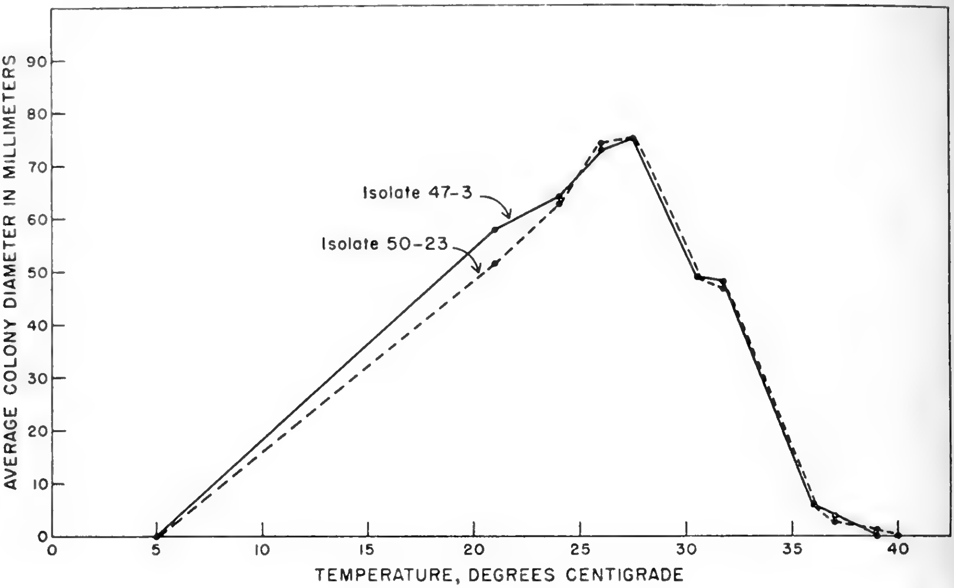

Fig. 8.—Effect of temperature on the colony size of two basal dry rot isolates of *Fusarium* grown 160 hours on Coons's agar.

several days. Five of the six isolates grew when moved to the lower temperature. Basal dry rot isolate 47-3 apparently had been killed by the 160-hour exposure to 40 degrees C.

In these studies the general shape of the curves of growth responses of all isolates to various temperatures was of the same general pattern, figs. 6, 7, and 8. The basal dry rot isolates agreed much more closely in their responses to temperatures than did the isolates from the other disease forms. The vascular isolates showed the greatest divergence in responses to temperatures. Isolates from the three disease forms could not be distinguished by their growth responses to various temperatures.

Reactions to Aniline Dyes

The 40 isolates of the gladiolus *Fusarium* listed in table 1 were grown on Coons's agar containing various concentrations of the aniline dyes malachite green, brilliant green, and crystal violet, according to the method developed by Coons & Strong (1931).

The malachite green and brilliant green media were made from preparations of stock agar containing 10 milliliters of 0.5 per cent dye solution per liter of Coons's agar. For each medium, four concentrations, tables 3 and 5, were prepared from the stock agar diluted with appropriate amounts of sterile, melted Coons's agar.

The crystal violet stock agar was prepared from 100 milliliters of 0.5 per cent dye solution added to a liter of Coons's agar, and the four concentrations, table 4, were made from this stock.

Inoculum was prepared in the manner described for the temperature studies. Four isolates were grown in each dish. The center of each quadrant of the dish was seeded with a 2-millimeter piece of *Fusarium*-infested thread. The cultures were run in duplicate and were incubated for 10 days at 25 degrees C.

Readings of the Petri dish cultures were made in accordance with the decimal numbering scheme used by Coons & Strong (1931). This scheme is as follows:

Color of mycelium	
White	10.
Red	20.
Breadth of mycelial mat	
No growth	0
Very slight growth	tr.
.5 cm. to 1 cm.	1.
1 cm. to 2 cm.	2.

2 cm. to 3 cm. . . . . 3.
3 cm. to 4 cm. . . . . 4.
4 cm. to 5 cm. . . . . 5.
Changes in medium color
No change 0
Halo 1
Strong decolorization 2
Color intensified in mycelium .3
Edge of colony
Even 00
Ramose 01
Frondose 02
Growth form of mycelium
Submerged 000
Cottony 001
Villous 002
Sericeous 003
Tufted 004
Submerged, cottony center. .005
Submerged, sericeous center .006
Submerged, with cottony fringe at edge, atoll. 007
Woolly 008

In the key to the species of *Fusarium* as arranged by Coons & Strong (1931), *F. orthoceras* and *F. oxysporum* are recorded as being moderately sensitive to malachite green, i.e., growth usually 1–2 centime-

Table 3.—Reactions* of isolates of the gladiolus *Fusarium* to four concentrations of malachite green in Coons's agar.

Isolate	Concentration of Dye				
	1:66,666	1:100,000	1:200,000	1:400,000	Control
45-73	0	tr	11.001	12.001	15.001
45-80	tr	tr	11.001	12.001	15.007
46-3	0	tr	11.001	13.001	15.000
46-5	0	tr	11.001	12.001	15.000
46-9	0	tr	11.001	12.001	15.007
46-14	0	tr	11.001	12.001	15.000
47-6	0	tr	12.001	12.001	15.001
47-10	0	0	tr	12.001	15.000
49-4	tr	11.001	12.001	14.003	15.007
49-15	0	0	tr	12.001	15.007
49-23	tr	11.001	12.001	15.001	15.004
49-30	tr	0	tr	12.014	15.007
49-31	0	tr	11.001	12.004	15.000
50-6	0	tr	11.001	13.001	15.001
50-24	tr	11.001	12.001	13.001	15.000
50-27	tr	tr	11.001	12.001	15.007
50-28	0	tr	11.001	12.001	15.007
45-8	0	0	11.001	13.001	15.001
45-74	0	tr	11.014	13.004	15.005
45-75	0	tr	11.001	13.001	15.001
45-78	0	0	0	12.001	15.001
46-4	0	tr	11.014	12.004	15.004
46-12	0	tr	tr	11.001	15.000
47-1	0	tr	12.004	14.003	15.004
47-8	0	tr	12.001	14.003	15.001
47-12	0	tr	11.001	12.001	15.000
47-19	0	tr	11.001	13.004	15.000
47-32	0	tr	11.001	12.001	15.001
49-1	0	tr	12.001	14.005	15.000
49-17	0	tr	11.004	12.012	15.001
49-19	0	tr	11.001	12.001	15.001
50-7	0	tr	12.001	14.001	15.001
50-22	tr	tr	12.004	14.005	15.001
50-25	0	tr	11.005	12.001	15.000
47-2	tr	tr	12.004	14.002	15.000
47-3	0	tr	11.005	12.001	15.001
49-8	0	0	11.001	12.001	15.007
49-20	0	tr	11.001	0	15.001
50-23	0	tr	11.001	12.001	15.007
50-26	0	tr	tr	12.001	15.001

*Reactions are expressed in the numbering scheme of Coons & Strong (1931), as explained in the text.

ters broad in the 1:400,000 and 1:200,000 concentrations. Growth on crystal violet extended to about 1:5,000 or 1:4,000. At this point in the key the two species are separated by their reactions to brilliant green, brilliant green not being decolorized by *F. orthoceras* but being decolorized by *F. oxysporum*. Also, a difference in growth form of the two species on crystal violet is noted, growth being submerged with sericeous center for *F. orthoceras* and cottony for *F. oxysporum*.

Diameters of the mycelial mats produced in different concentrations of dye were used by the writer to compare abilities of isolates to tolerate the dye in the culture medium. Considerable variation in diameters was shown by the 40 isolates of gladiolus *Fusarium*, tables 3, 4, and 5. Although of little diagnostic value, growth forms of the various isolates were probably the most striking characters, figs. 9 and 10.

When these isolates were taken through Coons & Strong's key, 26 keyed out to *Fusarium orthoceras* var. *triseptatum*. Since no isolates decolorized brilliant green, they did not fall into *F. oxysporum*. Vascular isolates 49-4 and 49-23, brown

Table 4.—Reactions* of isolates of the gladiolus *Fusarium* to four concentrations of crystal violet in Coons's agar.†

Isolate	Concentration of Dye			
	1:2,000	1:5,000	1:10,000	1:20,000
45-73	tr	11.011	11.011	11.001
45-80	0	11.001	12.001	11.000
46-3	0	11.001	12.001	12.001
46-5	0	11.004	12.000	12.000
46-9	0	11.001	12.001	12.001
46-14	0	11.001	12.001	12.001
47-6	0	11.001	12.001	12.001
47-10	0	11.001	12.001	12.001
49-4	tr	11.001	12.001	12.011
49-15	0	11.001	11.001	11.001
49-23	0	12.001	12.001	12.001
49-30	tr	11.014	12.001	12.014
49-31	tr	11.001	12.001	12.001
50-6	0	11.001	11.011	11.001
50-24	tr	11.001	11.001	11.001
50-27	tr	11.001	12.001	12.001
50-28	0	11.001	12.001	12.001
45-8	0	12.001	12.001	12.001
45-74	11.001	12.014	12.014	12.014
45-75	11.001	11.001	12.001	12.001
45-78	0	12.001	12.001	12.001
46-4	11.001	12.014	12.014	12.014
46-12	tr	11.001	12.001	12.001
47-1	tr	11.014	12.014	12.014
47-8	tr	11.001	12.001	12.001
47-12	tr	11.007	11.007	12.007
47-19	0	11.014	12.014	12.014
47-32	0	11.001	11.001	11.001
49-1	11.007	11.007	12.001	12.001
49-17	0	12.001	12.000	12.001
49-19	11.004	12.004	12.014	12.004
50-7	tr	12.014	12.014	12.014
50-22	tr	12.004	12.004	12.004
50-25	tr	11.000	11.000	11.000
47-2	11.001	12.004	12.004	12.004
47-3	tr	12.001	12.001	12.001
49-8	tr	11.001	12.001	12.001
49-20	tr	11.001	12.001	12.001
50-23	tr	11.001	11.000	11.000
50-26	tr	11.001	11.001	11.001

*Reactions are expressed in the numbering scheme of Coons & Strong (1931), as explained in the text.
†See table 3 for control readings.

rot isolates 47-1, 50-7, and 50-22, and basal dry rot isolate 47-8 keyed out to *F. euoxysporum.* Brown rot isolates 45-74, 45-75, 46-4, and 49-19 fell into *F. orthoceras* var. *longius,* and brown rot isolate 49-1 and basal dry rot isolate 47-2 keyed out to *F. moniliforme.* Basal dry rot isolates 46-12 and 49-20 keyed out to *F. filiferum,* but according to Coons & Strong (1931) this species decolorizes crystal violet. None of the isolates of the gladiolus *Fusarium* decolorized crystal violet.

Although, on the basis of their reactions to the three aniline dyes, the majority of the isolates of gladiolus *Fusarium* fell into the *F. oxysporum–F. orthoceras* group, reactions of so many of the isolates varied from typical reactions of this group that it would be impossible to use the aniline dye method of classifying *Fusaria* from gladiolus with any degree of certainty. Neither would it be possible to separate isolates of the three disease forms, vascular, brown rot, and basal dry rot, on the basis of their reactions to aniline dyes.

The results of this phase of the investigation agree with the results of Moore & Chupp (1952), who found that certain

Table 5.—Reactions* of isolates of the gladiolus *Fusarium* to four concentrations of brilliant green in Coons's agar.†

Isolate	Concentration of Dye			
	1:25,000	1:50,000	1:100,000	1:200,000
45-73	0	tr	12.001	12.301
45-80	0	0	12.024	13.004
46-3	0	tr	12.001	13.001
46-5	0	0	11.001	12.001
46-9	0	tr	12.001	13.001
46-14	0	0	12.001	13.004
47-6	0	0	12.001	13.001
47-10	0	0	12.001	12.001
49-4	0	12.001	14.001	15.001
49-15	0	0	12.001	13.001
49-23	0	12.001	14.001	14.001
49-30	0	0	12.014	13.001
49-31	0	0	11.001	13.001
50-6	0	0	12.001	13.001
50-24	11.001	12.001	13.001	14.001
50-27	0	11.001	12.001	13.001
50-28	0	tr	12.001	13.001
45-8	0	11.001	12.001	13.001
45-74	0	0	12.004	13.004
45-75	0	tr	12.001	13.001
45-78	0	0	tr	11.011
46-4	0	11.014	12.014	13.001
46-12	0	tr	11.001	12.001
47-1	0	11.014	13.014	14.014
47-8	0	11.014	13.001	14.001
47-12	0	tr	12.001	13.301
47-19	0	11.004	13.024	14.024
47-32	0	tr	11.001	12.001
49-1	0	11.001	12.005	13.005
49-17	0	12.014	13.014	14.004
49-19	0	12.004	12.014	13.004
50-7	0	12.011	13.011	14.024
50-22	0	11.011	12.005	14.005
50-25	0	tr	11.001	13.001
47-2	0	11.004	13.004	14.014
47-3	0	11.001	12.301	13.301
49-8	0	11.014	12.001	13.004
49-20	0	11.001	12.301	13.001
50-23	0	tr	11.001	12.001
50-26	0	tr	11.001	12.001

*Reactions are expressed in the numbering scheme of Coons & Strong (1931), as explained in the text.
†See table 3 for control readings.

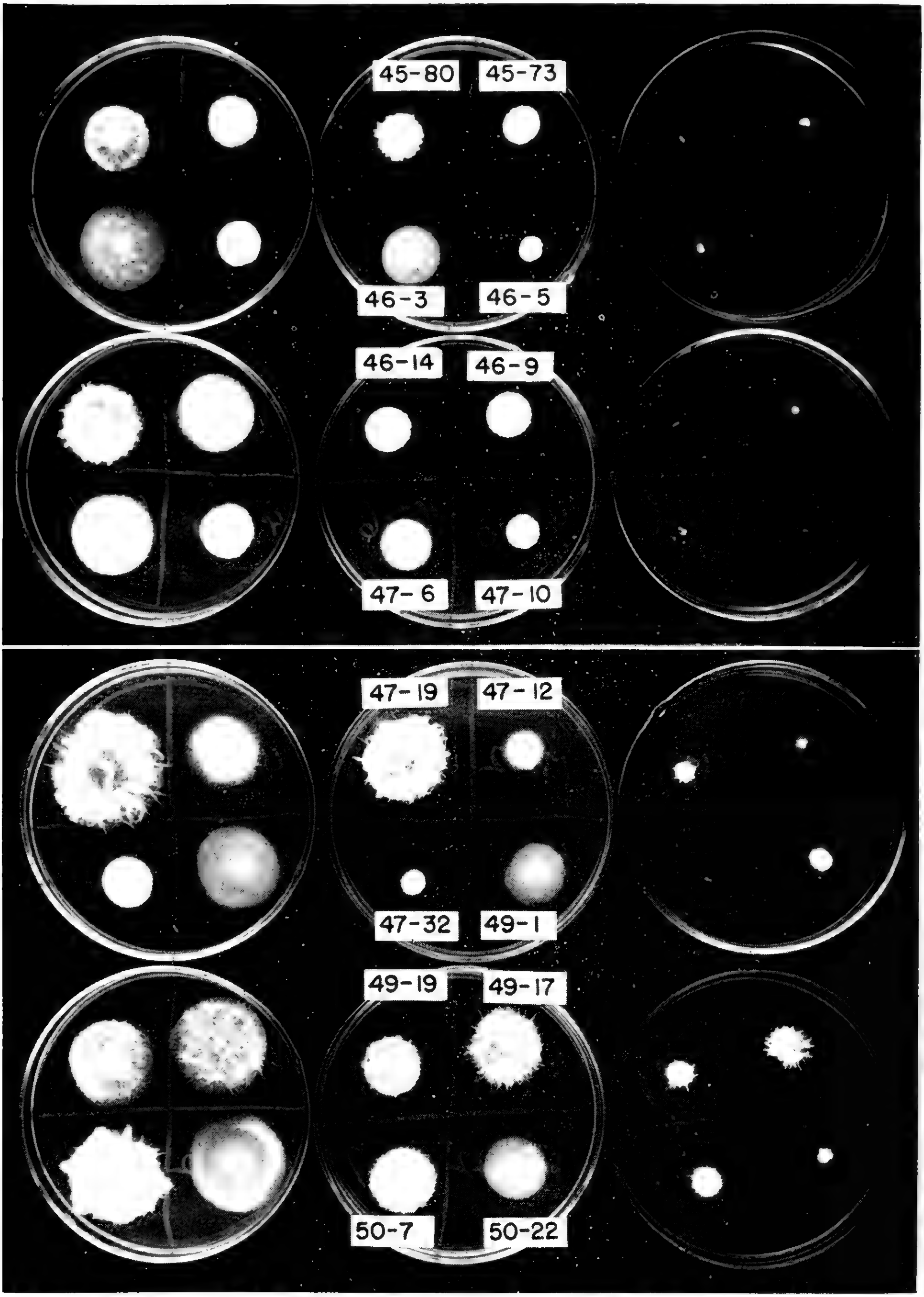

Fig. 9.—Isolates of *Fusarium* grown 10 days on Coons's agar containing three concentrations of brilliant green: left to right 1:200,000, 1:100,000, 1:50,000. Vascular isolates 45-73, 45-80, 46-3, 46-5, 46-9, 46-14, 47-6, and 47-10 are in the two top rows of dishes; brown rot isolates 47-12, 47-19, 47-32, 49-1, 49-17, 49-19, 50-7, and 50-22 are in the two lower rows. Isolates in the dishes at right and left are in the same relative positions as those in the center dishes. Other isolates in this series are shown in fig. 10.

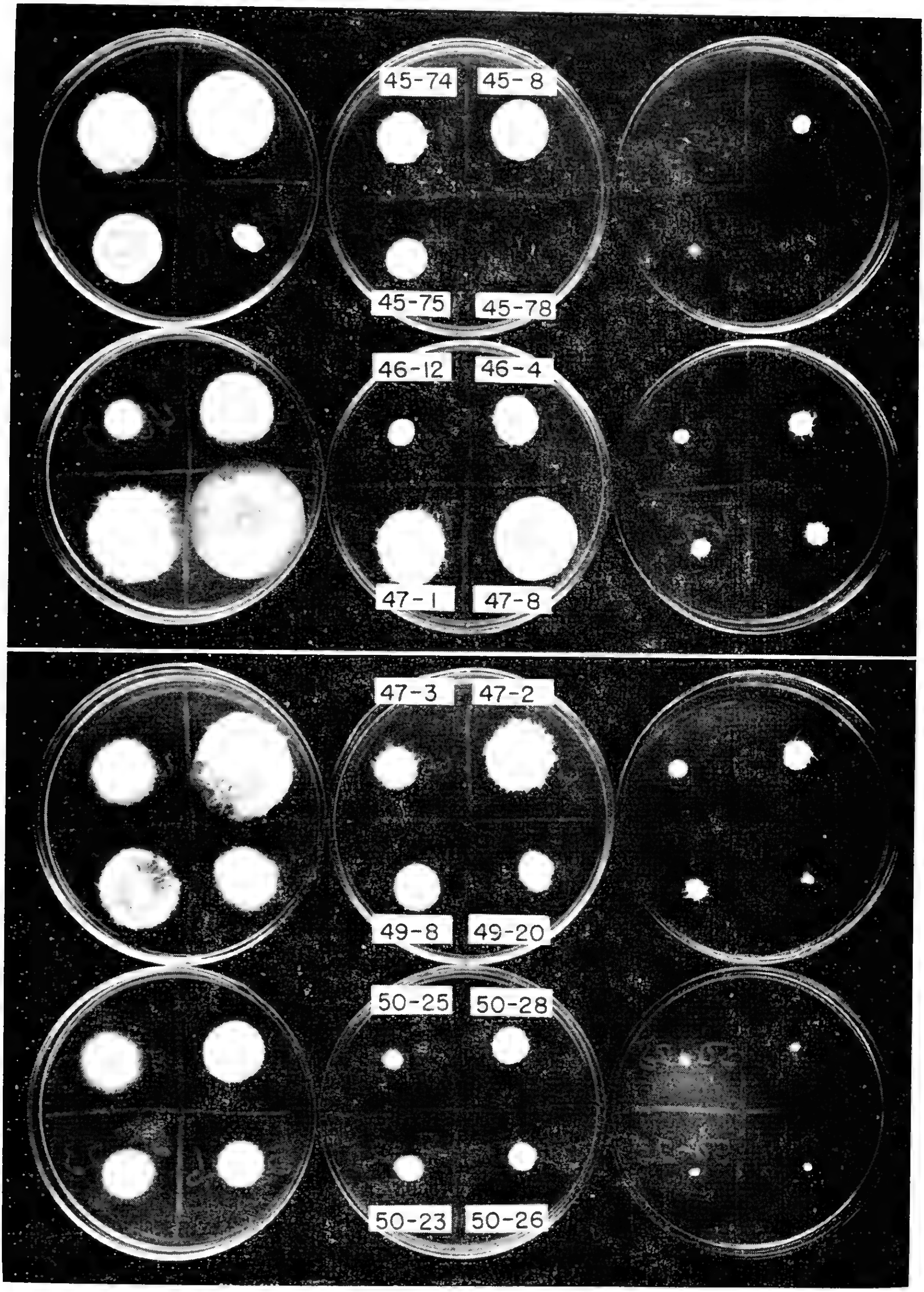

Fig. 10.—Isolates of *Fusarium* grown 10 days on Coons's agar containing the same concentrations of brilliant green as those shown in fig. 9: top row, four brown rot isolates; second row, brown rot isolates 46-4 and 47-1 and basal dry rot isolates 46-12 and 47-8; third row, basal dry rot isolates 47-2, 47-3, and 49-20 and brown rot isolate 49-8; bottom row, basal dry rot isolates 50-23 and 50-26, brown rot isolate 50-25, and vascular isolate 50-28. Isolates in the dishes at right and left are in the same relative positions as those in the center dishes.

isolates of *Fusarium* causing wilts of tomato, cabbage, and muskmelon did not react toward malachite green and crystal violet in the way described by Coons & Strong (1931) for those species.

Reactions to Copper Salts

Coons & Strong (1931) used copper sulfate in the culture medium in some preliminary tests and expressed the opinion that this salt might be useful in identifying some species of *Fusarium*. Nelson, Coons, & Cochran (1937) reported that two forms of *Fusarium* which cause two forms of the yellows disease of celery could be differentiated if isolates of them were grown on synthetic agar containing either copper sulfate or copper chloride.

The 40 isolates of gladiolus *Fusarium* used in the investigation reported here were grown on Coons's agar to which amounts of copper sulfate were added to make a series of concentrations that ranged from 1/100 molar (*M*/100) to 1/7000 molar, table 6. The strongest concentration, *M*/100, was prepared from 2.5 grams of copper sulfate (1 mole = 249.6

Table 6.—Reactions* of isolates of the gladiolus *Fusarium* to seven different molar (*M*) concentrations of copper sulfate in Coons's agar.†

Isolate	Concentration of Copper Sulfate						
	M/100	*M*/500	*M*/1000	*M*/3000	*M*/5000	*M*/6000	*M*/7000
45-73	0	0	tr	12.301	—	—	—
45-80	0	0	tr	tr	13.304	14.304	15.004
46-3	tr	11.329	12.301	13.001	—	—	—
46-5	0	0	tr	12.304	14.304	14.304	15.000
46-9	0	0	0	tr	11.301	13.301	15.001
46-14	0	0	0	tr	11.305	12.300	15.005
47-6	0	0	0	tr	12.305	13.305	14.001
47-10	0	0	0	12.301	14.305	15.005	15.001
49-4	tr	12.301	15.001	15.001	—	—	—
49-15	0	0	0	0	tr	11.000	14.000
49-23	0	tr	13.301	15.001	—	—	—
49-30	0	0	0	0	tr	12.000	15.001
49-31	tr	12.304	14.001	15.001	—	—	—
50-6	0	0	0	tr	13.001	13.301	14.301
50-24	0	0	0	14.001	—	—	—
50-27	tr	12.301	14.001	15.001	—	—	—
50-28	0	0	0	tr	11.300	12.305	14.305
45-8	0	0	0	0	tr	12.301	15.001
45-74	11.309	13.301	15.001	15.001	—	—	—
45-75	tr	12.301	14.301	14.000	—	—	—
45-78	tr	12.301	13.301	13.301	—	—	—
46-4	tr	12.301	14.001	15.001	—	—	—
46-12	0	0	0	tr	tr	12.000	13.000
47-1	tr	12.301	13.001	15.001	—	—	—
47-8	0	tr	12.001	14.001	—	—	—
47-12	tr	13.301	13.301	15.001	—	—	—
47-19	tr	12.301	13.301	15.001	—	—	—
47-32	0	0	0	tr	tr	12.000	13.000
49-1	tr	13.301	13.301	15.001	—	—	—
49-17	tr	12.301	14.001	15.001	—	—	—
49-19	0	0	0	tr	15.001	15.001	15.001
50-7	0	0	0	tr	15.001	15.001	15.001
50-22	tr	13.004	15.004	15.004	—	—	—
50-25	0	0	0	13.311	15.001	15.001	15.001
47-2	0	12.301	14.001	15.001	—	—	—
47-3	tr	12.301	14.001	15.001	—	—	—
49-8	0	0	0	tr	15.005	15.005	15.005
49-20	0	0	0	11.001	15.001	15.005	15.005
50-23	0	0	0	tr	tr	tr	15.001
50-26	0	0	0	tr	tr	tr	15.001

* Except for .009 (clumpy) of author, reactions are expressed in the numbering scheme of Coons & Strong (1931).
†See table 3 for control readings.

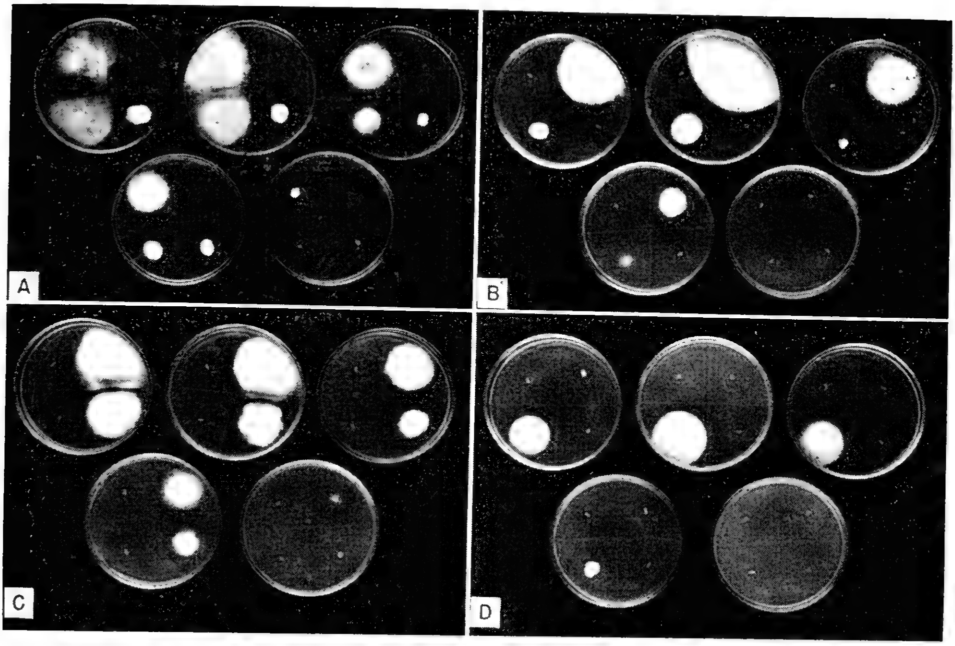

Fig. 11.—Isolates of *Fusarium* grown 10 days in plates of Coons's agar containing (upper rows, left to right: *M*/900, *M*/700, *M*/500, (lower rows, left to right) *M*/300, and *M*/100, copper sulfate. In each plate, clockwise from upper left, isolates are as follows: *A*, brown rot 45-74, 45-8, 45-78, 45-75; *B*, vascular 49-15, 49-4, 49-30, 49-23; *C*, vascular 50-6, 49-31, 50-27, 50-24; *D*, vascular 45-80, 45-73, 46-5, 46-3.

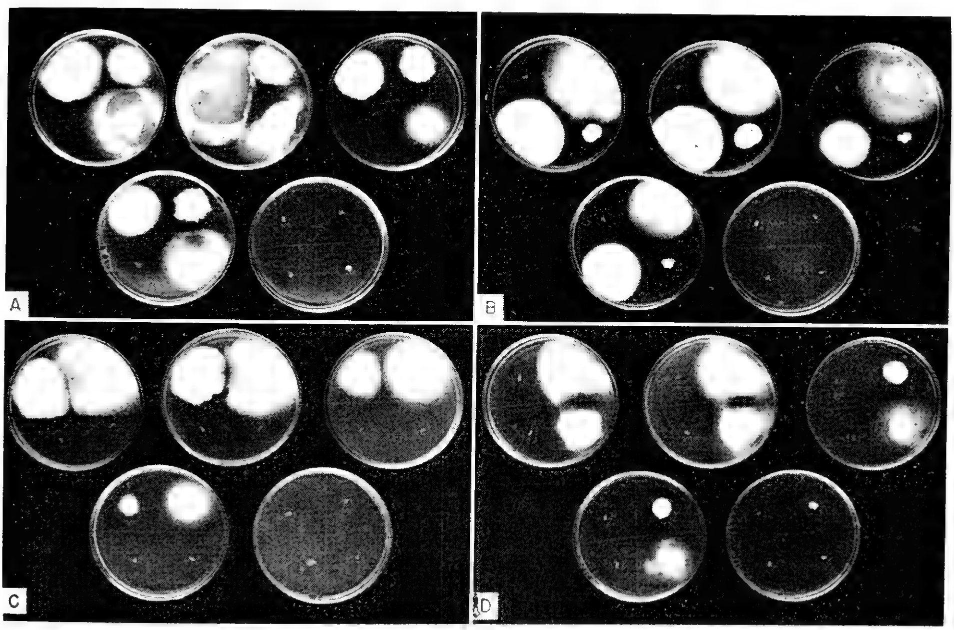

Fig. 12.—As for fig. 11, except *A*, brown rot 47-19, 47-12, 49-1, 47-32; *B*, basal dry rot 46-12, brown rot 46-4, basal dry rot 47-8, brown rot 47-1; *C*, basal dry rot 47-3, 47-2, 49-20, brown rot 49-8; *D*, brown rot 49-19, 49-17, 50-22, 50-7.

grams) dissolved in a liter of Coons's agar. The other concentrations were prepared from this stock diluted with Coons's agar. All dilutions were made immediately after the agar had been autoclaved, and the Petri dishes were poured immediately after the dilutions had been made. This procedure was necessary because it was found that Coons's agar containing copper salts, if remelted after being allowed to solidify, would not resolidify. Inoculum was prepared and the Petri dishes were inoculated in the same manner as that described for the aniline dye tests.

The reactions of the 40 isolates of gladiolus *Fusarium* to copper sulfate are very interesting because they show extreme variability in tolerance to the salt, figs. 11 and 12. One isolate, 45-74, produced measurable growth in the *M*/100 concentration. Seven isolates produced only traces of growth in the *M*/5000 concentration and two isolates produced measurable growth in only the *M*/7000 concentration, table 6. Although the reactions of the various isolates to copper sulfate failed to distinguish between isolates of *Fusarium* from the three disease forms,

Table 7.—Reactions* of isolates of the gladiolus *Fusarium* to four different molar (*M*) concentrations of copper chloride in Coons's agar.†

Isolate	Concentration of Copper Chloride			
	M/100	*M*/300	*M*/500	*M*/1000
45-73	0	0	0	0
45-80	0	0	0	0
46-3	11.301	12.101	12.301	12.301
46-5	0	0	0	tr
46-9	0	0	0	0
46-14	0	0	0	0
47-6	0	0	0	0
47-10	0	0	0	tr
49-4	tr	14.301	15.001	15.001
49-15	0	0	0	0
49-23	0	tr	11.301	15.001
49-30	0	0	0	0
49-31	13.301	14.301	15.001	15.001
50-6	0	0	0	tr
50-24	0	0	0	11.000
50-27	tr	14.301	15.001	15.001
50-28	0	0	0	tr
45-8	0	0	0	0
45-74	12.301	15.301	15.301	15.001
45-75	tr	13.301	14.301	15.001
45-78	0	11.301	12.301	13.301
46-4	0	14.301	15.001	15.001
46-12	0	0	0	0
47-1	0	13.301	13.301	15.001
47-8	0	tr	13.301	15.001
47-12	0	13.311	14.001	15.001
47-19	0	15.001	15.001	15.001
47-32	0	0	0	0
49-1	tr	15.001	15.001	15.001
49-17	tr	13.301	15.301	15.001
49-19	0	0	0	0
50-7	0	0	0	0
50-22	11.301	15.301	15.301	15.001
50-25	0	0	0	tr
47-2	tr	15.301	15.001	15.001
47-3	tr	13.301	14.001	15.001
49-8	0	0	0	0
49-20	0	0	0	0
50-23	0	0	0	0
50-26	0	0	0	0

*Reactions are expressed in the numbering scheme of Coons & Strong (1931), as explained in the text.
†See table 3 for control readings.

the brown rot isolates were, in general, less sensitive to copper sulfate than were the vascular and basal dry rot isolates.

Copper chloride was used in a way similar to that in which copper sulfate was used. The $M/100$ concentration was prepared from 1.7 grams of copper chloride dissolved in a liter of Coons's agar and the other concentrations were prepared from this stock diluted with Coons's agar. Only four concentrations, $M/100$, $M/300$, $M/500$, and $M/1000$, were used, table 7. Further dilutions of copper chloride were not used because the reactions of the isolates of *Fusarium* appeared to be following the same pattern with copper chloride as they did with copper sulfate.

Reactions to Mercuric Chloride

The preplanting treatment of gladiolus corms in a solution of mercuric chloride has been one of the methods used by growers to control the Fusarium disease. Because seemingly erratic results have sometimes been obtained from chemical treatment of corms, it was decided to test the 40 isolates of gladiolus *Fusarium* for sen-

Table 8.—Reactions* of isolates of the gladiolus *Fusarium* to six concentrations of mercuric chloride in Coons's agar.†

Isolate	Concentration of Mercuric Chloride					
	1:10,000	1:12,500	1:14,285	1:16,666	1:20,000	1:25,000
45-73	0	0	0	0	13.001	14.001
45-80	0	0	0	0	15.001	15.000
46-3	0	0	15.001	15.001	15.001	15.001
46-5	0	0	0	0	15.001	15.001
46-9	0	0	0	0	14.001	15.001
46-14	0	0	0	0	15.001	15.001
47-6	0	0	0	0	15.001	15.001
47-10	0	0	0	0	15.001	15.001
49-4	0	0	13.001	15.001	15.001	15.001
49-15	0	0	0	0	14.001	15.001
49-23	0	0	0	0	15.001	15.001
49-30	0	0	0	0	14.001	15.001
49-31	0	0	0	15.000	15.000	15.000
50-6	0	0	0	0	0	14.001
50-24	0	12.005	15.005	15.000	15.000	15.000
50-27	0	13.001	15.001	15.001	15.001	15.001
50-28	0	0	0	0	14.001	15.001
45-8	0	0	0	0	0	15.001
45-74	0	0	15.001	15.001	15.000	15.001
45-75	0	0	15.001	15.001	15.000	15.001
45-78	0	0	0	15.001	15.000	15.000
46-4	0	13.001	15.001	15.001	15.001	15.001
46-12	0	0	0	0	13.001	14.001
47-1	0	0	15.001	15.001	15.001	15.001
47-8	0	0	0	15.001	15.001	15.000
47-12	0	13.001	14.001	14.001	15.001	15.001
47-19	0	15.001	15.001	15.001	15.001	15.001
47-32	0	0	0	0	13.001	15.001
49-1	0	0	0	15.000	15.000	15.000
49-17	0	0	15.001	15.001	15.000	15.000
49-19	0	0	tr	tr	15.001	15.001
50-7	0	0	0	0	13.001	15.001
50-22	0	0	15.001	15.001	15.001	15.001
50-25	0	0	0	12.001	14.001	15.001
47-2	0	0	15.001	15.001	15.001	15.000
47-3	0	13.001	14.001	14.001	15.001	15.000
49-8	0	0	0	15.001	15.000	15.000
49-20	0	0	0	0	13.001	15.000
50-23	0	0	0	0	14.001	15.001
50-26	0	0	0	12.001	14.001	15.001

*Reactions are expressed in the numbering scheme of Coons & Strong (1931), as explained in the text.
†See table 3 for control readings.

sitivity to various concentrations of mercuric chloride in the culture medium.

A graded series of concentrations of mercuric chloride of 1:1,000 to 1:25,000 was prepared in a manner similar to that used in the tests with copper salts. Results of the test are shown in table 8. Because none of the isolates grew in concentrations of 1:1,000 to 1:10,000, only the dilutions of 1:10,000 and above are shown in table 8.

As in the tests with aniline dyes and copper salts, the isolates varied considerably in their sensitivity to mercuric chloride. One noticeable difference between the reactions to mercuric chloride and the reactions to the other growth-inhibiting substances was observed. In the various concentrations of aniline dyes and copper salts, size of the colonies of *Fusarium* increased as the dilution became greater. Although this reaction occurred to some extent with mercuric chloride, it was not so pronounced. In most cases, if growth occurred at all it was very vigorous and covered the maximum space available in the Petri dish. In tables 3, 4, 5, 6, 7, and 8, white mycelium and maximum growth are designated by 15, as derived from the

Table 9.—Color reactions of isolates of the gladiolus *Fusarium* on steamed rice. Colors are from the manual of Ridgway (1912).

Isolate	Color of Substratum	
	After 3 Weeks	After 11 Weeks
45-73	Thulite Pink	Pale Purplish Gray to Deep Purplish Gray
45-80	Dahlia Carmine	Bluish Black and Tawny Olive
46-3	White	Tawny Olive
46-5	Indian Lake	Dull Violet Black and Tawny Olive
46-9	Spinel Red	Dull Violet Black and Tawny Olive
46-14	Thulite Pink to Dull Dusky Purple	Dull Violet Black and Tawny Olive
47-6	Spinel Red	Dull Violet Black
47-10	Indian Lake	Bluish Black and Tawny Olive
49-4	Spinel Red to Indian Lake	Tawny Olive and Bluish Black
49-15	Indian Lake	Bluish Black to Tawny Olive
49-23	Indian Lake	Tawny Olive and Bluish Black
49-30	Indian Lake to Dull Dusky Purple	Dull Violet Black
49-31	Spinel Pink	Purplish Gray and Tawny Olive
50-6	Spinel Red to Indian Lake	Bluish Black
50-24	Salmon Buff, Thulite Pink, and Indian Lake	Purplish Gray and Tawny Olive
50-27	Thulite Pink to Dark Maroon Purple	Payne's Gray to Bluish Black
50-28	Indian Lake	Dull Violet Black
45-8	Spinel Red to Indian Lake	Dull Violet Black
45-74	Thulite Pink to Indian Lake	Tawny Olive to Dresden Brown
45-75	Indian Lake	Blackish Violet Gray and Bluish Slate Black
45-78	Indian Lake to Bordeaux	Dark Violet Gray
46-4	Spinel Pink to Spinel Red	Plumbago Slate and Old Gold
46-12	Dahlia Carmine	Dusky Slate Blue
47-1	Thulite Pink	Tawny Olive and Plumbago Slate
47-8	Light Buff	Clay Color to Saccardo's Amber
47-12	Thulite Pink	Deep Plumbago Gray and Tawny Olive
47-19	Thulite Pink to Indian Lake	Tawny Olive and Dusky Purplish Gray
47-32	Spinel Pink	Dull Violet Black
49-1	Thulite Pink to Indian Lake	Sudan Brown and Deep Purplish Gray
49-17	Indian Lake	Dull Purplish Black
49-19	Light Buff	Old Gold
50-7	Thulite Pink to Indian Lake	Dull Purplish Black and Dusky Slate Blue
50-22	Thulite Pink	Plumbago Slate and Old Gold
50-25	Dull Violet Black	Plumbago Slate
47-2	Spinel Pink to Indian Lake	Dull Violet Black and Dusky Slate Blue
47-3	Thulite Pink	Plumbago Slate and Old Gold
49-8	Indian Lake to Dull Violet Black	Dull Violet Black and Dusky Slate Blue
49-20	Cameo Pink	Raw Sienna
50-23	Indian Lake to Dull Violet Black	Dusky Slate Blue
50-26	Thulite Pink to Indian Lake	Plumbago Slate

Coons & Strong (1931) scheme shown on pages 458 and 459.

With the exception of isolates 50-26, 49-8, and 50-24, the isolates that were the most sensitive to the copper salts were also the most sensitive to mercuric chloride. Isolates from the three disease forms could not be separated on the basis of their reactions to mercuric chloride.

Although the isolates used in this study varied considerably in their sensitivity to mercuric chloride, as well as to other chemicals, more intensive work would have to be done before a conclusion could be reached that differences in sensitivity are responsible for differences in disease control obtained in tests involving chemical treatment of corms. However, sensitivity differences possibly could be factors contributing to control differences.

Color Reactions on Steamed Rice

Steamed rice was recommended by Wollenweber *et al.* (1925) as being especially useful in identification of groups of *Fusarium* because of the distinctive colors produced by cultures grown on it. Nelson, Coons, & Cochran (1937) reported that isolates from two forms of Fusarium yellows of celery fell into two groups when grown on steamed rice; in all instances the cultures which formed color on rice produced only form I of Fusarium yellows, while the cultures that were colorless produced only form II.

In the present study on the gladiolus *Fusarium,* 2 grams of rice and 6 milliliters of distilled water were placed in each of 80 test tubes. The tubes were plugged with cotton and steamed 1 hour on each of 3 successive days. Then a small amount of an agar slant culture was transferred to each tube of steamed rice. Two tubes of rice were used for each isolate. The test was run twice. In one trial the inoculated tubes were kept in the dark in an incubator held at 25 degrees C. In the other trial the tubes, in wire baskets, were placed on a cabinet shelf so that they were exposed to diffused light during the day. Colors produced in the rice substratum were, after 3 weeks and again after 11 weeks, compared with plates in the color manual of Ridgway (1912). The colors produced in the two trials were almost identical.

As shown in table 9, the 40 isolates of gladiolus *Fusarium* varied a great deal in the colors they produced on steamed rice. As will be described more fully in a section on pH studies, isolates of *Fusarium* caused progressive pH changes to occur in the culture medium. In the first 3 weeks, when the cultures were acid in reaction, the colors in most cases were forms of pink or red, although one isolate remained white and several others were shades of violet or purple. In the last 6 or 7 weeks, when the cultures were alkaline in reaction, the colors changed to blues, violets, or purples, in many of which olives and browns appeared. There was no relation between the disease form from which the isolates were obtained and the colors the isolates produced on rice.

VARIATIONS IN CULTURE TYPES AND PATHOGENICITY

Variability in culture types and in pathogenicity within a given species of *Fusarium* seems to be of almost universal occurrence. The only exception found in a search through the literature was in the report by Blank (1934) that different strains of the cabbage yellows organism were uniform in their cultural behavior and pathogenicity.

The relation between growth types of cultures of *Fusarium* on laboratory media and differences in pathogenicity has been studied by many workers. Ullstrup (1935) reported that with the *Fusarium* stage of *Gibberella saubinetii* (Mont.) Sacc. rapid mycelial growth and abundant aerial mycelium are directly correlated with a high degree of pathogenicity in the majority of cases. Earlier, Brown (1928), working with certain fruit-rotting species of *Fusarium,* had pointed out that the mycelial type of culture is the most pathogenic. He stated that this type of growth is the form generally obtained in first isolations from diseased tissues. Harvey (1929) reported that high virulence in various strains of *Fusarium fructigenum* Fries was correlated with vigorous mycelial growth. Armstrong, MacLachlan, & Weindling (1940) reported that in the cotton-wilt organism, *Fusarium vasinfectum* Atk., cultures that exhibited abundant aerial mycelium and grew rapidly were in the highly pathogenic group, but that variation from this cultural type may or may not be paralleled by decrease in pathogenicity. Wellman & Blaisdell (1941), in a study of pathogenic and cultural variation among single-spore isolates from strains of the tomato-wilt *Fusarium*, reported that the raised form is the most highly pathogenic, the appressed is mildest, and intermediate cultural types are intermediate in pathogenicity. In a later study, Wellman (1942) reported that these pathogenically and culturally variable strains of the tomato-wilt *Fusarium* also could be distinguished by differences in pH relations.

Many studies have been made on changes occurring in laboratory cultures of *Fusarium*. Burkholder (1925) reported that an isolate of *Fusarium martii phaseoli* Burkh. lost some of its virulence during its 5 years in culture. He noted changes in morphology and physiology, also. When first isolated, the pathogen produced on most media a blue-green slimy growth. At the end of 6 years the growth was white and fluffy. Armstrong, MacLachlan, & Weindling (1940) reported that variations of the cotton-wilt *Fusarium* were chiefly in two directions: decrease in abundance of aerial mycelium and decrease in the rate of radial growth. No changes occurred in the opposite direction. Isolates that had long been retained in culture were weakly pathogenic. Their cultural characteristics indicated that they were variants which had arisen in culture. These same authors reported that a cultural variant may or may not be less pathogenic than the isolate from which it has arisen.

McCulloch (1944) noted that variations and changes in pathogenicity occurred in isolates of the organism she called *Fusarium orthoceras* App. et Wr. var. *gladioli*. She observed that pathogenicity of this vascular *Fusarium* was reduced by long periods of culture in artificial media but she kept no extensive records of the changes. She also found that the isolates varied in their ability to infect different gladiolus varieties. Although she observed that some isolates produced dense aerial mycelium and others were of the appressed type, she made no attempt to associate these characters with differences in pathogenicity.

Several investigators have reported cases of physiologic specialization in certain species of *Fusarium*. Broadfoot (1926) reported that at least nine physiologic forms of *F. lini* Bolley can be distinguished by their parasitism on four varieties of flax. Armstrong & Armstrong (1950) wrote that there are definitely two

Table 10.—Growth forms of isolates of the gladiolus *Fusarium* when originally cultured on potato dextrose agar and when grown on Wellman's agar, August, 1953.

Isolate	Growth Form of Original Isolates on Potato Dextrose Agar	Growth Form on Wellman's Agar, 1953
45-73...	Not recorded	Raised
45-80...	Not recorded	Intermediate-appressed
46-3....	Not recorded	Appressed
46-5....	Intermediate	Intermediate-appressed
46-9....	Intermediate	Intermediate-raised
46-14...	Not recorded	Intermediate-raised
47-6....	Raised	Intermediate-raised
47-10...	Raised	Intermediate-raised
49-4....	Intermediate	Raised
49-15...	Raised	Appressed
49-23...	Raised	Raised
49-30...	Raised	Intermediate-raised
49-31...	Intermediate	Appressed
50-6....	Not recorded	Intermediate-raised
50-24...	Not recorded	Intermediate-raised
50-27...	Not recorded	Raised
50-28...	Not recorded	Intermediate-raised
45-8....	Raised	Raised
45-74...	Not recorded	Appressed
45-75...	Not recorded	Intermediate-raised
45-78...	Not recorded	Intermediate-appressed
46-4....	Appressed	Intermediate-raised
46-12...	Intermediate	Intermediate-raised
47-1....	Appressed	Raised
47-8....	Appressed	Intermediate-appressed
47-12...	Not recorded	Raised
47-19...	Appressed	Intermediate-raised
47-32...	Raised	Raised
49-1....	Intermediate	Appressed
49-17...	Appressed	Appressed
49-19...	Intermediate	Intermediate-raised
50-7....	Not recorded	Intermediate-appressed
50-22...	Not recorded	Intermediate-raised
50-25...	Not recorded	Intermediate-raised
47-2....	Appressed	Intermediate-raised
47-3....	Appressed	Raised
49-8....	Raised	Intermediate-raised
49-20...	Intermediate	Intermediate-appressed
50-23...	Not recorded	Raised
50-26...	Not recorded	Raised

and probably more biological races of *F. oxysporum* f. *tracheiphilum* Sny. & Hans. on the basis of pathogenicity on varieties of soybeans and cowpeas.

Studies on the relation of culture types and pathogenicity of the 40 isolates of gladiolus *Fusarium* listed in table 1 were undertaken by the writer with the hope of finding a possible relation between colony type, disease form, and degree of virulence. Methods of determining virulence are described under "Pathogenicity Tests."

Culture Types of the Gladiolus *Fusarium*.—Original isolations from diseased gladiolus corms were made on potato dextrose agar. Growth forms of the original cultures were not recorded for all isolates. However, 23 of the isolates were classified as belonging to the raised, intermediate, or appressed types on the basis of their aerial mycelium, table 10. Later, all isolates were grown on the medium found by Wellman (1942) to give more distinctive reactions between cultural variants. This medium, referred to as Wellman's agar in the present investigation, has the following composition: proteose peptone 5.0 grams, dihydrogen pc tassium phosphate 0.5 gram, magnesium sulfate 0.5 gram, maltose 15.0 grams, ferrous sulfate 0.03 gram, agar 12.0 grams, water 1,000.0 milliliters.

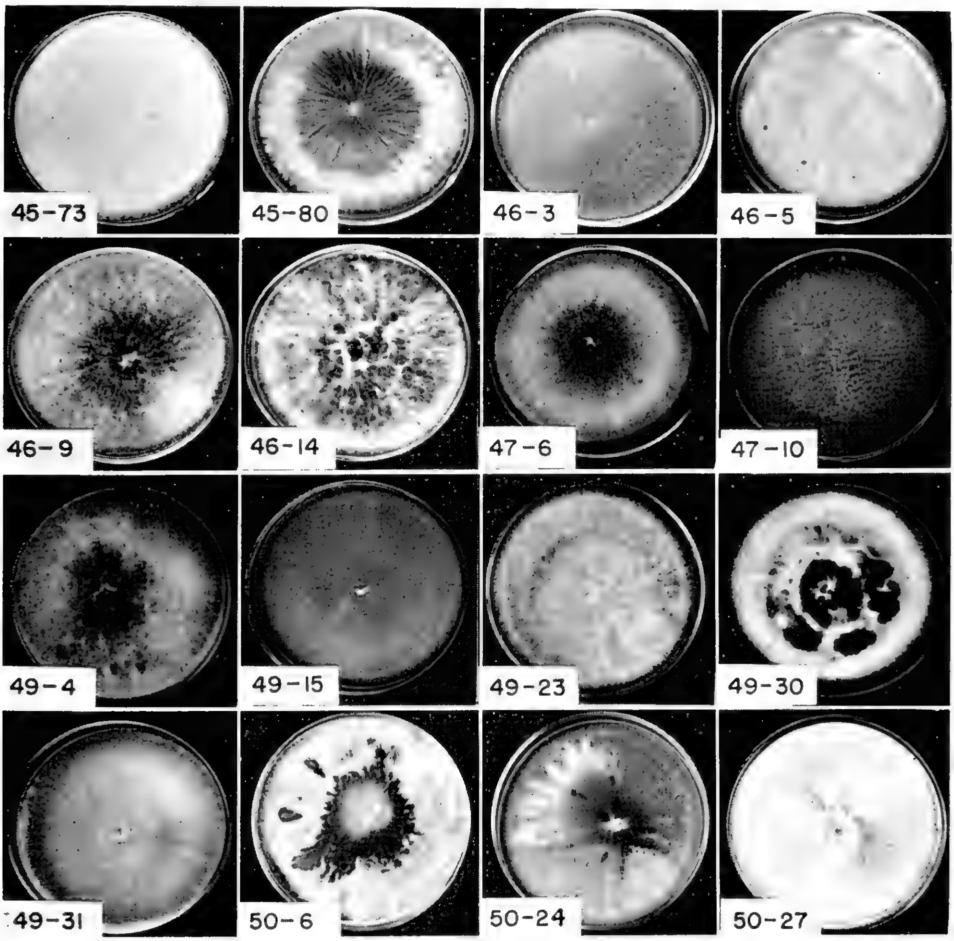

Fig. 13.—Raised, appressed, and intermediate growth forms of vascular isolates of *Fusarium* grown on Wellman's agar. The extreme raised and extreme appressed forms are shown in cultures 45-73 and 49-15, respectively. Cultures are 20 days old.

Growth forms, based on the classification of Wellman & Blaisdell (1941), of the 40 isolates of the gladiolus *Fusarium* as these isolates appeared in August, 1953, are given in table 10. When cultures of like form were grouped together, 11 were classified as raised, 17 as intermediate-raised, 6 as intermediate-appressed, and 6 as appressed. Photographs of 36 of the cultures are shown in figs. 13 and 14.

Table 10 shows that by 1953 some of the cultures were no longer of the same type as the original isolations. When these

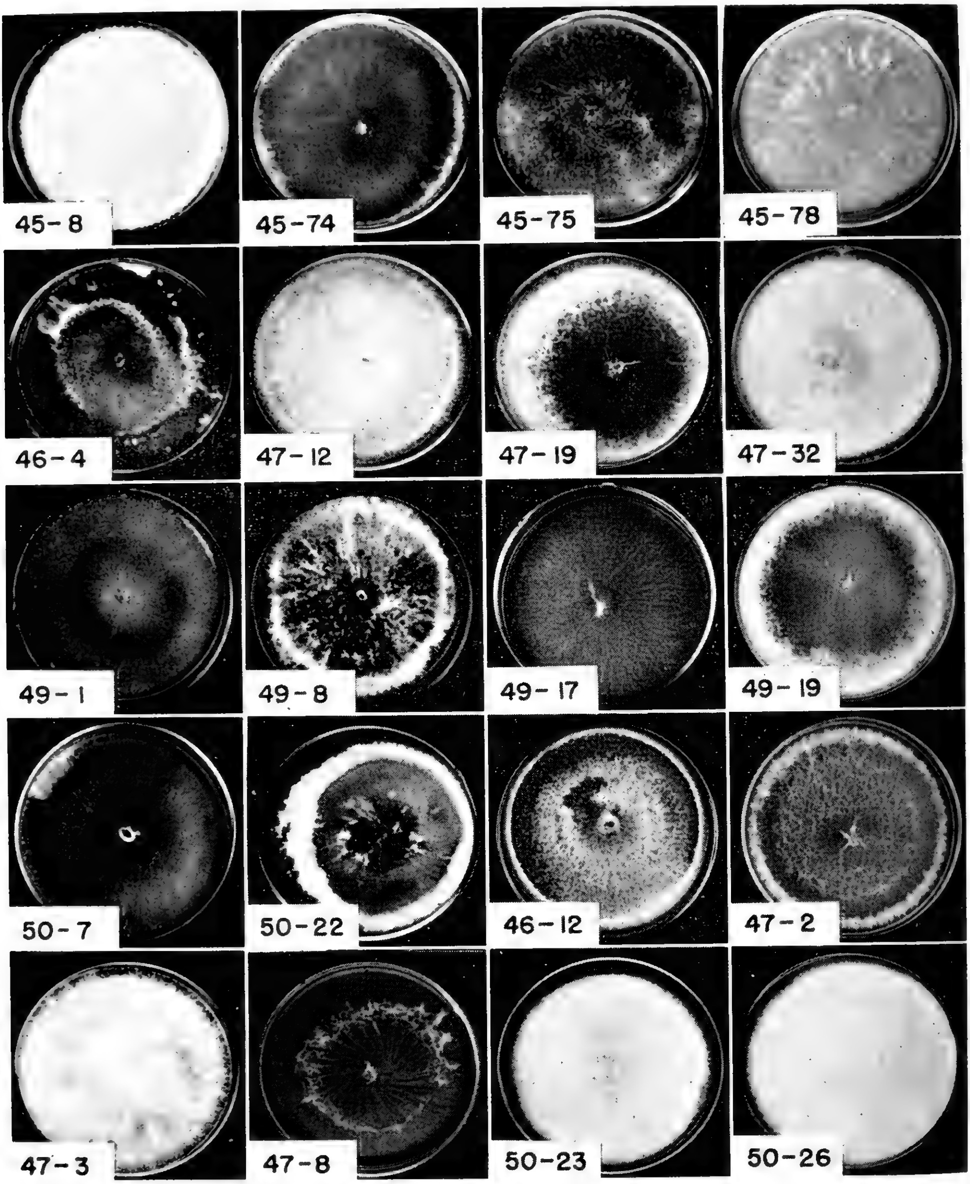

Fig. 14.—Raised, appressed, and intermediate growth forms of brown rot and basal dry rot isolates of *Fusarium* grown on Wellman's agar. Cultures 45-8 through 50-22 in the upper four rows are brown rot isolates; cultures 46-12 through 50-26 in the two bottom rows are basal dry rot isolates. Cultures are 20 days old.

Table 11.—Changes in growth form of isolates of the gladiolus *Fusarium* after being grown for various periods of time on laboratory media.

DIRECTION OF CHANGE	NUMBER OF ISOLATES
No change	9
Raised to intermediate	4
Raised to appressed	1
Intermediate to raised	1
Intermediate to appressed	2
Appressed to intermediate	4
Appressed to raised	2

changes were classified, with the two intermediate forms included in a single group, the results shown in table 11 were obtained.

Records show that variation in these cultures took place in both directions. Of the 14 isolates in which change in culture type was observed, 7 changed from raised to or toward appressed and 7 changed in the opposite direction.

pH Studies.—Wellman (1942) reported that raised (virulent) and appressed (mild) strains of the tomato-wilt *Fusarium* produced characteristic progressive pH changes in a liquid culture medium. Immediately after either of the strains began growing, acidity increased in the liquids for the first 5 days and became most intense in cultures of the appressed organism. The pH readings then gradually rose, but not at the same rate, until a maximum pH of about 8.7 was reached. With the raised strains, neutrality was reached at about the twelfth day, but with the appressed strains it was not reached until about the twenty-fifth day. By this time the pH of raised strains had nearly reached the maximum. The appressed strains did not reach the same point until after the fortieth day.

The 40 isolates of gladiolus *Fusarium* cultured in the studies reported here were grown in Tochinai liquid of the following composition: proteose peptone 10.0 grams, dihydrogen potassium phosphate 0.50 gram, magnesium sulfate 0.25 gram, maltose 20.0 grams, water 1,000.0 milliliters. The original pH of the medium was 6.21. Each isolate was grown in 100 milliliters of the culture medium in a 250-milliliter Erlenmeyer flask. Uniform disks of inoculum were cut from agar plate cultures with a sterile metal tube 9 millimeters in diameter. Each flask was inoculated with a single disk of inoculum. The flasks were shaken immediately and then left on the laboratory table. Small samples of liquid were removed from the flasks for pH determination after 3, 5, 8, 12, 15, 23, 28, 34, 41, 50, and 58 days. All pH determinations were made with a Beckman pH meter, standardized at frequent intervals against known buffer solutions.

The pH readings for 38 isolates are shown in table 12. As isolates 49-15 and 50-27 became contaminated early in the experiment they are not included in the table.

The progressive changes in pH produced by 16 of the isolates are shown in figs. 15, 16, 17, and 18. Pairs of isolates which had shown apparent differences in pathogenicity were selected from each disease form for comparison in pH reactions. The more virulent isolate of each pair, as determined by inoculation tests, is represented by the solid line in the graphs, and the milder isolate is represented by the broken line.

The figures show curves of the same general type as that obtained by Wellman for the tomato *Fusarium*. The liquid medium became more acid through the period of the first 5 days; then it gradually became less acid and more alkaline until a maximum of about pH 8.5 was reached.

In fig. 15*A*, vascular isolates 49-4 and 49-23 are compared. Both isolates were of the raised type on Wellman's agar, fig. 13. Isolate 49-4 was much more virulent than isolate 49-23 in pathogenicity tests in the greenhouse. Also, isolate 49-4 caused rot on corms inoculated in the laboratory; isolate 49-23 did not. The progressive pH changes produced by these two isolates were quite similar.

In fig. 15*B*, vascular isolates 50-24 and 50-28 are compared. Both isolates were of the intermediate-raised type on Wellman's agar. In pathogenicity tests, isolate 50-28 was the more virulent under both greenhouse and laboratory conditions. Isolate 50-28 reached a lower pH reading than isolate 50-24 and also required a longer time to reach maximum alkalinity. In these two isolates the relation between

Table 12.—Readings in pH of Tochinai liquid inoculated with different isolates of the gladiolus *Fusarium*; original pH 6.21.

Isolate	Days After Inoculation										
	3	5	8	12	15	23	28	34	41	50	58
45-73	5.68	5.25	4.87	4.84	4.97	6.99	7.45	8.36	8.48	8.47	8.32
45-80	6.10	4.78	4.94	5.52	6.06	7.10	7.68	8.27	8.52	8.52	8.47
46-3	5.63	5.10	4.93	5.30	6.03	6.50	7.38	8.29	8.54	8.58	8.45
46-5	5.51	4.85	4.73	5.60	6.65	8.49	8.72	8.72	8.55	8.15	8.59
46-9	5.50	4.84	4.75	5.49	6.06	6.85	8.22	8.63	8.61	8.48	8.41
46-14	5.55	4.83	4.78	5.78	6.03	6.57	7.90	8.40	8.59	8.54	8.45
47-6	5.60	4.78	4.63	5.52	5.84	8.53	8.50	8.61	8.48	8.32	8.12
47-10	5.33	4.78	4.63	5.73	6.68	6.77	6.47	8.21	8.44	8.54	8.61
49-4	5.55	4.90	4.95	6.20	6.47	6.32	7.53	8.44	8.62	8.42	8.45
49-23	5.78	4.92	4.90	6.48	7.03	6.25	7.07	8.31	8.46	8.50	8.38
49-30	5.94	5.30	4.88	5.79	6.88	7.93	8.40	8.58	8.52	8.32	8.15
49-31	5.27	5.03	4.83	4.98	6.00	7.50	8.02	8.53	8.51	8.44	8.43
50-6	5.59	4.85	4.89	6.08	6.42	6.68	6.98	8.45	8.48	8.65	8.62
50-24	5.41	4.92	4.95	6.38	6.98	8.37	8.50	8.50	8.40	8.23	8.09
50-28	5.55	4.75	4.61	5.38	6.07	6.53	6.71	7.82	8.45	8.55	8.53
45-8	5.60	5.00	4.88	5.89	7.38	8.49	8.55	8.45	8.47	8.32	8.15
45-74	5.70	5.03	4.92	5.95	6.67	6.63	7.58	8.37	8.43	8.61	8.50
45-75	5.45	4.88	4.91	6.18	7.00	6.98	7.32	8.19	8.44	8.51	8.40
45-78	5.88	5.21	4.78	5.61	6.70	8.34	8.37	8.48	8.58	8.55	8.38
46-4	5.75	5.45	5.27	5.58	6.26	7.33	7.33	8.40	8.48	8.64	8.51
46-12	5.51	4.74	4.60	5.12	5.50	5.93	6.17	8.20	8.42	8.58	8.45
47-1	5.69	5.05	4.93	5.55	6.38	6.95	7.84	8.48	8.59	8.50	8.39
47-8	5.59	5.27	5.04	5.91	6.38	6.77	7.61	8.37	8.57	8.65	8.45
47-12	5.64	5.18	4.94	4.90	5.10	6.55	7.59	7.48	8.43	8.58	8.45
47-19	5.68	5.12	5.00	4.96	5.24	6.60	7.54	8.08	8.62	8.49	8.42
47-32	5.69	5.12	4.86	5.16	6.15	8.28	8.40	8.62	8.48	8.44	8.28
49-1	5.83	5.10	4.89	5.75	6.70	7.19	7.35	8.48	8.61	8.59	8.41
49-17	5.42	4.89	4.77	6.00	6.67	7.29	7.44	8.29	8.54	8.54	8.46
49-19	5.53	4.95	4.89	6.40	7.10	6.47	8.15	8.40	8.52	8.62	8.47
50-7	5.50	5.21	5.07	5.96	6.17	6.70	7.27	8.40	8.64	8.49	8.46
50-22	5.66	4.95	4.78	5.74	6.73	7.48	8.06	8.44	8.43	8.50	8.52
50-25	5.48	5.09	4.95	6.50	6.85	7.51	7.69	8.29	8.60	8.65	8.49
47-2	5.72	4.87	4.55	5.02	5.81	7.15	8.02	8.48	8.37	8.60	8.48
47-3	5.51	4.90	4.88	6.15	7.08	7.94	8.39	8.45	8.55	8.58	8.42
49-8	5.72	4.90	4.62	5.67	6.38	6.32	6.10	8.23	8.41	8.47	8.51
49-20	5.53	4.93	4.80	6.13	6.64	6.52	7.38	8.32	8.43	8.65	8.59
50-23	5.52	4.85	4.71	6.04	6.60	7.34	6.50	8.36	8.39	8.56	8.43
50-26	5.67	5.20	4.85	4.83	5.68	8.00	8.48	8.48	8.38	8.33	8.23

pH changes and virulence is exactly opposite to that reported by Wellman for the tomato *Fusarium*.

In fig. 16*A*, brown rot isolates 47-12 and 50-25 are compared. Isolate 47-12 was of the raised type on Wellman's agar; 50-25 was intermediate-raised. Isolate 47-12 produced rot in inoculated corms; 50-25 did not. The pH curves of the two isolates show that in cultures of both isolates the same low point was reached at about the same time but that the rise in pH was much sharper in cultures of isolate 50-25 than it was in cultures of isolate 47-12. With isolate 50-25, neutrality was reached in about 17 days but, with isolate 47-12, not until after 25 days.

Brown rot isolates 49-17 and 49-19 are compared in fig. 16*B*. Isolate 49-17 was of the appressed type, and isolate 49-19 was intermediate-raised. Isolate 49-17 produced corm rot in laboratory tests in 1952 and 1953; isolate 49-19 produced corm rot in 1952 but not in 1953. The pH curves for these two isolates are similar except for a second drop in pH from the fifteenth to the twenty-third days in the culture of isolate 49-19.

Vascular isolates 45-73 and 46-3 are compared in fig. 17*A*. Isolate 45-73 was the more virulent in greenhouse tests in 1948 and 1953. In 1952, isolate 46-3 was slightly more virulent. Isolate 45-73 was of the raised type; 46-3 was appressed.

The pH curves for these two isolates are quite similar. Isolate 45-73 remained in the low acid range a little longer but reached the alkaline range ahead of isolate 46-3. After 30 days, the pH curves of these two isolates were nearly identical.

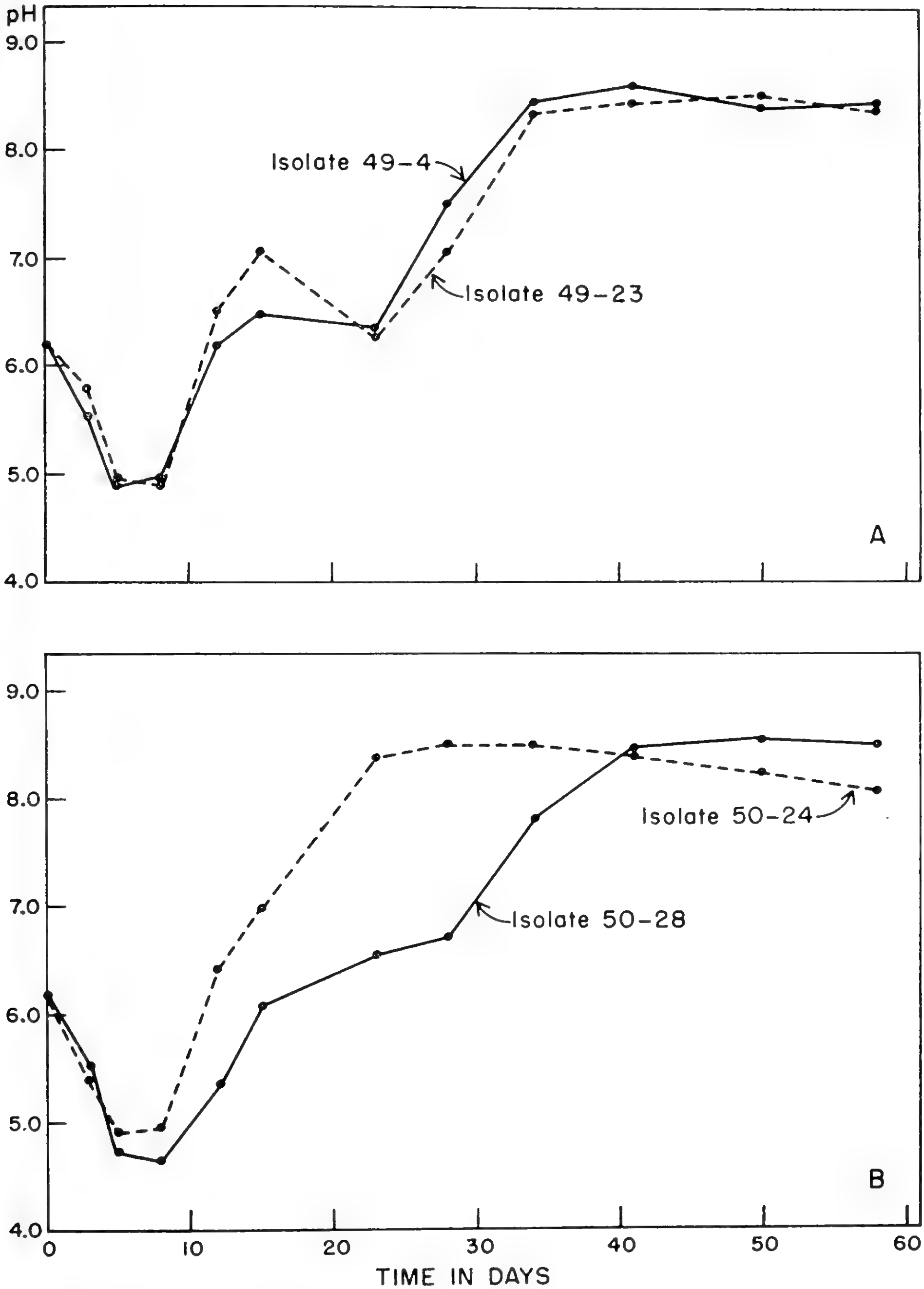

Fig. 15.—Progressive changes in pH produced in Tochinai liquid by four vascular isolates of *Fusarium*.

In fig. 17*B*, brown rot isolates 50-7 and 50-22 are compared. Isolate 50-7 was of the intermediate-appressed type; 50-22 was intermediate-raised. Isolate 50-22 was the more virulent in laboratory and greenhouse tests. The pH curves for

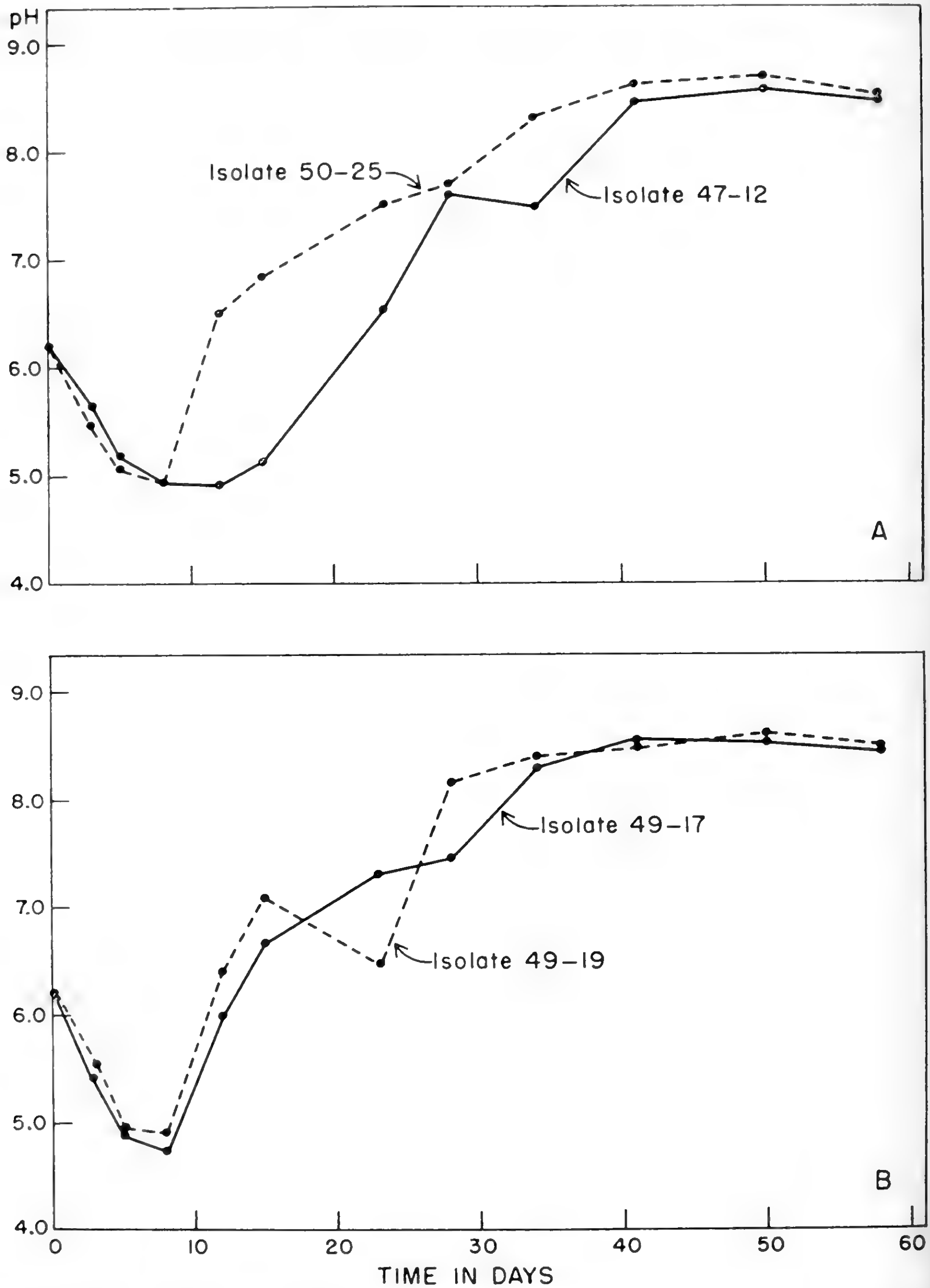

Fig. 16.—Progressive changes in pH produced in Tochinai liquid by four brown rot isolates of *Fusarium*.

these two isolates are similar except for a divergence that occurred between the twelfth and thirty-fourth days.

Two sets of basal dry rot isolates are compared in fig. 18. In fig. 18*A*, isolate 47-2 was of the intermediate-raised type

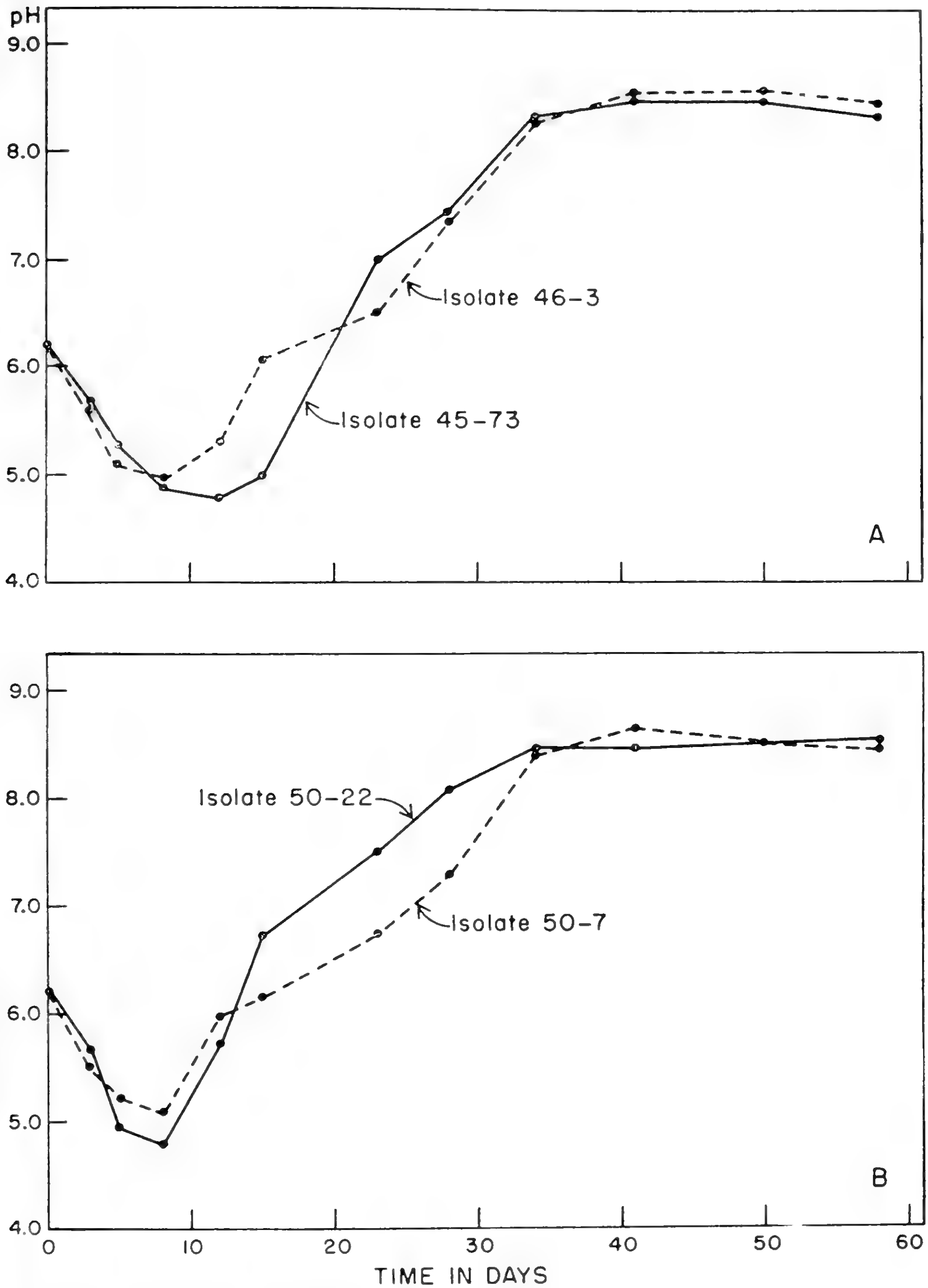

Fig. 17.—Progressive changes in pH produced in Tochinai liquid by, *A*, two vascular isolates and, *B*, two brown rot isolates of *Fusarium*.

and 47-3 was raised. Isolate 47-3 was the more virulent in greenhouse tests; 47-2 was slightly more virulent than 47-3 in the laboratory. Isolate 47-2 produced the greater amount of acid during early growth and its pH readings remained

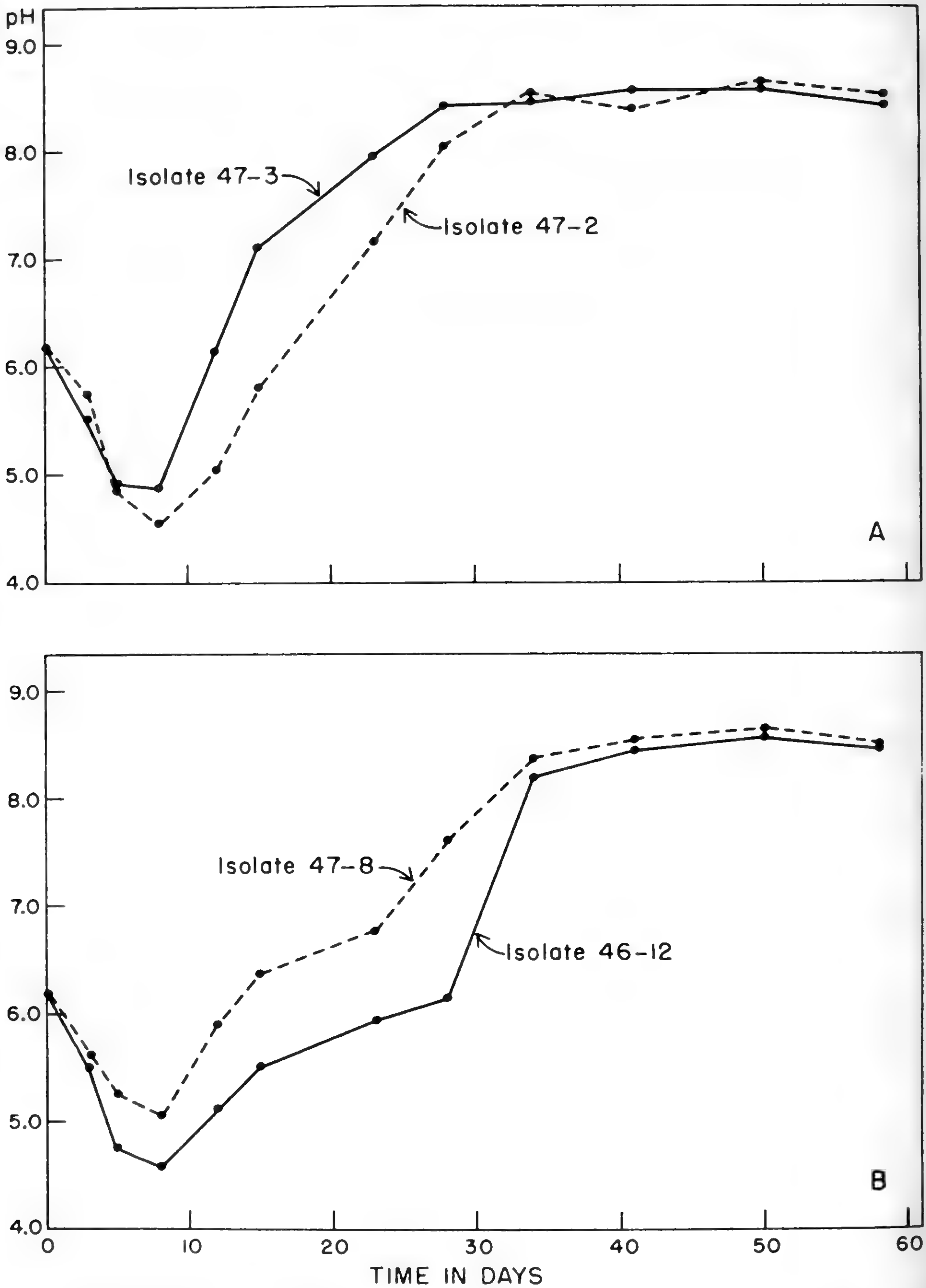

Fig. 18.—Progressive changes in pH produced in Tochinai liquid by four basal dry rot isolates of *Fusarium.*

lower than those for isolate 47-3 until the thirty-fourth day.

In fig. 18*B*, isolate 46-12 was intermediate-raised, and isolate 47-8 was intermediate-appressed. Isolate 46-12 was more virulent in laboratory tests. In this case the pH readings for the more virulent isolate were lower than those for the milder isolate from the beginning until the fifty-eighth day.

In these experiments no consistent relations between culture types, pH changes, or degrees of virulence were observed. In this respect, the gladiolus *Fusarium* appears to differ from the tomato *Fusarium*.

MORPHOLOGY

A complete morphological study of all the isolates from the vascular, brown rot, and basal dry rot forms of the gladiolus Fusarium disease was not attempted. Some of the isolates produced the typically 2- to 5-septate macrospores rather consistently, but many isolates produced only the single-celled type. In some isolates, septate spores were very abundant in the original cultures from diseased gladiolus corms, but, after one or two transfers, only single-celled spores could be found. Spores seemed to be produced more abundantly on Well-

Table 13.—Measurements of conidia produced by six isolates of the gladiolus *Fusarium* on Wellman's agar.

Disease Form	Isolate and Type of Conidia	Mean, Microns	Range, Microns
Vascular	Isolate 49-15		
	0-septate	9.2 x 3.3	5.5–13.1 x 2.8–4.1
	1-septate	16.0 x 4.0	6.9–27.6 x 2.8–5.5
	2-septate	26.2 x 4.1	16.6–34.5 x 3.4–4.8
	3-septate	32.1 x 4.1	23.5–45.5 x 3.4–4.1
	4-septate	45.3 x 3.9	37.3–56.6 x 2.8–4.1
	5-septate	53.8 x 4.1	Only 1 spore
Vascular	Isolate 50-27		
	0-septate	8.8 x 3.0	5.5–12.4 x 2.8–4.1
	1-septate	16.7 x 3.5	11.7–23.5 x 2.8–4.8
	2-septate	23.2 x 4.0	19.3–37.3 x 2.8–5.5
	3-septate	35.1 x 4.2	24.8–44.2 x 4.1–5.5
	4-septate	42.7 x 4.1	34.5–48.3 x 4.1–4.1
	5-septate	46.4 x 4.5	44.2–53.8 x 4.1–5.5
Brown rot	Isolate 45-74		
	0-septate	9.9 x 3.3	6.9–15.2 x 2.8–4.1
	1-septate	18.7 x 3.9	9.7–24.8 x 2.8–4.1
	2-septate	24.5 x 4.0	17.9–31.7 x 2.8–4.8
	3-septate	30.2 x 4.1	15.2–40.0 x 2.8–5.5
	4-septate	34.5 x 5.2	34.5–34.5 x 4.8–5.5
	5-septate	None	—
Brown rot	Isolate 50-25		
	0-septate	8.9 x 3.0	5.5–13.8 x 2.1–4.1
	1-septate	15.2 x 3.8	11.0–19.3 x 2.8–4.8
	2-septate	19.7 x 4.0	15.2–24.8 x 2.8–5.5
	3-septate	31.7 x 4.3	20.7–44.2 x 4.1–5.5
	4-septate	39.7 x 4.3	37.3–44.2 x 4.1–5.5
	5-septate	44.2 x 4.1	Only 1 spore
Basal dry rot	Isolate 49-20		
	0-septate	9.1 x 3.4	6.9–15.2 x 2.8–4.8
	1-septate	16.3 x 4.0	9.7–29.0 x 2.8–4.1
	2-septate	22.3 x 4.2	13.8–31.7 x 3.4–5.5
	3-septate	29.4 x 4.4	22.1–37.3 x 4.1–5.5
	4-septate	29.0 x 4.1	Only 1 spore
	5-septate	None	—
Basal dry rot	Isolate 50-26		
	0-septate	9.6 x 4.0	4.1–22.1 x 2.8–5.5
	1-septate	17.6 x 4.2	12.4–23.5 x 3.4–4.8
	2-septate	22.9 x 4.4	17.9–29.0 x 3.4–5.5
	3-septate	31.8 x 5.2	24.8–40.0 x 4.1–5.5
	4-septate	32.4 x 5.2	31.7–33.1 x 4.8–5.5
	5-septate	None	—

man's agar than on potato dextrose agar.

From several isolates which produced septate macrospores rather abundantly on Wellman's agar, two isolates from each disease form were selected for spore measurements. The only purpose of making spore measurements was to find out if isolates from the different disease forms

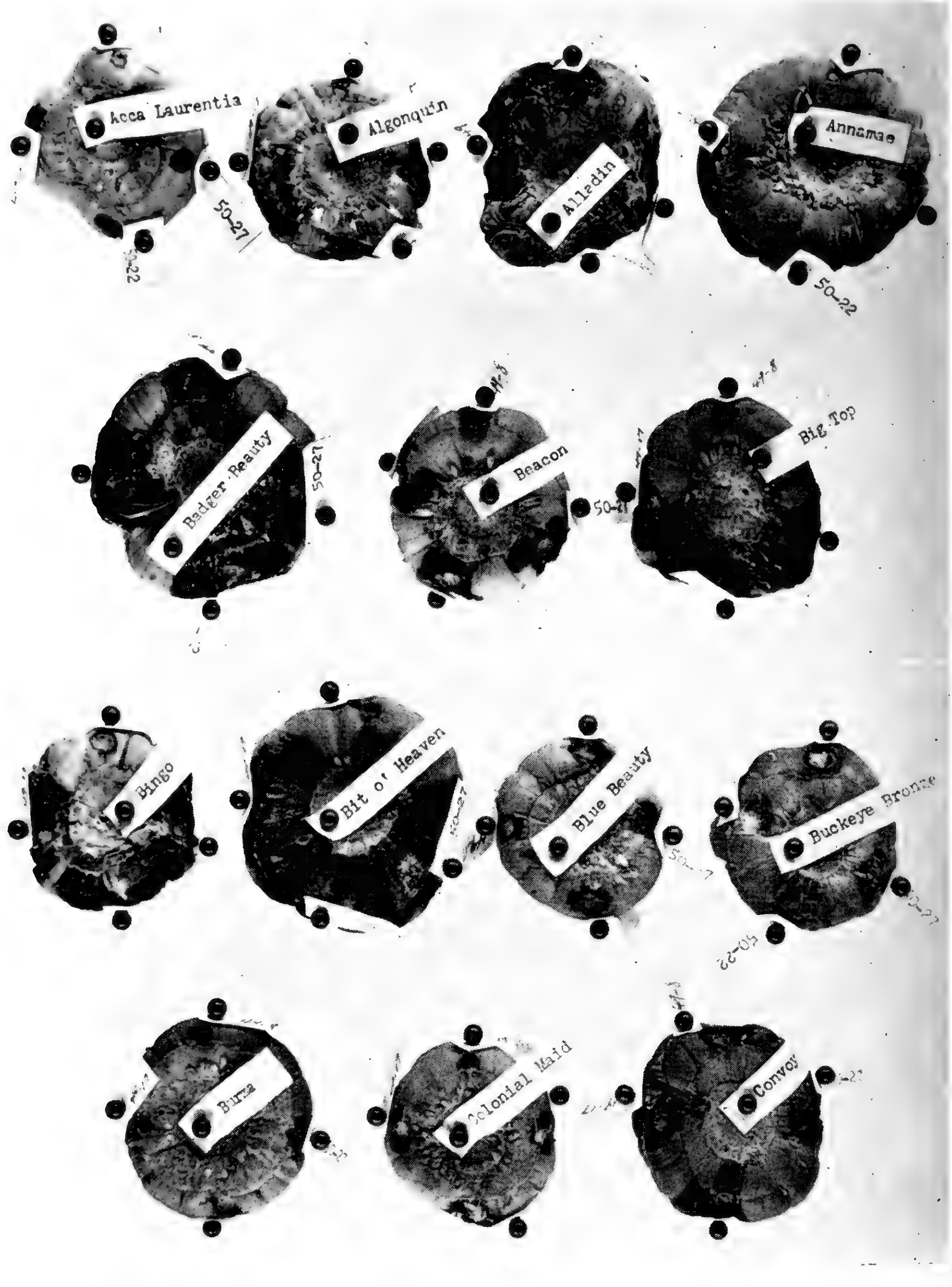

Fig. 19.—Corms of 14 gladiolus varieties, each corm inoculated with four isolates of *Fusarium*. The locations of the inoculations on each corm are as follows: top, isolate 49-8; right, 50-27; bottom, 50-22; left, 49-17. Photograph was taken 34 days after inoculation.

might be distinguished by differences in spore sizes. As pointed out by Harter (1939), several factors influence the size of *Fusarium* spores produced in laboratory culture. It is often difficult, if not impossible, by any means of manipulation of the culture to obtain a morphological agreement with the description of a given species. It seemed reasonable to assume, however, that a fair comparison could be made of spores from cultures which had been kept under the same conditions.

Six isolates were selected for use in making spore measurements and were grown on Wellman's agar in Petri dishes for 14 days in a location where the dishes were exposed to diffused light during daylight hours. All measurements were made within 2 or 3 days after the cultures were 14 days old. Cultures from which measurements could not be made immediately were placed in a refrigerator at 3–5 degrees C. until measurements could be made. The spores to be measured were mounted on 2 per cent plain agar on a microscope slide. Thirty spores of each septation type were measured from each culture in which this number of spores was available. The 4- and 5-septate types were so rare in most of the cultures that it was impossible to find 30 spores for measurement.

Mean measurements and ranges of measurements of spores from the six selected isolates are shown in table 13. The differences in spore sizes are not great enough to place the isolates in distinct groups on the basis of spore size.

PATHOGENICITY TESTS

In this investigation, the pathogenicity of the isolates of *Fusarium* was tested both in the laboratory and in the greenhouse. All 40 isolates were tested in the laboratory; 27 of them were tested in the greenhouse.

Laboratory Tests

Large mature gladiolus corms, free from blemishes, were selected for the laboratory inoculation tests. After the husks had been removed, the corms were washed well with water and then left on a table until dry. Four small wounds, approximately equal distances apart, were made on the basal area of each corm with a three-sixteenths-inch metal drill bit turned rapidly with thumb and index finger. Uniform disks of inoculum were cut from agar plate cultures with a sterile metal tube three-sixteenths inch in diameter. One disk of inoculum was pressed gently into each wound. Each corm was inoculated with four isolates; each isolate was used on four corms in each of the various tests.

Inoculations were identified by paper tags pinned near the points of inoculation, fig. 19. Immediately after they had been inoculated, the corms were placed in moist chambers and left for 48 hours. They were then removed and placed on a table in the laboratory. The corms were examined frequently, and at the end of 4 to 6 weeks final disease readings were made.

These inoculations resulted in the development of three general types of lesions: severe, in which the rot progressed steadily from the point of inoculation until most of the corm was rotted, shown in the Bit o' Heaven corm in fig. 19; mild, in which the rot progressed very slowly and only a narrow brown band appeared around the point of inoculation, shown in the Acca Laurentia corm in fig. 19; healed, in which no rot developed and the inoculation wound corked over, shown in the Annamae corm in fig. 19.

A basis on which to compare virulence of the isolates of *Fusarium*, as well as to compare susceptibilities of gladiolus varieties, was derived from a modification of McKinney's (1923) formula for disease evaluation. Class values of 0, 1, and 2, respectively, were assigned to the healed, mild, and severe types of lesions. Indexes of rot severity were calculated by use of the following formula:

$$\text{Rot severity index} = \frac{N_1 0 + N_2 1 + N_3 2}{2t} \times 100$$

where N_1, N_2, N_3 = number of corms in disease classes 1, 2, and 3, respectively

0, 1, 2 = values assigned to disease classes 1, 2, and 3 respectively

t = total number of corms used

Table 14.—Severity indexes for the rots produced by four isolates of *Fusarium* on 68 gladiolus varieties in 1951. The indexes were derived from the formula on page 481.

Variety	Isolate				Average
	49-8	49-17	50-22	50-27	
Abu Hassan	100.0	100.0	100.0	100.0	100.0
Acca Laurentia	37.5	50.0	50.0	25.0	40.6
Aladdin	75.0	100.0	100.0	87.5	90.6
Algonquin	50.0	100.0	100.0	100.0	87.5
Annamae	25.0	25.0	25.0	37.5	28.1
Badger Beauty	100.0	100.0	100.0	100.0	100.0
Beacon	62.5	87.5	100.0	100.0	87.5
Big Top	75.0	100.0	100.0	100.0	93.7
Bingo	75.0	100.0	100.0	100.0	93.7
Bit o' Heaven	62.5	100.0	100.0	100.0	90.6
Black Opal	87.5	75.0	100.0	100.0	90.6
Blue Beauty	62.5	50.0	87.5	62.5	65.6
Buckeye Bronze	37.5	75.0	87.5	87.5	71.9
Burma	50.0	12.5	50.0	50.0	40.6
Colonial Maid	37.5	75.0	100.0	100.0	78.1
Convoy	75.0	75.0	87.5	62.5	75.0
Corona	100.0	100.0	100.0	100.0	100.0
Crinkle Cream	87.5	100.0	100.0	100.0	96.9
Dieppe	50.0	100.0	100.0	100.0	87.5
Dr. F. E. Bennett	100.0	100.0	100.0	100.0	100.0
Dr. Whiteley	50.0	50.0	62.5	50.0	53.1
Dusty Miller	100.0	62.5	100.0	100.0	90.6
Early Rose	25.0	50.0	75.0	37.5	46.9
Elizabeth the Queen	75.0	100.0	100.0	100.0	93.7
Ethel Cave Cole	50.0	75.0	100.0	87.5	78.1
Fair Angel	50.0	75.0	87.5	50.0	65.6
Genghis Khan	100.0	100.0	100.0	100.0	100.0
Gloaming	62.5	100.0	100.0	100.0	90.6
Gold Eagle	50.0	37.5	62.5	62.5	53.1
Golden Dream	100.0	100.0	100.0	100.0	100.0
High Finance	62.5	100.0	100.0	100.0	90.6
Johan van Konynenburg	100.0	100.0	100.0	100.0	100.0
King Lear	75.0	100.0	100.0	100.0	93.7
King William	50.0	100.0	100.0	100.0	87.5
Lady Jane	12.5	75.0	87.5	87.5	65.6
Lantana	50.0	100.0	100.0	100.0	87.5
Larime	50.0	100.0	100.0	100.0	87.5
Leading Lady	50.0	100.0	100.0	87.5	84.4
Legend	50.0	75.0	87.5	50.0	65.6
Majuba	50.0	62.5	100.0	50.0	65.6
Malta	62.5	100.0	100.0	100.0	90.6
Margaret Beaton	50.0	50.0	50.0	50.0	50.0
Marguerite	62.5	75.0	100.0	100.0	84.4
Minuet	62.5	37.5	100.0	100.0	75.0
Miss Bloomington	50.0	50.0	50.0	50.0	50.0
Mother Kadel	50.0	100.0	100.0	100.0	87.5
Mrs. Lulu Hunt	50.0	50.0	50.0	50.0	50.0
New Europe	100.0	100.0	100.0	100.0	100.0
Ogarita	50.0	75.0	87.5	87.5	75 0
Ohio Nonpareil	50.0	87.5	100.0	87.5	81.2
Oklahoma	50.0	75.0	87.5	75.0	71.9
Oregon Gold	75.0	75.0	100.0	87.5	84.4
Pandora	75.0	100.0	100.0	100.0	93.7
Phyllis McQuiston	50.0	50.0	50.0	50.0	50.0
Prairie Gold	50.0	100.0	100.0	100.0	87.5
Purple Supreme	100.0	100.0	100.0	100.0	100.0
Red Charm	75.0	100.0	100.0	100.0	93.7
Rewi Fallu	75.0	100.0	100.0	100.0	93.7
Rosa Van Lima	25.0	75.0	62.5	37.5	50.0
Rose Ruffles	62.5	75.0	100.0	87.5	81.2

Table 14.—Concluded

Variety	Isolate				Average
	49-8	49-17	50-22	50-27	
Silentium	50.0	87.5	87.5	75.0	75.0
Silver Wings	75.0	100.0	100.0	100.0	93.7
Snow Princess	50.0	62.5	100.0	87.5	75.0
Southern Melody	100.0	100.0	100.0	100.0	100.0
Spirit of St. Louis	87.5	12.5	12.5	12.5	31.2
Valeria	37.5	37.5	87.5	50.0	53.1
Variation	100.0	100.0	100.0	100.0	100.0
Vulcan	50.0	75.0	100.0	87.5	78.1

Table 15.—Severity indexes for the rots produced by 40 isolates of *Fusarium* on seven gladiolus varieties in 1952. The indexes were derived from the formula on page 481.

Isolate	Gladiolus Variety							Average Index
	Ethel Cave Cole	Maid of Orleans	Miss Bloomington	Picardy	Rosa Van Lima	Snow Princess	Spirit of St. Louis	
45-73	0.0	12.5	0.0	37.5	0.0	0.0	25.0	10.7
45-80	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
46-3	0.0	0.0	0.0	25.0	0.0	0.0	0.0	3.6
46-5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
46-9	0.0	0.0	0.0	12.5	0.0	0.0	12.5	3.6
46-14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
47-6	0.0	0.0	0.0	50.0	0.0	0.0	0.0	7.1
47-10	0.0	0.0	0.0	25.0	0.0	0.0	0.0	3.6
49-4	12.5	0.0	0.0	100.0	0.0	62.5	0.0	25.0
49-15	0.0	0.0	12.5	0.0	0.0	0.0	0.0	1.8
49-23	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
49-30	0.0	0.0	0.0	100.0	0.0	0.0	0.0	14.3
49-31	0.0	0.0	0.0	25.0	0.0	0.0	0.0	3.8
50-6	0.0	0.0	12.5	75.0	0.0	0.0	0.0	12.5
50-24	0.0	0.0	0.0	25.0	0.0	0.0	0.0	3.8
50-27	0.0	0.0	0.0	75.0	0.0	0.0	0.0	10.7
50-28	0.0	12.5	12.5	75.0	0.0	0.0	0.0	14.3
45-8	0.0	0.0	0.0	62.5	0.0	0.0	0.0	8.9
45-74	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
45-75	12.5	0.0	0.0	75.0	0.0	0.0	0.0	12.5
45-78	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
46-4	12.5	0.0	0.0	25.0	12.5	0.0	0.0	7.1
46-12	37.5	0.0	25.0	100.0	0.0	0.0	0.0	23.2
47-1	87.5	0.0	37.5	87.5	12.5	0.0	0.0	19.6
47-8	0.0	0.0	12.5	37.5	0.0	0.0	0.0	7.1
47-12	0.0	0.0	0.0	100.0	0.0	0.0	0.0	14.3
47-19	0.0	0.0	12.5	100.0	0.0	0.0	0.0	16.1
47-32	0.0	0.0	25.0	100.0	0.0	0.0	0.0	17.7
49-1	0.0	0.0	0.0	100.0	0.0	0.0	0.0	14.3
49-17	25.0	12.5	37.5	100.0	0.0	37.5	0.0	30.3
49-19	0.0	0.0	50.0	100.0	0.0	37.5	0.0	26.8
50-7	25.0	0.0	50.0	100.0	0.0	37.5	37.5	35.7
50-22	100.0	12.5	62.5	100.0	0.0	100.0	12.5	55.3
50-25	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
47-2	37.5	37.5	62.5	87.5	50.0	12.5	87.5	53.6
47-3	62.5	12.5	50.0	100.0	25.0	12.5	12.5	39.3
49-8	12.5	0.0	12.5	87.5	0.0	0.0	75.0	26.8
49-20	0.0	0.0	50.0	87.5	0.0	0.0	25.0	23.2
50-23	12.5	0.0	25.0	100.0	0.0	0.0	12.5	21.4
50-26	0.0	0.0	25.0	100.0	0.0	0.0	0.0	17.8
Average	*10.9*	*2.5*	*14.4*	*59.4*	*2.5*	*7.5*	*7.5*	—

In 1951, four isolates were tested for ability to produce rot on corms of 68 varieties. Results are shown in table 14. Isolate 50-27 was a vascular isolate; the others were brown rot isolates. All four isolates caused rot on all varieties used in this test, but the severity of rot varied with isolates as well as with varieties. The average indexes in table 14 can be considered indicative of the relative susceptibility of the different varieties to Fusarium rot. Since the test was conducted under conditions that favored development of rot, varieties with an average index of 0 to 50 can be considered resistant and varieties with an index greater than 50 can be considered susceptible.

In 1952, all 40 isolates were tested on seven gladiolus varieties. The indexes of rot severity obtained in this test are shown in table 15. The isolates varied greatly in their ability to produce rot on corms of different varieties. Seven of the isolates failed to produce rot on any of the seven varieties tested. Only basal dry rot isolates 47-2 and 47-3 produced rot on all seven varieties. The average rot severity index for the 7 basal dry rot isolates was 26.5, for the 16 brown rot isolates it was 17.8, and for the 17 vascular isolates it was 6.7. Apparently vascular isolates are less capable of causing corm rot than are the brown rot and basal dry rot isolates. These results are in general agreement with those of McCulloch (1944), who found that the vascular isolates with which she worked caused only mild rot on corms inoculated in the laboratory, while isolates from corms having the disease type described by Massey (1926) caused severe rot.

In this test the average severity index for rot on the variety Picardy was 59.4 while on Maid of Orleans and Rosa Van Lima it was only 2.5. The difference in susceptibility indicated by these figures agrees well with what is observed in commercial stocks of these varieties. Fusarium rot is very rare in stocks of Maid of Orleans and Rosa Van Lima but it is extremely common in stocks of Picardy.

Six of the varieties used in the 1951

Table 16.—Severity indexes for the rots produced in 2 successive years by four isolates of *Fusarium* on six gladiolus varieties.*

Variety and Year	Isolate			
	49-8	49-17	50-22	50-27
Ethel Cave Cole				
1951	50.0	75.0	100.0	87.5
1952	12.5	25.0	100.0	0.0
Miss Bloomington				
1951	50.0	50.0	50.0	50.0
1952	12.5	37.5	62.5	0.0
Picardy†				
1951	75.0	100.0	100.0	100.0
1952	87.5	100.0	100.0	75.0
Rosa Van Lima				
1951	25.0	75.0	62.5	37.5
1952	0.0	0.0	0.0	0.0
Snow Princess				
1951	50.0	62.5	100.0	87.5
1952	0.0	37.5	100.0	0.0
Spirit of St. Louis				
1951	87.5	12.5	12.5	12.5
1952	75.0	0.0	12.5	0.0

*The indexes used in this table are taken from tables 14 and 15.
†In 1951, Silver Wings, a sport of Picardy, was used instead of Picardy.

test were used also in the 1952 test. The severity indexes for the rots caused by the same four isolates on corms of these varieties in the 2 years are shown in table 16. In 17 cases the rot indexes were lower in 1952 than they had been in 1951, in 5 cases they remained the same, and in 2 cases only they were higher.

A third test was made in 1953 when all 40 isolates were used on the varieties Picardy and Spirit of St. Louis. The results obtained with these varieties in 1952 and 1953 are shown in table 17. In the tests on Picardy the rot indexes in 27 isolates were lower in 1953 than in 1952, in 4 they were higher, and in 9 they remained the same. With Spirit of St. Louis the rot indexes in 5 isolates were lower in 1953 than in 1952, in 7 they were higher, and in 28 they remained the same. The indexes remaining unchanged included 7 instances in Picardy and 25 in Spirit of St. Louis in which no rot was produced in either year.

Although no attempt was made to maintain the same conditions for all tests, it is not likely that laboratory conditions varied greatly during the three tests. Differences in corm lots used in different years may have been partly responsible for

Table 17.—Severity indexes for the rots produced in 2 or 3 successive years by 40 isolates of *Fusarium* on two gladiolus varieties. Indexes were derived from the formula on page 481.

Isolate	Picardy			Spirit of St. Louis		
	1951	1952	1953	1951	1952	1953
45-73	—	37.5	25.0	—	25.0	25.0
45-80	—	0.0	0.0	—	0.0	25.0
46-3	—	25.0	0.0	—	0.0	0.0
46-5	—	0.0	0.0	—	0.0	0.0
46-9	—	12.5	0.0	—	12.5	12.5
46-14	—	0.0	0.0	—	0.0	0.0
47-6	—	50.0	0.0	—	0.0	0.0
47-10	—	25.0	0.0	—	0.0	0.0
49-4	—	100.0	75.0	—	0.0	0.0
49-15	—	0.0	0.0	—	0.0	0.0
49-23	—	0.0	0.0	—	0.0	0.0
49-30	—	100.0	0.0	—	0.0	0.0
49-31	—	25.0	50.0	—	0.0	0.0
50-6	—	75.0	0.0	—	0.0	0.0
50-24	—	25.0	0.0	—	0.0	0.0
50-27	100.0	75.0	75.0	12.5	0.0	0.0
50-28	—	75.0	25.0	—	0.0	75.0
45-8	—	62.5	50.0	—	0.0	0.0
45-74	—	0.0	62.5	—	0.0	0.0
45-75	—	75.0	100.0	—	0.0	0.0
45-78	—	0.0	0.0	—	0.0	0.0
46-4	—	25.0	12.5	—	0.0	0.0
46-12	—	100.0	37.5	—	0.0	0.0
47-1	—	87.5	100.0	—	0.0	12.5
47-8	—	37.5	12.5	—	0.0	0.0
47-12	—	100.0	75.0	—	0.0	0.0
47-19	—	100.0	75.0	—	0.0	0.0
47-32	—	100.0	75.0	—	0.0	50.0
49-1	—	100.0	75.0	—	0.0	25.0
49-17	100.0	100.0	87.5	12.5	0.0	0.0
49-19	—	100.0	0.0	—	0.0	0.0
50-7	—	100.0	25.0	—	37.5	37.5
50-22	100.0	100.0	75.0	12.5	12.5	37.5
50-25	—	0.0	0.0	—	0.0	0.0
47-2	—	87.5	75.0	—	87.5	25.0
47-3	—	100.0	100.0	—	12.5	0.0
49-8	75.0	87.5	12.5	87.5	75.0	37.5
49-20	—	87.5	37.5	—	25.0	0.0
50-23	—	100.0	62.5	—	12.5	0.0
50-26	—	100.0	75.0	—	0.0	12.5

Table 18.—Results of greenhouse tests on gladiolus variety Picardy inoculated with *Fusarium*, 1948.

Isolate	Symptoms and Numbers of Corms Affected			
	Vascular Discoloration	Basal Dry Rot	Completely Destroyed	No Symptoms
45-73	6	0	0	4
46-3	0	4	1	5
46-9	0	0	0	10
46-14	0	0	0	10
47-6	0	3	1	6
45-8	0	7	1	2
45-74	0	0	0	10
45-75	0	0	10	0
46-4	0	1	1	8
46-12	0	9	0	1
47-1	0	0	10	0
47-12	0	0	10	0
47-32	0	8	2	0
Check	0	0	0	10

differences in results, especially in the case of the variety Rosa Van Lima, which developed rot in 1951 but not in 1952. The over-all results seem to indicate that, as has been reported for many other pathogenic organisms, the isolates lose their virulence when maintained in laboratory culture over a period of time. More precise tests over a longer period of years would be necessary to establish this point with certainty.

Greenhouse Tests

In the greenhouse, corms were planted in soil which, after being steamed, had been infested with cultures of *Fusarium* that had been grown on autoclaved whole-grain oats in 250-milliliter Erlenmeyer flasks for 2 to 3 weeks. The flasks were shaken daily during the growth period of the *Fusarium*.

In order that the chances of using infected gladiolus corms in these experiments might be minimized, the husks were removed and the corms were soaked 15 minutes in a solution of 9 grams *New Improved Ceresan* (5 per cent ethyl mercury phosphate) in 1 gallon of water. The corms were then washed in several changes of tap water to remove the *Ceresan*. Cormels used in some of the tests were treated in this same way.

Furrows 2½ to 3 inches deep were marked out across a greenhouse bench. Depressions 4 inches apart were made in the bottoms of the furrows. One *Fusarium*-carrying oat grain was placed in each depression and covered lightly with soil. A gladiolus corm was then set over it. After the corms had been placed, the furrows were filled with soil.

No attempt was made to maintain a constant soil moisture content. Water was applied to the soil as often as necessary to maintain good growing conditions.

Tests in 1948.—Preliminary tests with 13 isolates of *Fusarium* were made in 1948. Ten Picardy corms, each approximately three-fourths inch in diameter, were used for each isolate. Planting was done March 1. All corms produced new plants. By April 19, yellow leaves indicated disease in some of the plants. New corms were examined August 5. Symptoms produced by the different isolates and the numbers of corms affected are shown in table 18.

Tests in 1952.—Twenty isolates of *Fusarium* were tested in 1952 for pathogenicity on the varieties Dr. F. E. Bennett, Margaret Fulton, Picardy, and Variation. Ten commercial size No. 5 (one-half to three-fourths inch in diameter) corms of each variety were used with each isolate. Three groups of checks, each consisting of 10 corms of each variety, were used in this experiment.

Planting was done on February 21 and 22. Differences in reaction of the four varieties to some of the isolates were quite pronounced by April 14, figs. 20 and 21.

The new corms were dug July 24; they were cleaned and examined August 13. They were then placed in a refrigerator at 5 degrees C. and left until November or December, when isolations from the affected corms were attempted.

Fig. 20.—Differences in reaction of, left to right in each picture, gladiolus varieties Dr. F. E. Bennett, Margaret Fulton, Picardy, and Variation to basal dry rot isolate 49-20 and vascular isolates 49-4 and 50-6 of *Fusarium*. Photographs were taken 52 days after planting date.

Results obtained in these tests are shown in tables 19, 20, 21, and 22. In the cases of the Dr. F. E. Bennett and Picardy varieties, the results cannot be considered conclusive, because disease symptoms developed in some corms of the checks. *Fusarium* was isolated from two corms of the Dr. F. E. Bennett checks. This finding

Fig. 21.—Differences in reaction of, left to right in each picture, gladiolus varieties Dr. F. E. Bennett, Margaret Fulton, Picardy, and Variation to four brown rot isolates of *Fusarium*. Photographs were taken 52 days after planting date.

indicated that the planting stock carried some *Fusarium*; so all of the symptoms that developed in the new corms probably did not result from the inoculations.

In the variety Picardy, five of the check plants died before reaching maturity and seven new corms had vascular discoloration. *Fusarium* was not isolated from any of these new corms. *Curvularia* sp. was isolated from four of them and *Penicillium* sp. was isolated from the other three. These two organisms appeared also in some isolations from corms in the inoculated series.

In the variety Variation, vascular discoloration developed in one corm; four corms of the 29 in the checks had slight basal rot lesions. Isolations from four of these affected corms yielded *Penicillium*; no organism was obtained from the fifth corm.

All plants from noninoculated Margaret Fulton corms remained healthy and produced healthy daughter corms. *Fusarium* was recovered from diseased corms in the inoculated series 36 times in 52 attempts.

Tests in 1953.—Varieties Dr. F. E. Bennett, Margaret Fulton, Spotlight, and Elizabeth the Queen were inoculated late in 1952 with 13 isolates of *Fusarium*. Size No. 4 (three-fourths to 1 inch in diameter) corms of the variety Elizabeth the Queen and large cormels of the other three varieties were used in this test. Treating and planting was done December 29, 1952. New corms were harvested June 5, 1953; they were cleaned and examined 2 weeks later.

In this trial, because no disease was found in the new corms produced in the noninoculated checks, and because only one Dr. F. E. Bennett and one Spotlight plant failed to live and produce new corms, it was assumed that the planting stock was practically free of disease. Cause of death

Table 19.—Results of greenhouse tests on gladiolus variety Dr. F. E. Bennett inoculated with *Fusarium*, February, 1952; new corms were examined in August of the same year.

Isolate	Plants Developed	Number of New Corms Obtained					Fusarium Recovered*
		Total	Healthy	Brown Rot	Vascular Discoloration	Basal Dry Rot	
Brown rot 45-8	10	9	2	0	7	0	3/8
Brown rot 45-74	10	8	8	0	0	0	0/0
Brown rot 47-1	9	0	0	0	0	0	0/0
Brown rot 47-12	8	0	0	0	0	0	0/0
Brown rot 47-32	10	5	0	0	5	0	5/5
Brown rot 49-8	10	10	4	0	6	0	1/5
Brown rot 50-7	10	8	6	0	2	0	2/2
Brown rot 50-22	7	0	0	0	0	0	0/0
Total	*74*	*40*	*20*	*0*	*20*	*0*	*11/20*
Vascular 45-73	10	6	0	0	6	0	3/4
Vascular 46-3	10	1	0	0	1	0	1/1
Vascular 46-9	10	10	0	0	10	0	0/0
Vascular 47-10	10	10	2	0	8	0	5/5
Vascular 49-4	9	0	0	0	0	0	0/0
Vascular 49-23	10	10	7	1	2	0	1/1
Vascular 50-6	8	0	0	0	0	0	0/0
Vascular 50-24	10	10	7	1	2	0	0/3
Vascular 50-28	10	5	0	0	5	0	0/0
Total	*87*	*52*	*16*	*2*	*34*	*0*	*10/14*
Basal dry rot 49-20	10	4	1	0	3	0	1/2
Basal dry rot 50-23	10	10	3	1	6	0	4/5
Basal dry rot 50-26	10	10	6	0	4	0	3/5
Total	*30*	*24*	*10*	*1*	*13*	*0*	*8/12*
Check No. 1	10	9	7	0	2	0	1/3
Check No. 2	10	10	7	0	3	0	1/3
Check No. 3	10	10	9	0	1	0	0/1
Total	*30*	*29*	*23*	*0*	*6*	*0*	*2/7*

*The numerator indicates the number of successful isolations, the denominator the number of corms from which isolations were attempted.

of the two nonsurviving check plants was not determined. As the results of this test are considered more conclusive than those of the previous test, they are given in detail by isolates and varieties.

Brown rot isolate 47-12

DR. F. E. BENNETT: Only 3 plants emerged; none produced a new corm.

MARGARET FULTON: 8 plants emerged; 1 survived and produced a new corm, which had thin basal rot.

SPOTLIGHT: 5 plants emerged; 4 survived and produced new corms, 3 of which had much of the bases rotted, but the rotted tissue was very thin. There was some vascular streaking, but it was not general. One corm showed no symptoms. *Fusarium* was recovered from all 3 affected corms.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms. Four of the new corms were badly decomposed; 6 had typical brown rot lesions. Of these 6 corms, 1 had numerous brown vascular strands; another had a single brown vascular strand in addition to the brown rot lesions. *Fusarium* was recovered from all 6 corms.

Brown rot isolate 47-32

DR. F. E. BENNETT: 6 plants emerged; 5 survived and produced new corms, all of which had core rot and brown vascular streaks. *Fusarium* was recovered from all 5 corms.

MARGARET FULTON: 10 plants emerged; all survived and developed new corms. Two corms had thin basal rot lesions; 8 showed no symptoms. *Fusarium* was not recovered from the affected corms.

SPOTLIGHT: 5 plants emerged; 7 survived and produced new corms, all of which had diffused basal lesions. There was no vascular discoloration. Cultures were made from 3 corms, and *Fusarium* was recovered from each corm.

Table 20.—Results of greenhouse tests on gladiolus variety Margaret Fulton inoculated with *Fusarium*, February, 1952; new corms were examined in August of the same year.

Isolate	Plants Developed	Number of New Corms Obtained					Fusarium Recovered*
		Total	Healthy	Brown Rot	Vascular Discoloration	Basal Dry Rot	
Brown rot 45-8	10	10	10	0	0	0	0/0
Brown rot 45-74	10	10	9	0	1	0	0/0
Brown rot 47-1	10	5	0	0	5	2	4/5
Brown rot 47-12	10	1	0	0	1	0	0/1
Brown rot 47-32	10	10	6	0	4	3	1/3
Brown rot 49-8	10	10	8	0	2	0	1/3
Brown rot 50-7	10	10	10	0	0	0	0/0
Brown rot 50-22	10	4	1	1	2	0	1/2
Total	*80*	*60*	*44*	*1*	*15*	*5*	*7/14*
Vascular 45-73	10	10	10	0	0	0	0/0
Vascular 46-3	10	9	3	0	6	0	3/4
Vascular 46-9	10	10	9	0	1	0	1/1
Vascular 47-10	10	10	9	0	1	0	1/1
Vascular 49-4	10	2	0	0	2	1	1/2
Vascular 49-23	10	10	10	0	0	0	0/0
Vascular 50-6	10	10	1	0	9	0	6/9
Vascular 50-24	10	10	7	0	3	0	0/4
Vascular 50-28	10	10	0	0	10	0	10/10
Total	*90*	*81*	*49*	*0*	*32*	*1*	*22/31*
Basal dry rot 49-20	10	10	0	0	10	0	5/5
Basal dry rot 50-23	10	10	8	0	2	0	2/2
Basal dry rot 50-26	10	10	10	0	0	0	0/0
Total	*30*	*30*	*18*	*0*	*12*	*0*	*7/7*
Check No. 1	10	10	10	0	0	0	0/0
Check No. 2	10	10	10	0	0	0	0/0
Check No. 3	10	10	10	0	0	0	0/0
Total	*30*	*30*	*30*	*0*	*0*	*0*	*0/0*

*The numerator indicates the number of successful isolations, the denominator the number of corms from which isolations were attempted.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms, 7 of which had very thin small lesions at the sides of the core bases. *Fusarium* was recovered from 2 of 4 corms cultured.

Brown rot isolate 50-7

DR. F. E. BENNETT: 8 plants emerged; all survived and produced new corms. All new corms had thin basal rot lesions. *Fusarium* was recovered from 2 of 5 corms cultured.

MARGARET FULTON: 10 plants emerged; all survived and produced new corms. No disease symptoms developed.

SPOTLIGHT: 10 plants emerged; all survived and produced new corms. Nine of the new corms appeared to have thin basal rot lesions developing when the corms were cleaned, but the symptoms were not distinct. The corms were placed in an incubator at 26 degrees C. and left for 15 weeks. The lesions did not develop further, and attempts to recover the *Fusarium* from these corms failed.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms, 9 of which had no disease symptoms. The remaining corm had a diffused basal rot lesion spreading halfway up the side of the corm. *Fusarium* was recovered from this lesion.

Brown rot isolate 50-22

DR. F. E. BENNETT: 6 plants emerged; 5 survived and produced new corms. Four of the new corms had typical thick brown rot lesions. One corm also had brown vascular strands. *Fusarium* was recovered from all 4 affected corms. One corm had no disease symptoms.

MARGARET FULTON: 10 plants emerged; 8 survived and produced new corms. Seven of the new corms had brown rot lesions on the bases and sides. Four

Table 21.—Results of greenhouse tests on gladiolus variety Picardy inoculated with *Fusarium*, February, 1952; new corms were examined in August of the same year.

Isolate	Plants Developed	Number of New Corms Obtained					Fusarium Recovered*
		Total	Healthy	Brown Rot	Vascular Discoloration	Basal Dry Rot	
Brown rot 45-8	9	1	0	0	0	1	0/0
Brown rot 45-74	10	3	2	1	0	0	1/1
Brown rot 47-1	6	1	0	0	1	1	0/1
Brown rot 47-12	4	0	0	0	0	0	0/0
Brown rot 47-32	10	2	0	0	0	2	0/0
Brown rot 49-8	10	9	6	0	3	0	2/6
Brown rot 50-7	10	2	2	0	0	0	0/1
Brown rot 50-22	7	1	0	1	0	0	1/1
Total	*66*	*19*	*10*	*2*	*4*	*4*	*4/10*
Vascular 45-73	10	9	3	0	6	0	6/6
Vascular 46-3	10	3	0	0	3	0	0/3
Vascular 46-9	10	10	10	0	0	0	0/0
Vascular 47-10	10	9	8	0	1	0	0/1
Vascular 49-4	7	0	0	0	0	0	0/0
Vascular 49-23	10	8	6	0	0	2	0/4
Vascular 50-6	10	9	5	2	2	0	0/4
Vascular 50-24	10	6	1	0	0	5	1/4
Vascular 50-28	9	8	1	0	7	0	7/7
Total	*86*	*62*	*34*	*2*	*19*	*7*	*14/29*
Basal dry rot 49-20	10	5	4	0	1	0	1/3
Basal dry rot 50-23	10	3	0	0	2	1	0/2
Basal dry rot 50-26	10	2	0	0	0	2	1/1
Total	*30*	*10*	*4*	*0*	*3*	*3*	*2/6*
Check No. 1	10	8	5	0	3	0	0/3
Check No. 2	10	8	4	0	4	0	0/3
Check No. 3	10	9	9	0	0	0	0/4
Total	*30*	*25*	*18*	*0*	*7*	*0*	*0/10*

*The numerator indicates the number of successful isolations, the denominator the number of corms from which isolations were attempted.

corms were cultured, and *Fusarium* was recovered from each of them. One corm remained healthy.

SPOTLIGHT: 10 plants emerged; 6 survived and produced new corms. Three of the new corms were completely mummified at cleaning time. One corm was three-fourths rotted; another contained a discolored vascular strand but had no external symptoms. *Fusarium* was recovered from the rotted corm but not from the discolored vascular strand. One corm remained healthy.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms. Two of the new corms were mummified at cleaning time, the other 8 had no disease symptoms. No attempt was made to recover the *Fusarium*.

Vascular isolate 45-73

DR. F. E. BENNETT: 7 plants emerged; 5 survived and produced new corms. Two of the new corms had brown vascular strands; 3 had no symptoms. *Fusarium* was recovered from both of the affected corms.

MARGARET FULTON: 10 plants emerged; all survived and produced new corms. One corm had brown vascular strands; 9 had no symptoms. *Fusarium* was recovered from the affected corm.

SPOTLIGHT: 10 plants emerged; all survived and produced new corms. Three of the new corms had brown vascular strands; 7 remained healthy. *Fusarium* was recovered from 2 of the affected corms.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms. Eight of the new corms had extensive discolored vascular strands; 2 of them had thick brown rot lesions also. No connections between the brown rot lesions and the vascular streaks were found in any of the corms. *Fusarium* was recovered from all 8 of the affected corms. Two of

Table 22.—Results of greenhouse tests on gladiolus variety Variation inoculated with *Fusarium*, February, 1952; new corms were examined in August of the same year.

Isolate	Plants Developed	Number of New Corms Obtained					Fusarium Recovered*
		Total	Healthy	Brown Rot	Vascular Discoloration	Basal Dry Rot	
Brown rot 45-8	10	7	2	0	5	0	0/4
Brown rot 45-74	10	8	6	0	2	0	0/0
Brown rot 47-1	10	3	2	0	1	1	1/1
Brown rot 47-12	10	6	0	0	6	5	2/4
Brown rot 47-32	10	6	0	0	6	6	3/5
Brown rot 49-8	10	10	3	0	7	0	4/7
Brown rot 50-7	9	7	0	0	0	0	0/0
Brown rot 50-22	10	3	1	1	1	0	0/0
Total	*79*	*50*	*14*	*1*	*28*	*12*	*10/21*
Vascular 45-73	10	9	1	0	8	0	5/6
Vascular 46-3	10	10	7	0	3	0	0/3
Vascular 46-9	10	10	6	0	4	0	3/3
Vascular 47-10	10	10	10	0	0	0	0/0
Vascular 49-4	10	8	0	0	1	7	0/0
Vascular 49-23	10	10	10	0	0	0	0/0
Vascular 50-6	10	10	7	0	3	0	0/2
Vascular 50-24	10	10	8	0	1	1	0/1
Vascular 50-28	10	9	0	0	9	0	1/3
Total	*90*	*86*	*49*	*0*	*29*	*8*	*9/18*
Basal dry rot 49-20	10	10	10	0	0	0	0/0
Basal dry rot 50-23	10	9	7	0	2	0	0/2
Basal dry rot 50-26	9	7	3	0	0	4	0/2
Total	*29*	*26*	*20*	*0*	*2*	*4*	*0/4*
Check No. 1	10	9	9	0	0	0	0/0
Check No. 2	10	10	6	0	0	4	0/4
Check No. 3	10	10	9	0	1	0	0/1
Total	*30*	*29*	*24*	*0*	*1*	*4*	*0/5*

*The numerator indicates the number of successful isolations, the denominator the number of corms from which isolations were attempted.

the 10 corms had no visible symptoms of disease.

Vascular isolate 46-3

DR. F. E. BENNETT: 7 plants emerged; all survived and produced new corms. One of the new corms was mummified; 2 had basal core rot but no extensive vascular discoloration. Four of the corms remained healthy. *Fusarium* was recovered from both corms with core rot. Isolations were not attempted from the mummified corms.

MARGARET FULTON: 9 plants emerged; all survived and produced new corms. One had a thin basal rot lesion; 8 remained healthy. *Fusarium* was not recovered from the affected corm.

SPOTLIGHT: 10 plants emerged; all survived and produced new corms. None had disease symptoms.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms. All of the new corms remained healthy.

Vascular isolate 47-10

DR. F. E. BENNETT: 7 plants emerged; all survived and produced new corms. Three corms had thin basal core rot but no vascular discoloration. Four corms had no disease symptoms. *Fusarium* was recovered from 2 of the 3 affected corms.

MARGARET FULTON: 9 plants emerged; 8 survived and produced new corms. One had extensive discolored vascular strands; 7 remained healthy. *Fusarium* was recovered from the affected corm.

SPOTLIGHT: 10 plants emerged; all survived and produced new corms. All of the new corms remained healthy.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms. All of the new corms remained healthy.

Vascular isolate 49-4

DR. F. E. BENNETT: 8 plants emerged; 7 survived and produced new corms. Two corms were mummified; 1 had a deep core rot extending to a thin lesion at the side of the core base. Three corms had deep core rot but no extensive vascular discoloration. One corm remained healthy. *Fusarium* was recovered from 3 of the affected corms.

MARGARET FULTON: 9 plants emerged; all survived and produced new corms. Eight corms had thin basal rot. There was no vascular discoloration. Three corms were cultured, and *Fusarium* was recovered from all of them. One corm had no disease symptoms.

SPOTLIGHT: 10 plants emerged; 9 survived and produced new corms. At cleaning time 2 of the corms were mummified; 6 had thin basal rot. *Fusarium* was recovered from 5 of the 6 corms affected with basal rot.

ELIZABETH THE QUEEN: 10 plants emerged; 9 survived and produced new corms. Four of the new corms had thin basal rot. In 1 corm, the brown discoloration extended from the base into one vascular strand. *Fusarium* was recovered from 1 of the 4 affected corms.

Vascular isolate 50-24

Eight DR. F. E. BENNETT, 9 MARGARET FULTON, 10 SPOTLIGHT, and 10 ELIZABETH THE QUEEN plants emerged; all survived and produced new corms. No disease symptoms developed.

Basal rot isolate 47-2

DR. F. E. BENNETT: 10 plants emerged; all survived and produced new corms. One of the new corms had one brown vascular strand; another had very short discolored vascular streaks around the core. *Fusarium* was not recovered from the affected corms. Eight corms had no disease symptoms.

MARGARET FULTON: 10 plants emerged; 9 survived and produced new corms. All new corms remained healthy.

SPOTLIGHT: 8 plants emerged; all survived and produced new corms. Six corms had thin basal rot lesions, most of which chipped out when the corms were cleaned. One corm also had pronounced vascular discoloration. *Fusarium* was recovered from 3 of the affected corms. Two corms remained healthy.

ELIZABETH THE QUEEN: 10 plants emerged; all survived and produced new corms. All new corms remained healthy.

Basal rot isolate 47-3

DR. F. E. BENNETT: 7 plants emerged; all survived and produced new corms. All

7 corms had brown core bases; 5 of these corms had brown vascular strands also. *Fusarium* was recovered from all 7 corms.

Margaret Fulton: 10 plants emerged; all survived and produced new corms. Each of the corms had a thin, light brown discoloration around the core base. Only 1 corm had a discolored vascular strand. Three of the corms were cultured; *Fusarium* was recovered from all of them.

Spotlight: 10 plants emerged; all survived and produced new corms. One corm had a hard core base and pronounced vascular discoloration. Two other corms had lighter vascular discoloration. *Fusarium* was not recovered from these corms. Seven corms showed no symptoms of disease.

Elizabeth the Queen: 10 plants emerged; all survived and produced new corms. Four corms had typical thin basal rot lesions; 2 had discolored vascular strands but no basal rot lesions. *Fusarium* was recovered from 5 of the 6 affected corms. Four corms had no symptoms of disease.

Basal rot isolate 50-23

Dr. F. E. Bennett: 6 plants emerged; all survived and produced new corms. One corm had a thin basal rot lesion; 1 had a brown vascular strand in the top half of the corm. *Fusarium* was recovered from both affected corms. Four corms remained healthy.

Margaret Fulton: 10 plants emerged; 9 survived and produced new corms. Eight corms had thin brown discolorations over the core bases. In 1 corm the discoloration extended slightly beyond the core. One corm had no symptoms. Attempts to recover *Fusarium* failed with all 8 affected corms.

Spotlight: 10 plants emerged; all survived and produced new corms. Nine corms had typical thin diffused basal rot lesions. There was no vascular discoloration. *Fusarium* was recovered from 8 of the 9 affected corms. One corm remained healthy.

Elizabeth the Queen: 10 plants emerged; all survived and produced new corms. No disease symptoms developed in any of the plants or new corms.

Basal rot isolate 50-26

Dr. F. E. Bennett: 8 plants emerged; all survived and produced new corms. Seven corms had brown core bases. One corm also had a thick brown rot lesion on its side; 1 corm had a thin brown rot lesion on its side, and 1 corm had a brown vascular strand. One corm had no disease symptoms. *Fusarium* was recovered from 5 of the 7 affected corms.

Margaret Fulton: 9 plants emerged; all survived and produced new corms. Six corms had brown core bases; 3 had no symptoms. *Fusarium* was recovered from only 1 of the affected corms.

Spotlight: 9 plants emerged; 8 survived and produced new corms. Two of the corms were mummies; 6 had typical thin basal rot lesions. *Fusarium* was recovered from all 6 of these corms.

Elizabeth the Queen: 10 plants emerged; all survived and produced new corms. Two corms had very small, thin basal rot lesions. *Fusarium* was recovered from both corms. Eight corms had no disease symptoms.

Noninoculated checks: Three sets of checks consisting of 10 corms of each variety in each set were planted.

Dr. F. E. Bennett: 24 plants emerged; 23 survived and produced new corms. No disease symptoms developed.

Margaret Fulton: 29 plants emerged; all survived and produced new corms. No disease symptoms developed.

Spotlight: 29 plants emerged; 28 survived and produced new corms. No disease symptoms developed.

Elizabeth the Queen: 30 plants emerged; all survived and produced new corms. No disease symptoms developed.

Fusarium reisolates: The cultures that were recovered from the new corms agreed closely in growth type on Wellman's agar with the growth types of the respective isolates used for inoculation.

Variation in Virulence of Isolates.—Relative virulences of the isolates used in the greenhouse tests were rated numerically by means of disease indexes computed as follows: Values were assigned to the disease symptoms in the new corms and these values were applied in a modification of the formula used in determination of rot severity indexes in the laboratory tests. Complete decomposition of the corms was considered the most severe result of the disease and was assigned a value of 3. Brown rot and vascular symptoms were considered equal in severity and were assigned a value of 2. Thin basal dry rot was considered less severe and was given a value of 1. Absence of symptoms rated

Table 23.—Severity indexes (obtained by use of formula on page 496) for the disease produced by 20 isolates of *Fusarium* on four gladiolus varieties in greenhouse tests, 1952.*

Isolate	Variety				Average Disease Index
	Dr. F. E. Bennett	Margaret Fulton	Picardy	Variation	
45-8	56.1	0.0	92.6	63.3	53.0
45-74	20.0	6.7	76.7	33.3	34.2
47-1	100.0	90.0	94.4	80.0	91.1
47-32	80.3	36.7	86.7	80.0	70.9
49-8	40.0	13.3	30.0	46.7	32.5
50-7	33.3	0.0	80.0	30.0	35.8
50-22	100.0	80.0	95.2	76.7	88.0
45-73	80.0	0.0	50.0	63.3	48.3
46-3	96.7	50.0	80.0	20.0	61.7
46-9	66.7	6.7	0.0	26.7	25.0
47-10	53.3	6.7	16.7	0.0	19.2
49-4	100.0	96.7	100.0	50.0	86.7
49-23	20.0	0.0	26.7	0.0	11.7
50-6	100.0	60.0	36.7	20.0	54.2
50-24	20.0	20.0	56.7	10.0	26.7
50-28	33.3	66.7	63.0	70.0	58.2
47-12	100.0	96.7	100.0	70.0	91.7
49-20	80.0	66.7	56.7	0.0	50.8
50-23	46.7	13.3	86.7	23.3	42.5
50-26	26.7	0.0	86.7	43.3	39.2
Check No. 1	23.3	0.0	40.0	10.0	18.3
Check No. 2	20.0	0.0	46.7	13.3	20.0
Check No. 3	6.7	0.0	10.0	6.7	5.8

*Symptoms in all varieties except Margaret Fulton were due in part to organisms other than the isolates used for inoculation, as explained in the text.

Table 24.—Severity indexes (obtained by use of formula on page 496) for the disease produced by 13 isolates of *Fusarium* on four gladiolus varieties in greenhouse tests, 1953.

Isolate	Variety				Average Disease Index
	Dr. F. E. Bennett	Margaret Fulton	Spotlight	Elizabeth the Queen	
47-12	100.0	91.7	60.0	66.7	79.6
47-32	72.2	6.7	76.7	23.3	44.7
50-7	33.3	0.0	0.0	6.7	10.0
50-22	61.1	66.7	73.3	13.3	53.6
45-73	47.6	6.7	20.0	53.3	31.9
46-3	28.6	11.1	0.0	0.0	9.9
47-10	28.6	18.5	0.0	0.0	11.8
49-4	62.5	29.6	50.0	30.0	43.0
50-24	0.0	0.0	0.0	0.0	0.0
47-2	13.3	10.0	41.7	0.0	16.2
47-3	66.7	36.7	20.0	26.7	37.5
50-23	16.7	63.3	30.0	0.0	27.5
50-26	50.0	22.2	40.1	66.7	44.7
Check No. 1	0.0	0.0	0.0	0.0	0.0
Check No. 2	12.5	0.0	0.0	0.0	3.1
Check No. 3	0.0	0.0	10.0	0.0	2.5

a value of 0. The formula used was as follows:

$$\text{Disease index} = \frac{N_1 0 + N_2 1 + N_3 2 + N_4 3}{3t} \times 100$$

where N_1, N_2, N_3, N_4 = number of corms in each severity class

0, 1, 2, 3 = values assigned to severity classes

t = total number of corms counted

The disease indexes obtained from these calculations are shown in tables 23 and 24. The isolates varied in their effects on the test varieties, but the variations did not follow any definite pattern.

The results obtained in the inoculation tests show that an isolate does not always produce the same form of the disease. For example, in the 1953 tests, all three forms of the disease appeared in plants inoculated with isolates 47-32 and 50-26. In most cases, more than one disease form was obtained from inoculations with a single isolate. A summary of the disease forms produced in plants inoculated with the various isolates is given in table 25.

Although the same methods were not employed, these results are in general agreement with those obtained by McClellan (1948), who used mass culture isolates of *Fusarium* for inoculations on the Picardy and Dr. F. E. Bennett varieties. Some isolates caused a vascular rot, some a surface rot, and others caused a combination of symptoms. McClellan mentioned that the pathogenicity of isolates varied from year to year but he did not describe the nature of the variation.

DISCUSSION AND CONCLUSIONS

The occurrence of different forms of a single fungus in laboratory cultures has been reported by many workers in many parts of the world. The terms "variation," "saltation," "dissociation," "mutation," and "sectoring" have been used to designate this phenomenon.

Most of the studies of variations in the genus *Fusarium* have been made on the relation of pathogenicity to forms of growth. Most of the workers have reported that cultures of *Fusarium* vary between a type with abundant aerial growth and a type with all the mycelium appressed in the nutrient substrate. The type of culture having aerial mycelium generally has been found to be most pathogenic, the type having only appressed mycelium least pathogenic, but observers on this point have not agreed unanimously (Armstrong, MacLachlan, & Weindling 1940, Burkholder 1925).

Numerous attempts have been made to account for these variations, but none has been entirely satisfactory. Leonian (1929, 1932) considered different cultural forms merely as phases in an orbit of variation of a species. Hansen (1938) explained variability in many of the Fungi Imperfecti as a "dual phenomenon" resulting from a segregation of genetically different nuclei in a multinucleate mycelium. Hansen & Smith (1932) earlier concluded that variable forms of the Fungi Imperfecti may owe their instability to nuclear heterogeneity, and that this condition can be brought about by nuclei of one strain entering the cells of another strain through anastomoses, and that reassortment of diverse nuclei can be accomplished by such mechanisms as anastomosis and unequal cell division.

Anastomoses, or fusions, between the hyphae and between the germ tubes of various fungi have been described by other workers. Zeller (1926) found conjugating macroconidia of *Nectria sanguinea* (Sibth.) Fr. in sporodochia on apple bark. He observed some comparatively long conjugating tubes connecting cells of one spore with those of another. In each case the nucleus had migrated from one cell to the other, producing a binucleate condition. Also, Zeller saw conjugation between two cells of the same spore. He did not discuss the significance of these conjugations.

Dickinson (1932) studied hyphal fusions in *Fusarium fructigenum* (Fries) and *F. vasinfectum* (Atk.). In no case did he observe fusion between segments (cells) of a conidium and only once did he find fusion between two segments of adjacent conidia. He concluded that in these species saltation was due to mutation rather than to heterocaryosis or cytoplasmic inheritance.

That germinating spores of the gladiolus *Fusarium* anastomose was observed in the studies reported here, fig. 22, but cytological studies were not made and no specific attempt was made to relate this phenomenon to subsequent variation of the isolates. If, however, the interpretation of Hansen & Smith (1932) is correct, this phenomenon could account for the variants both in form of growth and in pathogenicity of the gladiolus *Fusarium*.

Miller (1945*a*, 1945*b*, 1946*a*, 1946*b*), in studies of the muskmelon-wilt *Fusarium* and other species, reported that when

Table 25.—Disease forms produced by 27 isolates of *Fusarium* in experiments performed in 1, 2, or 3 years.

Isolate	Disease Form From Which Original Isolate Was Obtained	Year		
		1948	1952	1953
45-73	Vascular	Vascular	Vascular	Vascular, brown rot
46-3	Vascular	Basal dry rot	Vascular	Vascular, basal dry rot
46-9	Vascular	None	Vascular	—
46-14	Vascular	None	—	—
47-6	Vascular	Basal dry rot	—	—
47-10	Vascular	—	Vascular	Vascular
49-4	Vascular	—	Complete rot, vascular, basal dry rot	Basal dry rot, vascular
49-23	Vascular	—	Vascular	—
50-6	Vascular	—	Complete rot, vascular, brown rot	—
50-24	Vascular	—	Basal dry rot, vascular, brown rot	None
45-8	Brown rot	Basal dry rot	Vascular	—
45-74	Brown rot	None	Vascular, brown rot	—
45-75	Brown rot	Complete rot	—	—
46-4	Brown rot	Basal dry rot	—	—
46-12	Basal dry rot	Basal dry rot	—	—
47-1	Brown rot	Complete rot	Complete rot, vascular, basal dry rot	—
47-12	Brown rot	Complete rot	Complete rot, vascular, basal dry rot	Complete rot, brown rot, vascular
47-32	Brown rot	Basal dry rot	Vascular, basal dry rot	Brown rot, vascular, basal dry rot
50-7	Brown rot	—	Complete rot	Basal dry rot, brown rot
50-22	Brown rot	—	Complete rot, brown rot, vascular	Brown rot, vascular
47-2	Basal dry rot	—	—	Basal dry rot, vascular
47-3	Basal dry rot	—	—	Basal dry rot, vascular
49-8	Brown rot	—	Vascular	—
49-20	Basal dry rot	—	Vascular	—
50-23	Basal dry rot	—	Vascular, basal dry rot, brown rot	Basal dry rot, vascular
50-26	Basal dry rot	—	Basal dry rot, vascular	Basal dry rot, brown rot, vascular
50-28	Vascular	—	Vascular	—

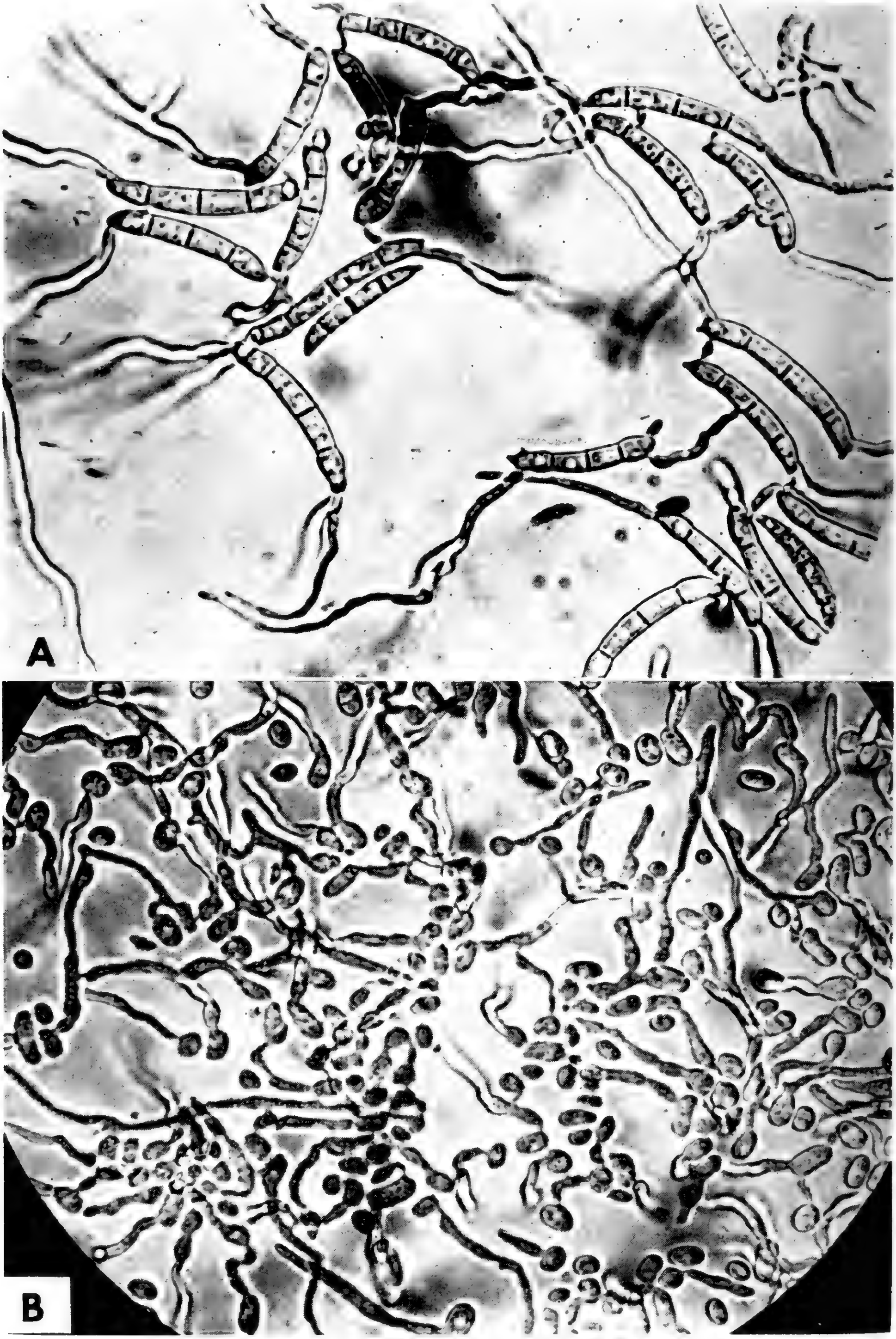

Fig. 22.—Anastomoses among germinating spores of the gladiolus *Fusarium*: *A*, macrospores; *B*, microspores.

monosporous isolations were made from an isolate derived from a diseased plant, all cultures were alike and of a form that produced abundant aerial mycelium on which conidia, mostly nonseptate, were borne rather sparsely. He called this form the wild type. Cultural variants that were derived from the wild type were considered to be laboratory mutants. Miller contended that the taxonomy of *Fusarium* should be based only on wild types and not on laboratory mutants.

The classification of Wollenweber & Reinking (1935) is based on the view that the macroconidia are the spore types on which species descriptions should be based and that those *Fusaria* which do not produce such spores when isolated from nature may be induced to do so by frequent cultural transfers. Such transferring gives rise to a cultural state characterized by abundant production of macroconidia, a condition that has been called "normal culture," "high culture," "Normkultur," and "Hochkultur." Miller contended that this method results in displacement of the wild type by mutants. According to Miller, most of the species descriptions appearing in the literature have been based on laboratory mutants rather than on natural types. Hence, he considered the classification of Wollenweber & Reinking unsatisfactory. The Snyder & Hansen (1940, 1941, 1945) revision disregards morphological criteria and places primary emphasis on the host relationship. Miller contended that this system also is unsatisfactory, stating that if proper cultural methods are employed the morphology of these organisms will be found sufficiently constant to warrant an attempt at morphological classification. He based this statement on two facts: (1) his original isolates were all of the raised type and (2) he was able to maintain this type by a soil culture technique in which the fungus was kept in a dried, inactive condition for long periods of time. From these two facts he concluded that variants of the types found in laboratory cultures do not occur in nature, or at least that variants are very rare. These conclusions do not agree with the report of Orton (1935), who found that several strains of *Fusarium niveum* Smith may change as readily in soil as upon laboratory media.

While an extensive study of the occurrence of changes in culture form of the gladiolus *Fusarium* was not made by the writer, such changes were observed, table 10. Since the raised, appressed, and intermediate forms were obtained in original isolations of the gladiolus *Fusarium*, it must be assumed that all of these forms occur in nature and that the wild types of this fungus are not all of one form.

The main object of this investigation was to determine if strains of *Fusarium* obtained from gladiolus corms having different disease symptoms could be fitted into well-defined groups on the basis of their pathogenicity and physiological characters. The isolates used in these studies do not fall into well-defined groups. Also the pathogenicity tests show that a single isolate is capable of producing more than one form of disease. Evidence obtained in the other tests in this investigation shows that the strains of the gladiolus *Fusarium* are extremely variable and some apparently are quite unstable. No definite pattern for association of the many variables could be determined; the variations seem to occur independently.

It was not intended that this paper should enter the controversy on the relative merits of the two available systems of classifying *Fusaria*. But, as both systems have been used in previous studies of the Fusarium disease of gladiolus, and at least two specific names under one system have been used for strains of the fungus associated with different forms of the disease, it becomes necessary to take a definite stand regarding the nomenclature and taxonomy of the gladiolus *Fusarium*. Since this investigation failed to establish the existence of well-defined strains of a *Fusarium* associated with the different forms of the disease, it seems most logical to regard all variants as members of a single species. Because the system of Snyder & Hansen is better suited for classification of this type of organism, it is proposed that all forms of the gladiolus *Fusarium* be included under the name *Fusarium oxysporum* f. *gladioli* (Massey) Snyder & Hansen.

SUMMARY

Three forms of the Fusarium disease of gladiolus, known as the vascular, brown rot, and basal dry rot forms, have been described by other workers. The agent or agents which cause these disease forms have been assigned various specific names, with the result that the exact relation of the different symptom types and their causal agent or agents has been in a state of confusion.

The purpose of this investigation was to rectify the confusion by determining if strains of *Fusarium* producing different symptoms could be fitted into well-defined groups on the basis of their pathogenicity and physiological characters.

From several hundred isolates of *Fusarium* that had been cultured from diseased gladiolus corms, 40 isolates were selected for comparison in pathogenicity tests and physiological studies. Comparisons of isolates from the three disease forms were made by means of their reactions to temperature, reactions to aniline dyes, reactions to copper salts, reactions to mercuric chloride, color reactions on steamed rice, growth types on differential media, pH changes produced in liquid media, spore measurements, and tendency to reproduce the same or different disease forms in inoculated plants and corms.

The isolates varied a great deal in their reactions in these tests, but no definite pattern for association of variables could be determined; the variations seemed to occur independently. The isolates did not fall into well-defined groups; the isolates from the three disease forms could not be distinguished by any of the tests used. The pathogenicity tests showed that a single isolate is capable of producing more than one form of the disease.

The evidence obtained in these studies shows that strains of the gladiolus *Fusarium* are extremely variable and that some of them apparently are quite unstable. It is proposed that all forms of the gladiolus *Fusarium* be included under the name *Fusarium oxysporum* f. *gladioli* (Massey) Snyder & Hansen.

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INDEX

The following index covers Articles 2, 3, 4, 5, and 6 of Volume 26 of the ILLINOIS NATURAL HISTORY SURVEY BULLETIN. An index of Article 1, *The Mayflies, or Ephemeroptera, of Illinois,* by B. D. Burks, begins on page 211 of this volume. Indexing of Articles 2, 3, 4, 5, and 6 has been limited for the most part to the names of birds, fish, insects, mammals, and plants mentioned in the articles. In most cases, the singular form of the word has been used in the index, even though the plural form has been used in the text, as *fungus* for both *fungus* and *fungi.* Place names have not been indexed.

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