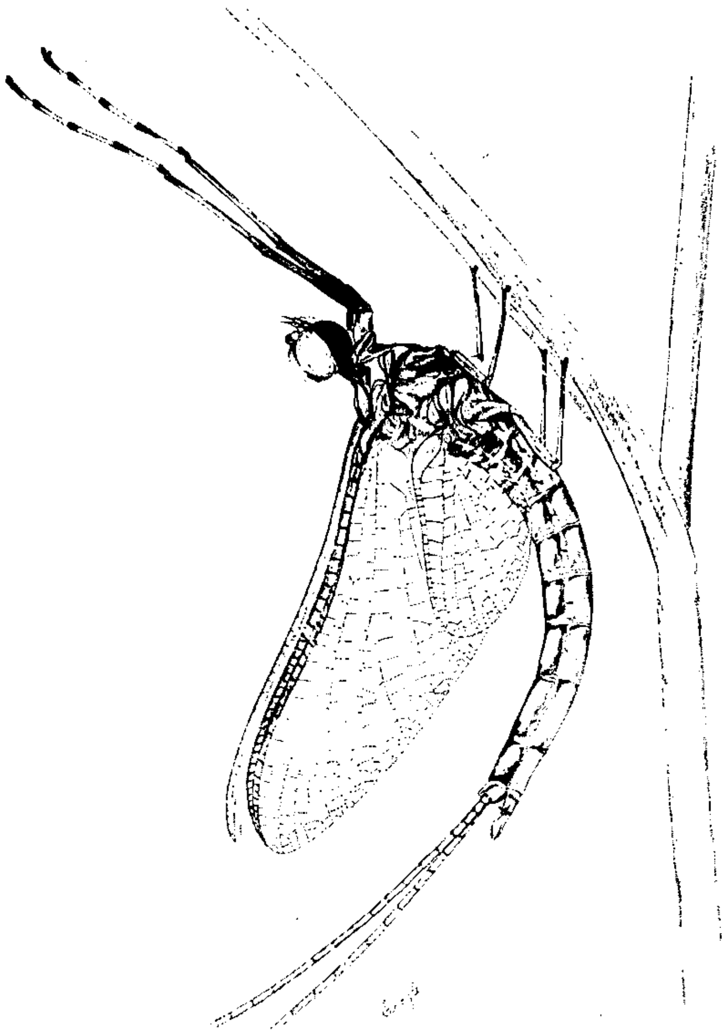
THE MAYFLIES OF FLORIDA

Revised Edition



Hexagenia orlando Traver, male imago

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Revised Edition

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University of Florida
and
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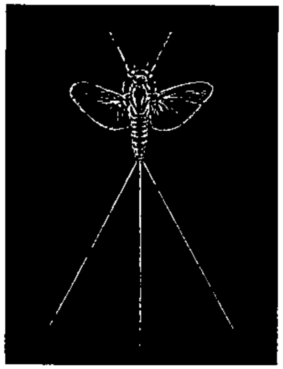

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TO DR. WILLIAM L. PETERS,
whose encouragement
stimulated us to undertake
this revision

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PREFACE

When the original edition of this book had reached the grand age of nearly thirty years, Bill Peters began needling me about preparing an updated revision to incorporate the many new findings. I toyed with the idea but balked at the work involved; however, I told him that when I retired, I would seriously consider undertaking the task. As I began working toward the project, it became obvious that I needed help; and so I recruited Manny Pescador to be coauthor of the revision.

In all, we devoted nearly three years to the revising and rewriting of the 1950 edition. Many sections were completely rewritten; the retained parts were updated where necessary. New keys to adults and nymphs were prepared. Under each taxonomic heading we have included chiefly those references published since 1950 when the original edition of *The Mayflies of Florida* appeared. However, our list of publications includes all papers or books mentioned in the text. Many new drawings were made. Where appropriate, we borrowed illustrations or diagrams from other authors. The format for treating species is much the same as in the original edition except that we have omitted detailing specific locality records. Instead, we have listed Florida counties from which specimens have been taken, and we have included new maps to show more clearly where a specific form occurs.

Many people have contributed in ways too numerous to mention. There are special ones, however, to whom we would like to call attention. Particularly, we are most grateful to Dr. William L. Peters, who allowed us free access to the excellent mayfly collections of Florida A & M University; Janice G. Peters and Ralph W. Flowers for helpful suggestions and valuable comments on the keys; Dr. Michael Hubbard for assistance with literature; Jerome Jones for his help in many ways; and Evelyn Sellars for secretarial assistance. All of these people are associated with Florida A & M University. A research grant (Flax 79009 and 85007) from CSRS, USDA, to Florida A & M University supported Manuel L. Pescador's research efforts in preparing this book.

Mr. Richard Cantrell, Florida Department of Environmental Regulation, provided his records of mayflies from southwestern Florida to help flesh out information about the insects in that region. Dr. Richard K. Allen allowed us to use some of his excellent illustrations, and Dr. George F. Edmunds, Jr., gave us free access to his illustrations as well. Dr. W. P. McCafferty generously allowed us to reproduce a table and diagram from one of his papers, and Dr. Boris Kondratieff furnished copies of his drawings of *Isonychia* structures. Dr. Tomas Soldán's paper on *Brachycercus* served as the source of drawings for that genus and for *Cercobrachys*. To these persons, Manny and I express our sincere gratitude.

A small grant from the Southern Regional Education Board provided financial help that supported three trips from Gainesville to Tallahassee. These visits offered us the opportunity to study the Florida A & M collections together and to plan the details of this monograph. We are grateful to the board for its help in our study.

The Department of Zoology of the University of Florida has provided so much assistance that without it this revision would not have been undertaken. The staff artists, Paloma Ibarra and Daryl Harrison, were most helpful in preparing maps, drawings, and plates. Mrs. Grace Kiltie was superb in her attention to detail while transcribing the manuscript onto a word processor. Her keen eyes detected inconsistencies and spelling errors, and her typing was impeccable. We are most grateful to her for her dedicated work. Others among the zoology department secretarial staff who assisted in entering the manuscript into the word processor were Carol Binello, Dawn Vallejos-Nichols, Alice McClaughry, and Janice Zeigler. We thank all of them.

The staff of the University Presses of Florida have been exceptionally cooperative in bringing this revision to fruition. Their attention to detail and their continued interest in this project over several years are reflected in the final product.

LEWIS BERNER

PREFACE TO THE FIRST EDITION

The present investigation was begun in 1937 after it was learned that almost nothing was known of mayflies in Florida. It was soon apparent that the study of these insects was far more complex than first appeared and that relatively few of the species inhabiting the state were recorded in the literature. As the insects became better known, wider vistas were opened and facets of the problem, which previously were only faint shadows, now began to manifest themselves. The real task soon became clear—it would consist of several phases, chiefly identifying those species of Ephemeroptera occurring in Florida, mapping their distribution, studying their ecology and habits, and learning as much as possible of their life histories. In all, seven years were devoted to this endeavor, in the course of which nearly all of Florida was covered, about fifty thousand specimens were collected and examined, numerous species of mayflies were reared, and much ecological information was obtained.

This work is an attempt to bring together all available data on Florida mayflies so that future students of the Ephemeroptera will have available a ready source of information on the group as it occurs in this southernmost extension of the Coastal Plain of the United States. Perhaps the material included here may serve as a starting point for some of the many problems still confronting the fresh-water biologist in Florida.

I wish to express my sincere appreciation to the many people who have helped in one way or another in this study. In particular, I should like to thank Professor T. H. Hubbell, of the University of Michigan, for his continual encouragement in this work, for many helpful criticisms, and for examination of the manuscript; Professor J. S. Rogers, also of the University of Michigan, whose aid, encouragement, and advice have been invaluable; and Professor H. H. Hobbs, of the University of Virginia, for numerous suggestions and discussions of the problem, aid in collecting, and help in preparing the illustrations. Various members of the faculty of the Department of Biology of the University of Florida have offered many suggestions and participated in discussions which have been very elucidating.

To the many friends who have collected mayflies for me, I wish to express my gratitude. In particular, Dr. H. H. Hobbs, Dr. F. N. Young, Dr. L. J. Marchand, and Mr. W. A. McLane have assiduously collected all ephemerids with which by chance or otherwise they have happened to come in contact.

All half-tone illustrations were prepared by Miss Esther Coogle, Staff Artist, Department of Biology, University of Florida, who spent countless hours perfecting techniques and laboring over the drawings. She was also most helpful in preparing the line drawings for publication by eradicating the discoloration caused by storage during my period of service in the army. Mr. William Brudon, Staff Artist, Museum of Zoology, University of Michigan, illustrated the distribution of mayfly nymphs on a rock.

The staff of the University of Florida Press has worked diligently in helping me get the manuscript in final form for publication. Dr. Lewis F. Haines, Director of the Press, has done a most careful job of editing the paper. Miss Penelope Griffin has read and reread the manuscript many times in an attempt to eradicate any possible discrepancies that may have crept into the writing. To these two people in particular, and to the other members of the Press staff, I should like to take this means of expressing my gratitude.

And finally, I wish to thank Dr. F. P. Ide, of the University of Toronto, Dr. H. T. Spieth, of the College of the City of New York, and Dr. J. R. Traver, of the Massachusetts State College, for examining and verifying identifications of many of the Florida species of mayflies.

LEWIS BERNER

University of Florida
October 1, 1949

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INTRODUCTION

When the first edition of this book was published, one of us (Berner) wrote: "Few orders of insects have been so little studied in Florida as the mayflies, or Ephemeroptera." The great upsurge in environmental studies changed this so that now it is possible to say that one of the best known orders of insects in Florida is the Ephemeroptera. Following World War II, there was a rapid expansion of the academic institutions in the state and an increase in the number of faculty and graduate students who devoted attention to the aquatic environment. The resultant studies revealed hitherto unknown dimensions in the size of the mayfly fauna, especially in northwestern Florida, where it was learned that only 70 percent of the insects were previously known. As more detailed investigations are undertaken in the panhandle, even more species will probably be discovered in some of the more remote and less accessible areas of the state.

Although the Ephemeroptera include no enemies of agriculture and therefore at first glance appear to have little or no economic importance, such an impression is altogether erroneous. The entire economy of aquatic life is intimately bound up with the presence and abundance of mayflies, and it has been demonstrated time and again that these insects, in both immature and adult stages, constitute an important item in the diet of many species of fish or of other organisms that are eaten by fish. The words of the late Dr. Frison (1935, pp. 284–285) apply with particular force to the study of ephemerids today:

> The insect life of our inland streams (and lakes) affords a most interesting and profitable field for investigation; and the sooner we learn to place and evaluate this fauna correctly, the sooner we will be in a position to formulate conclusions and generalizations of importance in our efforts to understand our aquatic resources and to forward their intelligent use.

In his *Travels* (1791), William Bartram beautifully describes the life and mating of the mayflies along the St. Johns River. Nearly 60 years passed before Ephemeroptera were again noted in the state, when Francis Walker (1853) described the tiny *Caenis diminuta* from the St. Johns Bluff on the St. Johns River. Not until 1900 was the group once more reported from Florida; in that year Dr. Nathan Banks described a new species, *Callibaetis floridanus*, from southern Florida. In 1931 the late Dr. J. R. Traver described *Hexagenia weewa* (*H. limbata*) and *Hexagenia orlando* from the state. *Oreianthus* sp. no. 1 (*Neoephemera youngi*) was recorded from Florida by Dr. Traver in 1935, and in 1937 she gave a full description of the nymph. Subsequently, with the increased interest shown in aquatic insects, other species were found and described, but during the years of World War II, work with such insects, other than mosquitoes, virtually ceased. Following the cessation of hostilities and with the population surge that occurred in the state and the concomitant growth in universities and environmental concerns, research related to aquatic environments and the organisms inhabiting them experienced a major revival of interest. Reflecting this growth, this edition will be concerned with 71 species of mayflies, 23 more than were treated in the earlier edition.

The Biology of Mayflies by J. G. Needham, J. R. Traver, and Yin-Chi Hsu summarized the knowledge of North American mayflies occurring north of Mexico up to 1935. This book provided a stimulus to a few workers, but the real growth of knowledge of this insect order did not occur until well into the 1950s. Many new and younger workers began to study these fragile but interesting insects, and with their publications there was a virtual explosion of knowledge concerning them. The most recent treatment of New World forms is found in *The Mayflies of North and Central America*, by G. F. Edmunds, Jr., S. L. Jensen, and L. Berner (1976). Species identification is still a difficult undertaking, and the newer book does not include keys at that level. The serious student must still return to the Needham, Traver, and Hsu volume or to subsequent revisional papers treating certain genera for aid in identification beyond the generic level. The most recent effort to bring together information that helps to identify mayfly immatures is that of J. D. Unzicker and P. H. Carlson, published in 1982 as a part of the volume *Aquatic Insects and Oligochaetes of North and South Carolina*, edited by A. R. Brigham, W. U. Brigham, and A. Gnilka. The keys in this volume are of only limited value in identifying Florida mayfly nymphs; however, they do include about 70 percent of the Florida species, those that are also found in the Coastal Plain habitats of South and North Carolina.

With increased emphasis on ecological investigations in recent years, mayfly immatures have taken their rightful place as important animals to be studied in evaluating human impact on natural environments. Environmental studies in which these insects have been key elements in evaluating pre- and postdisturbances have grown in number exponentially. At the same time, interest in taxonomic, phylogenetic, and distributional studies has also grown. Ecologists recognize the importance of specific identification of the organisms they are working with; as a result, the encouragement of taxonomic studies has led to a much firmer and more logical system than was formerly available.

With the recognition of the importance of aquatic insects to freshwater environments, emphasis has been placed on life histories and differentiation of the immature stages. Mayflies spend almost all their life as aquatic insects, and it is in the immature stage that the mayfly is important in the economy of fresh waters.

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THE ORDER EPHEMEROPTERA

The order Ephemeroptera is a natural grouping of primitive, pterygote insects. In general, the forewings are delicate, membranous, and triangular in outline; they usually have intercalary veins as well as many crossveins. The hind wings are much smaller than the forewings and may sometimes be wanting. The wings are normally held vertically over the back when the insects are at rest. The mouthparts of the adult are vestigial, and the alimentary tract has undergone modifications fitting it as an aerostatic organ. There are 10 abdominal segments, and from the posterior end of the abdomen either two or three caudal filaments arise. The immatures are aquatic and undergo a hemimetabolous development. The mouthparts of the nymphs are usually well developed for chewing. They have two or three caudal filaments, and gills are present on certain of the abdominal segments. Mayflies are the only insects that molt after they have attained functional wings; prior to this final molt they are spoken of as subimagoes. Although the extra subimaginal molt facilitates further changes in body form, Snodgrass (1954) and Schaefer (1975) still considered it to be a nonadaptive relict trait. Recently, the subimaginal molt of mayflies has been considered to be analogous to the pupal molt of holometabolous insects. According to Maiorana (1979), the pattern of retention or loss of the subimaginal molt in extant mayflies suggests that this molt may be necessary to complete elongation of caudal filaments and forelegs of adults.

The imago, or final adult form, in most instances can be easily differentiated from the subimago by several characteristics. The wings of the

subimago are dull and grayish, whereas those of the adult are normally glistening and iridescent; the hind margin of the wings of the subimago are ciliated, but those of the adult are usually bare; the body of the subimago is dull, and that of the adult is glossy; the forelegs of the subimago are relatively short, but in the imago they are much elongated, particularly in the male; the caudal filaments are somewhat hairy and relatively short in the subimago and usually lose this hairy condition when they elongate in the imaginal stage. Many of the males have divided compound eyes, which are less prominent and rather dull in the subimago and very prominent and glossy in the imago. The adult has nonfunctional mouthparts, and reduction to this condition has still not culminated during the subimaginal stage, as the mandibles, which are stunted and nonfunctional, are distinctly larger than they are in the imago.

The duration of the subimaginal stage varies from a few minutes to a few days. Temperature plays a decisive role. Pescador and Peters (1974) indicated that subimagoes of *Baetisca rogersi* lived for an average of 19 hours and 8 minutes when exposed at an average temperature of 79°F, while they survived for 24 hours and 9 minutes at an average temperature of 70°F. Under room temperatures (23°C–24°C), the subimaginal stage of *Neoephemera youngi* lasted from 12 to 16 hours (Jones 1977). The male subimagoes of *Dolania americana* have a brief adult life ranging from 12 to 15 minutes (Peters and Peters 1977).

Mayfly adults either have two caudal filaments, the cerci, and a vestige of a median terminal filament, or three caudal filaments—two cerci in addition to a fully developed median filament. The long caudal filaments, along with the forelegs, are reproductive adaptations of mayflies (Needham et al. 1935). The caudal filaments aid in the balance of the insect during flight, as a considerable share of the total drag of the body falls on the cerci and prevents the adult from the drifting that even a very light wind during swarming can cause (Brodskii 1973). Behavioral and electrophysiological experiments have shown that the principal function of the cerci of contemporary insects is sensory. In mayflies the long caudal filaments associated with the control of flight have giant axons, which provide considerable information at high speed from the cerci to the ganglia of the thoracic segments (Brodskii 1973). The long forelegs of the males play an essential part in the coupling of males and females during mating (Brinck 1957).

The eggs of nearly all mayflies (*Callibaetis* and *Cloeon* are ovoviviparous) are laid in fresh water, where varying periods are required for their development. Mayfly eggs are characterized by their attachment structures, micropyles, and chorionic sculpturings (Koss 1968). As the term implies, attachment structures are devices that prevent the eggs from being washed downstream or carried to an unfavorable environment. The three basic types of attachment structures in mayfly eggs are polar caps, accessory attachment structures, and external adhesive layers. Polar caps are found on one or both poles of the egg, while accessory structures are suckerlike discs, plates, or threads that are connected to the lateral surfaces of the eggs. Some eggs have only external adhesive coatings, which swell on contact with water and become effective attachment devices. The micropylar device is composed of the micropyle, the actual opening for sperm entrance, and the sperm guide, which presumably facilitates the funneling of sperm into the micropyle. Chorionic sculpturing in mayfly eggs may be peglike, netlike, or rugose. The manner of sculpturing is sometimes useful as a characteristic serving to establish generic-level phylogenies (Koss and Edmunds 1974).

The freshly hatched nymphs possess no gills, but within one to three molts these structures make their appearance; the mouthparts, however, are all present, though generalized and simple in form. Soon the nymphs assume the body shape and structures that they retain over most of their nymphal life. In the few species for which the life history has been completely worked out, there are at least 12 preadult molts, and in most cases more than this number are thought to occur; some species may require as many as 45.

The nymphs of mayflies are morphologically and behaviorally adapted to their environments in many and various ways. They all have certain features in common, such as gills, caudal filaments, and chewing mouthparts, although a few species are now known to be carnivorous and lack a molar area on their mandibles. The burrowing species exhibit some of the most remarkable adaptive characteristics; in these nymphs the legs have become flattened digging structures—the forelegs are used for pushing the silt aside, the hind legs for passing it back out of the burrow. The frontal process of the head and the greatly elongated tusks, or rami, of the mandibles first encounter the silt or sand in the digging process, loosening it so that the legs may complete the task of excavation and removal of the material. The gills of these burrowers are feathery and thoroughly penetrated by tracheae, providing a particularly efficient mechanism for obtaining oxygen. Even the feeding habits have become modified to such an extent that these nymphs, much like earthworms, eat the organic materials encountered in their burrowing in addition to other materials filtered from water moving past their bodies. It has been reported that some *Ephemera* nymphs are also carnivorous. The fact that little sand is found in their digestive tracts indicates that they feed selectively.

Numerous other distinctive modifications of form and structure encountered among the nymphs that do not burrow are directly related to their behaviors and the habitats in which they normally live. Dodds and Hisaw (1924) have shown that nymphs living on the undersides of rocks in midstream in the relatively still boundary layer have flattened bodies, whereas those inhabiting the swiftest waters have fusiform or torpedo-shaped bodies. Others with rounded, streamlined bodies dwell in ponds, but here the ability to swim and dart about rapidly is correlated with the streamlined form. Fusiform body shape offers the least resistance to fluids, and the mayflies having the nearest form to this are *Baetis* nymphs, which also have pilose caudal filaments that can move rapidly up and down, making an efficient paddle (Einsele 1960). Flattened bodies occur mostly among the heptageniid nymphs and some of the ephemerellids and leptophlebiids. Usually the dorsoventrally compressed bodies are pressed close to the substrate, allowing the current to flow over the nymph, technically making the whole body a part of the substratum (Illies 1968). Flattened nymphs adhering to substrate surfaces are often better protected from predation. For example, the flattened, clinging *Rhithrogena hageni* were more difficult for the predatory stonefly, *Isogenoides elongatus* (Hagen), to capture than the rounded, swimming *Baetis tricaudatus* nymphs (Corkum and Clifford 1981). Some nymphs with flattened ventral surfaces have devices that make their bodies come in close contact with the substrate. Nymphs of *Drunella doddsi*, a species occurring in fast-flowing streams of western North America, have the ventral surface of the abdomen covered with a mat of hairs, which increase resistance and minimize the danger of the nymph's being lifted from its attachment by the current (Hynes 1970).

We have found that there is a definite correlation between claw size and habitat. The species that dwell in ponds and in very slow-flowing water have thin, attenuated claws, which lightly touch the object to which the insect is clinging but do not form a strong clamp. A nymph with such long claws would probably have difficulty in maintaining itself in a strong current, for the claws could scarcely have sufficient leverage to support the insect in this situation. Mayfly nymphs living in swifter currents have short, thick claws, which clamp firmly into the substrate on which the insect is living. The stronger the current, in general, the shorter and thicker the claws. Nymphs from rapids have very short, thick claws, often with strong teeth on the underside; in the genera *Dactylobaetis* and *Camelobaetidius* pectination has converted the tarsal claws into comblike, powerful grasping structures. For the most part, the size of the tarsal claws is fairly uniform within a genus, but this is not always so. In one genus, *Centroptilum*, there are two Florida species: *viridocularis*, which occupies slow-flowing water, and *hobbsi*, which inhabits swift-flowing water. In *viridocularis* the claws are three-fourths as long as their respective tarsi; in *hobbsi* the claws are only one-half as long as their respective tarsi. All *Baetisca* nymphs, however, have curved and sharply pointed claws, providing a firm grip to the substrate on which they are living. Prior to emergence, the *Baetisca* nymphs crawl from the water and cling to solid objects a few inches above the water surface. When the nymphal skins are lifted and removed, the legs are often broken, with the detached claws still firmly anchored to the object on which the nymphs have crawled. Nymphal claws of some mayfly species are believed to have a sensory function. Recently, it was suggested by Corkum and Clifford (1981) that the subapical setae on the claws of *Baetis bicaudatus* and *B. tricaudatus* nymphs are probably mechanoreceptors that may be used to detect subtle changes in water flow and thus assist in orienting the nymphs to the current. In addition, all species of *Baetis* with subapical setae on the nymphal claws have a reduced terminal filament and inhabit fast-flowing water.

The nymphal leg structure, even in the nonburrowers, is correlated with the habitat. Species inhabiting ponds and relatively quiet waters have rather elongated limbs that stand out from the body and hold it above the object to which the nymph is attached. Quite an exception are the long, spiderlike legs of the sand-dwelling, rheophilic nymphs of *Pseudiron*. When at rest, the legs of the nymphs are spread out and have the long, thick, girdled tarsal claws deeply buried in the sand. The sprawlers have shorter, thicker legs, the femora being somewhat broadened; the legs are held out horizontally from the body and do not serve to lift the insect much above the substrate on which it is crawling. The clingers of swift water have thickened, shortened legs with a correspondingly greater development of their muscles. Their legs are held horizontally, with the femora close to the body; the latter are thin along the anterior edge but relatively thicker posteriorly, thus presenting lessened resistance to the current.

Mayfly nymphs usually have seven pairs of abdominal gills, although some groups have fewer to none as in the Chilean genus *Murphyella*. The gills are undoubtedly involved in respiration but to what extent largely depends on nymphal habits. The burrowing nymphs of *Ephemera* and *Hexagenia* use their gills primarily for respiration, but among such free-swimming forms as *Baetis* and *Cloeon* the gills are mainly involved in the production of water currents over the abdomen so that respiration, which is a function of the body surface, can be accomplished. This was demonstrated experimentally when the gills of *Baetis* and *Cloeon* nymphs were removed, and it was found that oxygen consumption was the same as that of nymphs with intact gills, so long as an artificial water current equal to that provided by the excised gills was provided.

Nymphal gills of mayflies have chloride cells similar to those found in freshwater fish gills. The chloride cells, which vary from a single cell to groups of organized complex cells, are involved in osmoregulation in the nymphs, and it seems that their chief function is probably the absorption of electrolytes (Wichard and Komnick 1971).

The caudal filaments show special features in the freely swimming and darting mayfly nymphs. In these species, there is a great development of hairs medially from the cerci or lateral filaments and laterally from the median filament so that the hairs overlap to form a paddle. By rapidly flicking their abdomens and straightening their tails, the insects develop very efficient swimming organs enabling them to move rapidly through the water. Those species that swim little or not at all have a correspondingly small development of hairs on the caudal filaments, and in some of these nymphs the tails are almost bare. In addition to swimming, the caudal filaments are known to aid some nymphs to live in fast-moving waters. Hora (1930) surmised that the caudal filaments might reduce drag on nymphs exposed to current flow. *Baetis* nymphs with progressively shorter terminal filaments live in habitats with increasing current velocities (Dodds and Hisaw 1924; Hora 1930). Interestingly, the rheophilic nymphs of *Baetis bicaudatus* and *B. tricaudatus* exhibit different altitudinal distributions in a particular mountain stream. Ward and Berner (1980) showed that the two-tailed nymphs of *B. bicaudatus* live at high altitudes while the three-tailed *B. tricaudatus* have an upstream limit in St. Vrain Creek in Colorado of about 2400 meters. Similarly, the upper limit of *B. tricaudatus* nymphs in the Highwood River in the Rocky Mountain Forest of Alberta is 1500 meters, while *B. bicaudatus* was found at an altitude of 1735 meters (Corkum and Clifford 1981). It has also been suggested, but not proved, that the caudal filaments of some mayfly nymphs are respiratory organs (Popovici-Baznosanu 1906). Corkum and Clifford (1981) suggested that since *Baetis* nymphs with a reduced terminal filament are found in rather specific habitats (altitude and latitude), gradual reduction of the appendage may be a response to lower respiratory demands in the cooler, fast-flowing waters.

PRIMITIVE AND SPECIALIZED CHARACTERS. It is frequently said that mayflies are primitive insects, and it is certainly true that many primitive characteristics are exhibited by this order. Snodgrass (1935, p. 12) wrote: "During the Carboniferous period, or probably earlier, a group of winged insects evolved a mechanism in the wing base for flexing the wings horizontally over the back when not in use. The descendants of this group (Neopterygota) include the majority of modern winged insects, while the more primitive non-wing-flexing insects are represented today by only two orders (Odonata and Ephemerida), both of which have descended from Carboniferous times but are not closely related to each other." The earliest known fossil insects identifiable as mayflies were taken from Permian shales. These early mayflies were long-winged, long-bodied insects with slender legs and three long tails. The forewings and hind wings were of nearly equal size and the wing veins were very well developed. Kukalova-Peck (1978) described a fossil nymph taken from the Lower Permian beds of Oklahoma in which there were "articulated and movable prothoracic wings which became in some modern insects transformed into prothoracic lobes and shields."

The forewings of the more generalized mayflies possess nearly all the veins of the archetype venation. The costal vein runs to the wing base and thence outward to the edge of the wing; the fore margin consists of a slightly thickened, folded wing membrane beyond the costa. The subcosta extends from the wing base to the apex of the wing, and the radius branches a short distance from the wing base to give rise to R_1, which runs parallel to the subcosta and to the radial sector, which in turn divides. The radial sector forms R_2, R_3, and R_4 plus R_5; R_4 and R_5 make up a single vein and the terminology is used only to prevent confusion. The media is represented by both its primitive branches, the anterior media (lost in the Neopterygota) and the posterior media; and the cubitus is likewise represented by the anterior and posterior cubitus. The Ephemeroptera are the only modern insects in which both branches of the media persist. The number of anal veins varies from one to three according to the genus.

In the hind wings of the more primitive genera the venation is but little modified from that of the forewings; however, with the shortening of the wing the area occupied by Rs has become smaller and R_5 has disappeared.

The genitalia of mayflies are likewise primitive. Imms (1931, p. 41) stated that "a very primitive condition is found among Ephemeroptera, where the penis lobes, instead of being fused to form an aedeagus, are relatively large and entirely free, with the parameres closely applied to them." A styliger plate is borne on the terminal end of the ninth sternite, and forceps originate at the posterior edge of the styliger plate. The penes belong to the 10th abdominal segment (Brinck 1957). According to Spieth (1933, p. 73), "the styliger plate of the mayflies is interpreted by Crampton and Walker as representing coxites, which have fused together to form a single structure. This structure, however, is separate from the ninth sternite. A parallel condition is to be found according to Walker, in the Phasmoidea and Acridoidea, except that in these groups the styli are lacking." The forceps (absent in *Homoeoneuria*) of male Ephemeroptera are homologues of styli, and in all mayfly genera, except for the known males of the Caenidae genera, are segmented. In the females, the oviducts open to the outside or into a common vestibule formed as a fold of the thin membrane joining the seventh and eighth segments. The sternum of segment 7 is produced backward to form a structure known as an egg valve, but no true ovipositor is formed; however, in some of the Leptophlebiidae there is the beginning of such a structure (fig. 171).

The abdomen of mayflies, although possessing only 10 distinct segments, is nevertheless considered to be quite primitive. The usual number of segments in the abdomen of modern insects is 10 or 11, but embryological evidence indicates that the number of segments of the early insects was 12. The generalized form of an abdominal segment is approximately retained in those larval forms that preserve rudiments of the abdominal appendages. In mayflies each gill-bearing segment is distinctly divided into a dorsum and a venter by large lateroventral lobes supporting the gill. These lobes represent the bases of abdominal appendages. Snodgrass (1935, p. 273) concluded that there is little doubt that the gills of mayflies are appendicular parts of abdominal limbs, of which the supporting lobes are the bases. He stated that "the gill stalk or gill plate, by its position on the basis and its basal musculature, suggests that it is the homologue of the stylus of the thysanuran abdominal appendages. The gill basis is very evidently the equivalent of the stylus-bearing plates of the Machilidae, though since it is immovable, there are no body muscles inserted upon it."

In order to arrive at any conclusions as to the primitiveness of the mouthparts of the Ephemeroptera, it is necessary to turn to the nymphal stages. The mayfly mouthparts are of the mandibulate type throughout the order, consisting of a labrum, hypopharynx, a pair of mandibles, a pair of maxillae, and a labium. The mandibles of most mayflies are very generalized in possessing a ventral incisor area and an inner or dorsal molar surface. Between the incisor and molar areas there is a small structure called the lacinia mobilis, the function of which is unknown. This structure has been interpreted by some as a mandibular palp and a prostheca, but according to Crampton (1921), it cannot represent a true palp. He has suggested that the mandibles of mayflies in some respects approach those found in the Crustacea. A pair of superlinguae is attached as lateral lobes of the hypopharynx. Superlinguae are best developed in apterygote insects and in some of the more primitive members of the Pterygota. The galea, lacinia, stipes, and palpifer are fused in the maxillae of all modern mayflies and form a structure called the galea-lacinia. In some of the more primitive genera it is thought that a line of separation can be seen between the galea and the lacinia. On the whole, the maxillae of mayflies must be considered as rather specialized.

The primitive condition of the tarsus of adult pterygote insects is believed to be five-segmented; tarsi having fewer than five segments have probably been specialized by the loss or fusion of some of the segments. In the adults of some of the more primitive mayfly genera, the tarsi are composed of five freely movable segments, but in most mayflies there is a certain degree of fusion. The legs, therefore, cannot be used as reliable indicators of the phylogenetic position of the Ephemeroptera with relation to other insects.

The gills of mayfly nymphs are considered to be homologous with abdominal legs—appendages that have been modified for respiratory purposes. Snodgrass states that there is no question but that the gills arise from limblike rudiments of the embryo, and that their structure and musculature suggest that they are parts at least of true abdominal appendages. Kukalova-Peck (1978, p. 68) summarizes the evidence homologizing the gills with the thoracic wings of adult mayflies, and she points out that pro-wings, or preflight wings, were the incipient functional "wings" of early flightless pterygotes and that they were present on all thoracic and abdominal segments. She further summarizes Wigglesworth's stylus theory thus: "the gill-plates of mayflies are segmentally arranged abdominal appendages, always located above the spiracle, which evaginate and develop very much like the thoracic wings; they are also provided with true venation, articulated between the subcoxa and tergum, and moved by the subcoxo-coxal muscles like thoracic wings." The most primitive of the modern mayfly genera bear gills on the first seven abdominal segments, and the earliest fossils known had these structures on the first nine segments. The retention of these abdominal structures appears to indicate primitiveness, even though they are present in highly modified and variable forms.

A consideration of the characters discussed above will also show that while generalized in many respects mayflies are at the same time highly specialized in certain features (Edmunds 1972; 1975). As Needham has said: "The group as a whole, while retaining a good many primitive characters, has gone a long way in specializing on lines of its own. There are no very primitive mayflies. There is no one genus or species that can be set down as nearest to the ancestral form in all particulars. The lines run criss-cross here as elsewhere; and do not lend themselves to a serial arrangement" (Needham et al. 1935, pp. 207–208).

One of the principal modifications and specializations undergone by the wings has been the cephalization of the flight mechanism, with relative enlargement of the forewings and corresponding reduction of the hind wings until, in some genera, the latter have entirely disappeared. In the specialized genera, venation tends to become reduced, with certain of the longitudinal veins becoming detached, some even being shifted at their bases and reattached. Paralleling this modification of the longitudinal veins is a tendency toward reduction in the number of crossveins in the forewings; in the highly specialized genera they may be almost completely absent.

The hind wings indicate degree of specialization very clearly, for in the Ephemeroptera there exists a whole series of species ranging from those with well-developed metathoracic wings to those showing complete absence of such structures. In certain of the highly specialized groups the hind wings are reduced to tiny threadlike rudiments, which are sometimes so small as to be difficult to find and which could hardly be of any use as organs of flight. The venation of these threadlike wings consists only of one to three longitudinal veins.

The form of the forewings in the primitive genera of Ephemeroptera is somewhat triangular. With increasing specialization, they have become more elongated and narrower, but in those genera with greatly reduced hind wings there is a tendency for the secondary development of a triangular wing with a well-developed anal angle, perhaps in compensation for the partial or complete loss of the hind wing. The return to a triangular wing shape reaches its culmination in the highly modified Caenidae, which lack metathoracic wings.

Not only is there a correlation between specialization and reduction in size of the metathoracic wings, but closely linked with this reduction is a decrease in body size. It is very likely that as wing size decreased a diminution in body size was a natural consequence. As the amount of wing surface for support of the insect lessened, the necessity for less body weight or an increase in wing surface of the other pair of wings was encountered. Both conditions have resulted. Diminution of body size parallels diminution in size of metathoracic wings, with concomitant changes in shape of the mesothoracic wings but with no relative increase in resulting wing surface. In *Caenis*, which has no hind wings and in which the body is thick and heavy by comparison with that of the Baetinae, the forewings have become enlarged and broadened considerably at the anal angle. Although certain other genera of mayflies have lost their metathoracic wings (*Pseudocloeon* and *Cloeon*), there has been no such increase in size of the forewings. In these dipterous mayflies, the body is lightened to accommodate the lessened wing surface.

There are few specializations in the genitalia of mayflies; however, in the more advanced genera there appears to be a fusion of segments of the forceps, and in *Caenis* and *Brachycercus* this fusion has reached its culmination, the claspers consisting of but a single segment. The males of the more specialized species also show a fusion of the paired penes, although the vasa deferentia still open to the outside separately, and in the Baetidae the penes have become internal.

Although the Leptophlebiidae are not the most highly specialized mayflies, certain of the females have the sternites of the seventh and eighth segments modified to form a simple "ovipositor" (Brinck 1957). The ovipositor is really nothing more than a prolongation of the egg valve of other mayflies, and its value in oviposition is unknown.

All mayflies have 10 abdominal segments; however, in *Baetisca* and *Prosopistoma* there seems to be some amalgamation of the segments, although it is claimed that 10 segments can be distinguished. The first abdominal segment of *Baetisca* is intimately related to the metathorax, and it is only with difficulty that this segment can be differentiated. Spieth (1933) considered that gills in the nymph of *Baetisca* occur on segments 1 through 5. Traver (1935) claimed that these structures are found on segments 2 through 6 but it has now been established that there are six pairs of abdominal gills on mature nymphs (Pescador and Peters 1974). Traver further stated that segment 1 is almost completely fused with the thorax, a statement with which we are in agreement. Thus this condition of decreasing the number of abdominal segments, although indicating specialization, is found in a genus that has many primitive characters.

The mouthparts of immature mayflies are relatively unspecialized. The greatest modifications occur in the burrowing species, where each mandible gives rise to a long tusk used in digging (fig. 112; plate 15). The fusion of the parts of the maxillae indicates a specialization in these structures. Spieth stated (1933, p. 81) that "even the most primitive maxilla of the mayflies (as is patent from the nature of the lacinia-galea) is specialized as compared with more generalized insect types." The degeneration evinced by the mouthparts of adult mayflies is a highly modified condition paralleled in relatively few other insects. The mouthparts of the adults are reduced in size, are asymmetrical in form, and lack sclerotization. Internally, the musculature degenerates. As a whole the mouthparts are shrunken very closely together into a single whitish mass beneath the clypeus.

One of the most interesting specializations shown by mayflies is the enormous development of the eyes in males. Baetid males have compound eyes divided into two parts, a lower rounded structure and a much larger "turbinate" portion capping the smaller part. The ommatidia of the turbinate eyes have become greatly elongated, and the shape of these eyes is extremely varied, ranging from a caplike, flattened structure closely hugging the lower eye to one that extends vertically from the head for some distance. In many species the turbinate eyes are brightly colored in shades varying from yellow to orange to brown. It is thought that this exceptional development of the male eye is correlated with the habit of aerial mating, for in the mating flight the male approaches the female from below (Brinck 1957). It has been pointed out by Cooke (1940) that the specializations have reached such a state of development that if a male (of *Stenonema vicarium*) is approached by a female from below, she will be completely ignored, probably because she is invisible to him; however, if the female is above the male, she is immediately seized, and copulation ensues.

The legs of mayflies, although primitive in some respects, are really highly modified organs. Adult mayflies do very little walking and no running whatsoever. In such groups as the genus *Tortopus*, for example, the legs (except the forelegs of the male) have become vestigial, and the adult can no longer alight but must remain on the wing during its entire imaginal life. The forelegs of male mayflies are elongated and have acquired a reversible joint at the base of the tarsus as an adaptation for seizing the female during the mating flight. The more specialized mayflies show a tendency toward a reduction in the number of tarsal segments in the two posterior pairs of legs by fusion of the basal segments with the tibia. The alteration of the alimentary tract to suit it for its aerostatic functions is a specialized character common to all mayflies.

The modification of the mouthparts, the overdevelopment of the ovaries, the enlargement and emptying of the alimentary canal, the enormous development of the eyes of the males, the elongation of the forelegs of the males, and the development of elaborate copulatory organs—all fit the adult mayfly for efficient mating and the certitude of continuing the species.

FAMILIES OF MAYFLIES. There have been many arrangements of mayflies in various families and much shifting back and forth of the genera. The latest, and the most firmly based on phylogenetic studies, is that of McCafferty and Edmunds (1979).* Their classification proposes two suborders of Ephemeroptera and recognizes the reclassification of several families and subfamilies.

Because the McCafferty-Edmunds classification scheme appears to be a logical arrangement based on contemporary studies, we will follow its arrangement in our treatment of Florida mayflies. The two suborders erected by these authors are the Pannota and the Schistonota. The Pannota are characterized in the mature nymphal stage by a fusion of the wing pads along the mesonotum with a general enlargement of that segment. Mature nymphs of the Pannota have less than half the developing forewing pad freely extending beyond its fusion to the thorax. Mature Schistonota nymphs usually have the forewing pads free from notal fusion for one half or more of their length.

According to McCafferty and Edmunds, the gill series of pannote nymphs tends to be reduced and protected in various ways, while that of Schistonota is usually well developed and highly variable and reflects a number of different adaptive modes and lineages. Behavioral differences are also generally apparent between the two lineages, with pannote nymphs being generally slow-moving, relatively inactive crawlers. Schistonota nymphs are swimmers, sprawlers, burrowers, or sometimes crawlers or clingers. Characteristics that will distinguish adults are not as easily seen as those separating nymphs of the two suborders.

We are including McCafferty and Edmunds's table 1 from their 1979 paper and have indicated by an asterisk those categories represented

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*The recent paper by Drs. V. Landa and T. Soldán, "Phylogeny and higher classification of the order *Ephemeroptera:* A discussion from the comparative anatomical point of view" (1985, Czechoslovakian Academy of Sciences, Prague, 121 pages), came to our attention after our manuscript was in press. The changes these authors propose are herewith recognized, but they do not significantly alter our taxonomic arrangements.—*LB* and *MLP.*

TABLE 1

EPHEMEROPTERA OF THE WORLD

Higher classification of the extant Ephemeroptera of the world, including suborders, superfamilies, families, and subfamilies. Distributional realms for each subfamily are indicated. Amphinotic distribution is southeastern Australia, Tasmania, New Zealand, and Chile and adjoining Argentina (from McCafferty and Edmunds 1979).

Suborder SCHISTONOTA*

- Superfamily Baetoidea*
  - Family Siphlonuridae
    - Subfamily Oniscigastrinae (Amphinotic)
    - Subfamily Ameletopsinae (Amphinotic)
    - Subfamily Siphlonurinae (Holarctic, Amphinotic)
    - Subfamily Rallidentinae (New Zealand)
    - Subfamily Acanthametropodinae (Holarctic)
  - Family Ametropodidae (Holarctic)
  - Family Baetidae*
    - Subfamily Siphlaenigmatinae (New Zealand)
    - Subfamily Baetinae (Widespread, except in New Zealand)*
  - Family Metretopodidae (Holarctic)*
  - Family Oligoneuriidae*
    - Subfamily Isonychiinae (Holarctic, Oriental)*
    - Subfamily Chromarcyinae (Oriental)
    - Subfamily Coloburiscinae (Amphinotic)
    - Subfamily Oligoneuriinae (Ethiopian, Neotropical, Holarctic)*
  - Family Heptageniidae*
    - Subfamily Arthropleinae (Holarctic)
    - Subfamily Pseudironinae (Nearctic)*
    - Subfamily Heptageniinae (Holarctic, Oriental, Ethiopian)*
    - Subfamily Anepeorinae (Nearctic, Holarctic?)
    - Subfamily Spinadinae (Nearctic)*
- Superfamily Leptophlebioidea*
  - Family Leptophlebiidae (Widespread)*
- Superfamily Ephemeroidea*
  - Family Behningiidae (Holarctic)*
  - Family Potamanthidae (Holarctic, Oriental)
  - Family Euthyplociidae (Oriental, Ethiopian, Neotropical)
  - Family Polymitarcyidae*
    - Subfamily Polymitarcyinae (Holarctic, Ethiopian, Oriental)
    - Subfamily Campsurinae (Neotropical, Nearctic)*
    - Subfamily Asthenopodinae (Neotropical, Ethiopian, Oriental)
  - Family Ephemeridae (Holarctic, Ethiopian, Oriental, New Zealand, Neotropical)*
  - Family Palingeniidae*
    - Subfamily Pentageniinae (Nearctic)*
    - Subfamily Palingeniinae (Palearctic, Oriental, Ethiopian)

Suborder PANNOTA*

- Superfamily Ephemerelloidea*
  - Family Ephemerellidae*
    - Subfamily Teloganodinae (Ethiopian, Oriental, Palearctic, Australian)
    - Subfamily Ephemerellinae (Holarctic, Oriental)*
    - Subfamily Melanemerellinae (Neotropical)
  - Family Tricorythidae*
    - Subfamily Leptohyphinae (Neotropical, Nearctic, Ethiopian)*
    - Subfamily Ephemerythinae (Ethiopian)
    - Subfamily Tricorythinae (Ethiopian, Oriental)
    - Subfamily Dicercomyzinae (Ethiopian)
    - Subfamily Machadorythinae (Ethiopian)
- Superfamily Caenoidea*
  - Family Neoephemeridae (Holarctic, Oriental)*
  - Family Caenidae (Widespread, except New Zealand)*
- Superfamily Prosopistomatoidea*
  - Family Baetiscidae (Nearctic)*
  - Family Prosopistomatidae (Ethiopian, Oriental, Palearctic)

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*These higher categories are represented by species occurring in Florida.

among the Florida mayflies. We have also reproduced their figure showing their interpretation of the phylogenetic relationships among contemporary suborders and superfamilies, as well as an illustration of the nymphal mesonotum and wing pads of the two suborders (fig. 1).

Table 1 reveals that all superfamilies have representatives in Florida and that 14 families are now known to occur in the state. Beyond the borders of Florida, the number of families occurring in adjacent states, where there is a greater variety of streams, increases to 16. Thus far there is no evidence that the two additional families, Siphlonuridae and Potamanthidae, might be found in Florida.

WING VENATION OF MAYFLIES. The wing venation of mayflies has been reviewed by numerous authors, especially by Martynov (1922), Tillyard (1923), Spieth (1933), Needham et al. (1935), and by Edmunds et al. (1976). The origin and evolution of wing venation and corrugation was treated in detail by Kukalova-Peck (1978) and discussed by Hubbard and Kukalova-Peck in 1980. Presently, there seems to be general agreement among Ephemeropterists that the terminology and interpretation given

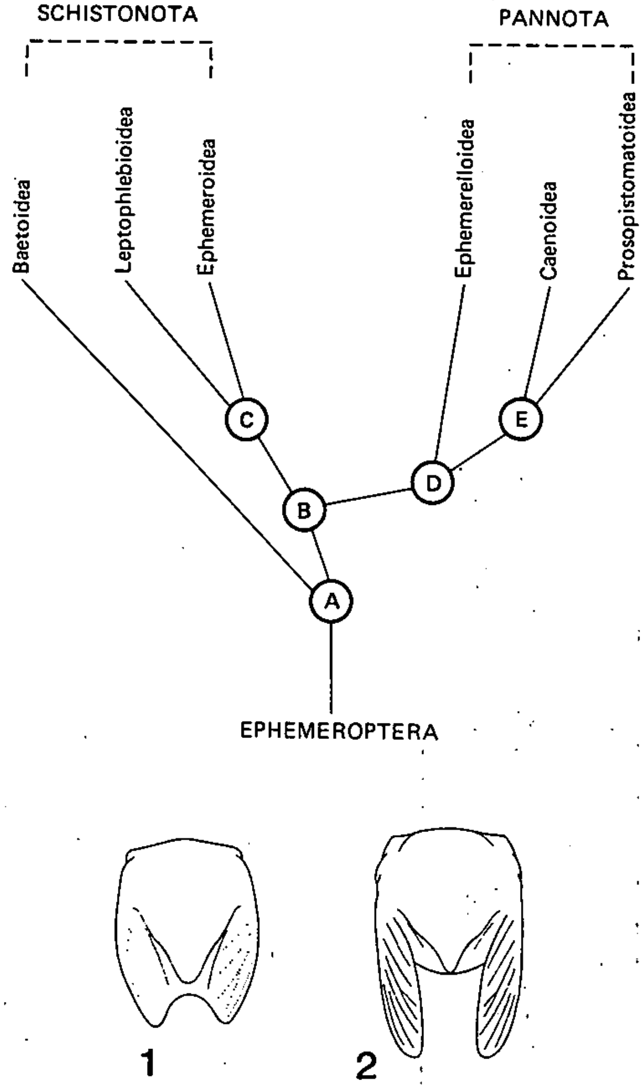


Fig. 1. The upper figure illustrates the present concept of the phylogeny of the extant superfamilies and suborders of Ephemeroptera (ancestors lettered). The lower figures show the nymphal mesonotum and wing pads of generalized mayflies. 1. Pannota. 2. Schistonota. (From McCafferty and Edmunds 1979)

by Edmunds et al. is a satisfactory one; it is the one we shall follow in this treatment of Florida mayflies.

Mayflies are unique among pterygote insects in completeness of fluting or corrugation of the wings. There is a regular alternation of high and low (convex and concave) veins. A very important feature of the mayfly wing, as shown by Spieth, is that all convex veins belong to the dorsal surface of the wing and all concave veins to the ventral surface. His findings (1933, p. 60) indicate that "the cross veins belong principally to the dorsal surface, i.e., at the base where they join the concave veins a stump of the cross vein is attached to the main vein, while on the dorsal surface the cross veins are always complete and vigorously developed. . . . It is important to note that veinlets at the edge of the wings are always restricted to the dorsal surface."

The triadic type of branching is also a characteristic feature of mayfly venation. When a longitudinal vein forks, there is interpolated between the two branches a third vein of opposite position, which does not reach the base of the fork. For example, the anterior media, a convex vein, forms a fork just beyond the middle of the wing. The two branches of this fork are convex; however, the intercalary vein lying between the two branches is concave. The system of fluting is primarily an adaptation for radial strengthening of the wing, and the crossveins serve chiefly to hold the ridges and furrows in place. In the more specialized mayflies, which have small hind wings or none at all, there is a decrease in the number of crossveins, while in those species that have large wings with prominent fluting, the crossveins are well developed, reaching a maximum in *Ephoron*, in which there are several hundred crossveins in the forewings.

The origin of the various wing veins has been studied in depth by proponents of the Comstock-Needham system. Ann Morgan (1912) investigated the origin of the definitive adult venation, but later studies by Tillyard and others show that some of Morgan's results were erroneous. She adopted for mayflies the same interpretation of the relationship of radial sector and media as that proposed by Needham for the Odonata wing, with Rs crossing M. More recent work, however, lends no support to the idea that this occurs in either order. In fact, Kukalova-Peck (1978, p. 64) refutes the Needham concept stating, "the 'media' comes out 'crossing' the 'sector radii,' which is never the case among the Pterygota and creates the false impression that the dragon flies are thus unique."

For the sake of consistency, in figure 2 we are reproducing the forewing illustration shown in the paper by Edmunds and Traver (1954). The abbreviations for the names of the wing veins are shown in the caption.

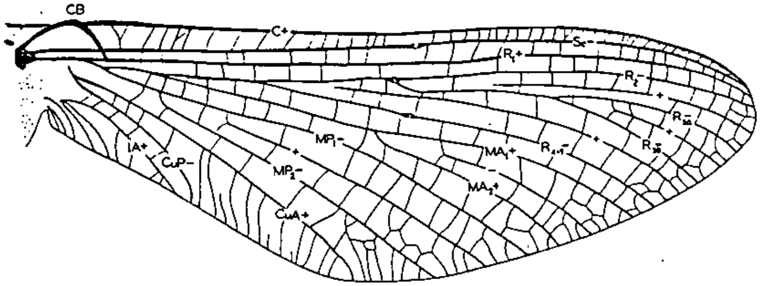


Fig. 2. Forewing of *Siphlonurus*, showing the bullae and concave (+) and convex (-) veins. (From Edmunds and Traver 1954)

C=costa
Sc=subcosta
R_1=radius$_1$
Rs=radial sector
R_2=radius$_2$
R_3=radius$_3$
R_{4+5}=radius$_{4+5}$
MA_1=media anterior$_1$
MA_2=media anterior$_2$
MP_1=media posterior$_1$
MP_2=media posterior$_2$
CuA=cubitus anterior
CuP=cubitus posterior
A_1=anal$_1$

Intercalary veins lie between the main veins, extend inward from the wing margin, and end in the wing membrane.

Other important landmarks in the forewing include the humeral, or costal, brace near the base of the wing; the bullae, which are apparently weak spots in some of the main veins providing flexibility in the outer portion of the forewings; and the stigmatic area, located near the wing tip between the costa and the subcosta. The disc of the wing is a central area that is sometimes pigmented with brown spots.

The venation of the hind wings is generally much reduced, with the venation difficult or impossible to interpret. The costal projection is present near the base of the hind wing in most genera and in some is strongly developed. Hind wings are absent in a few genera. In some of the smaller adults this characteristic may be difficult to determine because the wing may be threadlike.

TAXONOMIC CHARACTERS. Perhaps taxonomists in the past have not been sufficiently thorough in their treatment of mayflies. For the most part, external structures or features have been used in separating taxa and in developing phylogenies. However, in the past few years there has been a change brought about by the studies of a few ephemeropterists, particularly Dr. V. Landa, who undertook an intensive study of the comparative anatomy of mayfly nymphs (1969). Using his data as a basis, he developed a phylogeny for the order that employs internal structures such as the tracheal system, the Malphighian tubules, and the nervous system. More recently, Landa et al. (1980) have investigated the internal anatomy of nymphs of the family Leptophlebiidae in an attempt to understand the relationships of a rather unique family of Ephemeroptera.

In separating families, genera, and species of mayflies, the wing veins are utilized extensively. The wing veins of each genus of mayflies (particularly the longitudinal veins) are very constant in structure and position—so much so that only in a few groups can specific differentiation be found, and then only by reference to minute details. The highly modified hind wings are very useful in differentiating genera, and in many cases the shape of the costal angulation, the number of longitudinal veins, and the general shape and relative proportions of these wings are helpful even in distinguishing species.

The structure of male genitalia has been widely employed by taxonomists throughout the field of entomology and even in the study of other animals. These reproductive structures are particularly useful in the differentiation of ephemerid species and have been widely applied. Many of our more recently described species have been established on genitalic differences alone, but there are usually other characters that parallel such genitalic divergences. Each genus has its own peculiar penial shape, and within the genus there may be much variation. One of the best examples of this is seen in *Paraleptophlebia*, in which the penes of each species are distinctive. The shape, number of segments, and relative proportions of the forceps or claspers are also very useful in differentiating genera and, in some cases, species. The reproductive apparatus of the female mayfly is so poorly developed externally that it is of no use taxonomically, except in those few genera that possess a rudimentary ovipositor.

Dr. Osgood Smith studied the eggs of a number of genera of mayflies and found that within a genus the sculpturing and accessory structures are very uniform. He was able to construct a key to the known eggs of North American mayflies, which was incorporated in the book by Needham et al., *The Biology of Mayflies*. With the development of newer techniques such as provided by scanning electron microscopy, phase contrast, and Normarski interference contrast the study of mayfly eggs has become much more prevalent and has provided insight into phylogenetic relationships in the order. In 1974, Koss and Edmunds published their extensive studies of mayfly eggs and used the data to assist them in understanding mayfly phylogeny. Keys to the eggs of the insects studied were included in their monograph. We have discussed the egg in an earlier section on the order Ephemeroptera.

The number of tarsal segments in the posterior pair of legs of adult mayflies has proved useful as a familial character. Within some families, the length of tarsal segments of the forelegs of the males is used to distinguish genera, and in some cases this character has been relied on to such an extent that it is impossible to identify a female to genus, unless males can be definitely associated with her. Although some families have been studied intensively (e.g., Heptageniidae), females are still not easily differentiated even to genus! Within the genera, leg structure of adults is little used taxonomically, though careful study may prove that they are indeed helpful, as one of us (Berner 1978) recently showed in studying spination of the forelegs of *Siphloplecton basale* and *S. interlineatum*.

Another character frequently used, and rightfully so, is eye structure of adults, but this trait again is applicable only to males. Sexual dimorphism in mayflies is often so pronounced that unless one is familiar with the groups, males and females of the same species may easily be placed in different genera. Among the male ephemerids, there appear all gradations in structure of the compound eyes, from a simple type to those that are completely divided and enormously enlarged into bizarre shapes. The division, or lack of division, of the male eye is used as a criterion for separating some families, and in some cases this character is also used as a generic differentiator. There appears to be a definite correlation between eye size and shape and the night- or day-flying habits of the species. Those mayflies mating at dusk or after dark have small eyes that are approximately the same size in both sexes, or only slightly larger in the males. In *Palingenia*, widely distributed in the old world, the female is approached by the male as she floats on the water surface. In this genus the eyes of the male are a little smaller than those of the female. The males of day-flying species, on the other hand, have huge eyes that are far larger than those of the females, as shown in the illustration of the South American genus *Miroculis* by Savage and Peters (1983) (fig. 3).

The colors found in adult mayflies vary from white through yellow, orange, red, and brown, to black. All their colors, which are generally drab, aid in making mayflies inconspicuous. Spieth (1938) pointed out that the more primitive species have particularly dull and subdued colors. He found that in most mayflies the entire exoskeleton is transparent, and that if color is present in the chitin, it is always some shade of olive brown. The tissues immediately underlying the exoskeleton are often impregnated with pigments that are the principal cause of the distinct adult color

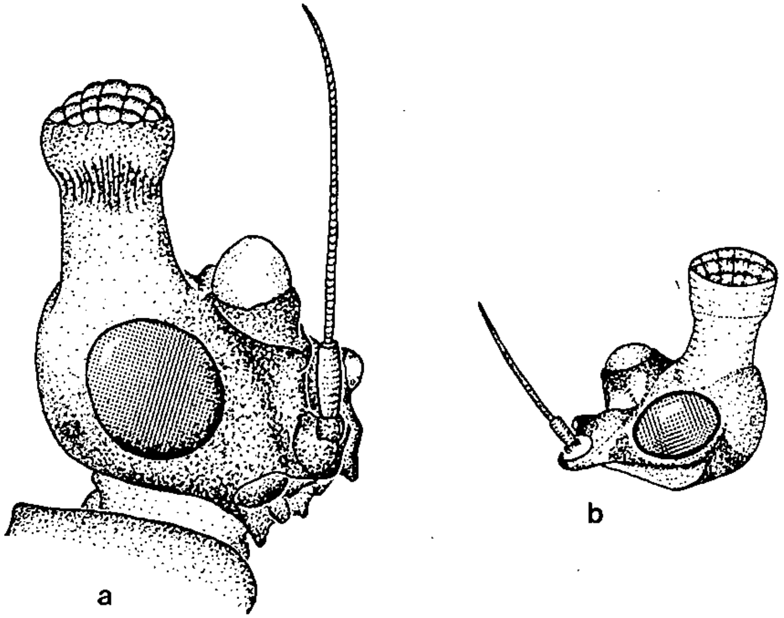


Fig. 3. Eyes of *Miroculis* male imago: (*a*) *M. rossi* (*b*) *M. fittkaui* (redrawn from Savage and Peters 1983).

pattern. Spieth found that the white colors in the Ephemeroptera are due to two distinct factors: (1) in all adults, a chalky white substance is present underneath the exoskeleton and epidermis but external to the musculature; and (2) certain species have a milky appearance that occurs not only in the body but also on the wings. This is a physical color, which disappears when the insect is immersed in liquids of the same refractive index as that of the white structure. The two types of white combine to form the color pattern of the adults showing this second type of coloration. He also pointed out that some of the oranges, bright yellows, and greenish yellows present in certain species are probably chlorophyll derivatives, since they deteriorate in dried specimens and are completely destroyed by preservatives.

The disposition of pigments in strongly sexually dimorphic species is particularly interesting. The wings and body of both sexes of these forms are brilliant. In the males, however, the pigments are no longer evenly

distributed in each abdominal segment but are concentrated in the first and last four, with the intervening ones hyaline white. There may be a definite color pattern overlaying the white of segments 2 through 6, but this is never conspicuous. In nearly all cases this strongly localized coloration is limited to specialized genera of mayflies in which the individuals are generally less than 10 mm in length. It is probable that the glistening wings and the hyaline segments help to render the insects inconspicuous, because there is such a great reduction in the amount of dark-colored abdomens, but it has been suggested that if the entire exoskeleton of these insects were transparent, the light-colored muscles as well as the egg masses would show through and the females would be easily seen.

Differences in maculation are reliable, in general, for distinguishing species, but the great degree of variability in some species causes misgivings whenever color pattern alone is used, unless it is absolutely distinctive. The genus *Stenonema* is one of the chief groups in which color has been used for the establishment of new species. Bednarik and McCafferty's study (1979) of *Stenonema* attempted to de-emphasize use of color for separating species; however, the differentiation of one from another is still difficult.

To distinguish between species, colorational differences have probably been employed more than any other character or group of characters. Spieth's study of coloration and its relation to seasonal emergence in the Ephemeroptera has indicated that some of the species, which have been described solely on the basis of maculational differences, are really only seasonal forms of the same species. As an example of this we have been told by Drs. Spieth, E. F. Lyman, and D. Jenkins, all of whom have worked in the Great Lakes region, that *Stenonema tripunctatum* (now *S. femoratum*) shows seasonal variation in coloration exceptionally well. Traver described several species differentiated from *S. tripunctatum* by colorational variations; but the other workers mentioned, through observations made during the entire emergence period of the mayflies of a restricted region, agree that all of these are merely seasonal forms of the one species. Bednarik and McCafferty's study considered the previously described subspecies of *femoratum* simply color phases within the range of variation of *S. femoratum.*

Size of adults, including both wing length and body length, has been used to some extent for the determination of species; however, so many factors modify size that it is not considered a safe criterion by itself for the erection of species. Wing length is much less variable than is body length, for body length is subject to shrinkage, elongation, swelling, and other distortions when the insect is killed. Although there has been little taxonomic use of relative proportions of wings, they may become more important as more is learned about them.

It is generally agreed that the present arrangement of mayfly families represents natural groupings. Evidence from the adults is substantiated by studies of the anatomy of the immatures (Landa 1969). In *The Biology of Mayflies*, Needham (1935, p. 208) stated that "in this order the struggle for existence has fallen largely upon the nymphs, which are better equipped to meet competitors. These show greater divergences in adaptation to their several types of habitat. These have differentiated on lines of their own, independently of the adults, and tell their own story. It goes without saying that our interpretations of nymphal and adult evolution will, when correct, be in agreement. One must corroborate the other; for nature preserves or eliminates species as wholes."

Mouthparts, head shape, and structure of gills are characters most often used to separate the families of mayflies in the nymphal stages. Gill shape and structure are extremely varied. The gills may be foliaceous, single, double, or recurved; they may be highly tracheate, or they may completely lack tracheae. Gills may be present on seven abdominal segments or absent from some of them. They may lie flat on the abdomen or be so shifted that they serve as suckers on the venter of the insect. They may be modified so that some form protective covers for others, or all may be completely exposed. They may be strongly muscled so that they can be vibrated very rapidly or so flabby that such reactions are difficult or impossible. They may be confined entirely to the abdomen or, in a few cases, may also occur at the base of the fore coxae or even on the maxillae. In short, the gills are probably the most variable structures to be found in nymphal Ephemeroptera.

As hind wings are absent in the adults of some species of mayflies, the immature stages of these naturally lacks hind wing pads. The presence or absence of metathoracic wing pads is used as a taxonomic character.

The caudal filaments (two cerci and one terminal filament) are very useful in studies of the nymphal forms. In some species, they are flexible organs; in others they are sturdy swimming structures. The cerci of many of the genera are densely clothed with hairs medially. The terminal filament has heavy growth laterally, forming a powerful propelling structure when the three filaments are overlapped. In many other genera the three tails are almost bare, having only a light covering of short hairs.

Color pattern, while frequently used for species determination, is much less often employed in nymphs than in the adults. Often when such characters are found to distinguish species, structural differences parallel them.

3

A COMPARISON OF FLORIDA MAYFLIES WITH THE NORTHERN FAUNA

TAXONOMY. Many of the genera of mayflies occurring in Florida are widely distributed over eastern North America. Some, however, are rather localized and rare, often because of the difficulty of collecting specimens or because the appropriate habitats have not been discovered or examined. The more distributionally restricted genera include *Homoeoneuria*, *Pseudiron*, *Macdunnoa*, and *Dolania*.

Of the 71 species now known from Florida, only six have not yet been encountered beyond the state's boundaries. The total list of 71 seems large for such an ecologically limited region where the land is mostly lowlying and the streams and rivers gently flowing or almost stagnant. When compared with the large number of species that may be taken from a single stream where the variety of habitats for the immatures allows for virtually every need, the number is actually quite small. Ide (1935) found 55 species in one stream in Ontario, and later he was able to collect more than one hundred from a single stream. No such concentrations of species are found in any Florida waters. Conditions in Florida streams are just not as favorable, as they lack the highly aerated, rapidly flowing water and rocky habitats characteristic of streams with a highly varied mayfly fauna.

COMPARATIVE ABUNDANCE. In Florida the actual number of individual mayflies present in a given habitat is generally smaller than in more northern, cooler streams. This is partly explained by the relatively small number of suitable nymphal habitats in any particular stream. That Florida streams are relatively depauperate in numbers is not always true. For instance, in the apparently sterile sandy bottom of the Blackwater River in northwestern Florida, the numbers of *Dolania* nymphs is significantly high.

In the smaller rivers and streams descending from the mountains along the eastern slopes in Mexico, the number of individual insects on a single rock is amazing. Nearly two hundred mayfly nymphs were taken by one of us (Berner) from one rock, approximately 15 × 15 × 8 inches, and on the same rock the caddis fly cases and blackfly larvae literally covered the surface. When a Florida stream is compared with such a river, it can be seen that even though mayfly nymphs are the predominant insects, they are so much less abundant that they can in no wise be as important in food chains as those of the rocky trout streams of the northern United States and the mountainous areas of North America in general.

Adults of the great majority of Florida species emerge throughout the year, and for this reason there are no great swarms (except of some of the burrowing forms and the tiny *Caenis*). The flights, which are small, are composed of inconspicuous insects that gather in groups to mate. The literature indicates that many of the small, more northern species collect in very large swarms to carry out their mating flights; but in the areas where such flights occur the emergence of those species forming the large swarms is limited to a short time period. It has been stated that the species that emerge over a long period—the entire summer—do not form large flights, and from these accounts it would seem that the flights of such species resemble in size the flights of the Florida ephemerids.

Prior to the extensive eutrophication of the lakes of central Florida, burrowing mayflies, being more or less seasonal, emerged in great numbers but never formed such tremendous swarms as occur in the more northerly parts of the country. The lake species, however, during their emergence period were a conspicuous part of the insect fauna in the Central Highlands of the state. When mating flights occurred, the adults constituted an important part of the food chains in the lakes of the region. The number of individuals in Florida lakes more closely approaches the abundance characteristic of unpolluted lakes of northern regions than do the numbers of mayflies occurring in any other type of situation in Florida. Only one larger stream among those examined—the Santa Fe River in north-central Florida—may perhaps compare favorably in abundance of mayflies with some of the small, more northern streams, and then only in its rapidly flowing stretches.

COMPARATIVE ECOLOGY. Naturally the conditions most affecting the distribution of mayfly species are the ecological factors of the aquatic environments where the nymphs occur. The great majority of mayflies are rheocolous, and the rate of flow of water is probably the most important single factor determining the presence or absence of a given species. The very swift, rocky streams preferred by many northern species are absent in Florida, but there are numerous streams in the northwestern part of the state that have a constant and fairly rapid movement. Nevertheless, many species that occur in streams with a similar rate of flow in north Georgia and North Carolina are not found in the Florida streams. The *interpunctatum* complex of *Stenacron* is represented in Florida by two species, *interpunctatum* and *floridense*, and this complex also occurs in the mountain streams of North Carolina. Yet *Epeorus*, which in North Carolina occurs in association with the *Stenacron* nymphs, for some unknown reasons does not extend its range south of the region of Atlanta, Georgia. Perhaps *Stenacron* possesses a greater tolerance to higher temperatures, or there may be differences in the feeding habits of the two that prevent the spread of *Epeorus* into the Coastal Plain.

Ide and others (i.e., Kamler, Hynes, Lager, Lehmkuhl, etc.) have shown that the entire stream fauna is very much affected by thermal conditions, and water temperatures are very closely tied up with rate of flow of streams. In Ontario, according to Ide, the number of mayfly species increases downstream owing to the higher temperatures that prevail in the lower stretches; the addition of species adapted to the higher temperatures is more rapid than the elimination of headwater species that require lower temperatures. His analysis of an Ontario stream in terms of temperature is very interesting; and although no similar studies have been made of Florida streams, Ide's results are not applicable to them since they have a nearly uniform temperature throughout. His conclusions would also suggest that the greatest number of species should be found in the southern part of North America where higher temperatures prevail throughout the year. The reverse is true in Florida, likely because of other ecological factors.

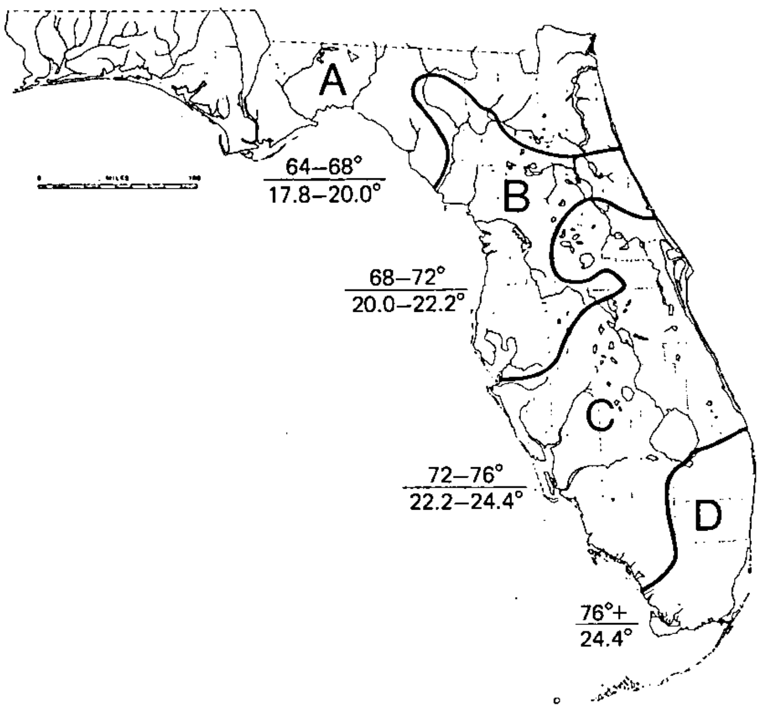
Habitats within Florida streams are apparently more limited in extent and variety than in more northern ones. A great many of the rapidly flowing streams of other states are filled with rocks and pebbles, a condition that evidently affords the optimum circumstances for great numbers of mayfly species. Combined with rocks are, of course, pools, vegetation, debris, and many other sites that offer refuge to the mayfly nymphs. Florida streams, mostly devoid of rocks and with much barren, sandy bottom (the Blackwater River is an exception), can offer little variety in comparison, even though all available habitats in these streams are utilized.

Perhaps the greatest barriers to the wide dispersal of more northern mayfly species in Florida are the large areas in which there are no constantly flowing streams. Thousands of square miles of the state, particularly in the coastal regions, are low and flat, and the grade of the lowlands is not sufficient to maintain permanently flowing creeks and rivers. Typical rheotropic species cannot exist for long in standing water, and even if a species were accidentally introduced while there was some flow, as soon as the flow ceased, the nymphs would probably die. The dry, sandy scrublands of southwest Georgia and of Florida also offer a serious barrier to less vagile species, and this has probably helped to keep the number of species in Florida less than in neighboring states and the northern part of the continent. Rogers (1933) found that the same conditions affected the distribution of crane flies. He wrote, "[O]ne of the most important barriers to the northern groups, the ranges of which extend into the Piedmont Province of Georgia and the Carolinas, is the monotonous, low pine-lands of the southern coastal plain with their dearth of clear, fairly rapid, pebble-bottom streams."

COMPARISON OF LIFE HISTORIES. Many differences in behavior would be expected between the mayflies of the northern parts of the United States and those of the south, but the most striking are found in life histories. The species of Ephemeroptera known to occur both in Canada and Florida show wide variations in emergence periods and might in consequence be considered different physiological subspecies. In Canada and the northern states, all these species have a rather limited period of emergence during late spring and summer; but in Florida every one of the species common to both north and south emerges throughout the year except during the short cold spells, and mating takes place at any time of the year except during cold weather, when the insects become lethargic.

Although Spieth had little definite information on the point, he stated rather accurately (1938, p. 214) that "in the southern part of the United States, the length of the emergence period of the group is much longer. There seems to be no reason why in the tropics and subtropics there should not be some species emerging during each month of the year." The greater part of Florida cannot be considered subtropical, yet Spieth's conjecture holds true for the whole area.

Not only are many of the mayflies nonseasonal in Florida, but this holds for other groups of animals as well. This characteristic of nonseasonal emergence has been found to be true particularly in the southern part of the peninsula.



Map 1. Temperatures of Florida streams. Zones A, B, C, and D show a north to south increase in stream temperatures. The upper figures in each zone show the average annual temperatures of Florida waters in degrees Fahrenheit, the lower in degrees Celsius. Many factors influence the stream temperatures, and the numbers should be considered only as generalizations. (Map and temperatures from Anderson 1971)

Map 1 shows that average temperatures in Florida are suitable, even in winter, for the adult stages of insects that are primarily of northern origin.

The few definitely seasonal Floridian species of mayflies are probably southern in origin; whereas those species emerging throughout the year are northern forms that have immigrated to Florida. This phenomenon has been noted by specialists working with the lycosid spiders, dragonflies, crane flies, and Orthoptera. The temperature factor appears to be linked with this unique behavior. The colder the water inhabited by immature mayflies, the shorter the period of adult emergence. In Florida the lowest winter temperature of the water is probably equal to, or only slightly below, that of many northern waters during the summer period of emergence. Consequently, mayflies in Florida are seldom, if ever, confronted with conditions unfavorable for transformation. For this reason a species (*Paraleptophlebia volitans*, for example) that emerges in Canada for about two weeks during the summer can emerge throughout the year in Florida. The generalization that species of northern origin are nonseasonal in Florida, and that seasonal forms in this state are all of southern origin, holds true; but this is not a complete statement of the facts. Many of the species believed to be southern in origin are nonseasonal, like the northern forms in this area. But this too may be explained on the basis of temperature if the southern forms arose in the cold waters of the southern Appalachians or the hilly regions of the Piedmont. There are, of course, some species that are strictly limited in their periods of emergence such as *Dolania americana*, *Neoephemera compressa* and *N. youngi*, and the Florida species of *Baetisca*.

Some species of mayflies are now known to have surprisingly brief development times, while others require more than one year. Individuals of the same species may require a long or short developmental time, depending on environmental conditions. Lawrence J. Gray (1981) reported that he had reared certain species from egg to adult in Arizona in incredibly short times, as noted in the following:

Baetis quilleri—7–13 days
Callibaetis montanus—9–14 days
Leptohyphes packeri—8 days
Tricorythodes dimorphys—8 days

Edmunds (1957) reported that *Parameletus columbiae* nymphs hatch in May or June from eggs laid in June of the previous year and complete nymphal life in from 16 to 22 days.

In Florida, Pescador and Peters (1974), studying *Baetisca rogersi*, found that the nymphs have 12 instars in their development and concluded that there is a single generation per year. Jones (1977) investigated the life history of *Neoephemera youngi* and found 15 nymphal instars. He reported that Dr. P. Tsui, also studying the same species, determined that there are 17 instars, based on a count of the rings in the Palmen organ. Jones also concluded that there is a single generation per year in *N. youngi*.

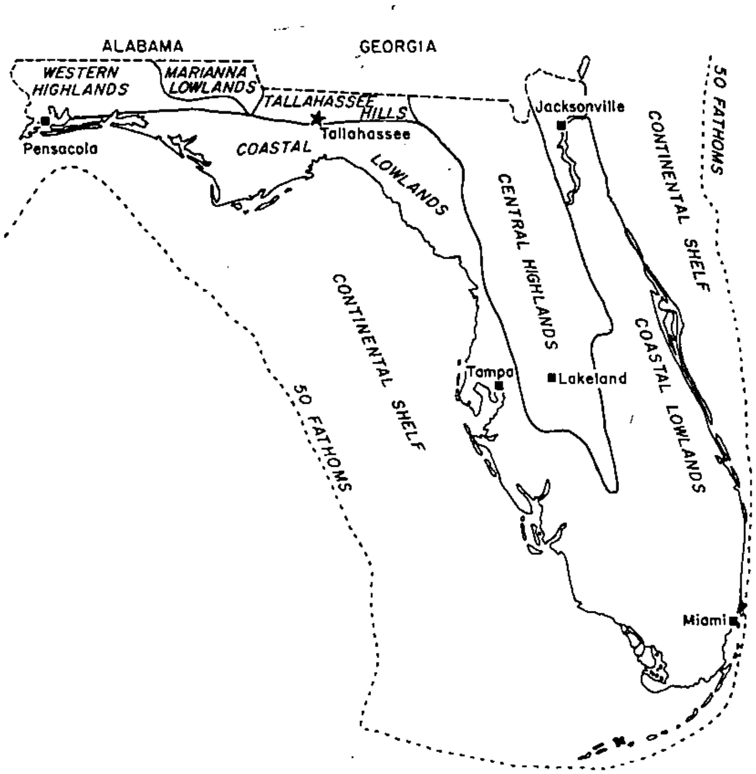
4

ZOOGEOGRAPHY

The topography of Florida has been described by C. W. Cooke (1939) in his *Scenery of Florida*. He divided the state into five natural areas (map 2) and these have been found to be closely related with differences in the mayfly fauna. Recently, Blanton and Wirth (1979) discussed the present physiography and climate of Florida and its geological history in relation to the distributional patterns of the native *Culicoides* species. In the same paper there is a brief review of previous accounts (Harper 1927; Howell 1932; Rogers 1933; Berner 1950; Young, 1954; Neill 1957; McPherson et al. 1976) of the biogeographic divisions in relation to the distributional patterns of the flora and fauna of the state. Our interpretations of the biogeographic division of Florida are discussed in the section treating the ecology of the mayflies.

Since mayflies are so limited ecologically, compared to other groups of aquatic insects, their introduction into a new area is subject to many obstacles. The various factors influencing drainage (stream flow, substrate, vegetation) are the dominant elements directing the movement of primarily aquatic insects. Hubbell and Stubbs (*in* Carr 1940) have suggested that the following events and conditions have occurred in the more recent geological history of Florida:

1. Persistence of a land area in central Florida, in the form of large islands or a group of keys, at least since the beginning of the Pleistocene and probably since Pliocene times.
2. The bridging of the gap to the mainland on one or more occa-



Map 2. The physiographic divisions of Florida (from Cooke 1939).

sions (perhaps first in the Pliocene), followed by renewed insular isolation.

3. Final establishment of peninsular conditions during the Pleistocene.
4. More or less extensive marginal submergences in late Pleistocene, reducing much of the eastern margin of the peninsula to a coastal archipelago.
5. Persistence of a salt-water barrier between Florida and the West Indies at least since pre-Cenozoic times and certainly throughout the period of derivation of the modern biota of the state.

It is unnecessary to hypothesize the existence of such islands in order to derive the Ephemeroptera fauna. The winged stage of mayflies and the

methods of dissemination of the insects would allow for rapid penetration of an area should ecological conditions become satisfactory for the maintenance of that species. Active or windblown dispersal of egg-bearing female mayflies can be propagules and a few individuals have been trapped as high as 3000 feet above the ground (Edmunds 1972; Glick 1939). Although Florida is geographically so situated as to receive maximum aerial and rafted dispersals from the neighboring West Indies, mayfly faunas of both these areas show no phyletic relationships. Based on his study of the leptophlebiid mayflies, Peters (1971) indicated that there is no evidence to suggest any dispersal from the West Indies to Florida.

Conditions today on many of the existing low-lying Bahamian Islands would not permit very extensive development of mayflies. It is not at all unlikely that as isolated islands were rising from the sea to form Florida, they were very similar to the present-day Bahamas. If the same conditions persisted until land connections were formed, the introduction of mayflies into the region has been very recent, and, as is suggested below, the fauna was derived mainly through the larger river drainages. Quite likely there were some mayflies inhabiting Florida islands, but they must have been pond forms and species that could withstand wide variations in ecological conditions. The species that may be endemic to Florida, *Baetisca escambiensis*, *Siphloplecton brunneum* Berner, *S. fuscum* Berner, *S. simile* Berner, *Stenacron floridense* (Lewis), and *Hexagenia orlando* Traver, could easily have arisen since the establishment of the peninsula in the Pleistocene.

As Florida rose, the streams draining the southeastern portion of the continent and carrying with them their northern fauna were extended onto this new area. In the western part of Florida, the Chattahoochee River, which drains the foothills of the Appalachians, and the Flint River, which drains the Piedmont of Georgia, came together to form the new Apalachicola River. As the Florida tributaries of this great stream began to erode back into the uplands, the conditions of their valleys tended to approach those of the more northern reaches of the river. As conditions in these tributaries became suitable, the mountain and Piedmont species came to occupy all available habitats within the small, rather rapidly flowing, sand-bottomed streams.

The Apalachicola River drainage has without doubt been the main highway of ingress to Florida for the great majority of animals that require flowing water or hardwood forests. Rogers (1933) found that ecological conditions in the Apalachicola drainage would admirably explain the distribution of many northern crane flies in Florida. Carr (1940) reported that the most extensive invasion of Florida by the northern element is encountered in that portion of the panhandle drained by the Apalachicola River. Hubbell (1936, p. 3354) stated that "in this particular environment [the deep ravines of the Apalachicola region] a great many northern plants occur, evidently the remnants of a northern flora left as relicts from the Pleistocene times in these deep moist cool ravines." It has also been noted that many northern plants reach their southernmost limits in these ravines and that many typically southern plants intermingle here with the northern species. Not only is this true of plants, but it has also proved to be the case in the crane flies, sand flies, the Odonata, the opilionids, the ichneumonids, the Orthoptera, the crayfish, the amphibians, and the reptiles. Cooler temperatures and/or higher rainfall during glacial times brought many plants and animals with northern distribution into Florida. Indeed, during the Wisconsin times Florida was too cool to support a tropical flora but cool and wet enough to support some organisms that now occupy the transition or even more northerly life zones (Neill 1957). According to Neill, deep embayments of the Gulf of Mexico along three river systems (the Escambia-Blackwater-Yellow River basin; the Choctawhatchee-Alaqua basin; and the Apalachicola basin) may explain the many peculiarities of east-west distribution in the Panhandle. Many mayfly species that have entered the state have probably spread out from these river systems and now occupy rather wide ranges in Florida (*Baetis* spp., *Eurylophella temporalis, Hexagenia limbata*); but certain forms (*Baetisca* spp., *Homoeoneuria dolani, Pseudiron centralis, Siphloplecton* spp.) seem to be more or less confined in these areas, particularly in the Apalachicola drainage.

Glacial events undoubtedly had a significant impact on the origin of the mayfly fauna of Florida. In our study of the biosystematics of the genus *Baetisca* (Pescador and Berner 1981), we suggested probable explanations for the origin of the species diversity of the group. "Speculation about the origin of the diverse Florida fauna lead us to the conclusion that the boreal endemic genus *Baetisca* (Edmunds et al. 1976) was pushed southward during the Pleistocene glaciation. With the receding of the ice sheet, the streams of northwestern Florida provided ideal conditions for speciation." Perhaps the same process has produced similar effects on the other faunal groups that are now established in the state.

The Apalachicola River was doubtless not the only route of entry from the north. It seems probable that the Suwannee and its tributaries may also have brought in certain northern elements, such as *Brachycercus maculatus, Cercobrachys etowah,* and *Stenonema exiguum.* Very likely there has been some migration along the more easterly Coastal Plain region, where the streams descend from the higher Piedmont. However, the forms that may have entered Florida over such routes are few in comparison with those that have come in by way of the western path. Perhaps some species have entered by more than one course, moving in from the west and meeting to form a unified population in northern Florida.

Traver's paper on the Ephemeropteran fauna of Puerto Rico (1938) and infrequent records of other species from the West Indies show that the species of mayflies found in Florida have few affinities with the insular fauna. No species are shared in common, and the genera that occur in both regions are very widely distributed. Although other species of insects have become established in both Florida and the West Indies, the mayflies have been unable to do this principally because of the ecological conditions of South Florida. The great majority of forms described from the islands are inhabitants of streams, particularly of mountain streams, and even if these mayflies were accidentally introduced into Florida, establishment would be impossible in the south. If, by some rare chance, a fertilized female were carried to one of the permanently flowing sand-bottomed streams, it is barely possible that the species might gain a foothold, but apparently this has not occurred.

Among the factors used to explain the present distribution of rheotropic mayflies in Florida, temperature exercises a considerable influence. In a study of stream temperatures, Anderson (1971) divided Florida into four geographic areas (map 1), which show a definite north-to-south increase in stream temperatures. An interesting pattern of faunal distribution and stream temperature relationship is established when the mayfly distribution is superimposed over the four geographic divisions of the state. All 71 mayfly species occurring in the state are found in areas where the average annual stream temperature ranges from 64°F to 68°F (20.0°C–24.4°C) and 76+°F (24.4+°C). The mayfly fauna of Florida is highly concentrated in the northwestern section, where the stream temperatures are comparatively lower than in the rest of the state. Since temperatures in streams are less subject to variations than those in air, it is likely that average annual temperatures are more important to aquatic organisms than to terrestrial forms, for which the extremes of temperature are more likely to be the critical factors. It seems reasonable to suppose that the score or so of mayfly species (*Callibaetis floridanus, Choroterpes hubbelli, Stenonema exiguum, Tricorythodes albilineatus,* etc.) common to peninsular Florida and the western part of the state must have relatively wide limits of temperature toleration. Those species having more restricted temperature toleration (*Baetisca* spp., *Pseudiron centralis, Siphloplecton* spp.) have remained confined to the northern and northwestern parts of the state.

DISPERSAL OF MAYFLIES. The two most important factors involved in the dissemination of mayflies are wind and water. Of these, water is by far the more important for the actual establishment of species, since the immature stages of Ephemeroptera (except for a very few brackish water species) require fresh water.

The ability to fly allows for the greatest amount of movement of ephemerid species, although the adults are more or less confined to moist situations. The relatively short life span of the imagoes must necessarily limit the flight range of the insects; however, the area occupied by a species can be extended somewhat through voluntary flight of the adults.

Such small, feeble insects as mayfly imagoes are easily carried by the wind. This can be seen in the present distribution of the more diminutive genera such as *Caenis*, *Baetis*, and others, which are found over most of the world. In 1939 P. A. Glick of the U.S. Bureau of Entomology conducted a thorough study of the distribution of insects, spiders, and mites in the air by using traps suspended from the wings of an airplane. Although they were not numerous, he did collect mayfly adults at altitudes from as low as 200 feet to as high as 3000 feet.

Dr. Glick's results show that mayflies can be carried to extreme heights, and by means of horizontal air currents, doubtless to considerable distances. Perhaps the greatest obstacles to be surmounted in aerial distribution at great heights are the short adult life and the necessity of the fertilized female's reaching fresh water. Even when these two obstacles are overcome, the chance of encountering satisfactory ecological conditions is slight; current-loving species could hardly develop in a pond, and vice versa. The possibility of distribution through wind currents at great heights, therefore, seems to be somewhat remote, but the chance nevertheless exists and must be considered.

Dr. Glick pointed out that the intensity of air currents is a great factor in the distribution and dispersal of insects. Most of the insects collected by him were taken at lower altitudes when the surface wind velocity was from five to six miles per hour, and fewest when it was calm. Winds at low altitudes are of importance in transporting adult flying insects from one region to another, but their effects are probably local; however, local spreading continued over a long period would eventually greatly increase the range of a species. A combination of strong winds at low altitudes, flight, and proper ecological conditions would allow rapid distribution of mayflies.

Within the continental area as a whole, stream piracy probably has acted as an important agent for the dispersal of mayflies. By this means, species may spread from one drainage system to another and from one region to another, gradually coming to occupy very wide ranges. This would be of particular importance in the case of those species that as adults have limited powers of flight and those that are unable to withstand desiccation.

Flood conditions also affect the spread of a species during the immature stages. Because of increased stream velocity during floods, rocks, logs, pebbles, and other objects are moved violently downstream. Although most of the animals on these objects are destroyed, a few may survive to carry the species far from its original home. From the lower reaches of the stream to which the nymphs have been carried, the species may extend its ranges into new drainages by the flight of the winged stages.

As a corollary to floods, the more modest phenomenon of stream drift might produce the same results but on a much slower and smaller scale. The importance of drift as a populating mechanism has been recognized only in recent times but now receives much attention from aquatic biologists. The reverse of stream drift, upstream repopulation by the species, has also become the subject of many studies, and it is now known that the winged stage plays a major part in stabilizing the population throughout the stream system. Additionally, downstream drift continuing over long periods of time might accomplish the same results slowly as floods do swiftly.

It is barely possible that wading birds might play a part in transporting mayfly nymphs or eggs from one body of water to another. Many water-dwelling organisms have been transported successfully on the legs of such birds. If the flights of the birds are short, necessitating only little time out of the water, it is possible that certain mayfly nymphs or mayfly eggs might survive a journey of this nature.

When the various postulated distributional agencies are analyzed, it can be seen that mayflies are disseminated principally by flight, by winds near the earth's surface, by floods, by stream drift, and more rarely by high air currents and stream piracy.

HABITATS OF FLORIDA MAYFLIES. It is generally recognized that the mayfly population of a region is intimately related to the aquatic conditions of that region. From the standpoint both of the ecological distribution of mayflies and of physiography, Florida can be divided into five natural areas, as proposed in 1939 by C. W. Cooke (map 2). Numerous papers dealing with the geography and geology of the state have appeared since Cooke's work, but for our purposes the five regions are still quite satisfactory. The boundaries of these natural topographic areas shown on the map are rather arbitrary. The aquatic conditions in the Coastal Lowlands overlap to a great extent those conditions found in the other areas, but these boundaries are useful in delimiting in a broad way the freshwater situations as they occur in Florida.

The Coastal Lowlands almost everywhere lie less than 100 feet above sea level; the height of the other regions varies from 100 to about 300 feet. The drainage of each of these subdivisions of the state is closely linked with the topography.

The Coastal Lowlands are swampy and marshy, including, in their southern reaches, the great expanse of the Florida Everglades, and continuing northward into the mucklands of the Lake Okeechobee region, which in turn is continuous northward on the east and west with the lowlands of the coast.

The Central Highlands may be divided into two areas. The southern half is entirely a lake region where almost every natural depression has its own pond or lake; the northern part of this division includes not only lakes and ponds but also numerous surface and subterranean streams of all sizes.

The Tallahassee Hills and Western Highlands are rolling areas composed of red-clay hills, well drained by many small streams. The Marianna Lowlands, on the other hand, are chiefly flatwoods, swampy areas, and rolling sandy hills covered by pine forests with few permanently flowing streams.

Several large rivers rising in Alabama and Georgia flow through northwestern Florida and empty into the Gulf of Mexico. In the east, the large St. Johns River flows north along the border between the Central Highlands and the Coastal Lowlands.

DESCRIPTIONS OF HABITATS. In the following descriptions of mayfly habitats, we have confined our discussion to include those factors that appear to be crucial in determining whether mayfly nymphs will inhabit them or not, assuming that pollution is not a factor. There have been many fine studies in recent years characterizing physical and chemical characteristics of natural waters, but we are not reviewing them here. We are listing the authors of some of those that pertain particularly well to Florida freshwater habitats: Beck (1965), Benke et al. (1984), Blanton and Wirth (1979), Brezonik et al. (1969), Gilmore (1977), Hellier (1967), Hubbell, Laessle, and Dickinson (1956), Hynes (1970), Johnson (1972), Macan (1961, 1974), Means (1981), Nordlie (1972), Rosenau et al. (1977), Sloan (1956), and Yount (1956).

INTERMITTENT CREEKS

In Florida, there are relatively few intermittent streams. These few are, for the most part, merely connecting canals between swamps, ponds, or other bodies of water, the levels of which fluctuate continually according to the amount of precipitation. Intermittent streams are rather poor habitats for mayflies. Only the very tolerant *Callibaetis* and *Caenis* nymphs can withstand the alternating conditions in the creeks produced by the continual changes in the levels of the bodies of water connected by the intermittent streams. Vegetation is usually abundant but differs from the type found in constantly flowing waters. Also, the drying of parts of the canal bed produces conditions that stream-inhabiting mayfly nymphs cannot long endure, so that even if by chance a species should become established during the period of flow, the cessation of this flow would bring about the death of the immatures.

PERMANENT CREEKS

Permanently flowing streams are the most important of the mayfly habitats in Florida. The creeks of this area may arbitrarily be divided into the following categories:

Sand-bottomed creeks with little vegetation
Sand-bottomed creeks choked with vegetation
Silt-bottomed creeks with little vegetation
Silt-bottomed creeks choked with vegetation

Sand-bottomed creeks with little vegetation. These are small, shallow, gently flowing streams with sandy beds. The creeks vary from 1 to 40 feet in width, and in depth from a couple of inches to as much as 5 feet. The bottom is composed of loose, rolling sand, which builds up in midstream into small ridges behind which small masses of debris accumulate. Large rocks almost never occur in Florida streams, but pebbles may be found imbedded in riffles where the water becomes quite shallow. There are occasional pools, but they are not a conspicuous element of the streams. The pools are usually small, quiet areas near the banks or at curves. Debris accumulates to a rather marked degree in some of the streams, almost any obstacle forming a nucleus for the accumulation of much leaf drift, sticks, and other objects. Tree trunks frequently form dams and give rise to riffles, while the tangle of branches and twigs provides a network in which much detritus becomes trapped. Silt accumulates near the shore and in places may produce rather thick deposits, in some streams even forming a layer more than two feet in thickness; however, the silt deposits in the sand-bottomed streams are usually sparse and of little consequence. Near shore, leaf drift becomes a fairly important habitat, for many insects are harbored in this material. In the almost stagnant shore pools the leaf debris, interspersed with silt, may be several layers thick. The flow of water in the sand-bottomed streams is never rapid; rather the flow is gentle, with the water surface seldom breaking. Most of these streams are circumneutral to slightly acid, but some may be pronouncedly acidic. Nearly all of them have tinted waters varying in shade from almost colorless to a strong tea color, according to the area drained and to the amount of rainfall. Most of the streams drain flatwoods, hammock lands (hardwood forests), or swampy areas, and are fed by springs or diffuse seepage areas. Vegetation is almost completely absent from the streams except for a few scattered *Orontium* plants and an occasional clump of *Polygonum* near the quiet shore zone; however, these plants are not particularly important from the standpoint of furnishing habitats for mayfly nymphs.

Sand-bottomed creeks choked with vegetation. Sand-bottomed streams occur mostly in the northwestern part of Florida beyond the Apalachicola River. The beds of the creeks are composed of fairly loose sand; instead of being almost bare, as in the type of stream mentioned above, they are filled with dense growths of *Vallisneria, Sagittaria,* and *Potamogeton,* which in turn are thickly covered with algae. There may be some debris collected in the slower areas near shore, but in midstream the vegetation is swept clean, although an occasional partially submerged log may lie among the plants. These streams are usually not much more than 20 feet across and may be as deep as 5 feet at the center. In their deeper parts, the vegetation tends to disappear and may be entirely absent from exceptionally deep stretches. The rate of flow is moderate but seldom strong enough to cause any marked disturbance of the water surface. Mainly, the creeks drain scrublands and high pine and hammock country. The water is much lighter in color than that of the sand-bottomed creeks with little vegetation; however, the water is usually definitely acidic, with a pH approximating 6.0. Silt deposits are not so pronounced in these streams as in those of the first class, and debris along the shore is likewise less in quantity.

Silt-bottomed creeks with little vegetation. Silt-bottomed streams are rather common in the northern part of the Central Highlands of Florida. The stream bottom is covered with a layer of silt overlaying the sand and varying from a few inches to several feet in depth. The rate of flow is comparatively slower than that of the sand-bottomed streams, but it is steady and quite perceptible. The water is definitely acidic and usually a rather strong tea color. The silt bottom is frequently overlaid by layers of leaves and strewn with much other debris, but there are few or no plants in the stream proper. Near shore, *Polygonum* and various sedges and grasses may be present, but they are not especially abundant. This type of creek averages about 20 feet in width and from a few inches to 3 feet in depth.

Silt-bottomed creeks choked with vegetation. Not especially common in Florida and confined mostly to the northwestern part of the state, silt-bottomed creeks choked with vegetation are shallow, one to three feet deep, often wide, very meandering in their courses, and sometimes braided. The vegetation is dense and may include plants characteristic of more slowly flowing or even stagnant water, such as *Ludwigia, Polygonum,* and *Pontederia.* Other plants also found in the course of the stream include *Vallisneria, Potamogeton,* and *Sagittaria,* as well as many algae. The silt in the streams is very loose and may be as much as three to four feet in thickness. This material is soft, fluffy, and somewhat sticky and at the slightest disturbance stirs up and clouds the water. There is usually a broad floodplain, over which the stream spreads during high water, until all vegetation except for larger bushes and trees is completely submerged. There is a constant flux of channels due to the flooding. In the shallower zones, the rate of flow of the water is negligible and during rare severe cold spells may partially freeze over.

RIVERS

Stagnant rivers. Stagnant rivers are confined chiefly to the southern portion of the Florida peninsula. Many have been dredged to serve as drainage canals for the Everglades. Strictly speaking, these rivers are not stagnant, but the flow is so slight that only rheotactic organisms that are very tolerant to stagnation can live in them. The Miami River, now heavily polluted, is an ideal example. Until the drainage plans were carried out, the much abused Miami River was in places a shallow, moderate- to swift-flowing stream cutting through the limestone that forms the bedrock of south Florida. In his book *Hunting and Fishing in Florida,* Charles B. Cory described and illustrated the Miami River as it was in 1895; the picture he painted differs enormously from the present state: "The Miami River, which runs from the Everglades into Biscayne Bay, is probably the only river in Florida which has a fall or rapid worthy of the name. For about a half a mile at the head of this stream there is considerable fall. At this point the river is shallow and not navigable for boats, and has a very rapid current, in which 'Cavalia' (*Caroux hippus*) are numerous and may be taken with an artificial fly." Dredging has completely eliminated all rapids from the river, and flow is not perceptible to any degree, even during the rainy season. The salt water of Biscayne Bay backs up into the river and produces a brackish condition some distance from the mouth of the canal.

Stagnant rivers have fairly heavy growths of aquatic vegetation near their shores, but they become deep rapidly, and in the deep regions the plants are quite limited. The rivers vary from 100 to 200 feet in width in the widest places, and usually range from 15 to 20 feet in depth. Some of the rivers show a pronounced flow during the rainy season and may even be subject to floods. Since the digging of the drainage canals, however, this is the exception rather than the rule. There is very little deposit of silt in these streams, and the bottom is mostly bare limestone.

Slow-flowing, deep rivers. Nearly all of the larger rivers of Florida, such as the Suwannee and the Apalachicola, are slow-flowing, deep rivers, draining extensive areas. The Suwannee drains the Okefenokee Swamp, and the Apalachicola, now dammed just at the Florida-Georgia state line, rises in the foothills of the Appalachians and the Piedmont of Georgia and Alabama. The larger rivers have continuous flow. During excessive rains they spread out over their floodplains. In the large rivers, vegetation is limited and occurs principally near the shores in protected places where the current is slow. The vegetation is more characteristic of standing water than of streams. Although there may be some rocks near shore in the shallow water and silt may be deposited in protected areas, for the most part the bottoms are composed of hard clay or limerock. The Apalachicola River is often very muddy owing to the heavy burden of silt it brings down from the Georgian highlands. The Suwannee is much clearer, although the water is generally strongly colored by the various organic acids coming from the swamps drained by the river. The St. Johns River has a much slower current than the other two streams; north of Lake George the flow is slight and is affected by the tides. The St. Johns has been plagued by masses of water hyacinths growing at the shore; in recent years, however, there has been a concerted effort to eradicate them. When the hyacinths were flourishing, conditions were not very different from conditions in the lakes of the Central Highlands, which supported luxuriant growths of this pest plant. Nearer the headwaters of the St. Johns, *Vallisneria* and *Sagittaria* grow in the stream, and water flow is more noticeable. Much of the water of the river originates in swamps, producing the brownish coloration of the stream.

Larger calcareous streams. The Silver River, the Wakulla River, and the Santa Fe River are examples of larger calcareous streams, which are, in general, distinctly basic in their reactions and smaller than those described above. Most of these streams rise from springs; they are clear, cool, and moderately flowing with rather dense growths of vegetation in the stream proper. Vegetation is composed chiefly of *Vallisneria, Sagittaria, Najas, Ludwigia,* mosses, and many algae, which in the shallower zones form dense mats completely covering the floor of the stream. The water may be colorless if the source is confined to springs, but if swamp waters also contribute to the stream the water may be brown. Many of these rivers have sand bottoms. Thick deposits of calcareous silt may occur in the quieter shallow zones. Leaf drift and other debris become entangled in fallen trees and other catchalls and form an important habitat for many mayflies and other organisms. In some of the rivers there are outcrops of limestone; in the Santa Fe River, specifically, there are many loose rocks that are important habitats for aquatic organisms. The depth of the streams varies from 3 feet to 20 feet or more, the width from 75 to 300 feet or more. Faunistically, this type of stream is the richest found within the boundaries of Florida, both in numbers of individuals and in species. Carr (1940, p. 25) stated that "optimum conditions [for fluvial organisms] apparently exist in those rivers which run over ledges of exposed limestone, or which receive most of their water from calcareous springs."

DITCHES AND POOLS

Roadside ditches. These are extremely rich situations for aquatic organisms if there is permanently standing water in them. The ditches are highly varied in appearance, but the fauna in them is fairly constant. In some ditches there are dense growths of *Pontederia,* which is the predominant plant. The water is shallow in the zone of pickerelweed but may become much deeper beyond this region; in the deeper parts other vegetation that can withstand greater degrees of submergence occurs. The bottom of the ditches is usually covered with grasses and may have heavy growths of *Micranthemum umbrosum, Ludwigia,* and *Polygonum.* Algae form dense mats in some of the ditches, along with *Utricularia, Ceratophyllum, Potamogeton,* and *Myriophyllum.* At times during the summer the water may become very warm; in winter it is often quite cold, with ice occasionally forming over the surface in the northern part of the state. The water in the ditches is usually acid but may be basic; the lowest pH we have recorded was slightly above 4.0. The depth of the water varies from a few inches to as much as 4 or 5 feet, and the width of the ditch (the part containing the water) may be from 1 to 15 or more feet.

Pools. Pools are the small and transitory bodies of water left by the retreat of a stream or formed by heavy rains. Very little or no aquatic vegetation occurs in them. Immature insects are only rarely found in the pools. They are usually entrapped stream insects, most of which perish when the pools disappear during dry weather. We have found mayflies in such places (*Baetisca obesa* nymphs in large numbers in puddles left by the receding Chipola River), but they cannot survive there for long. In some of the pools there may be several layers of leaf debris. Silt accumulates between the leaves, and algae begin to grow, continuing as long as the water remains.

PONDS

The ponds of Florida may be divided into several types, but nearly all of them share one characteristic in common—they seldom have surface streams draining into or from them.

Sinkhole ponds. Sinkhole ponds are formed by the dissolution of underlying limestone. Rainwater percolating downward to the water table dissolves vertical chimneys in the limerock into which the surface cover may collapse gradually or suddenly, producing a steep-walled, open sink. Where the cover is thicker or less compact, a saucer- or funnel-shaped depression may result. There are many of these ponds of sinkhole origin in Florida and particularly in the Gainesville area. Though some of the them are dry, the great majority have standing water maintained at a fairly constant level, because the water table is generally high enough to supply the ponds continually. The sides of the ponds both above and below the water level are steep, and the zone of rooted vegetation is very limited. The sides of the sinkholes above the water are usually covered with vegetation that extends from the edge of the water up to the rim of the depression. In many of the sinkholes a narrow sand beach may be formed where the slope of the sides levels off, but the shore zone extending into the water from this beach is very narrow, and the drop to deep water is rapid. The sinkhole ponds are usually about 100 to 300 feet in diameter and are mostly round in shape. Some of the larger ponds are formed by the coalition of two or more sinkholes.

There are two chief types of sinkhole ponds: (1) ponds with their surfaces free of vegetation; and (2) ponds with their surfaces covered by vegetation. The first of these is one of the common types of sinkholes encountered in peninsular Florida. The margin of the pond has a fairly rich growth of both submergent and emergent vegetation, which extends outward to the region where the drop-off to deep water occurs. The plants are principally *Sacciolepis striata, Polygonum, Mayaca fluviatilis, Panicum,* and some *Typha,* as well as numerous species of algae. The sudden drop to deeper water begins at a depth of about 4 feet and extends to a depth of about 10 feet; thence the drop continues more gradually to about 20 feet. In many of the ponds there may be deeper holes, such as the one found in Lake Mize (Harkness 1941), which reaches a depth of nearly 80 feet over a very small area. In the shallower portions the bottom is sandy and covered with patchy growths of *Utricularia.* There are only small deposits of silt in the shallower zones, but in the very deepest parts the bottom may be thickly covered with black, dense silt in which practically anaerobic conditions exist and from which larger organisms are almost entirely absent. The water varies from colorless to a strong tea color depending on the type of region drained by the pond. Many of the ponds are rather turbid, and this turbidity, combined with strongly tinged water, allows little penetration of light to the deeper parts. The water varies in reaction from pond to pond, being acidic, circumneutral, or slightly basic.

The second type of sinkhole pond includes two principal varieties: (1) those covered with water hyacinths, *Eichhornia crassipes*; and (2) those covered with duckweed, *Lemna obscura,* mud-marys, *Spirodela punctata,* and *Azolla caroliniana.* The first variety of pond may have a marginal ring of open water with the water hyacinths concentrated over most of the remaining area, or the entire surface may be covered with water hyacinths. If there is some open water, submergent vegetation may take root and become fairly well established, but usually the water hyacinths are the only plants of any importance in the ponds.

The duckweed-covered ponds seldom have any submergent vegetation growing in them, for the entire surface is covered with a single layer of duckweed that cuts off light from any rooted vegetation that might attempt growth on the pond bottom. When there is any wind the duckweed piles up and leaves clear areas on the water surface, but as soon as the wind dies down, the plants again spread evenly over the surface. Amphipods living among the duckweed are very numerous in the ponds, but bottom organisms are scarce, probably because of the small amount of available oxygen. The bed of the duckweed-covered pond has rather thick accumulations of black silt overlaying the sandy bottom. Almost anaerobic conditions exist in the silt, which is heavily loaded with hydrogen sulfide.

Fluctuating ponds. Fluctuating ponds constitute one of the more frequently encountered types of Florida ponds. Water fills shallow basins—some merely depressions in the original sea-laid sands, the majority produced by solution of underlying limestone or by wind action. The level of the water in these hollows varies with the amount of rain and surface runoff. Although there is great fluctuation in the area occupied by the water because a slight rise or fall causes marked spread or retreat of the margins, the depth usually does not change greatly because of the shallowness of the pond. True aquatic vegetation follows the rise and fall of the water to some extent, but it is chiefly confined to the part of the pond below the more permanent water level. Rogers (1933) stated that "these periodic and sporadic fluctuations (due to rainfall) prevent the development of any permanent vegetation within the broad zone of fluctuation. As the water recedes in the dry season, it leaves a belt of saturated earth in which some grasses and sedges spring up among mats of stranded algae and other aquatic vegetation. . . . The permanent water is usually filled with submerged, floating, and emergent aquatic plants and may support extensive floating mats of green algae."

The vegetation includes many true aquatics such as *Pontederia, Utricularia, Polygonum, Micranthemum,* and *Typha,* as well as *Hydrocotyle,* maiden cane (*Panicum*), and other semiaquatics. Many of the ponds have growths of *Nymphaea,* but very few are covered with water hyacinths. Plants are not confined to a shore zone as in the sinkhole ponds but may extend much farther out and, in some instances, may completely penetrate the ponds. Although the bottom of the fluctuating pond is mucky, the layer of silt is not deep. The water is subject to rapid changes in temperature and is much influenced by external weather conditions. There is normally a slight tint to the water, which is usually acidic.

Temporary woods ponds. Formed in depressions in hardwood hammocks, temporary woods ponds are of a more or less temporary nature. The vegetation present, however, is such as to indicate its habitual occupation of the depression. Blackgum (*Nyssa biflora*), button bush (*Cephalanthus occidentalis*), willow (*Salix nigra*), and bladderworts (*Utricularia* sp.) are frequently found in the ponds and around their margins. If the water remains for a sufficient length of time, other more succulent vegetation will become established. After the water has been standing in the depression long enough to allow growth of algae, many of the usual pond animals begin to migrate to and become established in the pond.

Sporadic ponds. The sporadic ponds, which are of a rather temporary nature, may disappear for a brief period or even permanently during the dry season. The ponds are shallow and may be large or small, depending on the depression and the drainage of the region.

Jerome sink. Because Jerome sink is so unusual, it deserves special classification. A description of the sink is included in the discussion of the ecology of *Choroterpes hubbelli.*

LAKES

Nearly all lakes in Florida are the result of solution of underlying limestone; however, such lakes as Lake Okeechobee seem to occupy basins that are natural depressions in the surface formed as the land rose during the last geologic period. Cooke (1939, pp. 100–101) stated: "Many Florida lake basins are simple sinks that have always been tributary to the groundwater supply and never have had a surface outlet. Others at one time or another formed part of the surface drainage and therefore were connected with the river system. Their history is complicated, for the fluctuations of sea level and the consequent fall or rise of the water table gave opportunity alternately to deepen the basins or to flood them. Some of them appear to have been estuaries during higher stages of the sea, for the sand-covered terraces around them stand within the limits of altitude of the coastal terraces." Cooke concluded that Lake Okeechobee, Lake Istopoga, Lake Kissimmee, Crescent Lake, Lake George, and others originated as hollows in the sea bottom.

Sand-bottomed lakes. The sand-bottomed lakes are the most common type of lake found in Florida. There are literally thousands of these lakes in the Central Highlands, being particularly numerous in Lake County, and many have undergone extensive eutrophication in recent years. The lakes vary in size from a quarter of a mile to 9 or 10 miles in width. The depth is not correspondingly great, and most of them are shallow, not more than 40 or 45 feet deep at their deepest holes. There is little vegetation except at the margin, and this is chiefly *Sacciolepis striata, Utricularia,* and algae. Wave action is slight, but it is probably sufficient to prevent the growth of other aquatic vegetation along the sandy shore. The *Sacciolepis* extends out into the lakes to a depth of five or six feet. Beyond this zone vegetation is limited to submergent plants such as *Utricularia,* which lie on the sand bottom as far out as there is sufficient light penetration for normal photosynthesis to take place. In this region; some silt is intermingled with the sand, but much of the sand is bare. Beyond a depth of about 20 feet, silt accumulates and covers the bottom sand with a layer several inches deep. With increase in the depth of the lake there is a direct increase in the amount of silt. The silt may reach a depth of a foot or more in the very deep parts of the lakes, where it is a very thick, black, fine, and oozy mud in which few organisms live. Along the shore some debris collects but is not abundant; the debris forms a habitat for many Florida insects that are normally found in streams. Probably the wave action in this region is sufficient to oxygenate the water and produce conditions that simulate those found in the moderately flowing streams of the state. The water of the lakes varies from very clear to strongly tea-colored. Turbidity is also variable according to the lake. Most of the lakes are circumneutral, ranging not much more than 0.5 on either side of a pH of 7.0.

Silt-bottomed lakes. Newnan's Lake near Gainesville is a good example of a silt-bottomed lake. The lake is large—about four miles long and two miles wide, averaging about six feet in depth (Brezonik et al. 1969). It is bordered by a ring of cypress trees that extends from dry land out into the water. A dense growth of water hyacinths, which were matted among the bases of the cypress trees and extended out onto the lake surface as far as there was a protected zone, formerly margined the lake. With every shift in the direction of the wind, masses of water hyacinths would break free and float across the lake, pushed onward by the wind. Frequently during a period of sustained moderate winds, the lake was dotted with numerous floating "rafts" of water hyacinths; eventually the plants piled up along one shore until the wind changed and sent them sailing back to the opposite shore. The continual rain of dead water hyacinths onto the bottom of the lake gave rise to a thick layer of loose fluffy silt that completely covered the bottom to a depth of several feet. Few living organisms could be found in these bottom deposits because such conditions are not conducive to life. In recent years the hyacinths have been controlled. The lake is now virtually free of them and appears to be recovering from the long invasion by this pest species. The water of the lake is brown-tinged and generally rather turbid.

Numerous other lakes in the Central Highlands belong in this same category. Orange Lake, one of the larger lakes of the region, is similar to Newnan's Lake in its type of bottom, but it is deeper, has much rooted vegetation such as water bonnets, and is somewhat exceptional in having numerous floating islands of vegetation. Some of the floating islands are large enough to support trees, but the great majority are composed of small clumps of vegetation that float about, changing location with each change in direction of the wind. An invasion of *Hydrilla,* an introduced plant, has occurred in recent years and the lake waters have become choked with it. What its ultimate effect will be is still unknown, but there is some belief that it may benefit certain species of fish living in the lake.

According to Rogers (1933), "[T]hese lakes show great variations in their aquatic vegetation; in many, the succession is directly toward swamp conditions with extensive development of cypress along the muddy shores; in others there is a distinct development and zonation of marsh vegetation before the shallow water is invaded by cypress or hardwood swamps."

Disappearing lakes. Certain large lakes in the northern part of Florida go dry during periods of drought. Lake Iamonia, which has gone dry several times since the area was settled, is an ideal example of a disappearing lake. There is another near Lake City that is said to go dry "once every seven years." These lakes are shallow and in most respects are similar to the silt-bottomed lakes in formerly supporting an abundant growth of water hyacinths (prior to control procedures) and in being ringed by cypress. Although at their maximum extent the disappearing lakes are fairly large, they vary greatly in size with seasonal fluctuation in depth.

MARSHES

Marshes are very common in peninsular Florida, particularly in the lower regions. Many of them have disappeared in recent years as they have been drained to accommodate the greatly increased human population of Florida. Marshes may be very limited in extent or quite large, according to the size of the original basin. Many ponds and lakes have become converted into marshes and many others are in the process of transition. The water is shallow and vegetation extends throughout, growing very profusely. The predominant plants are emergent and include cattail, pickerelweed, maiden cane, saw grass, water lilies, smartweed, and various grasses. Submergent plants are prominent and include *Ludwigia, Micranthemum, Myriophyllum,* and many algae. The water is rather warm during the summer and may freeze at the margins during prolonged periods of cold weather. The filling of lake and pond basins is rapid, and the great amount of decaying vegetation quickly builds up deposits of peat, which finally replace the water of the marshes. The level of the water is subject to great fluctuations according to the amount of rainfall, and at times the marshes go completely dry; however, during the greater part of the year when rainfall is normal, water remains in them. The marshes are distinctly acidic, some having a pH below 3.6; but this condition is local, and at different points in the same marsh the pH may range from 3.6 to 6.0 or higher. The organisms found in the marshes are not essentially different from those occupying similar habitats in ponds and along lake margins, for conditions in the marshes are very much like those of the pond margins. The principal differences are that emergent vegetation occurs throughout the water rather than being confined to a shore zone and that the marshes are shallow—not much more than three feet deep at their deepest point.

Another type of marsh found in the central part of Florida is very similar to the marshes just described, except that vegetation is composed principally of *Polygonum* and saw grass (*Cladium jamaicense*), with *Pontederia* much more limited in extent and with no *Nymphaea* present; however, the organisms inhabiting these marshes are identical with those found in the other types.

THE EVERGLADES

The Everglades are so distinctive that they require special treatment. Because they are so extensive and drain southward from Lake Okeechobee, they are sometimes referred to as a "river of grass." C. W. Cooke (1939, pp. 55–56) states:

> The Everglades occupy a nearly level plain, which slopes from 15 feet above sea level at the south shore of Lake Okeechobee to sea level at the tip of the Peninsula, a distance of more than one hundred miles. On the west the Everglades merge into the Big Cypress Swamp, which presumably is a few feet higher. On the south and southwest the Everglades are bounded by mangrove swamps, which separate them from the open waters of Florida Bay and the Gulf of Mexico. . . .
>
> The Everglades, as the name implies, are open grassy meadows. Here and there clumps of trees lend variety to the landscape. . . .
>
> The Everglades differ from most swamps and boggy places in the scarcity of trees and in their lack of ordinary mud and clay. The entire Everglades are underlain by hard limestone, which is cushioned in the lower, generally flooded parts by deposits of peat. . . . Where peat is absent, bare limestone shows at the surface.

Since drainage ditches have been put through the Everglades, during the dry periods the land becomes very susceptible to burning, and much of the peat has been destroyed by fire. In the rainy season most of the Everglades is covered to a depth of two or three feet by water, which overflows from the drainage canals. When this flooding occurs, the normal biocoenoses of the canals are no longer confined to the channels but

spread uniformly over the inundated areas; however, the density is thin compared with the concentration of organisms within the canals themselves. Only pond, swamp, and stagnant water animals can maintain themselves in this environment, and the mayflies associated with this region, *Callibaetis floridanus* and *Caenis diminuta*, are typical pond and swamp inhabitants that are found throughout Florida.

Saw grass is the predominant vegetation and grows profusely throughout the marsh. The lack of shade trees allows the water to become very warm, except in the canals where the water temperature is several degrees cooler. There is little submergent vegetation where the overflowing water has spread over the glades, but after it has stood for some time algae become noticeable.

SWAMPS

Cypress swamps. Cypress swamps are numerous in Florida. Some, such as the Big Cypress Swamp, occupy huge areas. The cypress swamps are formed in shallow depressions in flatwoods regions. Over most of the year during periods of normal rainfall standing water is present. Not only does cypress occur in them, but black gum is also very common. Herbaceous vegetation is, however, limited, though there may be clumps of *Polygonum, Utricularia,* and some sphagnum along with masses of algae. The water is usually tinted by humic acids and its reaction is definitely acidic. Depth of water varies considerably, but it is seldom over three or four feet.

Bayheads. Bayheads are very similar to cypress swamps, but the vegetation is much denser, and the bayheads often form the headwaters of small creeks. The plants consist mostly of small trees and shrubs and also include some cypress. The other trees are principally sweet bay, black gum, wax myrtle, red maple, loblolly bay, titi, Virginia willow, and dahoon holly. The growth of the shrubs is so dense as to be almost impenetrable in places. Water stands in the depressions for the major part of the year, and it is only during the very driest seasons that it entirely disappears from the bayheads.

SPRINGS

The most recent comprehensive description of the springs of Florida is that of Rosenau et al. (1977), in which each known spring is described in some detail. C. W. Cooke (1939, pp. 88–89) wrote of the Florida springs as follows:

> Most of the large springs of Florida are artesian. The water flowing from them rises through deep, generally vertical holes in limestone, some of which holes open into caverns, presumably nearly horizontal, through which flow underground rivers. . . .
>
> The cavity through which water ascends to an artesian spring is generally a former sink in which the direction of motion of the water has been reversed by the rise of the water table. If the water table were to fall below the mouth of the cavity, the spring would cease to flow and would revert to the form of a sink, provided the tubular cavity leading to the spring does not penetrate an impervious stratum, which might confine the water below it under pressure.

The runs of some of the larger springs have been discussed above under "Larger Calcareous Streams," but most spring runs are much smaller. Two of these, Homosassa and Weeki Wachee, were studied in detail by Sloan (1956). Vegetation is very dense just below the exit of the spring, but around the spring itself there is nothing but bare sand. Immediately beyond the periphery of the "boil," *Chara*, *Myriophyllum*, *Ceratophyllum*, *Vallisneria*, *Sagittaria*, and *Ludwigia* become very abundant. The surface of the vegetation close to the spring is usually covered with a coating of calcium carbonate deposited from the water as the bicarbonate exposed to the air changes to the carbonate. The low oxygen content of the water is reflected in the small populations of truly aquatic insects in this region; however, snails of the genus *Elimia* are exceedingly numerous on the vegetation, and *Pomacea* occurs frequently on the bottom sands. Approximately a quarter of a mile below the head of the springs a more abundant insect fauna becomes noticeable, and in this region the plants are quite free of the calcium carbonate. The water of the springs is crystal clear, cool, and alkaline.

5

KEY TO FLORIDA MAYFLIES

Adults

1 Forewing venation complete or only moderately reduced, numerous longitudinal veins present behind R_1 (fig. 11). Male genital forceps present (fig. 45) 2

Forewing venation greatly reduced with only three or four longitudinal veins behind R_1 (fig. 26). Male genital forceps absent (fig. 68) .... (Oligoneuriidae, Oligoneuriinae) .... *Homoeoneuria dolani*

2(1) Vein MP of hind wing forked near margin; stem longer than fork (fig. 34). Forelegs extensively dark brown; middle and hind legs pale .... (Oligoneuriidae, Isonychiinae) *Isonychia* . . . 3

Vein MP of hind wing (if present) simple and unforked or forked near base. Legs variable in color 6

3(2) Male subgenital plate broadly concave or with only a slight posteromedian emargination (fig. 71). Penes dorsally with acute sclerotized lateral and marginal serrations on incurved flap (fig. 73). Female subanal plate with no or only shallow posteromedian emargination (fig. 88) .... Subgenus *Prionoides*, *Isonychia* (*P.*) *sayi*

Male subgenital plate with deep posteromedian emargination (fig. 72). Penes dorsally without incurved flap bearing

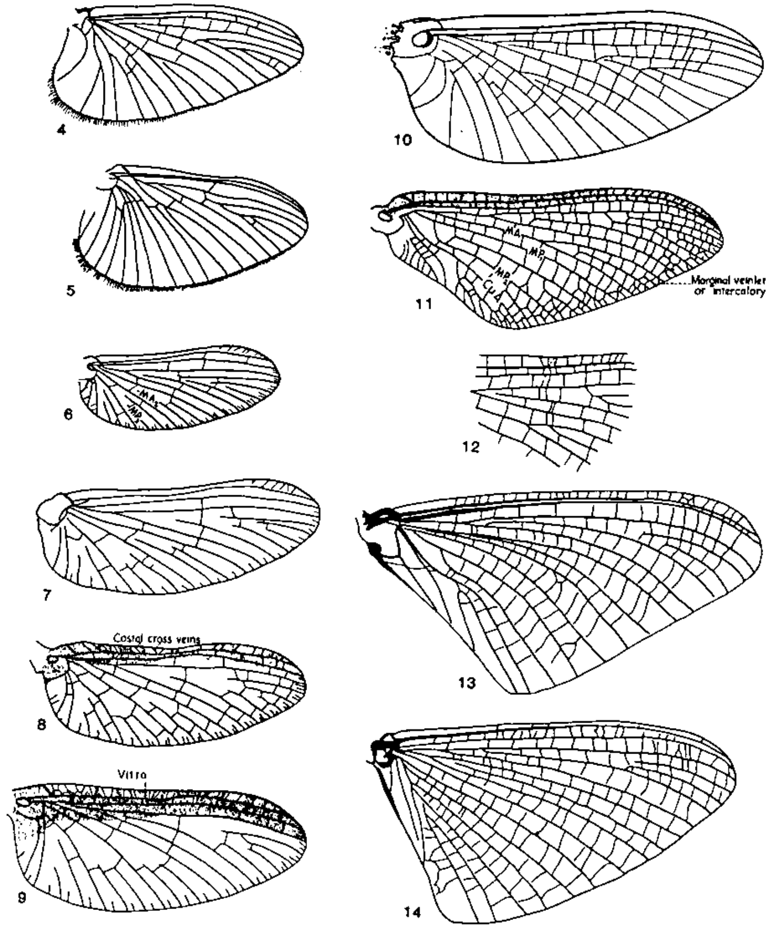


Fig. 4. *Tricorythodes albilineatus*, wing of male. Fig. 5. *Caenis diminuta*, wing of male. Fig. 6. *Baetis propinquus*, forewing of male. Fig. 7. *Centroptilum viridocularis*, forewing of male. Fig. 8. *Callibaetis pretiosus*, forewing of female. Fig. 9. *Callibaetis floridanus*, forewing of female. Fig. 10. *Leptohyphes berneri*, forewing of male (drawn by R. K. Allen). Fig. 11. *Hexagenia orlando*, forewing of male. Fig. 12. *Ephemera simulans*, midsection of forewing of male. Fig. 13. *Tortopus incertus*, forewing of male. Fig. 14. *Dolania americana*, forewing of male.

sclerotized teeth or serrations. Female subanal plate with a moderate to deep posteromedian emargination (fig. 89) .... Subgenus *Isonychia* . . . 4

4(3) Fore tibia white in middle, dark brown at base and at apex. Penes as in figure 76 .... *Isonychia* (*I.*) *arida*

Fore tibia entirely brown, sometimes darker at base and apex. Penes as in figures 74 and 75 5

5(4) Penis lobes narrowly rounded distally (fig. 75). Wing veins whitish to very light brown .... *Isonychia* (*I.*) *berneri*

Penis lobes broadly rounded to subtruncate distally (fig. 74). Wing veins yellowish brown to black ...... *Isonychia* (*I.*) *sicca*

6(2) Penes longer than forceps. Female antennae inserted on prominent anterolateral projections. Four or more long cubital intercalaries usually present in forewing (fig. 14) .... (Behningiidae) *Dolania americana*

Penes shorter than forceps (fig. 45). Female antennae not inserted as above. Three or fewer long, cubital intercalaries present (fig. 11) 7

7(6) Base of veins MP_2 and CuA of forewing strongly divergent from base of vein MP_1 as in fig. 11. Hind wing with numerous veins and crossveins (fig. 37) 8

Base of veins MP_2 and CuA of forewing slightly divergent from vein MP_1 as in figure 16. Hind wing not as above ... 15

8(7) Basal costal crossveins weak or atrophied; costal angulation of hind wings acute or at right angles. Median carina on prosternum................. (Neoephemeridae) *Neoephemera* . . . 9

Basal costal crossveins well developed (fig. 11); costal angulation of hind wings usually rounded (fig. 44). If nearly acute or at right angles, no median carina on prosternum 10

9(8) Small purplish band present in distal four-fifths of femora; tarsal segments 2–4 of middle and hind legs ringed with purplish gray. Caudal filaments annulate .... *Neoephemera youngi*

Legs extensively colored with purplish gray. Caudal filaments without annulations .... *Neoephemera compressa*

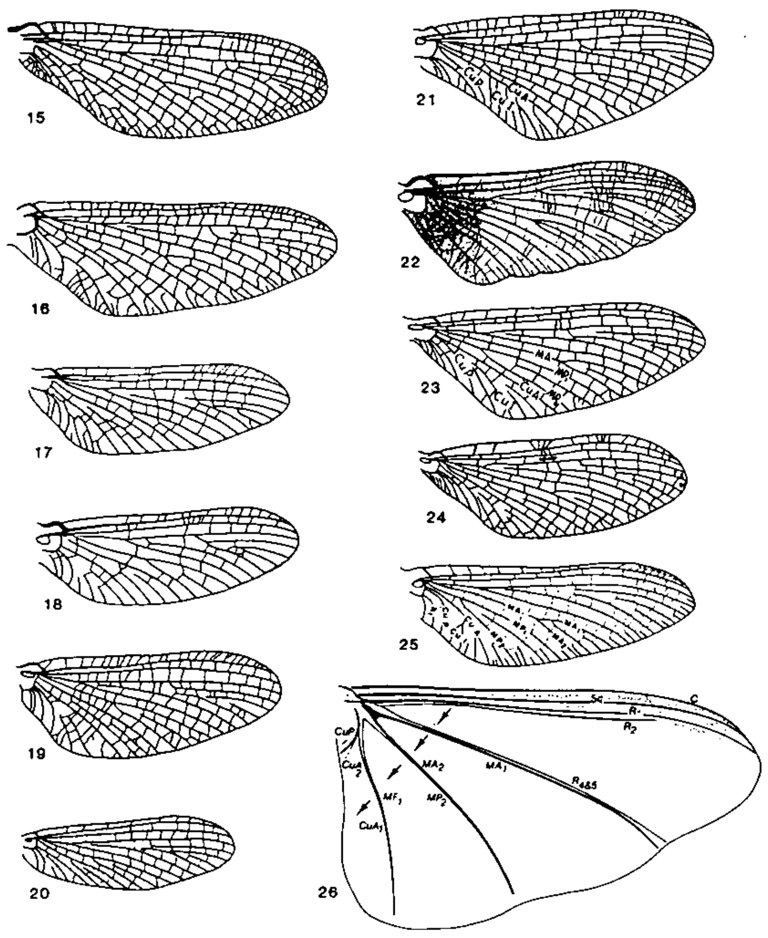


Fig. 15. *Siphloplecton brunneum*, forewing of male. Fig. 16. *Leptophlebia intermedia*, forewing of male. Fig. 17. *Habrophlebia vibrans*, forewing of male. Fig. 18. *Choroterpes hubbelli*, forewing of male. Fig. 19. *Paraleptophlebia volitans*, forewing of male. Fig. 20. *Habrophlebiodes brunneipennis*, forewing of male. Fig. 21. *Isonychia arida*, forewing of male. Fig. 22. *Baetisca rogersi*, forewing of male (from Berner 1940a). Fig. 23. *Stenonema smithae*, forewing of male. Fig. 24. *Stenacron interpunctatum*, forewing of male. Fig. 25. *Eurylophella temporalis*, forewing of male. Fig. 26. *Homoeoneuria dolani*, forewing of male.

10(8) Middle and hind legs of male and all legs of female feeble, nonfunctional. Basal segment of male genital forceps with lateral projections .... (Polymitarcyidae) *Tortopus incertus*

All legs of both sexes well developed, functional. Basal segment of male genital forceps not as above 11

11(10) Male pronotum well developed, no more than twice as wide as long. Penes variable, not long and tubular. Caudal filaments of female longer than body .... Ephemeridae ... 12

Male pronotum reduced, about three times as wide as long. Penes long and tubular (fig. 48). Caudal filaments of female shorter than body .... (Palingeniidae) *Pentagenia vittigera*

12(11) Crossveins of wings crowded together near bullae (fig. 12). Wings with distinct pattern of dark markings. Terminal filament as long as cerci .... *Ephemera simulans*

Crossveins of wings not crowded near bullae. Wings without a pattern of dark markings, although crossveins may be darkened. Terminal filament vestigial .... *Hexagenia* ... 13

13(12) Penes slender, somewhat beak-shaped (fig. 46). Abdomen banded longitudinally with dark and light areas .... *Hexagenia bilineata*

Penes more or less hooklike (fig. 47). Abdominal markings not as above (figs. 159, 160) 14

14(13) Hind wing with purplish brown border, large dark spots near middle; if brown border and blackish spots present, outer segment only of middle and hind legs dark on underside. Abdominal color pattern as in figure 159 ..... *Hexagenia limbata*

Hind wing without prominent purplish brown border and no large blackish spots (fig. 37); outer segment of middle and hind legs with dark brown markings on underside. Abdominal color pattern as in figure 160 .... *Hexagenia orlando*

15(7) Three well-developed caudal filaments present 16

Two well-developed filaments (cerci) present; terminal (median) filament rudimentary or absent 36

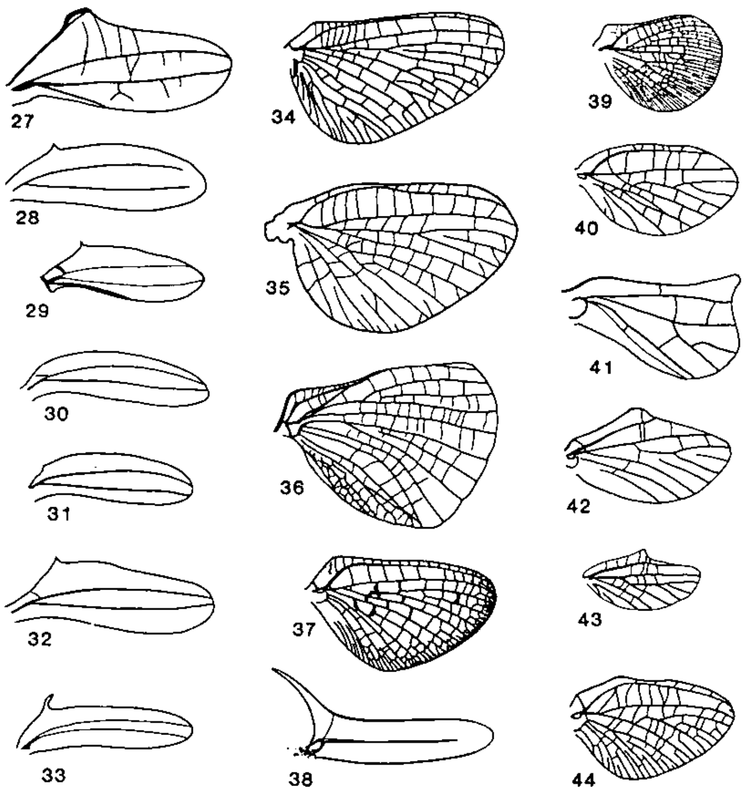


Fig. 27. *Callibaetis pretiosus*, hind wing of female. Fig. 28. *Baetis frondalis*, hind wing of male. Fig. 29. *Baetis intercalaris*, hind wing of male. Fig. 30. *Baetis ephippiatus*, hind wing of male. Fig. 31. *Baetis propinquus*, hind wing of male. Fig. 32. *Baetis pygmaeus*, hind wing of male. Fig. 33. *Centroptilum viridocularis*, hind wing of male. Fig. 34. *Isonychia arida*, hind wing of male. Fig. 35. *Leptophlebia intermedia*, hind wing of male. Fig. 36. *Tortopus incertus*, hind wing of male. Fig. 37. *Hexagenia orlando*, hind wing of male. Fig. 38. *Leptohyphes berneri*, hind wing of male (drawn by R. K. Allen). Fig. 39. *Baetisca rogersi*, hind wing of male (from Berner 1940a). Fig. 40. *Paraleptophlebia volitans*, hind wing of male. Fig. 41. *Habrophlebiodes brunneipennis*, hind wing of male. Fig. 42. *Choroterpes hubbelli*, hind wing of male. Fig. 43. *Habrophlebia vibrans*, hind wing of male. Fig. 44. *Eurylophella temporalis*, hind wing of male.

16(15) Hind wings present and relatively large with one or more veins forked; costal projection shorter than wing width (fig. 44) 17

Hind wings absent or small; if present, with two or three simple veins and long straight or recurved costal projection (1½–3 times the width of wing) (fig. 38) 29

17(16) Short, basally detached, marginal intercalaries present between veins along entire outer margin of wings (fig. 25). Genital forceps of male with one short or long terminal segment (figs. 65 and 69) . . . . Ephemerellidae . . . 18

No true, basally detached, marginal intercalaries in positions indicated above; usually absent along entire outer margin of wings (fig. 17). Genital forceps of male with two short terminal segments (fig. 62) . . . . Leptophlebiidae . . . 23

18(17) Terminal segment of male genital forceps six times as long as wide (fig. 69) . . . . *Attenella attenuata*

Terminal segment of male genital forceps less than four times as long as wide (fig. 65) 19

19(18) Penes with dorsal and ventral spines . . . . . . *Ephemerella* . . . 20

Penes without spines 21

20(19) Penes lobes short and broad with nearly parallel lateral margins. Fewer than 15 dorsal spines. Six or more ventral spines. Thorax and abdomen pale yellow . . . . *Ephemerella dorothea, E. choctawhatchee*

Penes lobes not so short and broad, usually with round lateral margins. More than 15 dorsal spines. Fewer than five ventral spines. Thorax yellow, shaded with brown. Abdominal terga yellow with a brown transverse band . . . . *Ephemerella rotunda*

21(19) Penes with lateral subapical projections (fig. 70) . . . . *Serratella deficiens*

Penes without lateral subapical projections (fig. 66) 22

22(21) Segment 3 of fore tarsi shorter than segment 2; penes basally swollen, narrow apically (fig. 65) . . . . . . *Eurylophella temporalis*

Segment 3 of fore tarsi longer than segment 2; penes basally narrow, expanded apically (fig. 66) .... *Dannella simplex*

23(17) Hind wings without costal projection (fig. 35) 24

Hind wings with distinct costal projection (fig. 41) 27

24(23) Terminal filament subequal to or shorter than cerci. Long, slender, anteriorly directed, ventral appendages arising at apex of penes lobes and often extending to base of lobes (fig. 64). Hind wings more than one-third the length of forewings .... *Leptophlebia* ... 25

Terminal filament as long as cerci. Ventral appendages of penes short and stout as in figure 60. Hind wings less than one-third the length of forewings .... *Paraleptophlebia volitans*

25(24) Terminal filament subequal in length to cerci. Ventral appendages of penes curved and spatulate. Basal one-fourth of penes fused (fig. 62) .... *Leptophlebia bradleyi*

Terminal filament distinctly shorter and thinner than cerci. Penes not as above (fig. 64) 26

26(25) Ventral appendages of penes extend to base of notch between divisions of penes (fig. 63). Terminal filament two-thirds the length of cerci .... *Leptophlebia intermedia*

Ventral appendages of penes shorter, do not extend to notch between divisions of penes (fig. 64). Terminal filament not more than one-third the length of cerci ... *Leptophlebia collina*

27(23) Vein Sc of hind wings extends well beyond costal projection (fig. 43). Each penis lobe with a mesal decurrent appendage (fig. 59). Combined length of two terminal segments of male genital forceps approximately equal in length to preceding segment .... *Habrophlebia vibrans*

Vein Sc of hind wings terminates at or slightly beyond costal projection (fig. 42). Penes not as above. Two terminal segments of male genital forceps short; combined length approximately one-fourth the length of preceding segment (fig. 67) 28

28(27) Costal projection of hind wings acute and located in apical half of wings (fig. 41). Penes with short, lateral decurrent appendages (fig. 67). Female subanal plate deeply cleft apically .... *Habrophlebiodes brunneipennis*

Costal projection of hind wings rounded and near midpoint of wings (fig. 42). Penes without appendages (fig. 61). Female subanal plate slightly emarginate .... *Choroterpes hubbelli*

29(16) Vein MA of forewings forming a more or less symmetrical fork, and veins MP_2 and IMP extending less than three-fourths of distance to base of vein MP_1 (fig. 4). Genital forceps of male two- or three-segmented (fig. 79). Thorax usually black or gray .... Tricorythidae ... 30

Vein MA of forewings not as above; MA_2 attached basally to MA_1 by a crossvein; veins MP_2 and IMP almost as long as vein MP_1 and extending nearly to base (fig. 5). Genital forceps of male one-segmented (fig. 78). Thorax usually brown .... Caenidae ... 31

30(29) Wings of male greatly expanded in cubito-anal area. Vein CuP evenly recurved (fig. 4). Hind wings absent. Genital forceps with an ovoid swelling at base of second segment on inner margin (fig. 79) .... *Tricorythodes albilineatus*

Wings of male not expanded in cubito-anal area; broadest near midpoint of length. Vein CuP abruptly recurved (fig. 10). Hind wings present in males (fig. 38), absent in females .... *Leptohyphes dolani*

31(29) Prosternum twice as wide as long. Fore coxae widely separated 32

Prosternum two to three times longer than wide. Fore coxae much closer together .... *Caenis* ... 35

32(31) Pedicel at least 1⅕–2 times the length of scape. Posterolateral spines on abdominal tergum 6 slightly bent dorsally .... *Brachycercus* ... 33

Pedicel only slightly longer than scape or equal in length. Posterolateral spines on abdominal tergum 6 strongly bent dorsally .... *Cercobrachys etowah*

33(32) Abdominal terga and sterna without dark brown markings .... *Brachycercus nasutus*

Abdominal terga and sterna with dark brown markings .. 34

34(33) Abdominal terga 1–6 with dark brown stippling. Penes approximately as long as wide with distinct posterolaterally rounded lobes .... *Brachycercus maculatus*

Abdominal terga 1–3 and sterna 1–3 with dark brown stippling. Penes longer than wide; weakly produced posterolaterally with slightly concave posterior margin (fig. 77) .... *Brachycercus berneri*

35(31) Stigmatic, dark brown streaks on posterior abdominal terga only. Head pale. Short, fine, black streaks on dorsal edge of each femur .... *Caenis hilaris*

Stigmatic, dark brown streaks on anterior abdominal terga. Head dark shaded. Hind femora with a dark apical band .... *Caenis diminuta*

36(15) Hind wings with numerous long, free, marginal intercalaries (fig. 39); cubital intercalaries absent in forewings, with vein A_1 terminating in outer margin of wings (fig. 22) .... (Baetiscidae) *Baetisca* ... 37

Hind wings not as above, sometimes absent; cubital intercalaries present in forewings, with vein A_1 terminating in hind margin of wings (figs. 6, 23) 42

37(36) Penes sharply tapered distally (fig. 87). Eyes striped .... Subgenus *Fasciculus*, *Baetisca* (*F.*) *escambiensis*

Penes smoothly tapered distally (fig. 86). Eyes uniformly colored .... Subgenus *Baetisca* ... 38

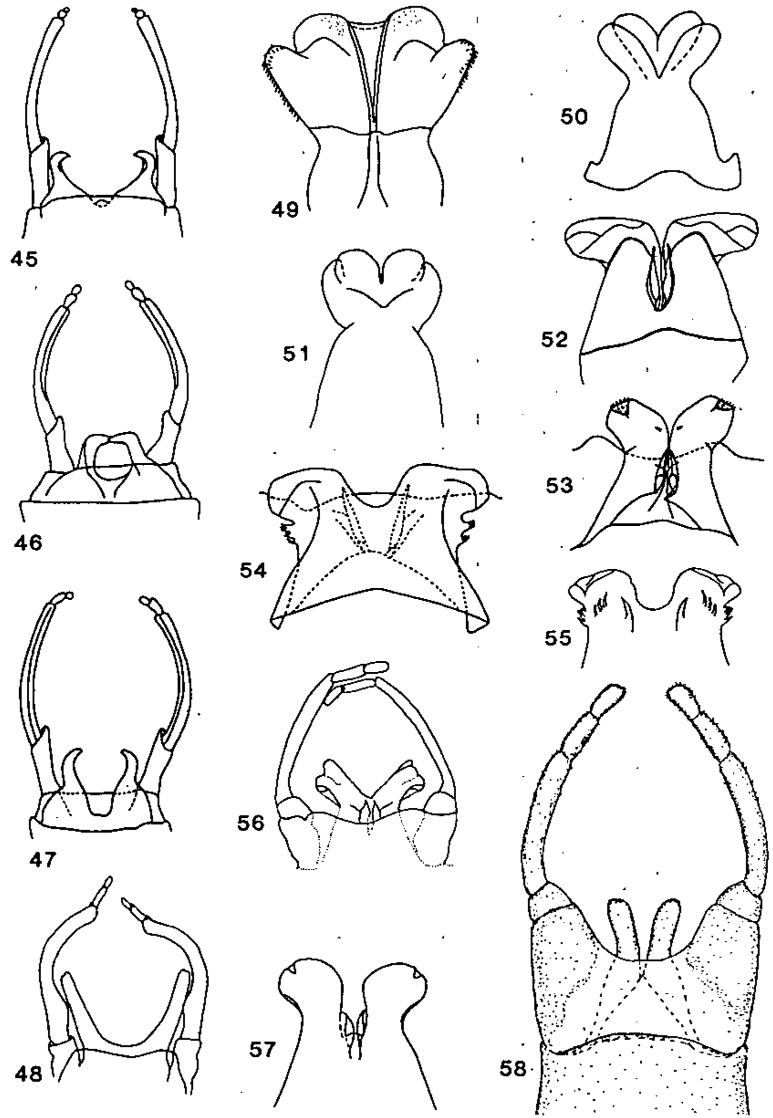


Fig. 45. *Hexagenia orlando*, male genitalia. Fig. 46. *Hexagenia bilineata*, male genitalia. Fig. 47. *Hexagenia limbata*, male genitalia. Fig. 48. *Pentagenia vittigera*, male genitalia. Fig. 49. *Siphloplecton fuscum*, male genitalia. Fig. 50. *Siphloplecton brunneum*, male genitalia. Fig. 51. *Siphloplecton simile*, male genitalia. Fig. 52. *Stenonema smithae*, male genitalia. Fig. 53. *Stenonema exiguum*, male genitalia. Fig. 54. *Stenacron interpunctatum*, male genitalia. Fig. 55. *Stenacron floridense*, male genitalia. Fig. 56. *Heptagenia flavescens*, male genitalia. Fig. 57. *Macdunnoa brunnea*, male genitalia. Fig. 58. *Pseudiron centralis*, male genitalia (from Pescador 1985).

38(37) Wings fully or partially flushed with orange, yellowish to reddish brown (figs. 22, 39) 39

Wings hyaline, rarely with brown tint at extreme base 40

39(38) Abdominal tergum 10 with a pair of small, dark brown spots. Basal one-third of hind wings faintly flushed with orange brown .... *Baetisca (B.) becki*

Abdominal tergum 10 without spots. Basal three-fourths of hind wings strongly flushed with dark reddish brown (fig. 39) .... *Baetisca (B.) rogersi*

40(38) Penes lanceolate, apically blunt (fig. 86) ... *Baetisca (B.) obesa*

Penes deltoid, apically pointed 41

41(40) Abdominal sterna dark brown; posterior margin of sterna 6–8 almost black; sterna with broad, brownish, elongate, anterolateral markings .... *Baetisca (B.) gibbera*

Abdominal sterna pale to light brown; markings absent .... *Baetisca (B.) laurentina*

42(36) Short, basally detached, single or double marginal intercalaries present in each interspace of forewings. Veins MA_2 and MP_2 detached basally from their respective stems (figs. 6, 7, 8). Hind wings small or absent. Penes membranous. Upper portion of male eyes turbinate (plate 1) .... Baetidae ... 43

Marginal intercalaries attached basally to other veins. Vein MA_2 attached basally (fig. 23). Hind wings larger. Penes well developed. Male eyes not turbinate 57

43(42) Hind wings present, although often minute 44

Hind wings absent 53

44(43) Hind wings with numerous crossveins, usually 10 or more; prominent, blunt costal projection (fig. 27). Abdomen with numerous, distinct dark spots .... *Callibaetis* ... 45

Hind wings with few crossveins, usually five or fewer; costal projection either sharply pointed, hooked, or absent but never blunt (figs. 29, 30, 33). Abdomen without speckled color pattern 47

45(44) Intercalaries in midposterior margin of forewing occur singly. Male abdominal segments 2–6 whitish hyaline with reddish shadings on dorsum. Female forewing with 20–25 crossveins posterior to vitta; vitta brown, margin straight; posterior margin of forewing unicolorous ...... *Callibaetis floridanus* ... 46

Intercalaries in midposterior margin of male forewing occur either in pairs or singly; female in pairs. Male abdominal segments 2–6 whitish hyaline with prominent brownish shadings on dorsum (plate 4). Female forewing with 35–40 crossveins posterior to vitta; vitta brown, undulating; posterior margin of forewing with alternate yellowish and brown areas; brown spots throughout membrane .... *Callibaetis pretiosus*

46(45) Forewings of female colorless or only slightly colored; spots covering body brown or reddish brown; body coloration somewhat dulled. Central and North Florida .... *Callibaetis floridanus* (form A)

Forewings of female tinged with brown; spots covering body red; body coloration intense. South Florida .... *Callibaetis floridanus* (form B)

47(44) Marginal intercalaries of forewings occur singly (fig. 7). Costal projection of hind wings hooked or recurved (fig. 33) .... *Centroptilum* ... 48

Marginal intercalaries of forewings occur in pairs (fig. 6). Costal projection of hind wings variable, sometimes absent .... *Baetis* ... 49

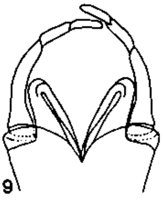
48(47) Abdominal terga 2–6 with reddish areas .... *Centroptilum viridocularis*

Abdominal terga 2–6 without extensive reddish areas .... *Centroptilum hobbsi*

49(47) Costal angulation present on hind wings (fig. 32) 50

No costal angulation on hind wings (fig. 30) .... *Baetis ephippiatus*

50(49) Segment 2 of genital forceps with prominent projection on inner margin (fig. 83). Female with large U-shaped figure on head .... *Baetis propinquus*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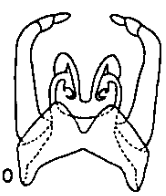
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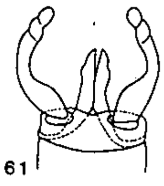
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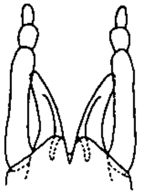
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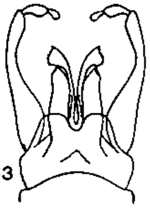
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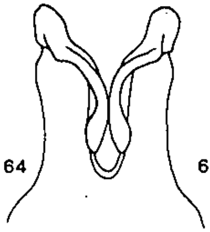
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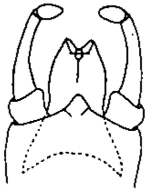
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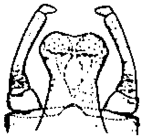
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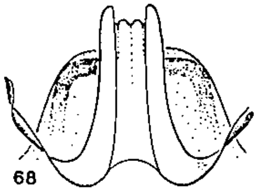
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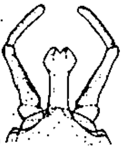
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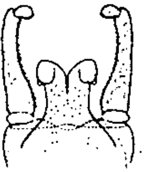
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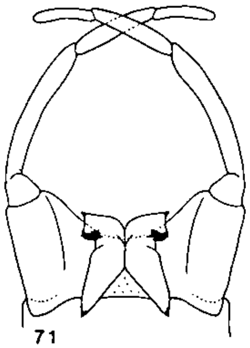
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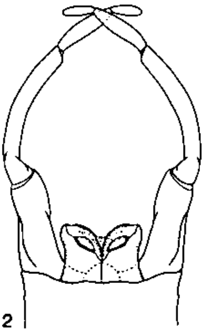
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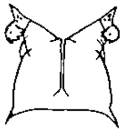
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Segment 2 of male genital forceps without projection on inner margin (fig. 81). Female head not as above 51

51(50) Abdominal segments 2–6 of male opaque brown. A small spine between bases of genital forceps (fig. 81). Costal angulation of hind wings much reduced (fig. 28) .... *Baetis frondalis*

Abdominal segments of male translucent white. No spine between bases of male genital forceps. Costal angulation of hind wings more prominent (fig. 32) 52

52(51) Hind wings with two longitudinal veins (fig. 32). Distal segment of genital forceps twice as long as wide (fig. 82). Male forewing about 3 mm long or slightly longer.. *Baetis pygmaeus*

Hind wings with three longitudinal veins (fig. 29). Distal segment of genital forceps about as long as wide. Male forewing approximately 5 mm long .... *Baetis intercalaris*

53(43) Marginal intercalaries single .... *Cloeon rubropictum*

Marginal intercalaries paired .... *Pseudocloeon* ... 54

54(53) Abdominal terga 2–6 with large ruddy patches 55

Abdominal terga 2–6 immaculate or with very limited markings 56

55(54) Middle and hind femora with a ruddy dash anteriorly on lower edge and a distinct, ruddy spot near the apex, well be-

Fig. 59. *Habrophlebia vibrans*, male genitalia. Fig. 60. *Paraleptophlebia volitans*, male genitalia. Fig. 61. *Choroterpes hubbelli*, male genitalia. Fig. 62. *Leptophlebia bradleyi*, male genitalia. Fig. 63. *Leptophlebia intermedia*, male genitalia. Fig. 64. *Leptophlebia collina*, male genitalia. Fig. 65. *Eurylophella temporalis*, male genitalia. Fig. 66. *Dannella simplex*, male genitalia (from Allen and Edmunds 1962a). Fig. 67. *Habrophlebiodes brunneipennis*, male genitalia. Fig. 68. *Homoeoneuria dolani*, male genitalia (from Pescador and Peters 1980). Fig. 69. *Attenella attenuata*, male genitalia (from Allen and Edmunds 1961). Fig. 70. *Serratella deficiens*, male genitalia (from Allen and Edmunds 1963a). Fig. 71. *Isonychia annulata*, male genitalia (from Kondratieff and Voshell 1984). Fig. 72. *Isonychia tuscalenensis*, male genitalia (from Kondratieff and Voshell 1984). Fig. 73. *Isonychia sayi*, male genitalia (from Kondratieff and Voshell 1984). Fig. 74. *Isonychia sicca*, male genitalia (from Kondratieff and Voshell 1984). Fig. 75. *Isonychia berneri*, male genitalia (from Kondratieff and Voshell 1984). Fig. 76. *Isonychia arida*, male genitalia (from Kondratieff and Voshell 1984).

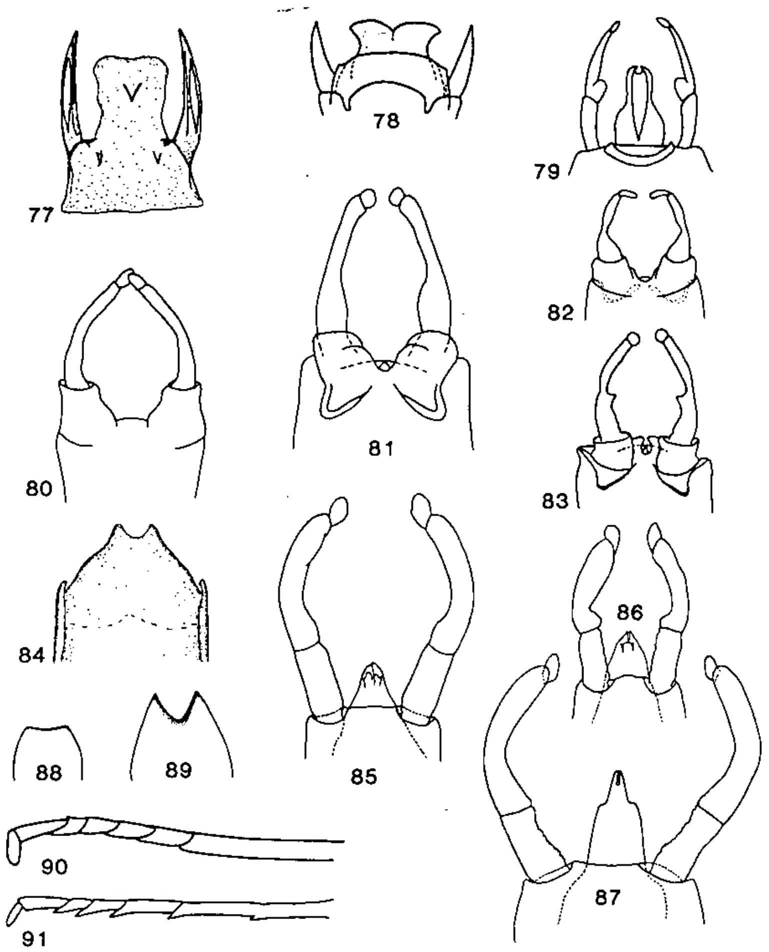

Fig. 77. *Brachycercus berneri*, male genitalia. Fig. 78. *Caenis diminuta*, male genitalia. Fig. 79. *Tricorythodes albilineatus*, male genitalia. Fig. 80. *Pseudocloeon alachua*, male genitalia. Fig. 81. *Baetis frondalis*, male genitalia. Fig. 82. *Baetis pygmaeus*, male genitalia. Fig. 83. *Baetis propinquus*, male genitalia. Fig. 84. *Pseudiron centralis*, female subgenital plate (from Pescador 1985). Fig. 85. *Baetisca rogersi*, male genitalia (from Berner 1955). Fig. 86. *Baetisca obesa*, male genitalia (from Berner 1955). Fig. 87. *Baetisca escambiensis*, male genitalia (from Berner 1955). Fig. 88. *Isonychia* (*Prionoides*) sp., female subgenital plate (from Kondratieff and Voshell 1984). Fig. 89. *Isonychia* (*Isonychia*) sp., female subgenital plate (from Kondratieff and Voshell 1984). Fig. 90. *Stenonema smithae*, male hind tarsus. Fig. 91. *Siphloplecton brunneum*, male hind tarsus.

yond the middle of the segment. Distal segment of male genital forceps much thinner than third segment . . . . *Pseudocloeon parvulum*

Legs without ruddy markings. Distal segment of male genital forceps as wide as third segment (fig. 80) . . . . *Pseudocloeon alachua*

56(54) Abdominal terga 2–6 without reddish markings. Posterior margin of sterna with a row of minute dots . . . . *Pseudocloeon punctiventris*

Abdominal terga 2–6 with small, paired red spots. Posterior margins of sterna without dots . . . . . . *Pseudocloeon bimaculatus*

57(42) Hind tarsi apparently four-segmented. Basal segment fused or partially fused to tibiae (fig. 91). Cubital intercalaries variable but may consist of one or two pairs (fig. 15) 58

Hind tarsi distinctly five-segmented (fig. 90). Cubital intercalaries consist of two pairs (fig. 23) . . . . Heptageniidae, in part . . . 62

58(57) Male eyes contiguous or nearly contiguous dorsally. Fore tarsi three times the length of fore tibiae. Female abdomen with apical and basal segments subequal to middle segments in length and width. Subanal plate evenly convex . . . . (Metretopodidae) *Siphloplecton* . . . 59

Male eyes separated dorsally by twice the width of median ocellus. Fore tarsi twice the length of fore tibiae. Female abdomen long and slender, with apical segments distinctly more elongate and slender than basal segments. Subanal plate with median emargination (fig. 84) . . . . (Heptageniidae, Pseudironinae) *Pseudiron centralis*

59(58) Crossveins of costal, subcostal, and radial spaces of forewings thickly infuscated with brown; membrane in region of bullae with brown stain 60

Crossveins not infuscated with brown; membrane without brown stain . . . . *Siphloplecton speciosum*

60(59) Venation of forewings dark brown. Crossveins of wing disc heavily infuscated. Brown stain at base of forewings extends to vein CuA. Basal one-fourth of male hind wings with brown stain. Female forewings and hind wings without stain. Penes as in figures 50, 51 61

Venation of forewings much lighter. Crossveins of wing disc not heavily infuscated. Brown stain at base of male forewings extends to vein CuP or absent. Male hind wings with brown stain mostly limited to subcostal space. Female forewings and hind wings without stain. Penes as in figure 49 .... *Siphloplecton fuscum*

61(60) Caudal filaments uniformly brown. Penes as in figure 50 .... *Siphloplecton brunneum*

Caudal filaments light brown or pale with strong brown annulations. Penes as shown in figure 51 .... *Siphloplecton simile*

62(57) Wings with two or three crossveins below bullae between R_1 and R_2 connected or nearly connected by dark pigmentation (fig. 24), rarely only a dark spot. Basal crossveins between R_1 and R_2 dark margined. Penes with well-developed lateral clusters of spines (figs. 54, 55) .... *Stenacron* ... 63

Wings with crossveins below bullae not connected as above (fig. 23). Crossveins between R_1 and R_2 rarely dark margined. Penes without lateral clusters of spines (fig. 52) 64

63(62) Penis lobes with clusters of lateral spines (fig. 54) .... *Stenacron interpunctatum*

Penis lobes with clusters of lateral and dorsal spines (fig. 55) .... *Stenacron floridense*

64(62) Penis distinctly L-shaped; median titillators usually well developed (fig. 52). Basal segment of fore tarsi usually one-third to two-thirds the length of segment 2 65

Penis not distinctly L-shaped as above; median titillators moderately to well developed (fig. 56). Basal segment of fore tarsi one-fifth to one-half the length of segment 2 .... *Heptagenia flavescens*

65(64) Apical lobes of penes without spines (fig. 57). Female abdomen without dark markings .... *Macdunnoa brunnea*

Apical lobes of penes with spines (fig. 53). Female abdomen with dark markings .... *Stenonema* ... 66

66(65) Dark gray, median longitudinal line on terga 3 and 6. Crossveins in bulla region and beyond arranged serially across wing, usually forming elongate cells. Spiracular marks, if present, consist of black, oblique streaks .... *Stenonema mexicanum integrum*

No dark gray, median longitudinal line on terga 3 and 6. Crossveins in bulla region and beyond not arranged serially across wing (fig. 23). Spiracular marks, if present, consist of black dots (plate 9) 67

67(66) Dark spiracular spots on abdomen. Tails narrowly annulate with purplish brown at joints. Posteromedial portion of penes angulate (fig. 52) .... *Stenonema modestum, S. smithae*

Dark spiracular spots on abdomen absent. Caudal filaments white. Posteromedial portion of penes rounded (fig. 53)..... .... *Stenonema exiguum*

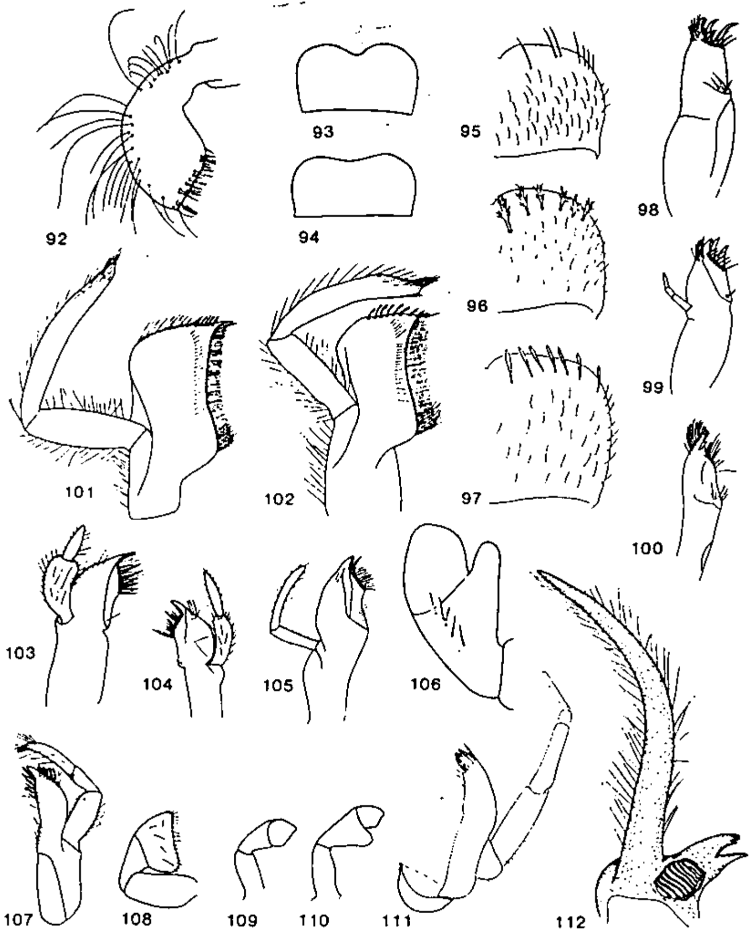

Fig. 92. *Hexagenia* sp., distal segment of labial pulp. Fig. 93. *Habrophlebiodes brunneipennis*, labrum. Fig. 94. *Paraleptophlebia volitans*, labrum. Fig. 95. *Baetis propinquus*, labrum (from Morihara and McCafferty 1979a). Fig. 96. *Baetis ephippiatus*, labrum (from Morihara and McCafferty 1979a). Fig. 97. *Baetis frondalis*, labrum (from Morihara and McCafferty 1979a). Fig. 98. *Eurylophella temporalis*, maxilla. Fig. 99. *Ephemerella choctawhatchee*, maxilla. Fig. 100. *Serratella deficiens*, maxilla. Fig. 101. *Stenonema smithae*, maxilla. Fig. 102. *Stenonema exiguum*, maxilla. Fig. 103. *Callibaetis pretiosus*, maxilla. Fig. 104. *Callibaetis floridanus*, maxilla. Fig. 105. *Cloeon rubropictum*, maxilla. Fig. 106. *Baetis pygmaeus*, labial palp (from Morihara and McCafferty 1979a). Fig. 107. *Caenis diminuta*, maxilla. Fig. 108. *Centroptilum viridocularis*, labial palp. Fig. 109. *Baetis intercalaris*, labial palp. Fig. 110. *Baetis propinquus*, labial pulp. Fig. 111. *Pseudiron centralis*, maxilla (from Pescador 1985). Fig. 112. *Hexagenia orlando*, mandible.

Nymphs

1 Thorax with well-developed mesonotal shield extended to abdominal segment 6. Gills enclosed beneath shield. Nymph as in plate 28 . . . . (Baetiscidae) *Baetisca* . . . 2

Thorax not as above. Gills exposed 7

2(1) Eyes striped (plate 25). Abdominal segments 6–9 with long, thick, lateral hairs. Claws more than two-thirds the length of tibiae . . . . Subgenus *Fascioculus*, *Baetisca (F.) escambiensis*

Eyes uniformly colored (plate 28). Abdominal segments 6–9 either glabrous or with few minute hairs. Tarsal claws less than two-thirds the length of tibiae . . . . Subgenus *Baetisca* . . . 3

3(2) Dorsal projections of mesonotal shield well developed; distinctly taller than medial hump 4

Dorsal projections on mesonotal shield weakly to moderately developed; height less than, or subequal to, that of medial hump 6

4(3) Lateral spines of mesonotal shield prominent, long, sharply pointed. Thoracic and abdominal markings as in plates 24a and b. . . . . *Baetisca (B.) becki*

Lateral spines of mesonotal shield shorter. Thoracic and abdominal markings not as above 5

5(4) Frontal projections of head well developed, distinctly extended beyond anterior margin of head (plate 27). Ventral margins of mesonotal shield lack dark brown outline. Abdominal sternites 2–6 with prominent dark brown spots near lateral margins . . . . *Baetisca* (*B.*) *obesa*

Frontal projections of head moderately developed, not extended beyond anterior margin of head (plate 24c). Ventral margin of mesonotal shield prominently outlined with dark brown (plate 24d). Abdominal sternites 2–6 lack prominent, dark brown sublateral spots but are freckled with brown (plate 24d) . . . . *Baetisca* (*B.*) *laurentina*

6(3) Mesonotal shield weakly flared (plate 28). Lateral margins of mesonotal spines serrate. Mesonotal shield distinctly longer than width. Lateral spines of mesonotal shield more than 1½ times as long as width at base. Abdominal sternites 7–9 with a pair of brownish black spots . . . . *Baetisca* (*B.*) *rogersi*

Mesonotal shield strongly flared (plate 26). Lateral margins of mesonotal spines smooth. Mesonotal shield length subequal to width. Lateral spines of mesonotal shield blunt, as long as width at base. Abdominal sternites 7–9 without defined spots . . . . *Baetisca* (*B.*) *gibbera*

7(1) Gills on abdominal segments 2–7 forked, with margin fringed. Mandibles usually with large tusks projecting forward and visible from above (plate 15; fig. 112). If tusks absent, head and thorax with pads of long spines (plate 14) 8

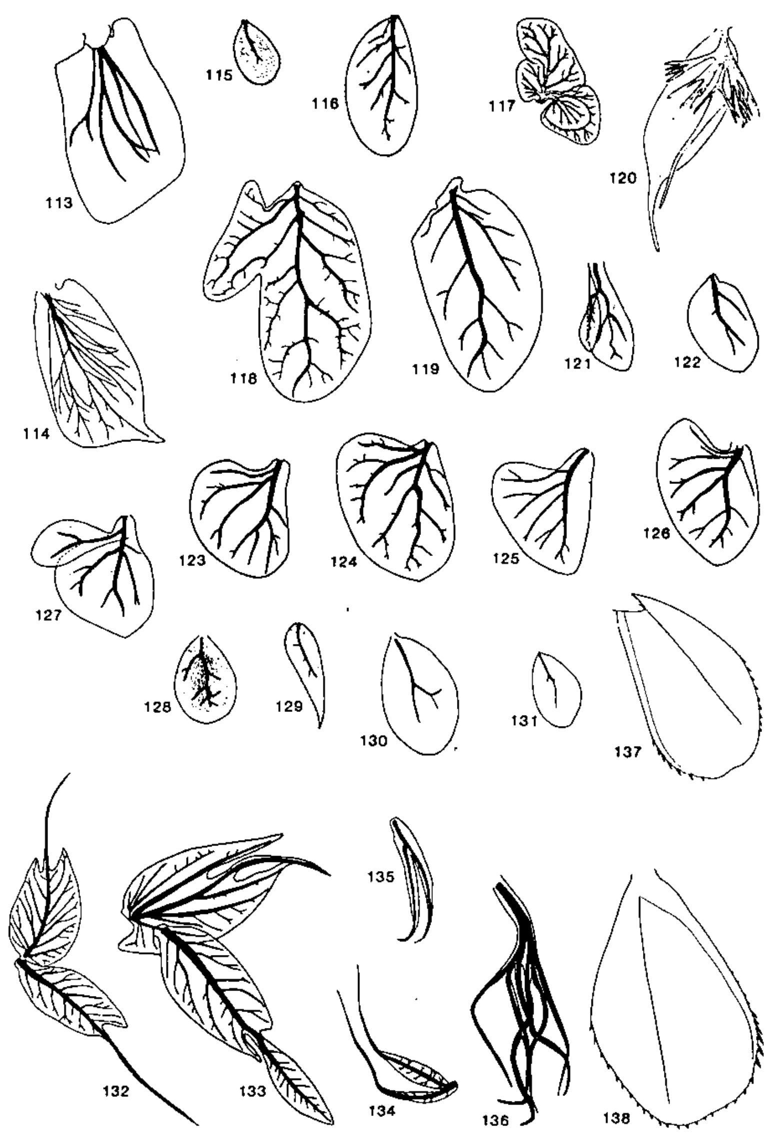

Fig. 113. *Stenonema smithae,* 4th gill. Fig. 114. *Stenacron interpunctatum,* 4th gill. Fig. 115. *Pseudocloeon bimaculatus,* 7th gill. Fig. 116. *Pseudocloeon parvulum,* 4th gill. Fig. 117. *Callibaetis* sp., 2d gill (from Spieth 1933). Fig. 118. *Callibaetis pretiosus,* 7th gill. Fig. 119. *Callibaetis floridanus,* 7th gill. Fig. 120. *Pseudiron centralis,* 7th gill (from Pescador 1985). Fig. 121. *Centroptilum hobbsi,* 1st gill. Fig. 122. *Centroptilum hobbsi,* 7th gill. Fig. 123. *Centroptilum viridocularis,* 1st gill. Fig. 124. *Centroptilum viridocularis,* 4th gill. Fig. 125. *Cloeon* sp. A, 1st gill. Fig. 126. *Cloeon* sp. A, 4th gill. Fig. 127. *Cloeon rubropictum,* 1st gill. Fig. 128. *Baetis ephippiatus,* 7th gill. Fig. 129. *Baetis pygmaeus,* 7th gill. Fig. 130. *Baetis propinquus,* 4th gill. Fig. 131. *Baetis propinquus,* 7th gill. Fig. 132. *Leptophlebia intermedia,* 3d gill. Fig. 133. *Choroterpes hubbelli,* 3d gill. Fig. 134. *Leptophlebia bradleyi,* 3d gill. Fig. 135. *Paraleptophlebia volitans,* 3d gill. Fig. 136. *Habrophlebia vibrans,* 3d gill. Fig. 137. *Isonychia* (*Prionoides*) sp., 7th gill (from Kondratieff and Voshell 1984). Fig. 138. *Isonychia* (*Isonychia*) sp., 7th gill (from Kondratieff and Voshell 1984).


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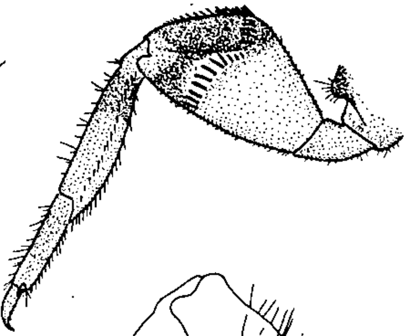
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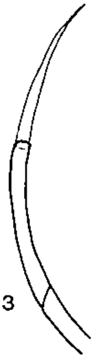
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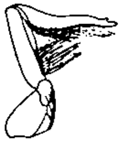
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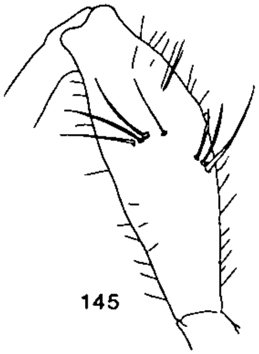
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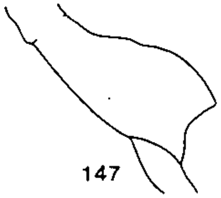
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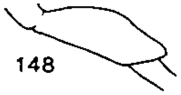
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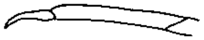
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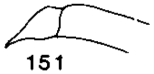
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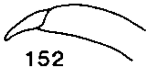
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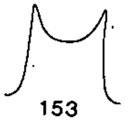
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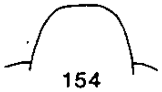
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Gills on abdominal segments 2–7 variable; if gills forked, margins not fringed (fig. 132). Tusks absent on mandibles 14

8(7) Head and prothorax with dorsal pads of long spines on each side (plate 14). Mandibles not modified into tusks. Gills ventral .... (Behningiidae) *Dolania americana*

Head and prothorax without pads of spines. Mandibles modified into tusks. Gills lateral or dorsal (plate 15) 9

9(8) Mandibular tusks apically curved upward when viewed laterally. Ventral apex of hind tibiae projected into distinct acute point.. 10

Mandibular tusks apically curved downward when viewed laterally. Ventral apex of hind tibiae rounded .... (Polymitarcyidae) *Tortopus incertus*

10(9) Mandibular tusks broadened laterally and with row of spurs along lateral margins. Terminal segment of labial palpi club-shaped, broadly rounded apically .... (Palingeniidae) *Pentagenia vittigera*

Mandibular tusks slender and without a row of spurs along lateral margins. Terminal segment of labial palpi pointed, truncate or falcate apically (fig. 92) ..... Ephemeridae ... 11

11(10) Frontal process of head distinctly bifid (fig. 153). Mandibular tusks with small group of basal and lateral spurs. Fore tibiae not emarginate apically and not greatly flattened (fig. 148) .... *Ephemera simulans*

Fig. 139. *Centroptilum viridocularis*, nymphal tarsal claw, hind leg. Fig. 140. *Centroptilum hobbsi*, nymphal tarsal claw, hind leg. Fig. 141. *Siphloplecton speciosum*, nymphal tarsal claw, foreleg. Fig. 142. *Leptohyphes sabinas*, foreleg of nymph (drawn by R. K. Allen). Fig. 143. *Pseudiron centralis*, nymphal tarsus and claw, foreleg. Fig. 144. *Homoeoneuria dolani*, nymphal foreleg (from Edmunds, Berner, and Traver 1958). Fig. 145. *Tricorythodes albilineatus*, nymphal fore femur. Fig. 146. *Ephemerella choctawhatchee*, nymphal fore femur. Fig. 147. *Hexagenia* sp., nymphal fore tibia. Fig. 148. *Ephemera* sp., nymphal fore tibia. Fig. 149. *Brachycercus nasutus*, nymphal fore tarsus and claw. Fig. 150. *Brachycercus maculatus*, nymphal fore tarsus and claw. Fig. 151. *Hexagenia bilineata*, nymphal hind claw (redrawn from Gooch 1967). Fig. 152. *Hexagenia limbata*, nymphal hind claw (redrawn from Gooch 1967). Fig. 153. *Ephemera* sp., nymphal frontal process. Fig. 154. *Hexagenia limbata*, nymphal frontal process.

Frontal process of head entire (fig. 154). Mandibular tusks without spurs but with long hairs. Fore tibiae slightly to distinctly emarginate along distal margin (fig. 147) .... *Hexagenia* ... 12

12(11) Color pattern of abdominal terga and sterna as in figure 160. Size relatively small (14–22 mm). Confined to sand-bottomed lakes in central Florida highlands .... *Hexagenia orlando*

Color pattern of abdominal terga and sterna not as above. Size relatively large (18–32 mm). Occurs throughout central and northern Florida 13

13(12) Mesotarsal claws swollen near base (fig. 151). Developing penes of mature nymph angulate and beaklike. Frontal process slightly conical .... *Hexagenia bilineata*

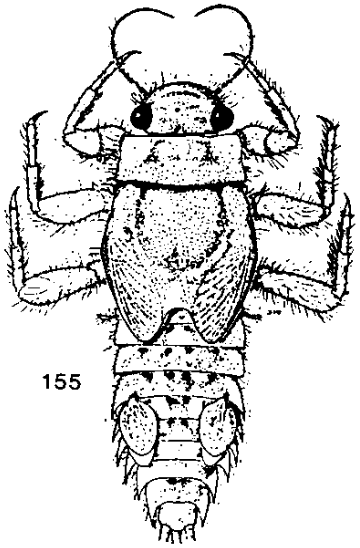
Mesotarsal claws slender for most of their length (fig. 152). Developing penes of mature nymph more evenly curved. Frontal process usually evenly rounded. Color pattern of mature nymphs as in figure 159 .... *Hexagenia limbata*

14(7) Inner surface of forelegs with a double row of long setae (fig. 144) .... Oligoneuriidae ... 15

Inner surface of forelegs not as above 18

15(14) Gills ventral on abdominal segment 1. Fore coxae without basal gill tufts. Fore tarsi reduced and papilla-like (fig. 144). Meso- and metatarsal claws nondenticulate .... (Oligoneuriinae) *Homoeoneuria dolani*

Gills dorsal on abdominal segment 1. Fore coxae with basal gill tufts. Fore tarsi normal with a double row of hairs. Meso- and metatarsal claws denticulate .... (Isonychiinae) *Isonychia* ... 16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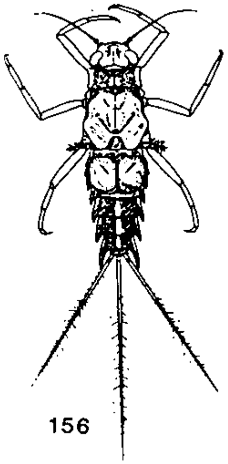
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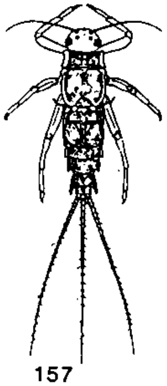
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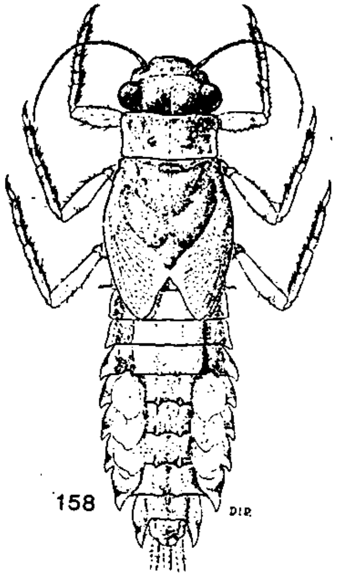
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159b


160a


160b

Fig. 155. *Dannella simplex*, mature nymph (from Allen and Edmunds 1962a). Fig. 156. *Neoephemera compressa*, half-grown nymph (from Berner 1956). Fig. 157. *Neoephemera youngi*, half-grown nymph (from Berner 1956). Fig. 158. *Attenella attenuata*, mature nymph (from Allen and Edmunds 1961). Fig. 159. *Hexagenia limbata*, abdominal color pattern (common Florida type), male (a) dorsal (b) ventral (from Spieth 1941). Fig. 160. *Hexagenia orlando*, abdominal color pattern, male (a) dorsal (b) ventral (from Spieth 1941).

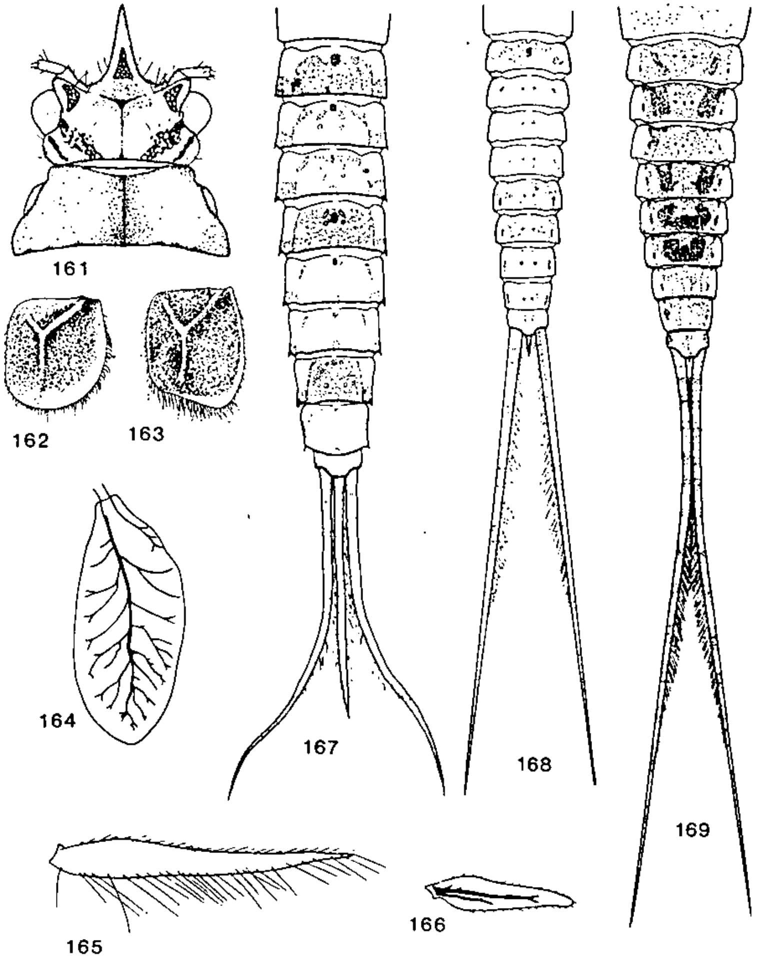

Fig. 161. *Brachycercus nasutus*, head of nymph (from Soldan 1986). Fig. 162. *Brachycercus maculatus*, operculate gill (from Soldan 1986). Fig. 163. *Brachycercus berneri*, operculate gill (from Soldan 1986). Fig. 164. *Heptagenia flavescens*, 7th gill. Fig. 165. *Stenonema smithae*, 7th gill. Fig. 166. *Stenacron interpunctatum*, 7th gill. Fig. 167. *Baetis ephippiatus*, nymphal abdomen. Fig. 168. *Pseudocloeon bimaculatus*, nymphal abdomen. Fig. 169. *Pseudocloeon parvulum*, nymphal abdomen.

16(15) Abdominal gill lamellae with stout, apical marginal spines (fig. 138). Fore coxal gills in tufts of multibranched filaments. . . . . Subgenus *Isonychia* s.s. . . . 17

Abdominal gill lamellae without stout, apical marginal spines (fig. 137). Fore coxal gills usually a single, stout filament . . . . Subgenus *Prionoides*, *Isonychia* (*P.*) *sayi*

17(16) Sclerotized distal edge of anterior margin of abdominal gill lamellae 6 and 7 usually with two or fewer indistinct rows of stout spines, and median sclerotized ridge usually with a row of spines along entire length . . . . *Isonychia* (*I.*) *sicca*

Sclerotized distal edge of anterior margin of abdominal gill lamellae 6 and 7 usually with three or more indistinct rows of stout spines and median sclerotized ridge usually with only scattered stout spines . . . . *Isonychia* (*I.*) *arida*

18(14) Gills on abdominal segment 2 operculate or semioperculate, covering succeeding pairs (plate 19) 19

Gills on abdominal segment 2 neither operculate nor semioperculate; either similar to those on succeeding segments or absent 28

19(18) Gills on abdominal segment 2 triangular, subtriangular, or oval, not meeting medially (plate 19). Margin of gill lamellae 3–6 not fringed . . . . Tricorythidae . . . 20

Gills on abdominal segment 2 quadrate, meeting, or almost meeting, medially (plate 20). Margin of gill lamellae 3–6 fringed 21

20(19) Operculate gill elongate-oval to oval. Fore femora with transverse band of moderately long to short, robust spines (fig. 142) . . . . *Leptohyphes dolani*

Operculate gill triangular or subovate (plate 19). Fore femora with transverse band of long, delicate setae (fig. 145) . . . . *Tricorythodes albilineatus*

21(19) Mesonotum with a distinct anterolateral lobe (plate 20). Operculate gills fused mesally. Developing hind wing pads present . . . . (Neoephemeridae) *Neoephemera* . . . 22

Mesonotum without anterolateral lobe. Operculate gills not fused mesally (plate 22). Without developing hind wing pads .... Caenidae ... 23

22(21) Posterolateral abdominal spines strongly produced (fig. 156). Posterior margin of abdominal segments 6–8 with median spines. Anterolateral corners of pronotum pointed. Pronotal submedian tubercles prominent ...... *Neoephemera compressa*

Posterolateral abdominal spines moderately produced (fig. 157). Posterior margin of abdominal segments 7–8 without median spines, slightly developed on 6. Anterolateral corners of pronotum rounded. Pronotal submedian tubercles inconspicuous .... *Neoephemera youngi*

23(21) Head with tubercles. Maxillary and labial palpi two-segmented. Depressed body form 24

Head without tubercles. Maxillary and labial palpi three-segmented (fig. 107). Compressed body form (plate 22) .... *Caenis* ... 27

24(23) Abdominal segments 7–9 without posterolateral spines. Anterior margin of mesosternum with long, anteriorly directed bristles. Abdominal segment 6 with spines arising anterolaterally .... *Cercobrachys etowah*

Abdominal segments 7–9 with posterolateral spines. Anterior margin of mesosternum without bristles. Abdominal segment 6 with spines arising posterolaterally (plate 23) .... *Brachycercus* ... 25

25(24) Frontal ocellar tubercle long, 1½ times longer than lateral ones (fig. 161), and twice as long as eye width .... *Brachycercus nasutus*

Frontal ocellar tubercle short, almost as long as lateral ones (plate 23), and at most 1½ times as long as eye width 26

26(25) Gill cover apically angulate (fig. 163). Pronotum with a pair of anterolateral spines .... *Brachycercus berneri*

Gill cover apically rounded (fig. 162). Pronotum without lateral spines .... *Brachycercus maculatus*

27(23) Length of mature nymph 3.9–6.7 mm. Pro- and mesonotum with numerous yellow spots. Predominantly pond forms .... *Caenis diminuta*

Length of mature nymph 2.6–3.8 mm. Pronotum without yellow spots; mesonotum with yellow spots at bases of wing pads, and a pair of submedian spots. Predominantly stream forms .... *Caenis hilaris*

28(18) Gills absent from abdominal segment 2; rudimentary on or absent from segment 1; present on or absent from segment 3. Paired tubercles often present on abdominal terga .... Ephemerellidae ... 29

Gills present on abdominal segments 1–7 or 2–7. Tubercles absent from abdominal terga 34

29(28) Lamellate gills present on abdominal terga 3–7 (plate 18) 30

Lamellate gills present on abdominal terga 4–7 (plate 17) 32

30(29) Caudal filaments with whorls of spines at apex of each segment and with only sparse intersegmental setae or none (plate 18). Maxillary palpi absent (fig. 100) .... *Serratella deficiens*

Caudal filaments rarely with whorls of spines at apex of each segment but with heavy intersegmental setae (plate 17). Maxillary palpi well developed (fig. 99) .... *Ephemerella* ... 31

31(30) Abdominal terga with paired submedian tubercles on segments 2–9. Tubercles small but discernible on terga 3–8, barely discernible on terga 2 and 9. Fore femur with moderately wide band of subapical spines ...... *Ephemerella rotunda*

Abdominal terga with paired submedian tubercles on segments 3–8, barely discernible on terga 3 and 8. Fore femur usually with a narrow band of only a few spines (fig. 146) .... *Ephemerella choctawhatchee*

32(29) Tarsal claws usually without denticles. Head, body, and appendages with long setae (fig. 155) .... *Dannella simplex*

Tarsal claws with denticles. Head, body, and appendages without long setae 33

33(32) Abdominal segment 9 distinctly longer than segment 8. Gills on tergum 4 semioperculate (plate 17) .... *Eurylophella temporalis*

Abdominal segments 8 and 9 about equal in length. Gills imbricate (fig. 158) .... *Attenella attenuata*

34(28) Nymphs distinctly flattened. Head capsule flattened and expanded, dorsally covering mandibles (plate 8) .... Heptageniidae ... 35

Nymphs spindle-shaped to slightly flattened (plates 2, 12). Head capsule not dorsally covering mandibles 43

35(34) Tarsal claws as long as or slightly longer than tarsi (fig. 143). Maxillary palpi four-segmented (fig. 111). Gills with finger-like branch arising near middle (fig. 120) .... (Pseudironinae) *Pseudiron centralis*

Tarsal claws shorter than tarsi. Maxillary palpi two-segmented. Gills variable but not as above 36

36(35) Abdominal gills all inserted dorsally or laterally. Lamellae broad on segments 2–6 or 2–7 (plate 8). Thorax without tubercles .... Heptageniinae ... 37

Abdominal gills on segments 2 and 3 inserted ventrally. Lamellae slender on segments 2 and 3, about same length as fibrilliform portion. Thorax with a pair of tubercles on each segment .... (Spinadinae) *Spinadis wallacei*

37(36) Gills on abdominal segment 7 similar to preceding pairs but smaller (fig. 164). Trachea of gill 7 with lateral branches .... *Heptagenia flavescens*

Gills on abdominal segment 7, if present, reduced to slender filaments or minute. Trachea of gill 7, if present, with few or no lateral branches (fig. 165) 38

38(37) Gills on abdominal segments 1–6 pointed at apex (fig. 114). Spinelike setae present on crown of maxilla (fig. 102) .... *Stenacron* ... 39

Gills on abdominal segments 1–6 truncated or rounded at apex. Hairlike setae, spinelike setae, or both present on crown of maxilla (fig. 101) 40

39(38) Middorsal pale streaks continuous or nearly so. Nine or 10 pectinate spines on crown of maxilla. More than 25 lateral setae on ventral surface of galea-lacinia .... *Stenacron interpunctatum*

Middorsal streaks, if present, discontinuous. Eight (rarely nine) pectinate spines on crown of maxilla. Fewer than 25 lateral setae on ventral surface of galea-lacinia .... *Stenacron floridense*

40(38) Gills on abdominal segment 7 greatly reduced, visible only under high magnification .... *Macdunnoa brunnea*

Gills on abdominal segment 7 distinct and elongate (fig. 165) .... *Stenonema* ... 41

41(40) Maxillary crown with fewer than 10 (usually 0) hairlike setae (fig. 102). Mesonotum of last-instar nymphs with conspicuous yellow band at base of wing pads (plate 8) .... *Stenonema exiguum*

Maxillary crown with 10 or more hairlike setae. Mesonotum of last-instar nymphs without yellow band 42

42(41) Abdominal terga 7–9 with distinct V-shaped pale mark. Two or three spinelike setae on crown of maxilla .... *Stenonema mexicanum integrum*

Abdominal terga 7–9 without V-shaped mark. Three to seven (rarely five) spinelike setae on crown of maxilla (fig. 101) .... *Stenonema modestum, S. smithae*

43(34) Fore claws bifid (fig. 141); middle and hind claws simple and pointed .... (Metretopodidae) ...... *Siphloplecton brunneum, S. simile, S. speciosum, S. fuscum*

All claws simple, sharply pointed 44

44(43) Abdominal gills on segments 2–7 either forked (fig. 135), in tufts (fig. 136), or with double lamellae terminating in filaments or points (fig. 132). Distal margin of maxillae with a dense brush of hairs .... Leptophlebiidae . . . 45

Abdominal gills not as above but either ovate (broad at base), obovate (narrowed at base), or subcordate; lamellae single, double, or triple (figs. 117, 125, 127). Distal margin of maxillae variable; never with dense brush of hairs .... Baetidae . . . 50

45(44) Abdominal gills on segments 2–7 with cluster of filaments (fig. 136) .... *Habrophlebia vibrans*

Abdominal gills 2–7 forked (fig. 135) or bilamellate (fig. 132) 46

46(45) Gills on abdominal segment 1 differ in structure from those on succeeding segments (plate 10) 47

Gills on abdominal segment 1 similar in structure to those on succeeding segments (plate 12) 49

47(46) Gills on abdominal segment 1 single; gills 2–7 with dorsal lamellae ending in a single, spatulate filament (plate 10; fig. 133) .... *Choroterpes hubbelli*

Gills on abdominal segment 1 forked; gills 2–7 not as above (plate 13; fig. 132) .... *Leptophlebia* . . . 48

48(47) Gill lamellae relatively slender, smoothly tapered toward apex (fig. 134). Tarsal claws slender and gradually tapered distally .... *Leptophlebia bradleyi*

Gill lamellae broad, produced into one or two blunt lobes at base of terminal filament (fig. 132). Tarsal claws moderately broad at base and abruptly tapered toward apex .... *Leptophlebia intermedia*

49(46) Labrum with moderately deep V-shaped median emargination (fig. 93). Lateral spines on abdominal segment 9 half as long as the length of that segment; small row of spines present only on posterior margins of dorsum of abdominal segments 6–10 .... *Habrophlebiodes brunneipennis*

Labrum with broad and shallow median emargination (fig. 94). Lateral spines on abdominal segment 9 no more than one-fourth the length of that segment; small row of spines present on posterior margins of dorsum of abdominal segments 1–10 .... *Paraleptophlebia volitans*

50(44) Two caudal filaments; if small terminal filament present, no longer than length of abdominal tergum 10 (fig. 169) .... *Pseudocloeon* . . . 51

Three caudal filaments; terminal filament developed, either shorter than or equal in length to cerci (fig. 167) 54

51(50) Caudal filaments with a brown band at the middle 52

Caudal filaments without brown band 53

52(51) Abdominal gills 1–6 unicolorous, tinged with brown; gills on abdominal segment 7 with lateral two-thirds reddish brown, inner margin clear (fig. 115). Band on caudal filaments dark brown .... *Pseudocloeon bimaculatus*

Abdominal gills 1–7 unicolorous, tinged with brown. Band on caudal filaments light brown .... *Pseudocloeon punctiventris*

53(51) Length of terminal filament less than width of cerci at base. Cerci prominently banded with alternate dark and light brown annulations (fig. 169). Grayish area in gills (fig. 116)......... .... *Pseudocloeon parvulum*

Length of terminal filament greater than width of cerci at base. Cerci faintly or not at all annulate with brown. No grayish area in gills .... *Pseudocloeon alachua*

54(50) Terminal filament shorter and often thinner than cerci. Abdominal gills with single lamella (fig. 130) ...... *Baetis* . . . 55

Terminal filament about equal in length and width to cerci. Gill lamellae double, single, or single with dorsal recurved flap (figs. 121, 127) or flaps (fig. 117) 59

55(54) Gills on abdominal segment 7 slender, asymmetrically teardrop-shaped (fig. 129). Segment 2 of labial palpi with median lobe thumblike, projecting anteriorly (fig. 106) .... *Baetis pygmaeus*

Gills on abdominal segment 7 rounded apically (fig. 131). Segment 2 of labial palpi variable 56

56(55) Second segment of labial palpi not distally expanded (fig. 109) . . . . *Baetis intercalaris*

Second segment of labial palpi expanded distally (fig. 110) 57

57(56) Labrum with submarginal setae slender and unbranched, reduced in number, and often paired (fig. 95) . . . . *Baetis propinquus*

Labrum with submarginal setae either branched (fig. 96) or somewhat spatulate (fig. 97) 58

58(57) Labrum with submarginal setae branched (fig. 96). Gill 7 reddish brown (fig. 128) . . . . *Baetis ephippiatus*

Labrum with submarginal setae spatulate, often fringed apically (fig. 97). Gill 7 not deeply colored . . . . *Baetis frondalis*

59(54) Hind wing pads absent . . . . *Cloeon* . . . 60

Hind wing pads present 61

60(59) Gills double on abdominal segment 1 (fig. 127) . . . . *Cloeon rubropictum*

Gills single on all abdominal segments (figs. 125, 126) . . . . *Cloeon* sp. A

61(59) Gills on all segments with a single lamella or with a small dorsal recurved flap on first gill (fig. 121). Apex of labial palpi truncate (fig. 108) . . . . *Centroptilum* . . . 62

Gills on abdominal segments 1–4 and usually 5–7 with ventral recurved flap or flaps, making each gill appear double (fig. 117) or triple. Apex of labial palpi rounded . . . . *Callibaetis* . . . 63

62(61) Gills double on abdominal segment 1 (fig. 121). Branching of gill tracheae asymmetrical, mostly on inner side (fig. 122). Abdominal segments 8–10 with spines on lateral margins. Sternites unmarked. Tarsal claws shortened (fig. 140) . . . . *Centroptilum hobbsi*

Gill single on abdominal segment 1. Branching of gill tracheae symmetrical (figs. 123, 124). Abdominal segments 4–10 with spines on lateral margins (plate 5). Row of large brown spots on lateral borders of sternites 2–9, becoming large and elongated transversely on 8 and 9. Tarsal claws attenuated (fig. 139) . . . . *Centroptilum viridocularis*

63(61) Maxillary palpi shorter than body of maxilla (fig. 103). Segment 2 of maxillary palpi about half the length of segment 1, and width of segment 1 about half its length. Gill 7 with small recurved flap (fig. 118) . . . . *Callibaetis pretiosus*

Maxillary palpi equal in length to body of maxilla (fig. 104). Segment 2 of maxillary palpi approximately equal in length to segment 1, and width of segment 1 less than one-third its length. Gill 7 without recurved flap (fig. 119) . . . . *Callibaetis floridanus*

6

SPECIES OF FLORIDA MAYFLIES*

Suborder SCHISTONOTA

- Superfamily Baetoidea
  - Family Baetidae
    - Subfamily Baetinae
      - *Baetis ephippiatus* Traver
      - *Baetis frondalis* McDunnough
      - *Baetis intercalaris* McDunnough
      - *Baetis propinquus* (Walsh)
      - *Baetis pygmaeus* (Hagen)
      - *Callibaetis floridanus* Banks
      - *Callibaetis pretiosus* Banks
      - *Centroptilum hobbsi* Berner
      - *Centroptilum viridocularis* Berner
      - *Cloeon rubropictum* McDunnough
      - *Cloeon* sp. A
      - *Pseudocloeon alachua* Berner
      - *Pseudocloeon bimaculatus* Berner
      - *Pseudocloeon parvulum* McDunnough
      - *Pseudocloeon punctiventris* McDunnough
  - Family Metretopodidae
      - *Siphloplecton brunneum* Berner
      - *Siphloplecton fuscum* Berner
      - *Siphloplecton simile* Berner
      - *Siphloplecton speciosum* Traver

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*Our arrangement follows the scheme proposed by McCafferty and Edmunds (1979).

  - Family Oligoneuriidae
    - Subfamily Isonychiinae
      - *Isonychia arida* (Say)
      - *Isonychia berneri* Kondratieff and Voshell
      - *Isonychia sayi* Burks
      - *Isonychia sicca* (Walsh)
    - Subfamily Oligoneuriinae
      - *Homoeoneuria dolani* Edmunds, Berner, and Traver
  - Family Heptageniidae
    - Subfamily Pseudironinae
      - *Pseudiron centralis* McDunnough
    - Subfamily Heptageniinae
      - *Heptagenia flavescens* (Walsh)
      - *Macdunnoa brunnea* Flowers
      - *Stenacron floridense* (Lewis)
      - *Stenacron interpunctatum* (Say)
      - *Stenonema exiguum* Traver
      - *Stenonema mexicanum integrum* (McDunnough)
      - *Stenonema modestum* (Banks)
      - *Stenonema smithae* Traver
    - Subfamily Spinadinae
      - *Spinadis wallacei* Edmunds and Jensen**
- Superfamily Leptophlebioidea
  - Family Leptophlebiidae
      - *Choroterpes hubbelli* Berner
      - *Habrophlebia vibrans* Needham
      - *Habrophlebiodes brunneipennis* Berner
      - *Leptophlebia bradleyi* Needham
      - *Leptophlebia collina* (Traver)
      - *Leptophlebia intermedia* (Traver)
      - *Paraleptophlebia volitans* (McDunnough)
- Superfamily Ephemeroidea
  - Family Behningiidae
      - *Dolania americana* Edmunds and Traver
  - Family Polymitarcyidae
    - Subfamily Campsurinae
      - *Tortopus incertus* (Traver)
  - Family Ephemeridae
      - *Ephemera simulans* Walker
      - *Hexagenia bilineata* (Say)
      - *Hexagenia limbata* (Serville)
      - *Hexagenia orlando* Traver
  - Family Palingeniidae
    - Subfamily Pentageniinae
      - *Pentagenia vittigera* (Walsh)

**Occurrence of this species in Florida has not been confirmed.

Suborder PANNOTA
Superfamily Ephemerelloidea
  Family Ephemerellidae
    Subfamily Ephemerellinae
      Attenella attenuata (McDunnough)
      Dannella simplex (McDunnough)
      Ephemerella choctawhatchee Berner
      Ephemerella dorothea Needham
      Ephemerella rotunda Morgan
      Eurylophella temporalis (McDunnough)
      Serratella deficiens (Morgan)
  Family Tricorythidae
    Subfamily Leptohyphinae
      Leptohyphes dolani Allen
      Tricorythodes albilineatus Berner
Superfamily Caenoidea
  Family Neoephemeridae
      Neoephemera compressa Berner
      Neoephemera youngi Berner
  Family Caenidae
      Caenis diminuta Walker
      Caenis hilaris (Say)
      Brachycercus berneri Soldán
      Brachycercus maculatus Berner
      Brachycercus nasutus Soldán
      Cercobrachys etowah Soldán
Superfamily Prosopistomatoidea
  Family Baetiscidae
      Baetisca becki Schneider and Berner
      Baetisca escambiensis Berner
      Baetisca gibbera Berner
      Baetisca laurentina McDunnough
      Baetisca obesa (Say)
      Baetisca rogersi Berner

7

ANNOTATED LIST OF MAYFLIES

BAETIDAE

When Needham, Traver, and Hsu's book was published in 1935, the family Baetidae was broad in scope, including the majority of North American genera of mayflies. Subsequently, most of the subfamilies were raised to family level and the definition of the Baetidae was severely restricted.

As now interpreted by Edmunds et al. (1976), the family includes the following Florida genera: *Baetis, Callibaetis, Centroptilum, Cloeon,* and *Pseudocloeon.* Another of the Baetidae, *Paracloeodes,* which occurs in the southeastern United States, eventually may be found in Florida. All of the genera have suffered great reduction in the size of, or complete loss of, the hind wings; and the main veins, IMA, MA_2, IMP, and MP_2, are detached basally in the forewings. The difficulties in assigning placement of species are summarized by Edmunds et al. as follows: "The absurdity of the present classification does not escape us. We are plagued further by the knowledge that a series of adults collected in Idaho, which appears to represent one species, has hind wings in the males but not in the females. There is also a species of Baetidae in Argentina in which only the males have hind wings" (1976, p. 155).

The members of the family are distributed worldwide, being present on all continents and many islands.

Much work still remains to be done to untangle the puzzles presented by the Baetidae and to establish some clear understanding of the relationships of the genera. Edmunds et al. point out that the primary center of evolution of the Baetidae was South America, with dispersion from that continent. The recognition of South America as a major center of evolution has important implications for the taxonomy of the family.

Baetis Leach

Berner 1950, pp. 204–205 (*Acentrella*); pp. 209–211.
Burks 1953, pp. 122–126.
Edmunds, Jensen, and Berner 1976, pp. 158–164.
Morihara and McCafferty 1979a, pp. 139–149.
Unzicker and Carlson 1982, p. 3.91.

Baetis, one of the first-known mayfly genera, was described by Leach in 1815. *Brachyphlebia*, which Westwood described in 1820, proved to be synonymous with *Baetis*, and in 1843 a portion of *Baetis* was synonymized by Pictet. The genus *Acentrella*, split off in 1912 by Bengtsson, is no longer recognized as a valid taxon. During its long existence, many species of mayflies were described under the genus *Baetis* before this all-inclusive category was divided into several smaller genera. In the latest treatment of the genus (Morihara and McCafferty 1979), 39 North American (north of Mexico) species are included as being valid forms.

Morihara and McCafferty suggested that the North American species might be divided into species groups in the way that Müller-Liebenau (1969) divided the European species of *Baetis*. Morihara and McCafferty decided not to establish the group names as taxonomic categories but to use them simply as a convenience. They found that some species are not assignable to a group because their relationships are unclear or they are relatively unique. Two of Morihara and McCafferty's groups are represented by Florida species—the *B. fuscatus* group includes *B. intercalaris;* their *B. propinquus* group includes *B. ephippiatus*, *B. frondalis*, and *B. propinquus*. Only *B. pygmaeus* remains unassigned to a group. Müller-Liebenau (1981), reviewing the Baetidae from the Sunda Islands and the Philippines, confirms that *propinquus* and *ephippiatus* belong to the genus *Baetis*, not to *Acentrella*.

The species of *Baetis* are rather generally distributed throughout the world. In the Nearctic and Neotropical regions, the genus is widely dispersed from southern South America to the Arctic region in North America; its only requirement apparently is the presence of permanently moving fresh water.

The morphological similarities of the adults make identification rather difficult; so identification must be based on male characteristics such as eye shape and color, abdominal color pattern, genitalia, and hind-wing venation and shape. Females are so similar that species identification must be dependent on relating them with identifiable males or by rearing them from nymphs that may be identified. Identification of nymphs can be made with some degree of accuracy when one works in a restricted geographic region where the mayfly fauna is rather well known. Morihara and McCafferty constructed a key to the known nymphs of 21 North American species, which now permits identification with some reasonable degree of certainty. This key makes extensive use of taxonomic characters and methods of preparing specimens that were developed by Müller-Liebenau (1969) in her excellent study of European species of *Baetis*.

From a consideration of the hind wings of *Baetis* there appear to be at least three lines of development: enlarged wings with three or more longitudinal veins and a small costal process; medium-sized wings, usually with three longitudinal veins and a rather large, hooklike costal process; and smaller hind wings with two longitudinal veins and usually a small, or no, costal process. From the standpoint of nymphs, other lines of development may have evolved: those nymphs with three caudal filaments and those with only two. The former group can be further subdivided into those possessing rounded seventh gills, and those with lanceolate seventh gills. Again, the former group can then be subdivided into those species with an expanded second segment of the maxillary palp and those in which this segment is not expanded.*

Ecologically, the nymphs are confined to water in which there is constant motion. In Florida, *Baetis* nymphs mostly occur in streams, although Richard Cantrell reports finding them at lake margins in the central part of the state.

Baetis ephippiatus Traver

(FIGS. 30, 96, 128, 167. MAP 3)

Berner 1950, pp. 205–208 (*Acentrella ephippiatus*); 1958, p. 30; 1977, p. 16.
Morihara and McCafferty 1979a, pp. 180–182.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 205.

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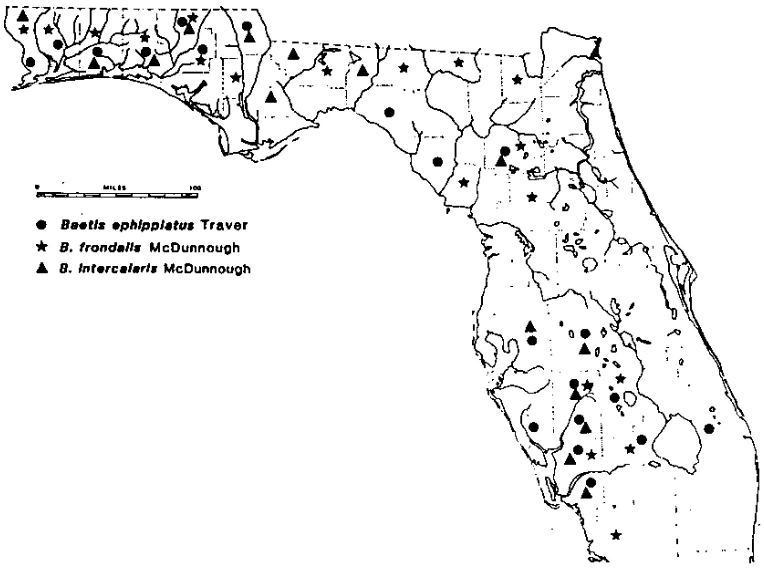
*The 1987 paper by R. D. Waltz and W. P. McCafferty (New genera of Baetidae for some Nearctic species previously included in *Baetis* Leach [Ephemeroptera]. Ann. Entomol. Soc. Amer. 80: 667–670) was received after this book was in press. They have restricted Nearctic *Baetis* and erected three new genera to include species formerly included in *Baetis*. Future papers by them are likely to modify further the concept of *Baetis*.

TAXONOMY. Traver described *Baetis ephippiatus* in *The Biology of Mayflies* (Needham, Traver, and Hsu 1935) but based her description on males only. In 1937 she re-erected *Acentrella*, and by this action removed *ephippiatus* to Bengtsson's genus. The nymph of this species was described (by Berner) in 1940, at which time it was pointed out that the species, on the basis of the nymph, formed an intermediate between *Baetis* and *Acentrella*. Subsequently, with the synonymizing of the two genera, the generic name of the species is now settled.

The adult male is easily distinguished from the various *Baetis* species found in Florida by the absence of the costal process from the metathoracic wings and by the presence of a truncate penis cover; the adult female is less easily separated. We have found that the best trait for separating these females from those of *B. propinquus* and *B. pygmaeus* is the presence of a distal femoral band on each leg of *B. ephippiatus*. The nymphs are distinct from all other Florida species in having a strongly colored seventh pair of gills; without the use of this characteristic, many of the nymphs might be confused with those of *B. propinquus*, for the labial palpi of the two species are very similar. Morihara and McCafferty (1979) have noted that the form of the submarginal labral setae of *ephippiatus* is distinctive in being branched. In well-marked nymphs, the prominent red-brown tergites of segments 2, 5, and 8, and the reddish markings on the venter easily separate this species from others.

In the first edition of this monograph, a group of specimens lacking abdominal markings was assigned the name *Baetis propinquus* (Walsh). In the discussion it was mentioned that they could be differentiated from *ephippiatus* only by the fact that adult males of *ephippiatus* have dorsal markings on the pale abdominal tergites. Several specimens of *ephippiatus* have since been found on which the markings are obsolescent. Because of this and the very similar hind-wing venation and male genitalia, it was suggested that these specimens called *propinquus* might be merely variants of *ephippiatus*. Morihara and McCafferty (1979a) substantiated the suggestion that the Florida specimens named *propinquus* really belong to the species *ephippiatus*.

GEOGRAPHIC DISTRIBUTION. *Baetis ephippiatus* is widely distributed in northwestern Florida and in the two southernmost counties of Alabama. Cantrell has found the species to be the second most common *Baetis* in the central and southwestern counties of Florida. *B. ephippiatus* was described by Traver from specimens collected at Fort Valley and Rome, Georgia. Rome is located near the southern tip of the Valley and Ridge physiographic province; Fort Valley is on a plateau just below the Fall Line Hills.



Map 3. The distribution of *Baetis ephippiatus*, *B. frondalis*, and *B. intercalaris* in Florida.

The Florida and Alabama records are from typical Coastal Plain country. *B. ephippiatus* is known from the following Florida counties (map 3): Alachua, Bay, Charlotte, Columbia, DeSoto, Dixie, Escambia, Glades, Hardee, Highlands, Hillsborough, Holmes, Jackson, Lee, Martin, Okaloosa, Santa Rosa, Sarasota, Taylor, and Walton.

ECOLOGY. Nymphs inhabit sand-bottomed streams and margins of large lakes where they cling to the vegetation. We have found them most frequently in those creeks emptying into the Choctawhatchee Bay in northwestern Florida. The streams have dense growths of *Vallisneria*, *Potamogeton*, *Sagittaria*, and algae in all parts except the deepest, and in them, *ephippiatus* nymphs are the most frequently encountered of the ephemerids. The nymphs cling to the vegetation in the swiftest, as well as the slowest, parts of the creek, but are seldom found on submerged logs and boards or in the very slow-flowing water near shore. Many of the creeks in the panhandle region of Florida are small and shallow and have very little submergent vegetation, but nymphs manage to live in them by clinging to the small bits of plant material and to the accumulated debris. In these streams there is a paucity of habitats, which is reflected in the smaller number of nymphs present, for there are far fewer insects per cubic foot of area than in the streams first described.

In Alachua County, the nymphs and adults have been taken only from Hatchet Creek which, prior to modification, had one of the richest mayfly faunas in central Florida. In the shallower parts of the creek, there were dense growths of *Potamogeton, Fontinalis,* and other plants among which the nymphs lived. Nymphs seldom venture into the quieter water nearer shore where the kindred nymph, *B. propinquus,* is often found. Even the more rapid water of Hatchet Creek is fairly slow when compared to many northern streams, but the flow is continuous and the current is quite noticeable, particularly in the shallower portions.

Subimagoes only are known from the Hillsborough River; they were collected where it is fairly shallow, rapid, and filled with vegetation, principally *Vallisneria.*

Every stream from which we have collected nymphs of *B. ephippiatus* and at which we have taken pH readings showed a definitely acidic reaction. In no case did the acidity range below 5.8; all readings were by the colorimetric method. The Hillsborough River, from which we have only adults, is slightly basic. The acidic streams drain flatwoods or swampy areas and usually are lightly to strongly brown-tinted.

SEASONAL DISTRIBUTION AND LIFE HISTORY. *B. ephippiatus* occurs in Hatchet Creek near Gainesville, but the species has been taken only intermittently on many collecting trips to the stream; consequently, seasonal data are not very complete. Though a study of the specimens from west Florida and from Hatchet Creek indicates that the species emerges throughout the year, adults in our collections were taken only in March, April, May, June, August, October, and November. Nymphs in their last instar were collected in August and September, whereas half-grown specimens are known for April, May, and June, and very immature nymphs for June only. These latter specimens seem to indicate that emergence occurs during the winter and fall. However, we have no definite information for the remainder of the year, owing primarily to lack of collecting in the other months. The late P. W. Fattig collected the type specimens in Georgia on June 1 and August 3, 1931.

Nymphal life probably lasts only a few months. The matter of developmental time is much in need of detailed investigation, especially following the findings of L. J. Gray (1981), who reared *Baetis quilleri* in from 7 to 13 days. Eggs that he obtained from reared adults hatched in 1 or 2 days; subimagoes emerged in from 9 to 11 days. Nymphs with fully developed wing pads were present after 6 days. Gray's study was conducted in a Sonoran Desert stream in Arizona. Jacobi and Benke (1985) conducted growth-rate studies of *B. ephippiatus* collected from the Ogeechee River in east-central Georgia. They estimated that during the summer months this mayfly completed its development in 24 days.

When the subimago is ready to emerge, the nymph swims to the surface, its thoracic covering splits, and in an instant the subimago rises from the water. This speed is particularly necessary in streams, for if the adult is thrown off balance and the wings become wet, they crumple when freed from the water. The insect is then doomed, for it cannot again straighten its wings. When the subimago rises from the water, it flies upward and may reach a support close to the stream. Usually, the flight is upward until the insect is out of sight some 25 feet in the air. It then probably flies to one of the trees that line the stream margin, where it sits quietly and awaits the ultimate molt. The shedding occurs within eight or nine hours. In the field, adults have been observed emerging just after sunset, and in the laboratory the performance is the same. Nothing is known of the mating flight or oviposition. Females of some species of *Baetis* have been seen crawling beneath the water surface to glue their eggs to objects embedded in the streambed (Thew 1957; Edmunds et al. 1976).

BEHAVIOR. The nymphs of this species are rapid swimmers that cling gracefully to vegetation, their heads facing upstream and their tails waving as the current swings their bodies from side to side. As they move slowly over their supports, they graze on the materials covering the plants and occasionally dart to another plant, but always facing upstream. The nymphs, which seldom go deep into the clumps of vegetation, remain mostly near the outer leaves and stems away from accumulations of silt and detritus.

The body of the nymph is quite rounded, and when a specimen is placed in a pan or dish, it usually falls on its side and can move only by flicking its abdomen. If the insect falls on its belly surface, it can crawl, but not so rapidly as the leptophlebines.

Examination of the alimentary tract of west Florida specimens indicates that the nymphs feed predominantly on filamentous algae, but an occasional diatom is picked up along with the filaments.

Baetis frondalis McDunnough

(FIGS. 28, 81, 97. MAP 3)

Berner 1950, pp. 218–221 (*B. australis*); 1958, p. 30 (*B. australis*); 1977, p. 15 (*B. australis*).
Morihara and McCafferty 1979b, p. 133 (*B. frondalis* = *B. australis*); 1979a, pp. 182–185.
Needham 1949, p. 457 (*B. australis*).
Peters and Jones 1973, p. 30 (*B. australis*).
Schneider 1969, p. 205 (*B. australis*).

TAXONOMY. *Baetis frondalis* was first reported from Florida in 1940 (Berner) as *B. australis*. This latter name was used for the species until Morihara and McCafferty (1979a) synonymized it with *frondalis*. They pointed out that Traver had erected *australis* on the basis of some rather trivial and subjective criteria and that their study had demonstrated Traver's differences were inconsistent. In Morihara and McCafferty's paper figure 17 is apparently mislabeled as being the forceps of *B. frondalis;* in reality it is a drawing of *B. tricolor* (fig. 111a of Müller-Liebenau), a European species that resembles *frondalis*.

Morphologically, the male is distinct from all other *Baetis* adults in North America and can easily be separated from other Florida *Baetis* by the dark coloration of abdominal segments 2 through 6. The genitalia of *frondalis* resemble those of *propinquus* but lack the inwardly directed medial projection of the basal enlargement of the forceps of that species. The metathoracic wings of the two species are very similar in that they are long and narrow, the longitudinal veins are reduced to two (the third being variable), and the costal process is obsolescent.

None of the females we have examined can be assigned with any degree of certainty to *frondalis;* some are doubtless included among the specimens we have identified as *propinquus*. The differences are so slight that the females of the two species are virtually indistinguishable. The nymphs are likewise very difficult to separate, and we have found no characters that are easily used to distinguish them. Examination of a large series of specimens shows that the cerci of *propinquus* are shorter than those of *frondalis*. In the last-instar male nymphs, the abdomen of *frondalis* is unicolorous while that of *propinquus* is more variegated. Gills and mouthparts of the two species are very similar; however, Morihara and McCafferty (1979a, p. 182) have separated nymphs of *ephippiatus, propinquus,* and *frondalis* on the basis of the dorsal setal arrangement on the labrum: "The labrum of *B. frondalis* has an irregular row of subapical setae composed of a variable number of distally expanded setae . . . ; in *B. ephippiatus* this row is composed of setae which are branched . . . ; and in *B. propinquus* the submarginal setae are simple and occur in small aggregates."

GEOGRAPHIC DISTRIBUTION. Traver described *B. australis* in 1932 from specimens taken at Goshen Swamp, at Burncoat Swamp, and in Lenoir County, North Carolina. Later, she recorded *B. frondalis* (as *australis*) from Fort Valley, Georgia, which is in the more hilly section of the Coastal Plain. We have specimens collected from Alachua County to the Alabama state line. Needham (1949) mentioned that he had taken specimens (identified for him by Traver as *B. australis*) from Highlands County but we have no adults from this far south and our nymphs show only *propinquus* characteristics. We also have a few nymphs from Lee County in extreme southwestern Florida. *B. frondalis* is known from Ontario and Quebec in Canada and from the southeastern and central United States. We have recorded specimens from the following Florida counties (map 3): Alachua, Calhoun, Collier, Columbia, DeSoto, Escambia, Glades, Gulf, Hamilton, Highlands, Jackson, Lee, Leon, Levy, Liberty, Madison, Marion, Okaloosa, Santa Rosa, and Walton.

ECOLOGY. Identifiable nymphs and adults have been collected only from acidic streams, all of which fall into the sand- and silt-bottomed categories. In the former streams, the nymphs can be found living on the vegetation in the most swiftly flowing portions as well as in the slowest areas. Like *propinquus*, the nymphs tend to remain near the distal parts of the plants where there is the greatest flow and the smallest deposit of silt. Nymphs may occur on all sorts of stream debris. Submerged logs, in particular, are sought by the nymphs, which hide in the cracks and crevices on the downstream side. In the Alachua County creeks, the nymphs were found principally on *Panicum* and on a moss that grows profusely in certain parts of some of the streams where the flow is at least perceptible. The west Florida nymphs were chiefly inhabitants of the dense mats of *Vallisneria* and *Potamogeton* that choke the streams. Cantrell has told us that *B. frondalis* is one of the few species inhabiting seasonal, intermittent streams in southern Florida.

The silt-bottomed streams from which nymphs were taken had luxuriant growths of *Ludwigia, Polygonum,* and eelgrass. Despite this plentiful vegetation, the mayfly fauna was not excessively large.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults have been reared or collected in each month except January, June, and July; and it is likely that adults occur then, but we have not been fortunate enough to encounter them. The rate of development of the immatures is probably temperature-dependent, so that during most of the year it occurs rapidly, especially in southern peninsular Florida.

The process of emergence is like that of *B. propinquus*. The subimago emerges during the afternoon about two or two and one-half hours before sunset. All subimagoes that were observed in the field emerged from very small streams, and in every case the insect flew to the nearest support and settled about three or four feet above the water surface. The subimaginal molt takes place after 7 to 10 hours, and the imago remains quiescent until time for the mating flight. We have not observed the flight nor has it been reported by other workers. Most flights of *Baetis* occur in late morning or early afternoon, and the swarms are highly variable in size. Generally they occur over water or a stream bank at heights varying from a few feet to as high as 15 feet above the water.

BEHAVIOR. We have noted no differences in the behavior of nymphs of *B. propinquus* and those of *B. frondalis*. Observations relating to the former species will apply equally well to *frondalis*.

Baetis intercalaris McDunnough

(FIGS. 29, 109. MAP 3)

Berner 1950, pp. 221–224; 1958, p. 30; 1977, p. 16.
Cowell and Carew 1976, pp. 590–591.
Jones 1977, p. 65.
Lanquist 1953, pp. 50, 53, 66.
Morihara and McCafferty 1979a, pp. 168–171.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 205.
Sloan 1956, p. 92.

TAXONOMY. McDunnough's taxonomic work on the Ephemeroptera began with his description of *Baetis intercalaris* in 1921. The species was again described by McDunnough in 1923 when he examined living insects in order to clarify the differences existing in the eyes of certain species of *Baetis*. Traver (1935) redescribed the male adult in the taxonomic portion of *The Biology of Mayflies*, and Ide (1937) completed the life history with his description of the nymph. In 1940 the species was reported from Florida (Berner 1940); the identification was tentative as only nymphs and females were available at that time. Subsequently, the correctness of the identification has been confirmed.

The shape of the labial palp, which is not expanded, easily separated the nymphs of *intercalaris* from most other Florida *Baetis*. The relatively long cerci and the mode of banding of these structures are also characteristic. The rounded seventh gills immediately separate the nymphs from those of *B. pygmaeus*. The adults, male and female, are easily separated from other Florida species by the large hind wing, which has a definite costal projection and a third longitudinal vein.

Morihara and McCafferty (1979b) separated the nymph of *intercalaris* from its very similar relative *B. flavistriga* on the basis of color pattern of the abdominal terga. As *flavistriga* is not known to occur south of the mountainous regions of Tennessee and North Carolina, there are no other species with which *intercalaris* might be confused in Florida.

GEOGRAPHIC DISTRIBUTION. For many years after the first report of *intercalaris* occurring in Florida and Ontario, there were no further records between these widely separated localities. The species is now known to be widespread throughout eastern and central North America. We have records of *intercalaris* extending its range from Hillsborough County in peninsular Florida to the Alabama state line in the northwestern part of the state. Our county records include the following (map 3): Alachua, Calhoun, Charlotte, DeSoto, Escambia, Gadsden, Hardee, Hillsborough, Holmes, Jackson, Jefferson, Lee, Liberty, Okaloosa, Sumter, Walton, and Washington.

ECOLOGY. Basic streams, where the flow is swiftest, support the largest populations of *B. intercalaris* nymphs. Although the species does inhabit acid water, the creeks are usually only slightly acidic, and they have sand bottoms. In the central portion of Florida, nymphs have been collected in greatest numbers from the Santa Fe River and from the Hillsborough River, both of which are alkaline streams. The nymphs are very rare in the sand-bottomed streams of peninsular Florida, but Cantrell has found them to be very common in the Peace River drainage of west-central and southwest Florida. In Alachua County where collecting has been most intensive, nymphs have been taken only at the Santa Fe River.

In the Santa Fe River, the number of immatures fluctuates greatly from one time to another, but the population is never so great as that of *B. propinquus*, with which *intercalaris* is associated. Both species inhabit eelgrass in the swiftest water; but in more rapid currents the *intercalaris* nymphs congregate in greater numbers than do those of *propinquus*. In the slower areas the ratio of *intercalaris* to *propinquus* is reversed.

There are never large concentrations of nymphs in the sand-bottomed streams. Frequently, even though other species of *Baetis* are fairly common, only one or two specimens of *intercalaris* are taken. The nymphs inhabit the vegetation and debris wherever the water is permanently flowing. If there is debris in the middle of the stream, the nymphs will more likely be found there in greater numbers than near the shore. In the creeks of Gadsden County there are often masses of exposed roots of terrestrial plants that are washed by rather rapidly flowing water. *B. intercalaris* nymphs can usually be collected from these mats. Submerged logs in the swifter water are also productive situations; but examination of such logs is a rather arduous task and less profitable than root collecting.

The size of the stream evidently has no bearing on the presence or absence of nymphs, as the insects have been found in brooks as narrow as three feet across and as shallow as three inches deep, as well as in creeks and in rivers. In the smallest streams there was no vegetation, and the nymphs inhabited debris lodged in the streambed. The bottom of one small creek, about three or four inches in depth, was covered with a thin growth of algae, in which several nymphs were found.

Cowell and Carew (1976), while studying stream drift in Blackwater Creek in Hillsborough County (a small stream draining into the Hillsborough River), found that *Baetis intercalaris* nymphs formed a significant component of the complex of drifting insects. The stream has dense growths of *Vallisneria, Potamogeton,* and *Egeria.* Ephemeroptera formed 17% of the benthic fauna; however, Cowell and Carew found marked differences in the composition in the three benthic habitats sampled: riffles, pools, and aquatic vegetation. These authors noted that major peaks in drift rates occurred in December and March, and the rates were low in late December and in January; they also tended to be low during the warmer months of April to late August.

Cowell and Carew found *Baetis intercalaris* to be the most abundant organism in the drift, comprising 35.2% of the total. Seasonal changes in the drift of *intercalaris* accounted for much of the variability in the total drift. There was a marked night-active periodicity in the drift rate. In their four diel studies peak drift rates that were 700–800 times greater than daytime levels occurred within one hour after sunset.

The data showed peak drift rates in winter and early spring dropping to minimal values during the summer. Cowell and Carew (1976, p. 593) concluded that "different life history patterns related to the marked differences in environmental conditions (e.g. temperature, photoperiod, patterns of allochthonous import, etc.) found between northern and southern streams are probably responsible for the differences in seasonal drift patterns."

SEASONAL DISTRIBUTION AND LIFE HISTORY. That *B. intercalaris* emerges throughout the year is clear from the fact that adults or last-instar nymphs have been collected in each month of the year. There is some indirect evidence lending credence to the belief that this species does have a tendency to form broods within a particular stream. The collections from the Santa Fe River seem to indicate that March and October are important months for emergence because the mature nymphs were very common during these periods; however, mature nymphs were also found on other dates but not in such numbers. Nymphs collected from Sweetwater Creek in northwestern Florida were predominantly in the last nymphal stage during December, but mature nymphs were also present in other months in which collections were made there.

In their study of stream drift, Cowell and Carew reported that large numbers of last-instar exuviae were collected in their drift nets at Blackwater Creek on March 28, July 25, and October 3, 1972, indicating that adults were emerging at that time.

When McDunnough (1921; 1923) collected the type specimens of *intercalaris* at the Rideau River, Ottawa, from June 11 through June 14, 1920, and other specimens two years later, he noted that there were apparently two generations, one emerging in early June and the other from the middle of August until early in September. McDunnough also noted that individuals of the second generation were somewhat smaller than those of the first.

Ide (1935), working on the effect of temperature on the distribution of mayflies in a stream in Ontario, found that in the lower, warmer reaches of the stream, *intercalaris* gave definite evidence of the occurrence of two generations in the same season, the first during the early part of June, the second starting in July and proceeding until the middle of August. Collections from the upper part of the stream indicated that there is probably only one generation produced at the upper stations in a season.

Harper and Harper (1984) found small numbers of adults emerging in September in southern Ontario, and Burks (1953) observed them throughout the summer in Illinois. Bergman and Hilsenhoff (1978) noted the same behavior in Wisconsin.

At the same time that Jacobi and Benke (1985) were studying growth rates of other mayflies collected from the Ogeechee River in east-central Georgia, they investigated those of *B. intercalaris* in an artificial stream using water from the river. They estimated that during the summer months development was completed in 24 days.

Because the limits of tolerance of *B. intercalaris* are not very great, rearing in the laboratory presents some difficulties. Many attempts were made to bring live specimens to Gainesville from the Santa Fe River, but most of them died en route. However, a few were successfully transported to the laboratory and several lived for slightly more than two days in an aerated aquarium. Of these, only females emerged. Essentially emergence is like that of *propinquus*. The nymph makes a few rapid dashes that end at the water's surface, the thoracic covering splits, and the fully emerged subimago immediately appears and at once flies to the nearest support. Emergence has also been observed in the field, where it was seen that the insects do not at once head for shore, but fly directly upward until lost to sight. They probably seek refuge among the protecting leaves of the higher trees.

The subimagoes begin rising just about sundown and continue for approximately 30 minutes, the peak being about 15 minutes after emergence starts. In the laboratory a subimago emerged an hour after dark, at 7:30 P.M., and underwent its imaginal molt at 8:07 A.M. This is an excessively long subimaginal period and is probably atypical for a member of the genus *Baetis* because most specimens that were observed in the laboratory molted within 8 to 10 hours after transformation.

The mating flight of *B. intercalaris* has not been described, nor have we ever observed it.

BEHAVIOR. The living nymphs can usually be distinguished from those of *B. propinquus* and *frondalis* without microscopic examination, although they are superficially similar and agree in body size and in length of caudal filaments. When nymphs of *B. intercalaris* are placed in a small amount of water in a white-enameled pan, the gills are spread outward from the abdomen so that they overlap its borders considerably. Furthermore, the gills, as seen against the white background, frequently have a greenish tinge. *B. propinquus* and *frondalis*, on the other hand, usually hold their relatively colorless gills much closer to the body. In addition the caudal filaments of *intercalaris* are usually less intensely banded than those of *propinquus* and *frondalis*. Swimming and clinging activities of *intercalaris* are very similar to those of *propinquus*.

The nymphs live on vegetation growing in the swift water and cling near the upper, free ends of the leaves where the full force of the current can strike them. Remaining on the undersurface of the leaves, they feed on the materials covering the plants. The food consists chiefly of algae, but diatoms, desmids, and plant epidermis are frequently eaten.

Although the upper surfaces of the rocks in the Santa Fe River are completely covered with the moss *Fontinalis*, this moss does not serve as a habitat for *intercalaris* nymphs, probably because of the slowness of the current through the plant and because of the heavy silting where it grows. *B. intercalaris* has one of the most rheotactic nymphs of all the mayflies inhabiting Florida streams.

Baetis propinquus (Walsh)

(PLATE 1. FIGS. 6, 31, 83, 95, 110, 130, 131, 170.
MAP 4)

Berner 1950, pp. 211–218; 1958, p. 30; 1977, p. 18 (*B. spinosus*).
Jones 1977, p. 65 (*B. spinosus*).
Lanquist 1953, pp. 23, 24, 27, 40, 44, 50, 53, 62, 66 (*B. spinosus*).
Morihara and McCafferty 1979b, p. 130 (*B. propinquus* = *B. spinosus*); 1979a, pp. 185–187.
Peters and Jones 1973, p. 246 (*B. spinosus*).
Schneider 1967, p. 205 (*B. spinosus*).
Sloan 1956, p. 92 (*B. spinosus*).
Wurtz and Roback 1955, p. 194 (*B. spinosus*).

TAXONOMY. For many years the Florida species now recognized as *B. propinquus* was called *Baetis spinosus* McDunnough. Morihara and McCafferty (1979b, p. 130), after carefully examining the male lectotype of *B. propinquus* at the Museum of Comparative Zoology, stated that "the name *B. spinosus*, commonly and incorrectly applied to this species in the past, must be regarded as a junior synonym. The incorrect usage is a result of the male genitalia of *B. propinquus* never having been described or figured."

These authors point out that the male genitalia have "a distinct, medially directed projection of the basal enlargement of the forceps . . . , which readily distinguishes *B. propinquus* from any other North American *Baetis*."

Another trait that has caused confusion in the past is the presence or absence of a small costal projection on the hind wing of the male. Burks

Plate 1. *Baetis propinquus* (Walsh), male imago

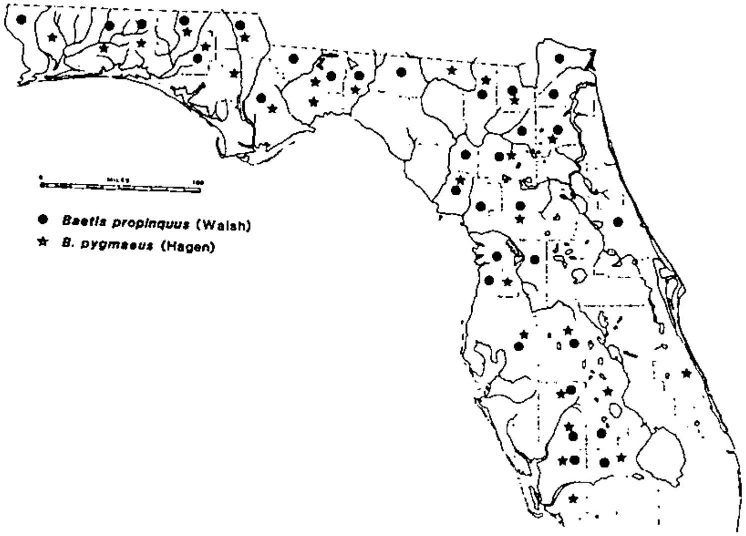
(1953), in his discussion of *B. spinosus* in Illinois, found the structure to be vestigial or absent. He described *propinquus* as lacking the projection. Our Florida male specimens from which we have removed the hind wing for examination show a very small, but distinct, costal projection, but it is obsolescent in the female. We do not consider the presence or absence of this structure to be of sufficient importance to retain the name *spinosus* for the Florida form and concur with Morihara and McCafferty in the synonymy.

Walsh described *B. propinquus* from specimens collected in Illinois. This widespread species is now known to occur throughout eastern North America. Males are easily distinguished from the other species of *Baetis* by the characteristics described above. Generally, females cannot be separated from those of other species.

Nymphs are easily differentiated from all other Florida species by the shape of the seventh gill, which is rounded, the enlargement of the second segment of the labial palpi, and the submarginal setae of the labrum, which are slender, unbranched, reduced in number, and often paired. Mature nymphs can be separated from those of *ephippiatus*, which they resemble, by the more strongly marked abdominal tergites of *ephippiatus*. They are less easily distinguished in the field from the nymphs of *frondalis* and the submarginal lateral setae must be examined microscopically for their differentiation.

GEOGRAPHIC DISTRIBUTION. *Baetis propinquus* is distributed over the entire eastern portion of North America from Manitoba to south Florida. In Florida, *B. propinquus* is one of the most widely dispersed of all the mayflies. It is found from the southwestern border of Alabama to the northeastern corner of Florida, and from this latter locality as far south as Collier County. In the panhandle of Florida, nymphs can be found in every unpolluted stream in which there is permanently flowing water, and in peninsular Florida this is true almost without exception. *B. propinquus* specimens have been collected in the following Florida counties (map 4): Alachua, Baker, Bay, Charlotte, Citrus, Clay, Collier, Columbia, DeSoto, Escambia, Gadsden, Gilchrist, Glades, Hamilton, Hardee, Hernando, Highlands, Hillsborough, Holmes, Jackson, Jefferson, Leon, Levy, Liberty, Madison, Marion, Nassau, Okaloosa, Polk, Putnam, Sumter, Suwannee, Taylor, Volusia, Walton, and Washington.

ECOLOGY. Without doubt, this is one of the most adaptable of all Florida mayflies. The following instance is a fairly good example of its ubiquity. Nymphs were observed in a flume leading to a dam at the origin of Little



Map 4. The distribution of *Baetis propinquus* and *B. pygmaeus* in Florida.

Sweetwater Branch in Liberty County. The sides of the flume, constructed of wood, were covered with a thin growth of algae, and there was a continuous flow of water through the trough. The level of the water was not much over two or three inches, yet it supported a rather large population of *B. propinquus* nymphs of all sizes. We have found immatures along the edges of creeks where the water was practically stagnant and the nymphs were living under accumulated masses of dead leaves and silt. Conversely, the nymphs have been found in the most rapid parts of the most rapidly flowing Florida streams, where they can be found in all regions ranging from the slowest to the swiftest.

Those streams in which there are dense growth of *Vallisneria*, *Sagittaria*, and *Potamogeton* support the largest populations of *B. propinquus* nymphs. The reason for this abundance is seen in the tremendous amount of surface presented by the thick masses of this submerged vegetation. An abundance of food materials in the form of algae and diatoms covers the surfaces of the leaves. An excellent example of this type of stream is the Santa Fe River in the vicinity of Poe Springs. There, the *Vallisneria* and *Sagittaria* grow so thickly that in wading the stream one might easily walk almost across it without touching the streambed. During the late winter, spring, or summer, 50–100 nymphs may be collected with a few strokes of the dip net through this tangle of vegetation. In this mass, the nymphs seem to prefer the more distal or free portion of the leaves and become less numerous near the base of the plants.

The spring runs in the west-central and the north-central parts of Florida are usually similar to the Santa Fe River in having great growths of eelgrass. Near the head of the runs, where the springs emerge, mayflies are very rarely found, although within a short distance downstream they become noticeable. Their absence from the head of these runs may possibly be explained by the fact that the water emerging from the ground carries in solution large amounts of bicarbonate which are deposited as carbonate when the water reaches the surface. By forming a covering over the surface of the plants this salt prevents the mayflies from securing sufficient food to survive. Another explanation of the absence of mayflies from the springheads might be the lack of sufficient oxygen in the water just after it emerges from its subterranean channels. As surface water, it has not yet had time to become sufficiently oxygenated for the maintenance of mayfly populations. At the head of the springs the snail *Elimia* normally occurs in almost unbelievable numbers. We have almost filled a dip net with them after taking a few strokes through the eelgrass; these snails may also be a factor in restraining the introduction of mayfly nymphs into springheads.

Sloan (1956), in his study of insects in two Florida springs, found that ecological niches in them are relatively few in number. He demonstrated that the general trend in the rivers formed by the springs is for species numbers to be low initially at the spring pool, to increase rather sharply further downstream, and to decline gradually as the water moves toward the brackish estuary. Sloan also found a striking correlation between the distribution of the insects and the oxygen concentration and partially confirmed the hypothesis that in the springhead areas this may be an important limiting factor that explains the paucity of aquatic insects here.

Any slightly acidic stream containing detritus, submerged logs, leaf drift, or vegetation in midstream or near shore will ordinarily have nymphs, even though they may occur in very limited numbers. Many of these streams have so little vegetation and other suitable habitats for development of nymphs that only small numbers can be supported. Only rarely do nymphs enter such dense mats of algae as those formed by *Spirogyra* and *Batrachospermum*.

Physically, the water inhabited by the nymphs of *B. propinquus* shows a wide range. The immatures are found in streams with a pH as low as 5.0, as well as in alkaline streams, with a pH as high as 7.8. In general, it seems that the nymphs thrive better in slightly alkaline water with a pH of about 7.3. The temperature factor is not particularly important in Florida, although during a cold spell the degree of emergence greatly lessens and may completely stop. As the water gradually warms, the nymphs again become active enough to attain the adult state.

Nymphs can apparently tolerate standing water for a time because we have been able to keep them alive in unaerated aquaria for as long as two days, and in shallow pans of water for as long as three. If the water is aerated, however, the life of the insect may be prolonged as much as two weeks in the laboratory. This ability to tolerate standing water is probably one of the factors accounting for the wide distribution of the species. If the nymphs can live in intermittent streams and in those that flow most of the time but that occasionally become stagnant, it would greatly increase the adaptability of the species. There is some field evidence to indicate such tolerance. We have collected nymphs from several streams that connect two bodies of standing water. Normally there is a slight movement of water from one of these bogs to the other, but during low water the flow ceases. If the flow ceases for too long a time, the nymphs die off; but as soon as the water begins moving again, these intermittent creeks become repopulated from nearby permanently flowing streams.

Even though *B. propinquus* is so tolerant, it has not yet become adapted to lake margins in Florida as have *Eurylophella temporalis, Choroterpes hubbelli,* and *Stenacron interpunctatum.* Our examination of the margins of many sand-bottomed lakes has produced not a single immature even though we often found nymphs of the other species.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Among the materials at hand, there are adults or nymphs in their last instar taken during each month of the year, clearly indicating that *B. propinquus* is one of the many species of mayflies that emerges throughout the year in Florida. In the northern part of its range, *propinquus* has a short seasonal emergence, but the farther south it occurs, the longer the season, until in Florida seasonal limits disappear.

Many unsuccessful attempts have been made to hatch eggs in the laboratory. Adult females forced to oviposit produced eggs that failed to develop; artificial fertilization also failed. Bergman and Hilsenhoff (1978) reported successful parthenogenetic reproduction when studying Wisconsin females collected in June and August. They incubated 1503 eggs from four females and of these 41% hatched when kept at a temperature

of 19°–23°C with an incubation period of 19–20 days. Another female collected in June produced 258 eggs, of which 38% hatched in 32 days at a temperature of 13°–15°C. McCafferty and Morihara (1979, p. 27) suggest that "[p]arthenogenesis is evidently the most selectively favored form of reproduction in relatively colder, or stressed, environments for some species [of *Baetis*]." We have no evidence of parthenogenetic reproduction in the Florida population of *propinquus.*

Published data record the detailed rearing of only a single species, *B. vagans,* which Dr. Helen Murphy (1922) raised from egg to adult both in the laboratory and in the field at Ithaca, New York. She found that under laboratory conditions the nymphs went through 27 instars, and, depending on temperature, the developmental period was six to nine months. Definite broods emerged in May, August, and October. Gray (1981) reared *B. quilleri* from egg to adult in from 7 to 13 days in Arizona. In Florida where year-round emergence occurs, brooding has not been observed and, moreover, would not be expected of *B. propinquus.*

Emergence occurs in late afternoon, usually just after sundown or as the sun is setting. The period of transformation lasts 15 to 30 minutes, with the peak occurring about 10 minutes after the first subimago rises. As the subimago lifts itself from the stream, it can be seen as a slow-moving, grayish body rising upward. If it encounters a tree or bush, the insect stops; if not, it continues its upward flight until it is lost to sight. When sufficiently high, it probably flies horizontally to a nearby tree or bush. We have seen the subimagoes fly almost straight up for 30 or 40 feet before they were lost to sight. When the insects begin to emerge, one can easily spot the area of transformation by observing the path of the giant dragonflies which begin to patrol the stream as the sun sets. The slow flight of the mayflies makes them easy and choice prey for these Odonata. "One day during the spring, as I stood in midstream netting subimagoes, a large dragonfly darted in front of me, grasped a mayfly which was at the mouth of the net, and darted away without even entering the moving bag" (Berner 1950, p. 216). Another excellent indicator of emergence is the increased activity of the insectivorous birds along the stream margins.

Spiders, numerous along the streams, are among the most important decimators of *Baetis propinquus* subimagoes and adults. Many adult mayflies and subimaginal skins have been found entangled in the meshes of spiderwebs under bridges. If the subimago does not entangle itself too badly, and if the spider does not kill the insect at once, there is some chance of its becoming free at its final molt; this is, however, a comparatively rare occurrence.

If the subimago escapes predators, it alights and becomes motionless and inconspicuous, hardly moving during the entire period of its life as an immature adult. After a period varying from 7 to 10 hours, the final shedding occurs. The imago remains in a resting state until time for the mating flight. While resting, adults of *Baetis*, both male and female, frequently twitch the abdomen and swing the caudal filaments from side to side. At Ithaca, New York, *Baetis* performs the mating flight in the forenoon; the time of the event in Florida *propinquus* is not known.

Emergence of the subimago has been observed frequently in the laboratory. When ready for emergence to occur, the nymph floats freely at the surface of the water and almost immediately the subimago pops free, the whole process taking not more than 5 to 10 seconds. Naturally, in such rheotactic forms, rapid emergence is an absolute necessity unless the nymphs migrate into slow water; even those *Baetis* nymphs that happen to be in almost stagnant water emerge very rapidly.

Numerous attempts to rear the species in quiet water in the laboratory failed. Individuals were successfully reared, however, in a cage through which a slow but steady stream of tap water was allowed to flow. The use of an aquarium equipped with an aerator gave an even greater degree of success. The aerator emitted a steady stream of bubbles that disturbed the surface. Apparently, water agitation helps the subimago release itself from the nymphal skin, perhaps by battering; or perhaps the increased amount of dissolved gases in the water aids the nymph in obtaining the air necessary for flotation and loosening of the skin.

With respect to the longevity of the adult, the male shows almost no signs of life about 38 to 40 hours after emergence. The female adult in the subimaginal and imaginal stages may live as long as 48 to 50 hours. Mating obviously must occur very soon after the subimaginal molt and oviposition shortly thereafter.

BEHAVIOR. The habits of posture and movement easily distinguish *B. propinquus* from other mayfly nymphs when they are examined in the laboratory. Usually the insect swims to some point of attachment, grasps it with the claws, and raises the abdomen well above the support. If there is nothing to which it can cling, the nymph swims to the perpendicular sides of the container and hangs there until motivated to move. The gills are held close to and over the abdomen in contrast to *B. intercalaris*, one of the species with which *propinquus* may be most easily confused in the field. When stimulated, the nymphs dart in short spurts from one spot to another by rapidly moving the caudal filaments up and down. The hairs on the filaments overlap and form a very effective organ for rapid propulsion by vibration.

Certainly as swift or swifter than *Callibaetis* nymphs, those of *Baetis propinquus* are less graceful in their resting attitudes. They cling rather closely to their resting place, with their heads upstream and their abdomens swinging from side to side in the current. Slowly, the nymphs crawl over the surface of the leaves or rocks as they search for new and tender bits of food. During this slow movement, the orientation to the current is maintained no matter whether the nymph is on the upper or the underside of the leaf; in a current, however, the insect rarely moves to the upper side of its support, for there it is less protected from the force of the moving water and the food supply is more limited. While feeding, the nymph swings its head from side to side as the maxillary palpi, continually moving, aid it in bringing its food within reach of the maxillae and mandibles.

The food found in the alimentary canals of nymphs indicates that mastication is very thorough, for in every specimen studied, the diatoms were broken and the remainder of the food was destroyed almost beyond recognition, even though it was still in the anterior portion of the tract. The food of the Santa Fe River nymphs proved to be predominantly filamentous algae and plant epidermis, although an occasional diatom was noted.

Adults are only mildly phototactic, with the taxis more pronounced in the subimaginal stage.

Baetis pygmaeus (Hagen)*

(PLATE 2. FIGS. 32, 82, 106, 129. MAP 4)

Berner 1950, pp. 224–229; 1958, p. 30; 1977, p. 17 (*B. spiethi*).
Jones 1977, p. 65 (*B. spiethi*).
Lanquist 1953, pp. 20, 34 (*B. spiethi*).
Morihara and McCafferty 1979a, pp. 190–198 (*B. pygmaeus* = *B. spiethi*).
Peters and Jones 1973, p. 246 (*B. spiethi*).
Schneider 1967, p. 205 (*B. spiethi*).

TAXONOMY. *Baetis spiethi* Berner, synonymized with *pygmaeus* by Morihara and McCafferty (1979a), was described from a large series of both reared and wild-caught specimens in 1940. After examining nymphs and paratypes of *spiethi* from Florida and comparing them with *B. pygmaeus* speci-

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* Waltz and McCafferty (1987) have assigned *B. pygmaeus* to their new genus *Acerpenna*. See footnote, page 97, this volume.

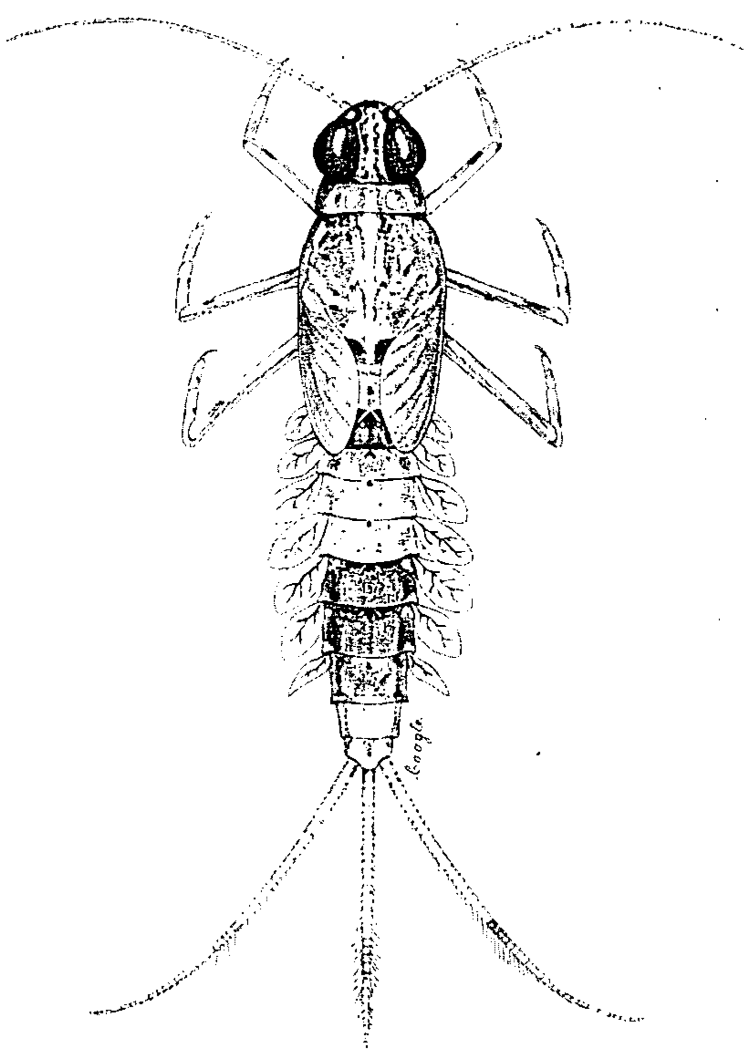


Plate 2. *Baetis pygmaeus* (Hagen), nymph

mens gathered by Ide in Canada, as well as specimens from geographically intermediate populations, Morihara and McCafferty concluded that the nymphs were identical. Adults could be separated only on the basis of a marginal intercalary vein in the first interspace of the forewing, a trait that they believed to be variable.

The male of *pygmaeus* is easily distinguished from all other Florida species of *Baetis* by the shape of the genitalia, the coloration of the abdomen, and, most readily, by the structure of the hind wings, which have only two longitudinal veins and a much more prominent costal projection than does *propinquus*. The differentiation of the females is a more difficult matter. Compared with those of *propinquus* (with which they can most easily be confused), the metathoracic wings of *pygmaeus* are minute—being barely visible against the dark background of the thorax with the highest magnification of the dissecting microscope—and the head of *pygmaeus* is more yellowish. The females of *B. ephippiatus* have a distal brownish band on the femora that distinguishes them from the females of *pygmaeus*. Nymphs are immediately separable from all other known southern baetid mayflies by having lanceolate gills on abdominal segment 7.

GEOGRAPHIC DISTRIBUTION. *B. pygmaeus* is known to occur from Hillsborough County in west-central Florida northward to the Georgia state line and westward to Mobile County, Alabama. According to Morihara and McCafferty, the species is distributed throughout eastern North America from southeastern Canada to Florida and westward to Louisiana. *B. pygmaeus* is as widespread in Florida as *propinquus*, although we have not yet recorded it from the northeastern counties of the state. Florida counties from which specimens have been collected include (map 4): Alachua, Bay, Calhoun, Charlotte, Columbia, DeSoto, Glades, Hamilton, Hardee, Hernando, Highlands, Hillsborough, Holmes, Indian River, Jackson, Jefferson, Lee, Leon, Levy, Liberty, Madison, Marion, Okaloosa, Polk, Putnam, Santa Rosa, Wakulla, Walton, and Washington.

ECOLOGY. *B. pygmaeus* has been found most frequently in the smaller, more slowly flowing creeks. Within a particular stream, they are very similar in habitat preference to *B. propinquus*. In general, the nymphs seem to remain in quieter and shallower water than do those of *propinquus*, but almost always the two live side by side. They are most frequently found in sand-bottomed streams where the vegetation is scattered along the edge of the stream and where the flow is still evident and constant. The nymphs thrive among these plants, and with other Baetidae form the major faunal element. Hatchet Creek, which has been described elsewhere in this monograph, is a typical example of a stream in which *pygmaeus* prospers. In this creek the small bed of *Potamogeton, Micranthemum umbrosum*, and mosses make up the predominant vegetation from which the nymphs have been collected. There they may be found in the swiftest as well as in the slowest parts of the current. In the Torreya State Park region of northwestern Florida, the nymphs are also abundant among the exposed, but submerged, roots of terrestrial plants growing along the banks of the streams that drain into the Apalachicola River.

In every stream from which *pygmaeus* nymphs were collected, *propinquus* or *frondalis* nymphs were also collected or seen, but not all streams from which *propinquus* was taken contained *pygmaeus* nymphs. The size of the stream does not affect the presence or absence of nymphs, as they have been collected from brooks that were merely trickles, as well as from streams as large as the run of Wakulla Springs. This river, like other west Florida streams from which collections were made, has dense growth of *Vallisneria*. Although the nymphs have not been found to be exceedingly numerous in the eelgrass, they do occur there. Some of the streams near the western border of the state have thick mats of *Potamogeton* in which *pygmaeus* nymphs occur as commonly as in Hatchet Creek near Gainesville.

The nymphs live on the undersides of the leaves near the free ends, where they are protected from the current and find food plentiful. Near shore among the vegetation, they may be found most often on the stems about halfway up from the streambed. Occasionally nymphs are found in leaf drift, and somewhat more frequently on submerged logs in the current.

B. pygmaeus nymphs are the most tolerant of all the Florida species of the genus. We have kept nymphs alive in a shallow pan of water without aeration for as long as a week, and they have remained alive in an aerated aquarium for as long as 14 days. The percentage of nymphs transforming in an aerated aquarium is usually greater than that of the other *Baetis* species, except perhaps *propinquus*.

Although nymphs of *pygmaeus* do inhabit alkaline streams, they seem to thrive far better in circumneutral or slightly acidic creeks. These usually have a high content of humic and other organic acids that give the water a brownish tinge.

Adults are often encountered in spiderwebs under bridges. The bridges are also the most productive places for securing free adults or subimagoes, as the humidity over the streams is fairly high and shade is plentiful—two qualities that the subimagoes and adults seem to demand. Apparently the subimagoes of *Baetis* can tolerate a much dryer atmosphere than can the Leptophlebiidae for they can molt where the leptophlebiids would perish in the process.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Seasonally, *Baetis pygmaeus* is not restricted in Florida. While emergence is, of course, greater in the summer than during the colder months, no month is entirely free of adults. Farther north, the species is strictly seasonal, adults emerging during the summer only.

Nymphal life probably occupies a period of less than six months, but as we were not successful in rearing the species from egg to adult, the length of time required must remain conjectural. At all times of the year, nymphs of all ages can be found in Florida waters.

When the nymph is mature and ready to transform, it swims to the surface. As a subimago, it suddenly bursts free of the nymphal skin, floats on the discarded exuviae for a moment, and then flies away. Emergence takes place in the slower-flowing parts of the stream where upsetting is least likely to occur and where the insect may rest before testing its newly opened wings. After this short rest, the subimago rises to nearby bushes or trees where it remains, unless disturbed, until the ultimate molt takes place. The subimaginal stage lasts from 7 to 10 hours, and the males may live about 24 hours longer.

The transformation to the subimago takes place from perhaps an hour before sunset until sunset, but before darkness has fallen. The height of emergence occurs just after sunset, and lasts for about 15 minutes.

We have observed the mating flight of *pygmaeus* on only one occasion. While one of us (Berner) was collecting nymphs at the Waccasassa River on October 13, 1946, a swarm of small mayflies was seen gathering at 10:15 A.M. in the warm sunlight. The males came together in small groups and then amalgamated into one large swarm of about 200 individuals. They flew about 6 feet above the water, near the south shore of the stream, confining themselves to the bank and seldom moving out over the water. The swarm hovered over the vegetation, now and then rising to a height of about 15 feet above the water, but rarely more than 6 or 8 feet above the highest ground level. Only males were observed and collected from the swarm. The group would fly over the bank for a few minutes and then move away from the water only to return again within a short time. The presence of a black railroad bridge and the very dark water outlined the adults clearly so that they were easily observed as long as they remained in the vicinity of the stream.

The up-and-down flight varied greatly, having a rise and fall from six inches to three or four feet. After a period of about an hour, the swarm apparently dispersed. No females were seen joining the males and none was noted until 3:00 P.M. when a single individual was collected while it was flying close to the water.

From a distance, the mating flight resembled the swarming of midges so commonly observed along the margins of the lakes of Florida. It was only by approaching the swarm closely and noting the trailing caudal filaments that the members were identified as mayflies.

BEHAVIOR. The habitats of *pygmaeus* nymphs are not essentially different from those of *propinquus*. The food we examined was so finely masticated that it was difficult to determine its nature from a study of the contents of the alimentary canal. Some of the identifiable fragments included algae, parts of diatoms, small roots, and plant debris.

Callibaetis Eaton

Berner 1950, pp. 193–194.
Edmunds, Jensen, and Berner 1976, pp. 165–169.

When Eaton treated the North American species of *Callibaetis* in his monograph (1883–88), he described only four, three of which were already named. Between 1900 and 1918, Banks added eight additional species, among which were included *floridanus* and *pretiosus*, the two Florida forms. Since the publication of *The Biology of Mayflies* in 1935, five additional species of *Callibaetis* have been described, making a total of 24 known from North America north of Mexico. Though adults as well as nymphs of the genus are distinct and easily separable from other genera, within *Callibaetis* taxonomic characters are not so well defined, making differentiation of most of the species difficult and determinations often questionable.

The genus is one of the unique groups in which ovoviviparity appears to be universal. *Callibaetis vivipara* from South America was first found to exhibit this condition. In 1935 a specimen of an unidentified species from New York was reported to contain first-instar nymphs. In 1941 one of us (Berner) reported the phenomenon of ovoviviparity in *C. floridanus*, *C. pretiosus*, and another species from Michigan and noted that apparently many, if not all, of the species of this genus are normally ovoviviparous. Subsequently Edmunds (1945) confirmed that this method of reproduction occurs in two Utah species.

Callibaetis is both a Neotropical and Nearctic genus, distributed widely over both continents. In North America, it is found from coast to coast in mountainous as well as level regions and its range extends northward to Alaska. *Callibaetis* is one of the most difficult of all mayflies with which to deal; hence published distributional records are few and far between, although the genus is often encountered. Marked sexual dimorphism, especially in the wings, makes association of males and females especially difficult. As there are only two species known with certainty to occur in Florida, identification of males can be made only by assuming they are the same species when they are collected along with the more distinctive females.

Callibaetis floridanus Banks

(PLATE 3. FIGS. 9, 104, 119. MAP 5)

Berner 1950, pp. 194–201; 1958, p. 31; 1977, p. 18.
Berner and Sloan 1954, p. 98.
Frost 1967, p. 281.
Lanquist 1953, pp. 23, 24, 27, 31, 40, 44, 57, 63.
Schneider 1967, p. 205.
Sloan 1956, pp. 92–94.
Trost and Berner 1963, pp. 285–299.

TAXONOMY. In the latter part of the nineteenth century, Mrs. A. T. Slosson collected *Callibaetis floridanus* in the vicinity of Biscayne Bay in south Florida and submitted her specimens to Dr. Banks for identification and description. Her series consisted entirely of females, and the species was known only from this sex until 1940 when a description of the male and nymph was published (Berner 1940b). Our specimens from north Florida, which we are calling *C. floridanus* (form A), may ultimately prove to be a new species. For the present, we are not considering them as such. The north Florida forms differ in certain minor respects from the south Florida insects as follows:

North Florida

Callibaetis floridanus (Form A)
Forewings colorless or only lightly tinted
Spots covering body are brown or reddish brown
Coloration somewhat dulled

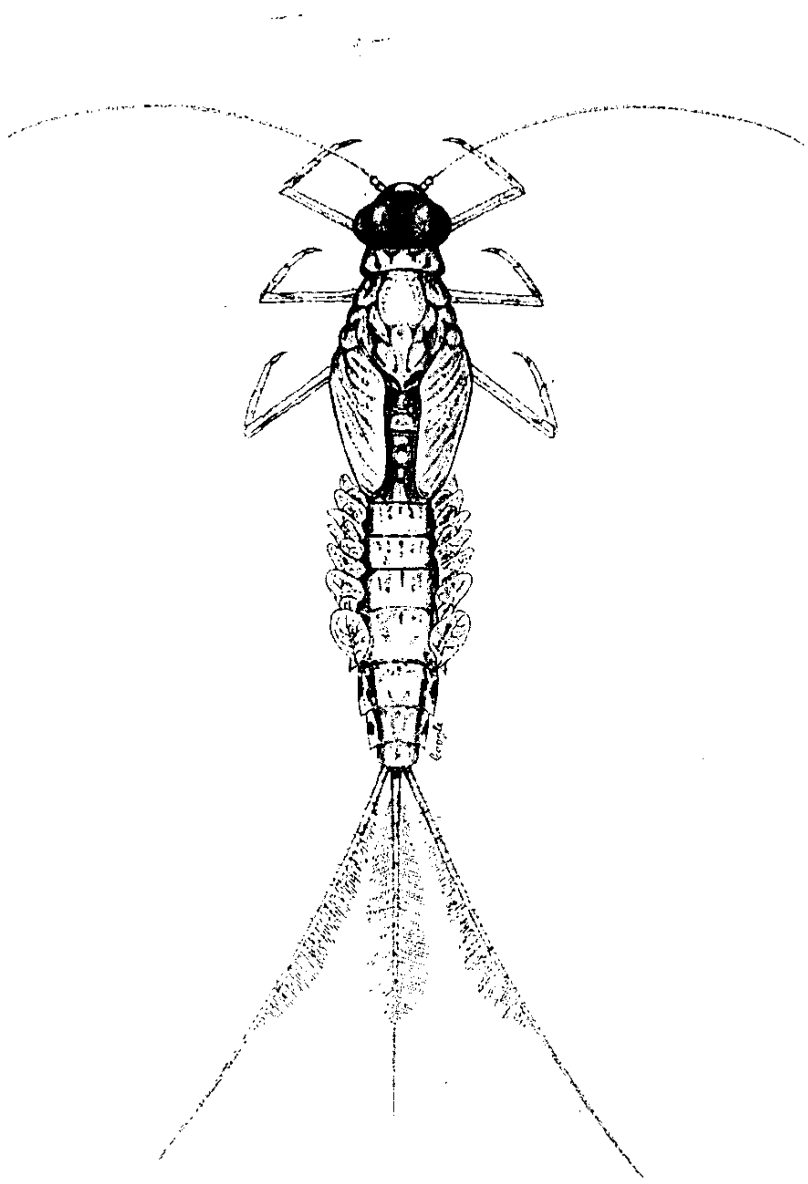


Plate 3. *Callibaetis floridanus* Banks, nymph

South Florida

Callibaetis floridanus (Form B)
  Forewings strongly tinged with brown
  Spots covering body are red
  Coloration intense

Although in south Florida there are no mayflies that show the characteristics of the north Florida *Callibaetis*, we have taken specimens in the Gainesville area that are very similar to the south Florida forms. From an examination of the specimens at hand, it would appear that two forms of *C. floridanus* that inhabit Florida have their region of intergradation in the central part of the state.

In the taxonomy of the genus *Callibaetis*, males are much more difficult to identify than are females. In the Florida species, the males are not exceptional, and unless associated females are available, identification must be tentative.

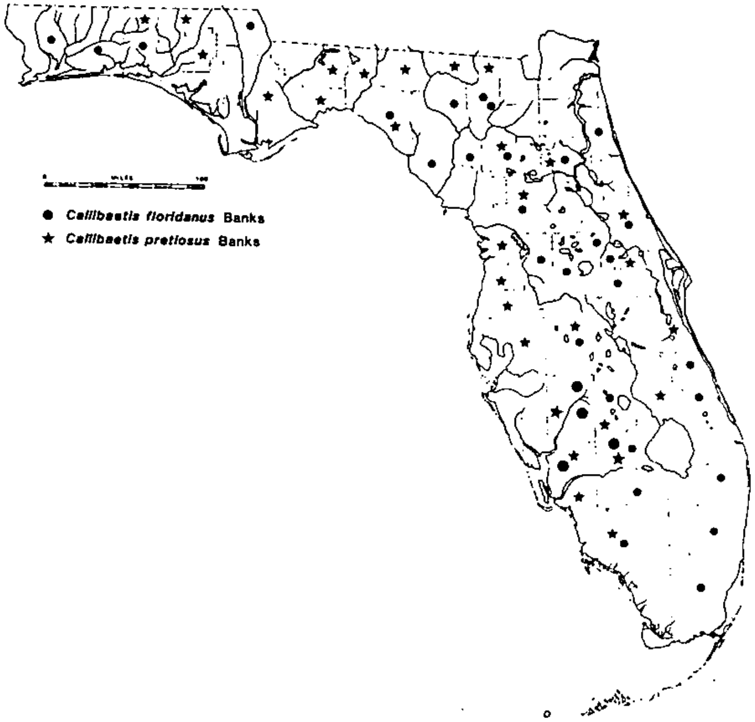
GEOGRAPHIC DISTRIBUTION. *C. floridanus* (form B) is distributed throughout the southern tip of Florida and is known with certainty to spread as far north as Highlands County. It has been collected throughout the Everglades and as far south as Key Largo.

C. floridanus (form A) occupies a range extending from Lake County northward into Georgia and throughout the northwestern panhandle.

The species has been recorded from the following Florida counties (map 5): Alachua, Broward, Charlotte, Citrus, Collier, Columbia, Dade, DeSoto, Dixie, Gilchrist, Glades, Hardee, Hendry, Hernando, Highlands, Indian River, Jackson, Lake, Lee, Levy, Marion, Monroe, Okaloosa, Orange, Palm Beach, Polk, Putnam, St. Johns, St. Lucie, Santa Rosa, Seminole, Sumter, Suwannee, Taylor, Volusia, and Walton.

ECOLOGY. *Callibaetis floridanus* nymphs have the widest limits of tolerance of any mayfly in Florida and can be found in a wide variety of aquatic habitats.

The Everglades, which have been described many times and in many places, are broad open expanses of saw grass, partially submerged by water accumulating on the surface of the exposed pitted limestone (Miami oolite) during the rainy season. An occasional hammock (hardwood forest) indicates a slightly higher mass of rock on which water does not stand. Almost stagnant drainage canals that are filled with gar and other fish, turtles, and vegetation penetrate much of the Everglades. During



Map 5. The distribution of *Callibaetis floridanus* and *C. pretiosus* in Florida.

the dry season, mayfly nymphs develop in the canals, but in the rainy season, when most of the land is under water and the Everglades is truly a "river of grass," mayfly nymphs can be found in almost any area where the water has been standing for a few weeks. At that time not only the mayflies but also crayfish, minnows, beetles, water bugs, and other members of the canal association become widely disseminated. The water in the "glades" is shallow, one to three feet in depth, fully exposed to the sun, and consequently quite warm. The population of mayfly nymphs tends to thin out over this region and the mayfly fauna in a particular area would be smaller than the fauna in an area of equal size in the canals.

In south Florida, nymphs have also been taken from temporary ponds, roadside ditches, and small pools in abandoned rock pits. The species has even been found breeding in a small, artificial fish pond. A collection taken at Key Largo included nymphs that were living in water where mangrove trees were growing. The nymphs were collected not more than 10 feet from the roots of the trees. Although the water from which the nymphs came tasted brackish, analysis showed that it had a salinity of only 1.7%. Later studies of the occurrence of nymphs in brackish water (Berner and Sloan 1954) reported the salinity at high tide to be near 10 parts per 1000 of chloride. *C. floridanus* nymphs were the only Ephemeroptera found in an estuary during a study of the distribution of insects in two Florida springs from their origin to their estuaries in the Gulf of Mexico (Sloan 1956). Another report (Trost and Berner 1963) claimed that experimentally nymphs were able to live in, and emerge normally from, water with salinities up to 12 parts per 1000, approximately one-third that of sea water. The late Jack Russell, while working on salt-marsh mosquitoes near New Smyrna, frequently took mayfly nymphs along with mosquito larvae. He neglected to save the nymphs, but he did notice that they occurred in water that ranged from fresh to definitely brackish. On June 30, 1939, one adult female came to his light at Coronado Beach; Mr. Russell informed us that the location is an island some distance from the mainland and as its surface water was brackish, the nymphs must have developed in the saline water. Moreover, we collected immatures from canals in the city of Miami not more than one or two miles from Biscayne Bay. These almost stagnant canals are brackish, particularly at high tide. We have been told that during the early part of the twentieth century Biscayne Bay, described by Banks as the type locality of *C. floridanus*, was distinctly brackish to saline. *C. floridanus* is one of the few mayfly nymphs known with certainty to inhabit saline waters (Davis (1980) reported finding *Choroterpes mexicanus* to be euryhalinous). Eaton (1895) recorded a Cingalese *Palingenia* that inhabits an estuary where the water "occasionally must be brackish." He also recorded *Cloeon dipterum* and *Caenis halterata* from brackish water streamlets of Hamman-es-Salakin, Biskra, Algeria. Brittain (1982), in summarizing the biology of mayflies, stated that a few species of Baetidae, Caenidae, and Leptophlebiidae occur in brackish water habitats. Wichard et al. (1973), studying the chloride cells of *C. floridanus* in the gills of nymphs and their relationship to osmoregulation, used nymphs collected from brackish water ponds in the St. Marks National Wildlife Refuge in northwestern Florida. In comparing nymphs from fresh and brackish water, the samples contained 0.5 and 26 mmoles of NaCl per liter, respectively.

In north Florida, the habitat of *C. floridanus* is similar to that of the south Florida form. The nymphs are most common in roadside ditches where they live among the stems and leaves of submerged vegetation, clinging to the plants, darting swiftly from one stem or leaf to another, or moving slowly and gracefully over the surface of the plant. In the roadside ditches the water is usually not more than three to four feet deep, choked with vegetation, and stagnant. The plants most commonly include *Pontederia, Polygonum, Micranthemum, Saururus, Ludwigia, Websteria,* and many algae. The nymphs are seldom found where the algae form mats, for the insects' movements would be much too restricted by the entangling strands. Normally, the nymphs can be found where the vascular plants are most dense.

Numerous *Callibaetis* nymphs are usually found in temporary woods ponds, sinkhole ponds with open surfaces, and lakes with marginal vegetation. Cypress swamps, marshes of various types, and margins of slow-flowing streams where there is vegetation suitable for harboring nymphs also maintain their populations of *C. floridanus.* The immatures cannot withstand a strong flow of water, and we have never taken them from rapidly flowing creeks unless these streams formed pools or had thick growths of shore vegetation that helped to slow the current in this zone.

Those sinkhole ponds in which the surface is covered with duckweed usually do not have mayfly nymphs. Several factors may account for their absence: the covering of plants makes it impossible for adults to oviposit successfully; an absence of submergent vegetation provides no protection; there is a lack of food materials; or there may be an abundance of predators. In this sort of place, mayflies find it difficult to live and the normal pond-margin inhabitants are also absent. Sinkhole ponds and lakes in which the margins are either permanently or intermittently covered by water hyacinths are usually not inhabited by *Callibaetis* nymphs, probably for the same reason that they are absent from the duckweed-covered ponds.

The ditches, pond, swamps, and other bodies of water that *Callibaetis* nymphs inhabit may range from being very acidic to very basic. Nymphs have been collected from a *Pontederia* marsh where the pH (colorimetric measurement) was lower than 4.0, which was below the lowest range of the instrument. In Biven's Arm, a small lake in Alachua County choked with submergent vegetation, principally *Myriophyllum,* nymphs were common at a pH above 10.0 (glass-electrode measurement).

In the standing fresh waters of Florida, the only ephemerid associates of *C. floridanus* are *C. pretiosus* and *Caenis diminuta.* Along the margins of slow-forming streams where *C. floridanus* nymphs may occasionally be found are also *Caenis diminuta, Callibaetis pretiosus, Eurylophella temporalis, Leptophlebia bradleyi, L. intermedia, Baetis pygmaeus, B. propinquus,* and *Stenonema smithae.* The usual associates other than mayfly nymphs in the ponds and ditches include Odonata nymphs, Hemiptera, various water beetles, caddis fly larvae, and other still-water forms.

The adults of *C. floridanus* remain in a fairly moist situation, although we have collected a large series of specimens from a burnt-over field adjacent to one of the canals in the Everglades. In the rock pits of south Florida, there are few or no bushes, but there are relatively dense growths of grasses where the mayfly adults remain hidden in the low vegetation until time for the females to release their young. In one section of the Everglades, which is in part a cypress swamp with emergent grasses scattered throughout the area, we collected some 90 mayflies by sweeping the low plants. Apparently the adults preferred to remain close to the water rather than to fly into the trees.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The following discussion is quoted from a paper concerned with the biology of *Callibaetis floridanus* by Trost and Berner (1963, pp. 287–291).

> The life cycle of *Callibaetis floridanus* is comparatively short and all stages can be found at all times of the year. Mature nymphs have been collected during every month and collections made at any time of the year will produce nymphs of all instars. We also have records of adults for all months of the year in Florida, even as far north as Gainesville. In this study it was found that the length of time required for nymphal development varies with the time of year during which the nymphs are studied. We believe this variation in time of development is primarily due to temperature. The shortest time recorded from oviposition to emergence of the subimago was 27 days (August 19 to September 14), although other nymphs from the same brood and reared under the same conditions took up to 35 days to complete their life history. These results were duplicated in the laboratory and in the field. During this period water temperature fluctuated between 28° and 32°C. In late October and early November the complete nymphal cycle took approximately 60 to 75 days. At this time the average water temperature ranged from 18° to 20°C. However, in these latter rearings, the nymphs were kept in the laboratory

because there was no convenient standing water in the ponds used for the study and it was extremely difficult to obtain gravid female imagoes. The mortality of the nymphs in this later period also seemed to be much higher than that which occurred during the summer.

Needham (1935) stated that the nymphal stage lasts five to six weeks from the laying of the eggs to emergence, however, he gave no data to substantiate his estimate. [Needham was unaware of the universality of ovoviviparity in *Callibaetis.*] Dickinson (1948) found mature *Callibaetis floridanus* (form A) nymphs in temporary ponds in the Gainesville area within five to six weeks after the first water appeared in the ponds.

Our observations indicate that *Callibaetis floridanus* nymphs apparently pass through 9 to 11 instars with the most common number being 10 prior to emergence. Taylor and Richards (1963) state, "Judging from the number of rings in the Palmen body of an adult mayfly, which Needham et al. state as representing successive molts, the mayfly *Callibaetis* appears to undergo approximately 15 molts." If their estimate is correct, there are 16 instars in the nymphal life of the insect.

Although 235 nymphs were reared and measured, it was difficult to determine the number of molts with certainty. In the early instars the nymphs are of such minute size that it is virtually impossible to find the exuviae to provide conclusive proof of molting. The number of instars was determined by measurement of the living nymphs every other day with an ocular micrometer. Because of the relative size constancy of the head exoskeleton, we selected change in width across the eyes as a criterion of growth. Using this measurement it was usually possible to ascertain size changes in the nymphs. At times, however, very likely due to errors introduced in measuring active, live nymphs, this value seemed to grow smoothly from one size interval to another. Usually there is an easily observable difference in this measurement between instars, but the value does not hold constant. The first two instars are generally rigidly set in size and the nymphs are very similar, but following this stage much variation develops. . . .

On September 14, 1962, a collection of 650 *Callibaetis floridanus* nymphs was made at random from Stengel Field pond. These specimens were immediately preserved for later measurement to attempt to establish a size range for particular instars. That such conclusions as to correlation of size range and instar cannot be drawn is obvious. . . . The curve is bell-shaped which simply means that the great bulk of the nymphs were in the intermediate-size range. The early instars were too small to be collected in the field and the later instars were small in number, probably because of the greater natural death rate of older nymphs, predation, and emergence. Further, there are size differences because of sexual dimorphism. The measurement of the head was selected for the study because the changes in abdominal length between instars produces too many inaccuracies to give a reliable indicator of size changes. Additionally, the length of the caudal filaments varies too much to be of any use as a marker for a particular instar.

When a series of nymphs of a selected instar is measured there is a considerable amount of variation within that one instar. . . . From our observations, it seems that the general size of the population varies as a unit. From April to August, specimens taken from the Stengel Field pond were predominantly in the smaller size range. During late August and early September there was a trend toward increase in size, until in late September and October the large size predominated. At that time the pond dried and the study, of necessity, ceased. . . .

The newly hatched nymph is quite active. . . . Five ocelli are present on the dorsal surface of the head, the two posterior ones will become the compound eyes and the three anterior will remain as the true ocelli. However, in the first instar this division is not obvious. There are no gills. . . .

Transformation of the first to the second instar takes approximately three to four days under summer conditions, where the water temperature ranges between 28 and 32 degrees centigrade. The second instar nymph is quite different from the first instar and more closely resembles the later instars. Now there are six pairs of gills, all single and minute; the eyes have differentiated enough to distinguish the simple from the compound. . . . The median tail has still not developed, but the cerci are between 1.00 and 1.08 mm in length.

The median caudal filament first appears as a stump at the beginning of the third instar. . . . All seven pairs of gills are developed but they are still single and minute. . . . The time

> interval between the second and third and between the third and fourth instars, lasts from two to five days with the most common period being three under summer conditions when the temperature ranges between 28 and 32 degrees C. The time interval is consistent with the suggestion of Taylor and Richards (1963) of an average of two to three days for each instar.
>
> The fourth instar, also lasting from two to five days, cannot be differentiated from the third except in size. . . .
>
> Beginning with the fifth instar, the gills are all present and are compound as in mature nymphs. From this stage onward the variability becomes so great that development or size change in each instar cannot be characterized.

Subimagoes emerge in late afternoon or early evening. We have observed emergence in February between 3:45 and 4:00 P.M. In summer, the subimagoes begin rising between 6:00 and 9:00 P.M. We believe that there is a correlation between light intensity and time of emergence. Trost and Berner (1963) found that nymphs kept in the laboratory seemed to lose their normal synchronization of emergence time, with subimagoes appearing either earlier or later than they would have in the field.

The subimaginal molt occurs about seven to nine hours following emergence of the winged stage. This means that the adult stage is reached early in the morning following emergence. The time of molting appears to be correlated with weather conditions, but there seems to be some synchronization as subimagoes mostly molt at about the same time. It was noted by Trost and Berner that the molt occurred in the field approximately 15 minutes after the subimagoes were exposed to bright sunlight.

After dark the subimagoes move away from the water's edge and fly to vegetation 200 or more feet away, where they await the final molt in preparation for the mating flight.

Mating flights, observed on several occasions, occur during the morning hours. They begin within about 20 to 30 minutes after the subimaginal molt. The flights have been seen as early as 6:50 and as late as 10:30 A.M.

Occurring over an open field, the flight follows a zigzag path upward to a height of from 4 to 25 feet. The abrupt rise and fall of the males ranges from a few inches to 2 feet. As the females fly into the swarm, they rise and fall in the same rhythm as the males.

After mating, the females return to rest on the vegetation, and the males rejoin the swarm. Some of the swarms may be very small, consisting of only a few males, while others may be quite large. The late Dr. Maurice Provost wrote in a letter to one of us (Berner):

> As I was leaving my home [Indrio Rd., 4 miles W of U.S. 1 in northern St. Lucie Co.] this morning [October 17, 1956] at about 7:45, I was at once struck by the fantastic numbers of male May flies dancing from 2 to 10 feet above the ground everywhere. It was partly cloudy, the sun shining brightly, the temperature about 70°F and a wind of about 2 miles an hour blowing intermittently. The insects looked like snow and were very uniformly distributed over lawns, fallow fields, pastures, flatwoods, roadsides,—i.e. everywhere over an area of at least 100 acres and possibly much more. The individual dance was up and down over some 8 to 16 inch distance, and the mayflies were spaced at roughly one to 2 or 3 square feet of ground-surface with no sign whatever of groupings.
>
> There is a shallow *Typha* pond of some 15 acres in a pasture in the middle of the involved area, and roadside ditches and drainage canals everywhere in this citrus-grove and pasture region. Monday [Oct. 15] there was a rainfall of 6 to 10 inches throughout this region and by nightfall we were pretty much under water, the flatwoods looking like cypress swamps. Tuesday there was very little rainfall, and I assume the mass emergence of May flies occurred that afternoon.

As adults, females have been kept alive for a maximum of 13 days. In natural habitats, however, the imaginal period is undoubtedly several days shorter. The male dies within two days after emergence. Longevity of the females is probably correlated with ovoviviparity. Normally the life span of adult mayflies is from less than an hour to two or three days, but a female *Cloeon dipterum*, the European ovoviviparous mayfly, survived for 21 days. After mating, the female of *C. floridanus* becomes quiescent until the eggs are ready to hatch. When the time arrives, the female takes to the wing, flies to a body of somewhat stagnant water, and releases the eggs, which hatch at the moment of laying. When the female oviposits, she places her abdomen against the water surface, releases her eggs, and then floats with wings held upright. Afterwards, as she attempts to leave the water, she generally fails, struggles, and her wings become trapped in the surface film. She dies within 20 to 30 minutes unless earlier captured by some predator.

BEHAVIOR. *Callibaetis* nymphs are the most graceful of all the mayfly immatures found in Florida waters. Its body arched, the green insect hangs from a plant stem and blends almost perfectly with its background. Only the delicate movements of the antennae and the shuttling motion of the large, foliaceous gills draw one's eyes to the nymph. If disturbed, the insect darts rapidly away from the disagreeable area by rapid flicks of the caudal filaments. Its streamlined shape, hairy caudal filaments, and ability to become motionless in an instant assure *Callibaetis* maximum efficiency in its darting actions.

When collected and placed in a white-enameled pan in which the water has been drained away from them, the nymphs hop about very much like small minnows if one attempts to lift them. This action is particularly evident in larger nymphs, especially those in the penultimate or last instar. Frequently the nymphs can be detected in the pan only by draining the water away from them and watching for their kicking and hopping as they attempt to return to the water.

Examination of the contents of the alimentary tract of nymphs showed that they feed predominantly on algae, but they also eat plant material of other sorts. The nymphs graze on the algae covering plant stems and leaves in the ponds and ditches rather than move into the algal mats that sometimes form in these places. Food material passes through the gut rapidly, and it was reported (Trost and Berner 1963) that during active feeding the nymphs extrude a mass of fecal matter in volume equal to one-third to one-fourth the volume of the digestive tract every 20 to 40 seconds.

Callibaetis pretiosus Banks

(PLATE 4. FIGS. 8, 27, 103, 118. MAP 5)

Berner 1950, pp. 201–203; 1977, p. 18.
Frost 1967, p. 281.
Lanquist 1953, p. 27.
Peters and Jones 1973, p. 246.
Sloan 1956, p. 92.

TAXONOMY. We have examined the specimens that we named *Callibaetis pretiosus* with great care, compared them with *pretiosus* from other areas,

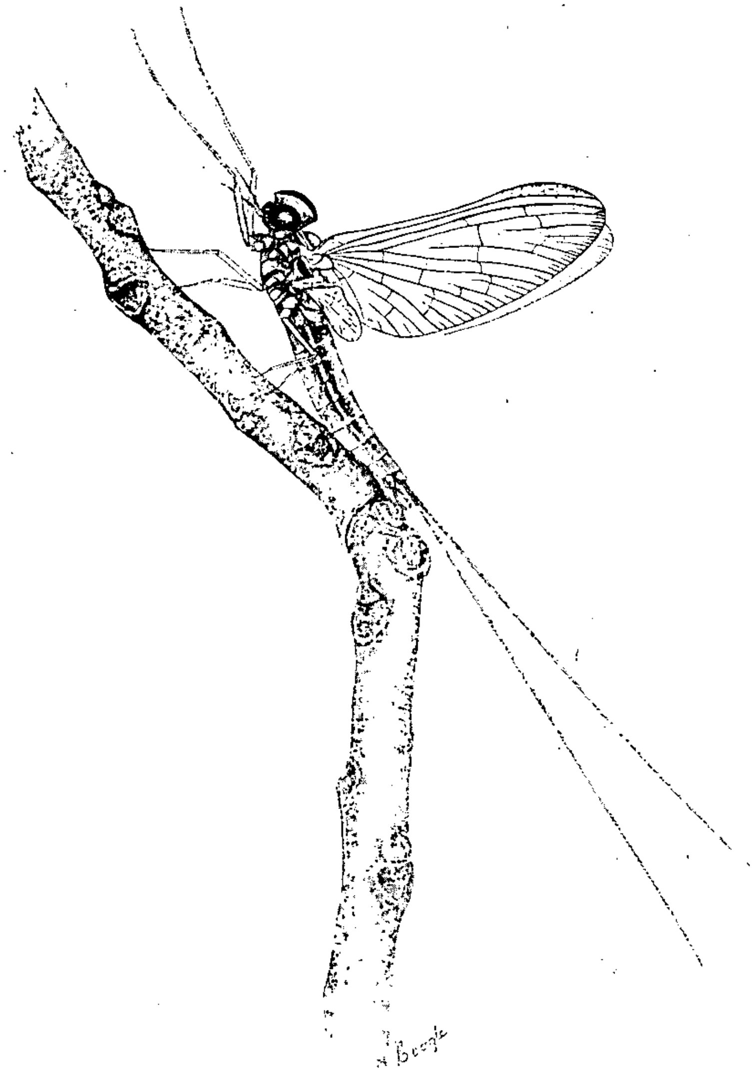


Plate 4. *Callibaetis pretiosus* Banks, male imago

studied specimens identified by Banks to be this species, and concluded that we are correct in assigning this name to the Florida specimens. Our earlier doubts arose because of the wide degree of variability in the pattern of pigmentation that occurs in the forewings of the females, the only sex that can be identified with any degree of certainty.

Banks first described the species from Virginia in 1914 and we are unaware of any published reports of its occurrence other than in Florida since its description, except those of Berner (1977). In Traver's presentation (1935) of *Callibaetis* the species was redescribed, but as only the female was known at that time, it was the only stage included. The male and nymph still remain to be described.

In *Callibaetis* imagoes there is a very marked sexual dimorphism. The female *pretiosus,* as is usual for the genus, is strongly marked over the body and has a brown vitta in the forewing, numerous crossveins behind this vitta, double intercalaries along the outer margin of the forewing, and generally brown clouds of pigment in its membrane. The male has the normal darkened thorax and darkened distal abdominal segments with the pale intermediate area in common with many other species of *Callibaetis.* In the forewings behind R_1, there are, as in the male of *C. floridanus,* relatively few crossveins, and the marginal intercalaries are usually single. Even though the Florida females of *floridanus* are very easily distinguished from those of *pretiosus,* the males of the two Florida species are so similar that they can be differentiated only on the basis of coloration of the abdominal tergites, a characteristic that is not at all reliable. The nymphs, on the other hand, are easily separated from those of *floridanus* by the presence of a small recurved flap on the seventh gill of *pretiosus* and its absence in *floridanus.* There is also a difference in the size of the distal segment of the maxillary palp in the two nymphs.

GEOGRAPHIC DISTRIBUTION. The distribution of *C. pretiosus* is much the same as that of *C. floridanus* (form A) in Florida. We have examined specimens collected in the following Florida counties (map 5): Alachua, Bay, Brevard, Charlotte, Citrus, Collier, Columbia, DeSoto, Glades, Hamilton, Hernando, Highlands, Hillsborough, Holmes, Jefferson, Lee, Leon, Liberty, Madison, Marion, Monroe, Okeechobee, Pasco, Polk, Putnam, Seminole, Taylor, Volusia, Wakulla, Walton, and Washington.

ECOLOGY. *Callibaetis pretiosus* nymphs are ecologically very similar to *C. floridanus,* except that they have never been found living in saline or brackish waters and the range of acidity-alkalinity appears to be somewhat narrower than that of *floridanus.* Frequently the nymphs of the two species can be found together in the same roadside ditches, ponds, or lakes.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The adults of this species emerge throughout the year in peninsular Florida. In the northwestern part of the state, emergence of adults generally occurs during the warmer months of the year.

Dr. S. W. Frost, while in residence at the Archbold Biological Station in Highlands County, collected mayflies in light traps he operated over a period of four years during the months of November through April. In 418 nights of trapping, he found that *C. pretiosus* imagoes were caught during hours of darkness as follows:

6–8 P.M., 356 individuals
8–10 P.M., 674
10 P.M.–2 A.M., 964
2–7 A.M., 1089

He also sorted the adults trapped during January through April by sex and reported their frequencies as follows:

6–8 P.M., m. 59, f. 123
8–10 P.M., m. 99, f. 318
10 P.M.–2 A.M., m. 118, f. 371
2–7 A.M., m. 173, f. 263

Frost attributed the greater number of females in the collections to the fact that females are long-lived while males die soon after mating.

The life history of *C. pretiosus* is believed to be very similar to that of *floridanus,* but as no detailed studies of the species have yet been made, we cannot confirm this.

BEHAVIOR. The behavior of nymphs and adults is like that of *C. floridanus,* and nymphs of the two species cannot be separated in the field to make possible observations of any distinctive actions.

Centroptilum Eaton

Berner 1950, p. 230.
Burks 1953, pp. 119–120.
Edmunds, Jensen, and Berner 1976, pp. 169–172.
Jones 1977, p. 65.

Eaton (1869) established *Centroptilum* to accommodate those European Baetidae that possess metathoracic wings and in which the intercalaries of the forewings are single. In his taxonomic revision of the mayflies, he included in the genus a species from Cuba as well as a species close to the European *C. luteolum* (Muller) (later described as *C. semirufum* McDunnough) from the Hudson Bay region. Eaton (1892) again wrote of *Centroptilum* when he treated the Ephemeroptera of Central America and added to the list an undescribed species from north Sonora, Mexico. The status of the genus in the western hemisphere remained unchanged until McDunnough (1923) published descriptions of *C. fragile* and *C. curiosum* (= *Heterocloeon curiosum*). Following this publication, descriptions of new species of *Centroptilum* began to appear frequently, and now there are 24 species known to occur in North America north of Mexico, 14 of which were described by Dr. McDunnough.

Prior to 1946, the genus was unknown from either the Coastal Plain or Piedmont provinces although Traver recorded *C. album* (?) from the mountains of North Carolina and *Centroptilum* sp. from the mountains of Alabama. Several species, two of which were described from Florida, are now known from the southeastern United States in all of the physiographic provinces represented there. *Centroptilum* occurs in the Holarctic, in Africa, in the Australian and Oriental regions, and generally in the Nearctic.

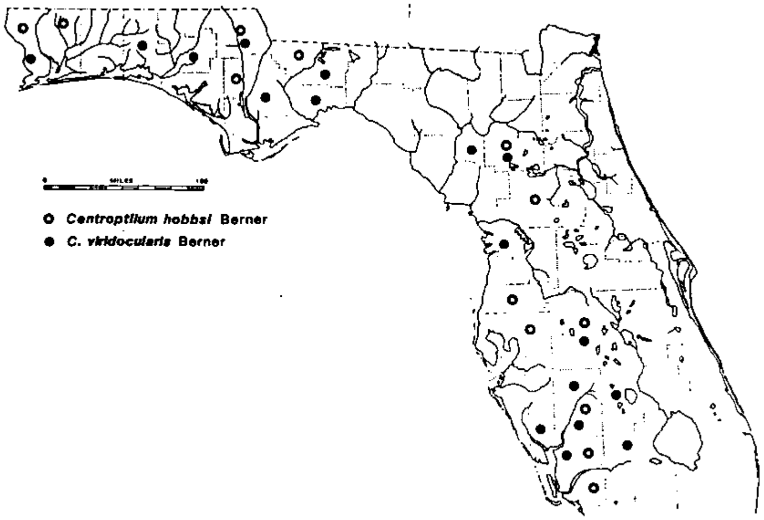
Ide (1930) very briefly mentioned the habitat preference of *C. convexum* and *C. bellum* nymphs. Beyond this, little has been written about the ecology of the nymphs. Of the former species Ide reported that nymphs were abundant in the Mad River at Horning's Mills, where they lived among the lily pads and pond weeds. The nymphs of *C. bellum*, he continued, were numerous in moderately swift water, where they clung to the upper surfaces of stones. Edmunds et al. (1976) added that some nymphs may be found on the sand along the margins of a large river and others may be found along the edges of lakes where there is wave action.

Centroptilum hobbsi Berner

(FIGS. 121, 122, 140. MAP 6)

Berner 1950, pp. 236–237; 1958, p. 31;
 1977, p. 19.
Lanquist 1953, pp. 21, 23, 62.
Schneider 1967, p. 205.

TAXONOMY. The species was described in 1946 from a few nymphs and three female adults that were sufficiently different from any described species to warrant their receiving a new name. Traver (1935) described *C. rivulare* in the adult stage but dismissed the nymph with the assertion that it has small dorsal flaps on the basal pairs of gills. *C. bellum* has double gills on the basal segments at least. *C. hobbsi*, which also has double gills on the first segment, is certainly different from *bellum* as drawn and described by Ide (1930), and is probably just as distinct from *C. rivulare* and *C. ozburni*. All four of these have double gills. The uniqueness of the Florida species lies in the fact that only the first pair of gills is doubled and that these gills are markedly different in form from the other six pairs. All seven pairs of abdominal gills of *C. viridocularis* are single and similar in shape. Burks (1953) did not separate the nymphs of the three Illinois species he treated.



Map 6. The distribution of *Centroptilum hobbsi* and *C. viridocularis* in Florida.

GEOGRAPHIC DISTRIBUTION. Records of the occurrence of *C. hobbsi* are few and scattered, but they are sufficient to permit us to know that the species inhabits peninsular Florida from DeSoto County northward to the extreme northwestern part of the state. The species is also known from Alabama, Georgia, and Mississippi (Berner 1977). We have records from the following Florida counties (map 6): Alachua, Calhoun, DeSoto, Escambia, Gadsden, Hillsborough, Jackson, Marion, Pasco, and Santa Rosa.

ECOLOGY. Though the ecological factors limiting *C. hobbsi* are complex, two are rather obvious. In the first place, the species is confined to streams; and second, these streams are all believed to be basic in reaction. In regard to the second characteristic, nymphs have been taken most commonly from the Santa Fe River at Poe Springs in which the pH ranges close to 7.3, but other streams in which the nymphs were living have measured up to and above 8.0.* For the most part, the rivers and creeks in which *C. hobbsi* nymphs occur are spring-fed and in some cases are the main spring runs.

As noted elsewhere in this study, both spring runs and the Santa Fe River have abundant growths of *Vallisneria* and other water plants in midstream. *C. hobbsi,* an inhabitant of this vegetation zone in streams, has rarely been collected from other regions. The nymphs are clingers that attach their claws to the long, trailing strands in moderately swift to swiftly flowing water. The immatures occur in as swift water as the *Vallisneria* can tolerate; they can also be found in the more slowly flowing portions where *Najas* and other aquatic vegetation predominate. The claws of this species are proportionately much shorter and stouter than those of *C. viridocularis*—a condition correlated with the fact that *C. hobbsi* nymphs inhabit faster-flowing water.

In Jackson County, two nymphs were taken from a stream with a pH of 7.8 and with no vegetation in the flowing portions. The immatures were found clinging to submerged logs in the swiftest part of the creek. Farther west in Florida, along the Choctawhatchee Bay region, there are a number of small creeks with dense mats of *Vallisneria, Sagittaria,* and other aquatic plants in midstream. We found nymphs of *C. viridocularis* but none of *hobbsi.* These streams are all clearly acidic with a pH ranging to not much above 6.0. It would seem, therefore, that *C. hobbsi* is quite sensitive to conditions of alkalinity and that this sensitivity is probably the major limiting factor in the distribution of the species.

SEASONAL DISTRIBUTION AND LIFE HISTORY. From the paucity of records, little can be said with certainty about the seasonal occurrence of *C. hobbsi.* Adults are likely on the wing each month of the year, weather permitting, as we have adult females collected in February, March, June, July, August, September, and October.

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*Cantrell, working in southwest and south-central Florida, has taken specimens from streams that are seasonally acidic; however, all of his nymphs were collected during periods when the water had a basic pH. He has pointed out that in southwestern Florida the summer rainy season causes extensive swamp drainage into the streams creating acidic conditions. He has no summer nymphal specimens.

Nothing is known of the life history, but it is probably not different from that of *C. viridocularis.*

BEHAVIOR. We have observed no differences in the behavior of this species from any other *Centroptilum.* Examination of the contents of the alimentary tract of nymphs from the Santa Fe River showed the food to consist mostly of diatoms with a few interspersed strands of algae.

Centroptilum viridocularis Berner

(PLATE 5. FIGS. 7, 33, 108, 123, 124, 139. MAP 6)

Berner 1950, pp. 230–236; 1958, p. 31; 1977, p. 19.
Frost 1967, pp. 281.
Lanquist 1953, pp. 20, 21, 23, 24, 63.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 205.

TAXONOMY. *Centroptilum viridocularis* has been described in both the nymphal and the adult stages. Adult males may be distinguished from other species by the mesothoracic color, the red markings on tergites 2 through 6, the color of tergites 7 through 10, and the presence or absence of a projection on the inner margin of the second forceps segment. Because both wings and genitalia are similar to those of *rufostrigatum,* known only from Illinois and Wisconsin in the United States, these two species appear to be closely related.

GEOGRAPHIC DISTRIBUTION. The nymphs of this species are usually difficult to find, but the specimens in our collections indicate that they occur in all parts of Florida where there are permanently flowing streams. Specimens have been taken as far south as DeSoto County, where nymphs were found living in the Peace River (Lanquist 1953), in Hillsborough and Alachua counties, and from the Suwannee River as well as throughout northwestern Florida. The species is known to occur in Alabama, Georgia, and Mississippi (Berner 1977). Florida counties from which specimens have been collected are (map 6): Alachua, Charlotte, Citrus, DeSoto, Escambia, Gilchrist, Glades, Hardee, Highlands, Hillsborough, Jackson, Leon, Liberty, Polk, Sarasota, Wakulla, Walton, and Washington.

ECOLOGY. The nymphs of *viridocularis* prefer moderately swift streams, the size of the channel seemingly being of no consequence. After spending many hours searching for nymphs of this species in Hatchet Creek near Gainesville, a catch of two or three immatures was considered to be

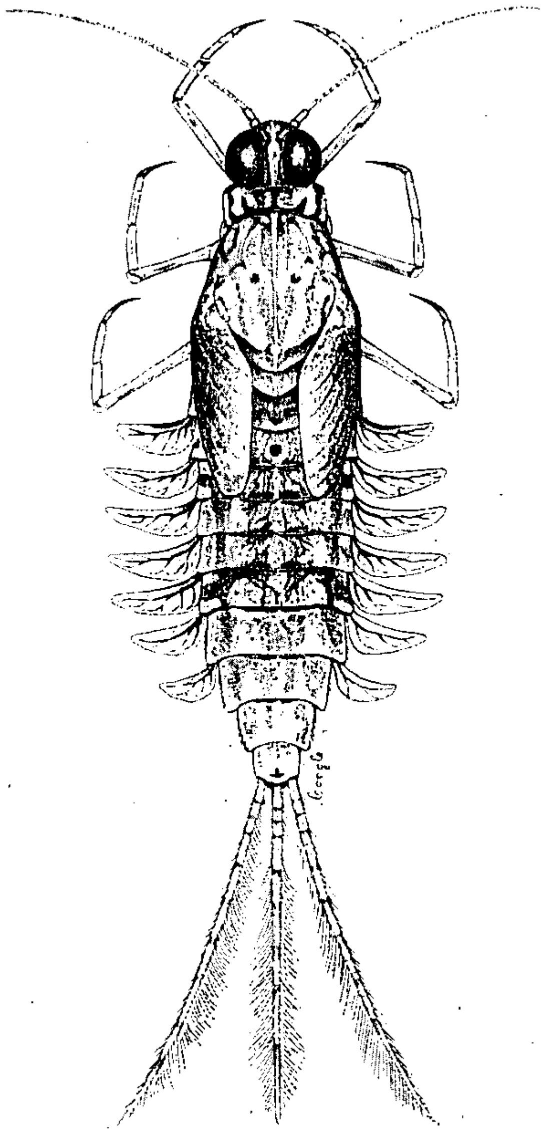


Plate 5. *Centroptilum viridocularis* Berner, nymph

good; yet examination of the stomach contents of several small bass (*Micropterus salmoides*) revealed that *C. viridocularis* was their food of choice and that each fish had eaten 15 to 25 nymphs. After this discovery, a diligent search was made without success in the place from which the bass were seined; examination of other habitats in the creek resulted in the capture of only two nymphs. Subsequently, collections made from a much smaller stream near Gainesville have yielded significantly more nymphs than did the larger Hatchet Creek. Some of the latter nymphs were reared to the adult stage.

Hatchet Creek is a sand-bottomed stream, rather deep in places, but for the most part, a shallow, moderately rapid creek. The depth varies from six or seven feet in a dredged area at a bridge to as little as six inches in the more swiftly flowing portions. Near the shore there are dense growths of parrot's feather (*Myriophyllum* sp.), and in the stream proper there are clumps of *Potamogeton, Panicum, Micranthemum umbrosum,* and some *Fontinalis.* Near the shore in quieter areas there are rather large accumulations of leaf drift, and the stream is margined with various partially submerged grasses. Though two nymphs were collected from the leaf drift, most of the insects lived near the base of the grasses where there was a silty accumulation and very little current.

Little Hatchet Creek, from which most of the nymphs have been taken, falls into the sand-bottomed category; it is about three feet wide and one foot deep. In the shallower parts where the current is more rapid there are growths of *Panicum;* in the more slowly flowing, deeper regions the mosses become the dominant element of the flora. Nymphs of *C. viridocularis* were frequently found on the silt-covered mosses, and a few nymphs were also present in the detritus that accumulated between the projecting roots of large trees along the stream margin.

As previously stated, the Santa Fe River at Poe Springs is one of the swiftest of Florida streams. It is only in the most slowly flowing parts of the river that nymphs of *viridocularis* cling to the vegetation, principally *Najas.* They never venture into the swifter waters where *hobbsi* occurs. In their choice of environment within the river itself the two species of *Centroptilum* afford one of the best examples of the theory that claw size is directly related to habitat. The claws of the quiet-water form, *C. viridocularis,* are thin and attenuated, being three-fourths as long as the tarsi, whereas the claws of *C. hobbsi,* from swift water, are shorter and thicker, being about one-half as long as the tarsi.

The streams inhabited by *C. viridocularis* nymphs may be either slightly acidic or slightly basic. In Hatchet Creek, an excellent example of a swamp stream in which the water is heavily tinted with organic acids, the coloration is so intense at times that the water takes on the appearance of strong tea. On the other hand, the Santa Fe River, fed by springs, is normally lightly colored and slightly basic in reaction. Although the species is tolerant of very slowly flowing water, it is not known to inhabit ponds and other standing bodies of water. The nymphs live in places in Hatchet Creek where there is no perceptible current; yet in standing, unaerated water in the laboratory they can survive only a few days.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults of *C. viridocularis* emerge throughout the year in Florida. Adults have been collected in some part of the state in every month except November and December. We have been unable to determine whether there is a synchronization of emergence with the tendency to form broods, but we consider it unlikely as nymphs of all sizes may be found throughout the year.

The length of nymphal life has not been determined, but it probably extends over a period of just a few months in peninsular Florida. Emergence of the subimago during the summer occurs in late afternoon, just before or at approximately the same time as sunset. The final molt to the imagal state takes place within 10 to 12 hours. In the laboratory a female emerged as late as 6:30 P.M. on August 23, just at sunset. Although it was still lively on the morning of August 25, by 9:00 P.M. of that day it had begun to shrivel and showed only the slightest signs of life. Under ideal conditions it would seem that maximum longevity for females of this species is approximately 50 hours.

Some of the nymphs that were kept in the laboratory in an effort to rear adults were rather immature and remained alive long enough to undergo ecdysis. The following is a summary of the data on molting:

Nymph 1.	Two-thirds grown	
	Collected at 3:00 P.M.	8/13
	Molted about 1:00 P.M.	8/15
	Molted between 9:15 P.M., 8/19, and 9:30 A.M.	8/20
	Molted	8/21
	Died	8/24
Nymph 2.	One-third grown	
	Collected about 10:00 A.M.	8/10
	Molted between 10 A.M. and 4:00 P.M.	8/14
	Died	8/16
Nymph 3.	Penultimate instar	
	Collected about 10:00 A.M.	8/10
	Molted between 6:00 and 9:00 P.M. to last instar	8/10
	Wing pads blackened	8/13
	Died without emerging	8/13

The mating flight of *C. viridocularis* has not been observed but, as the sun was setting in late October, a single female was seen flying over midstream about 6 to 10 inches above the water and apparently ovipositing.

BEHAVIOR. The nymphs of *Centroptilum* are very easy to distinguish from other mayflies (except *Cloeon*) in the field. When the live nymph is placed in water, the tails are not held straight out as in *Baetis* but are depressed slightly at the tips. Moreover, a brown band is usually prominent on the caudal filaments of those mayflies likely to be confused with the nymphs of *Centroptilum*. In addition, the long hairs on the tails of *Centroptilum* are not evident, and the shape of the head is quite different from that of many of the other genera of the Baetidae. The rather abrupt frontal margin gives the *Centroptilum* nymph the appearance of having pulled the lower part of its head close in to the sternum, and its frontal margin is not so rounded as that of *Baetis*. Finally, the body of *Centroptilum* is shorter and thicker than that of *Baetis*.

The nymphs swim adeptly by rapidly flicking the abdomen and holding the tails stiffly out from the body. The movement is slower than that of *Baetis*.

When placed in a white-enameled pan without water, the nymphs, in common with other Baetidae, usually fall on their sides where they remain helpless. If stimulated, they begin to hop about, flipping the abdomen like small minnows, but with much less vigor. The older and more rounded the nymph, the more helpless it becomes when stranded out of water. The young nymphs, because of their more flattened bodies, often fall with the dorsal side up, and they are then able to crawl over the surface.

In feeding, the nymphs do not often use their legs for bringing food to the mouth. As the nymph comes upon food material, the head is moved into a position best suited for seizing the food, which is taken into the mouth by means of the maxillae as they shuttle rapidly inward and outward. The food is made up of plant materials of various sorts, principally epidermis, algae, and, to a slight extent, diatoms.

Cloeon Leach

Berner 1959, p. 21.
Burks 1953, p. 141.
Edmunds, Jensen, and Berner 1976, pp. 172–174.

Cloeon, described by Leach in 1815, occurs virtually worldwide. The similarities between *Cloeon* and *Centroptilum* are striking in both the adult and the nymphal stages; however, adults of *Cloeon* lack metathoracic wings while they are present in *Centroptilum.* Nymphs are separated from those of *Centroptilum* most readily by the fact that *Cloeon* nymphs have no hind wing pads.

In common with *Centroptilum,* the marginal intercalary veins of the forewing are single and the nymphal mouthparts are very similar in structure. The two genera are, in fact, so similar in most respects that Edmunds et al. (1976) questioned the validity of separating the two merely on the presence or absence of minute hind wings.

In Florida we have found two species that occur in the panhandle section of the state. They differ, as far as we can tell, in gill structure only. For the present, we will not consider *Centroptilum* and *Cloeon* to be synonymous; when a sufficient number of study specimens becomes available, we may be moved to unite the two under a single name, *Cloeon.*

Cloeon rubropictum McDunnough

(FIGS. 105, 127. MAP 7)

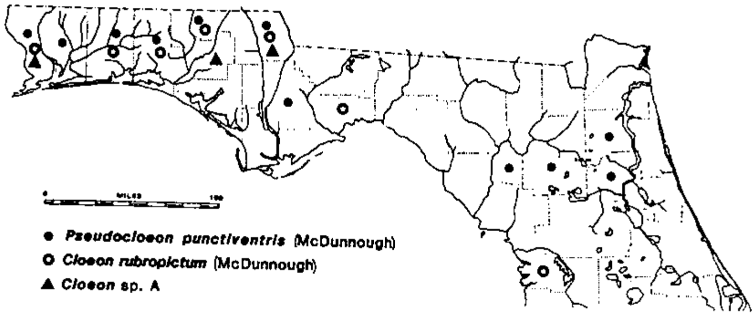
Berner 1950, pp. 237–240; 1958, p. 31; 1977, p. 20.
Jones 1977, p. 65.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 205.
Sloan 1956, p. 92.
Wurtz and Roback 1955, p. 194.

TAXONOMY. A series of nymphs from Florida is being referred to *Cloeon rubropictum,* as these nymphs fit the criteria established for it better than any other described species. At this point, we do not consider the specimens to represent a new species. We have made many attempts to secure adult males of this species but have taken only nymphs and one female. Specific identification of nymphs in this genus is not yet possible as so many of the immatures remain unknown. We communicated with Dr. F. P. Ide some years ago concerning the identity of our specimens and he suggested that they might be *rubropictum.* Careful study of our nymphs still leads us to accept the name with some skepticism, yet we are not prepared to say that they are not *rubropictum.* Therefore, for the present we are retaining our specimens under this name. Our nymphs have a recurved dorsal flap on the first gills only, a characteristic that distinguishes them from the other Florida species that has all gills single.

The known nymphs of *Cloeon* can be divided into three groups based on gill structure: those with double lamellae on segments 1 through 6 or 1 through 7; those with single lamellae on all segments; and those with double lamellae on segment 1 only. The Florida nymphs we have designated as *rubropictum* fit into the last group.

GEOGRAPHIC DISTRIBUTION. *C. rubropictum,* described from Ontario in 1923, has since been recorded throughout the eastern United States and from eastern Canada. Nymphs are known chiefly from a rather restricted portion of Florida—that part in which the streams most closely resemble those found in the Appalachians—except for Sloan's (1956) collection of nymphs from Homosassa Springs Run in Citrus County. The eastern spread of the species in Florida may have been stopped by the wide area of dry, sandy country that separates the Aucilla River from the Suwannee drainage. This distribution would seem to support the theory that the species moved into the state along the western side of the Appalachians and gradually spread into western Florida. *C. rubropictum* has also been recorded from Alabama, Georgia, and Mississippi in the southeast. In Florida, it is known from the following counties (map 7): Bay, Citrus, Escambia, Holmes, Jackson, Okaloosa, Wakulla, Walton, and Washington.

ECOLOGY. *C. rubropictum* nymphs are inhabitants of slowly flowing water. Of the numerous Florida streams we have examined, only a few supported populations of the species in numbers sufficient to indicate that it was a highly successful form in the creek. The first of these, from which we have collected on several different occasions, is located 5.6 miles north of Panama City in the panhandle region. The creek is about 15 feet across and varies in depth from 1 to 3 feet. Attached to the pilings supporting one of the two bridges over the stream where collections were made were large clumps of a densely growing moss which was also attached to all other firmly anchored objects in the stream. When collections were first made there, the water was somewhat contaminated with masses of tar that had been discarded during road construction. Wherever the moss occurred, the current was slow and the movement of the water scarcely suf-



Map 7. The distribution of *Pseudocloeon punctiventris*, *Cloeon rubropictum*, and *Cloeon* sp. A in northern Florida.

ficient to cause the plants to stream out in the direction of the flow. Farther upstream, where the water was shallower, there was much less moss. A species of *Polygonum*, which is common in very slowly flowing water where the movement is barely perceptible, now became evident. The first trip to the creek yielded only a few specimens; on the second, about 25 nymphs; and a still later trip produced more than 100 nymphs. In every case, the immatures were collected from the moss and, although the *Polygonum* was thoroughly examined, not a single specimen could be found there. The density of the nymphal population in the stream was high, as shown by the fact that 67 nymphs were collected in one sweep of a dip net through the moss.

At Wakulla Springs Run, about four miles below the springhead, 10 nymphs were collected in about an hour. This stream, as is usual in spring runs, has dense growths of *Vallisneria* both in the slow current of the shore region and in the deeper, more swiftly moving central part. The river is about 75 yards wide and has a soft, sandy bottom that is overlaid with a deposit of calcium carbonate. The many *Elimia* snails taken in the dip net, as well as the numerous large *Pomacea* snails, indicated a high alkalinity in the stream. Collections could be made without a boat only near shore because the river deepened rapidly, and even though all types of habitats were examined in the shallower zones, *C. rubropictum* nymphs were found only on eelgrass. The sole report of the species from peninsular Florida is that of Sloan (1956), who collected nymphs from *Vallisneria* growing in the bed of Homosassa Springs Run from one to three

miles below the springhead. The greatest concentration of nymphs was found at Sloan's three-mile station. Both Homosassa Springs Run and Wakulla Springs Run drain into the Gulf of Mexico.

Other streams from which nymphs of this species have been collected are derived from swamps, are slowly flowing, have tinted waters, and usually have much vegetation. Never have the immatures been found by us other than in protected places located in vegetation. Schneider (1967) reported that while working in the Apalachicola River system, he collected nymphs from vegetation or on boards or logs.

The kinds of streams in which the nymphs live do not seem to be limited by pH, as individuals have been found both in basic and acidic waters. Rather low temperatures in the northwestern part of the state during the winter seem to interfere with emergence. Our evidence, from nymphal specimens, suggests that such interference occurs only intermittently during sharp drops in temperature.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The specimens at hand indicate a year-round emergence for the species. We have a single adult collected in July and mature nymphs taken in May, June, July, November, and December. The lack of material for other months is due to our failure to encounter this rather rare species. In the November collection, the presence of very immature, half-grown, and last-instar nymphs certainly indicates that emergence is continuous throughout the year.

There is no definite seasonal emergence of the species, and the few references to it give little indication of its life history or mating habits. Available evidence seems to indicate that the entire period from egg to adult probably requires less than six months. Ide (1930) has suggested that the species that Clemens (1913) called *Cloeon dubium* is, in reality, *C. rubropictum*. Clemens described the flight of the adults as he observed it at Station Island, Georgian Bay, Lake Huron, in July. The adults flew in small swarms along the shore at a height of from 10 to 15 feet about 7:45 P.M. Ide (1930) found the adults swarming in late evening July 4–20, 1929, at Lake Nipissing, Ontario. Our single female flew into our automobile as we stopped to collect at Sandy Creek in northwestern Florida.

BEHAVIOR. The living nymphs resemble, in morphology and behavior, those of *Centroptilum hobbsi* to such an extent that they cannot be differentiated in the field. The food of *C. rubropictum* nymphs consists of diatoms, algae, and plant epidermis.

Cloeon species A

(FIGS. 125, 126. MAP 7)

Berner 1950, p. 241.
Edmunds, Jensen, and Berner 1976, p. 173 (*Cloeon* = *Neocloeon*).
Schneider 1967, p. 205.
Wurtz and Roback 1955, p. 194 (*Neocloeon* probably *alamance*).

TAXONOMY. A small number of nymphs collected in northwestern Florida were assigned the name *Cloeon* sp. A in the first edition of this study. We have had no success in clarifying the status of these insects and are, therefore, leaving them in limbo. In the original treatment of the nymphs, it was indicated that they fit the criteria established by Traver for her genus *Neocloeon*. Since that time *Neocloeon* has been synonymized with *Cloeon* (Edmunds et al. 1976). These Florida nymphs, which are characterized by having all gills single, clearly fall into the group of *Cloeon*, having single gills as described under *C. rubropictum*. For a time we considered assigning them the name *C. alamance*, but we now believe that it would be better to assign no specific name until additional specimens, especially adults, can be obtained for study.

GEOGRAPHIC DISTRIBUTION. *Cloeon* sp. A has been taken by us at only two localities, both in northwestern Florida. Three nymphs were collected from Holmes Creek, a part of the Choctawhatchee River drainage, and the remainder from a small stream draining into the Chipola River, one of the Apalachicola River tributaries. Schneider (1967) also recorded the species from the same stream systems, but we believe he was citing those given in the first edition of this monograph. Wurtz and Roback's (1955) listing of the species from the Escambia River provides the westernmost report of the species. *Cloeon* sp. A has been taken in the following counties (map 7): Escambia (Wurtz and Roback's record), Jackson, and Washington.

ECOLOGY. From an ecological standpoint, the species is virtually unknown. In the center of one of the branches of Holmes Creek from which the nymphs were collected, there was an old stump of a hydrophytic tree (*Nyssa* sp.) that on its downstream side had a small amount of *Polygonum* that grew in the sand and silt covering the dead roots. Intermingled in this mass was an accumulation of leaf drift, silt, and other debris. Behind the stump the water was about two feet deep and there was no perceptible current. It was here that the nymphs were found. A single nymph from the Chipola River drainage was collected from either the vegetation near the shore or the leaf drift that had accumulated in this zone.

Both streams described above are distinctly acidic and derived from swamps; the water is colored deep brown.

SEASONAL DISTRIBUTION AND LIFE HISTORY. So little evidence is available about these subjects that we can only comment that mature nymphs were taken in July, and a nymph in the penultimate instar was collected in December. Very likely the species emerges throughout the year just as does *C. rubropictum*.

BEHAVIOR. Probably the behavior of these nymphs is like that of *C. rubropictum* and *Centroptilum*.

Pseudocloeon Klapalek

Berner 1950, pp. 242–243.
Edmunds, Jensen, and Berner 1976, pp. 178–181.
Keffermüller 1980, pp. 115–121.
Müller-Liebenau 1981, pp. 201–203.
Provonsha and McCafferty 1982, pp. 29, 31.

From the standpoint of phylogeny, *Pseudocloeon* is one of the most confusing genera of the Baetidae. The lack of metathoracic wings in the adult and the vestigial median caudal filament of the nymph are characteristics that indicate a rather high degree of specialization. The genus was not erected until 1905, when Klapalek considered that the group of species lacking hind wings and possessing doubled intercalaries in the mesothoracic wings should, on the basis of these characteristics, be separated from the all-inclusive *Cloeon*, in which the intercalaries occur singly. Further, the nymphs of the two genera form compact assemblages, the nymphs of *Cloeon* being three-tailed and those of *Pseudocloeon* two-tailed. In the former genus the labial palpi are truncate; in the latter they are rounded. Both genera occur in Florida. *Pseudocloeon* is very closely related to *Baetis* and whether to name our species *Pseudocloeon* or *Baetis* or give them a new generic title is still open to question.

Müller-Liebenau (1981, p. 201), reviewing *Pseudocloeon* in the Sunda Islands and the Philippines, the area from which *Pseudocloeon* was described, concluded that the genus is confined to the Oriental Region. She stated: "As Edmunds et al. (1976:155) point out, 'the genus *Pseudocloeon* was established from a species from Java, and it is not certain, that the American species are congeneric with the Javanese species.' In my opinion this is true not only for the American species but also for all '*Pseudocloeon*' from outside the Oriental Region. These have to be studied carefully and than [*sic*] possibly gathered into one or more new genera."

Keffermüller (1980, p. 120) contends that *Pseudocloeon* should be eliminated and the species transferred to *Baetis*, as all the characteristics "known to be typical for *Baetis* in both nymphs and winged forms are also found in *Pseudocloeon*, with the exception of the existence of hind wings. All the intermediate forms exist from the fully developed hind wings in *Baetis* to their complete reduction in *Pseudocloeon*. Thus hind wings must be excluded from the diagnostic characters for the genus *Baetis*." And Provonsha and McCafferty (1982, pp. 29, 31) wrote, "Although some authors (e.g., Keffermüller 1979 [*sic*]), would choose to no longer recognize *Pseudocloeon* as a valid genus because of apparent polyphyly in other parts of the world, we believe the distinction between *Baetis* and *Pseudocloeon* in North America remains practical."

Long ago Spieth (1933, pp. 338–339) wrote:

> The genus *Pseudocloeon* is like *Baetis* in every item of nymphal and adult structure considered here [venation, genitalia, mouthparts, and gills], except that the adult lacks hind wings and the nymph has only two caudal setae. McDunnough has established a genus *Heterocloeon* (of which the nymphs are also unknown [these are now described]) for those species in which the hind wings are present, but are reduced to a mere thread. . . . Considering wing characters alone, a graded series can be found which extends from the condition found in *Baetis parvus* to that found in *Pseudocloeon*. . . . It is possible that even *Pseudocloeon* [as well as *Acentrella* and *Heterocloeon*] should be considered part of the genus *Baetis*, comparable with the short winged forms known among *Drosophila*, leaf hoppers, beetles, parasitic hymenoptera, gall wasps, etc. Each of the types of reduced wings in these mayfly groups may have arisen by direct and independent mutation from a form such as *B. parvus*. It is not necessary that there has been a gradual decrease in the size of the hind wings. The *Pseudocloeon* species may be more closely related to a species of *Baetis* than are two species which are now unquestionably regarded as members of that genus.

Although Spieth's reasoning seems fairly sound, and although *Pseudocloeon* may represent only a subgenus of *Baetis*, we feel that the convenience of arrangement justifies the retention of the genus for the present as recommended by Provonsha and McCafferty (1982). Further evidence to substantiate Spieth's argument is shown by the gradual diminution in size of the hind wings of females of certain Florida species of *Baetis*. Specifically, the metathoracic wings of *B. pygmaeus* females are so minute that in some specimens they are almost invisible and can be detected only by closest scrutiny of the lateral surfaces of the metathorax. Then, too, a series of *Baetis* nymphs of various species can be arranged to show all gradations in size of the median caudal filament.

The species of North American *Pseudocloeon* are differentiated on the basis of rather minor characteristics, of which the color pattern on the abdomen of the male adults is the most significant. We believe that when the presently described species of this genus are better known, color differences will be shown to be more variable than now supposed, and many of the species will become invalid. Provonsha and McCafferty (1982) pointed out that when adults of *Pseudocloeon* are preserved in alcohol, rapid fading of red color occurs so that identifications using color patterns are often useless.

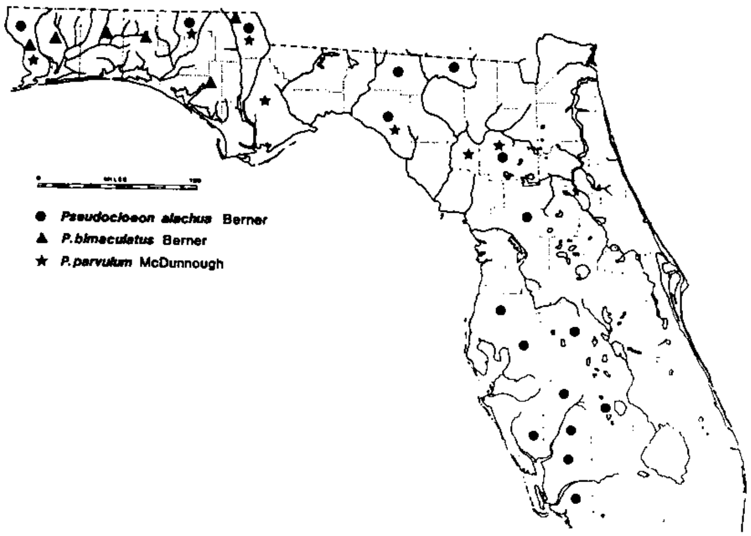
The genus is widely distributed over the eastern portion of North America. There are also records from the central United States and from eastern and western Canada but only a single species is known from the southwestern United States and one from the northwest.

In Florida the nymphs of *Pseudocloeon* are confined to running water, although in the north some species have been reported to inhabit lake margins.

Pseudocloeon alachua Berner

(FIGS. 80, 170. MAP 8)

Berner 1950, pp. 243–248; 1977, p. 21.
Hynes 1970, p. 128.
Lanquist 1953, pp. 50, 53.
Schneider 1967, p. 205.



Map 8. The distribution of *Pseudocloeon alachua, P. bimaculatus,* and *P. parvulum* in Florida.

TAXONOMY. *Pseudocloeon alachua* was described from Florida in 1940. Although it is similar to *P. parvulum,* it differs in having long, thin forceps, no intercalary veinlets in the first interspace of the forewing, and abdominal segments 2 through 6 are whitish hyaline but marked with brownish red patches dorsally. The nymphs are much like those of *P. parvulum* but are easily separated by having faintly banded cerci and by lacking coloration in the gills.

GEOGRAPHIC DISTRIBUTION. The distribution of *P. alachua* is rather interesting, for the species is confined to the middle and western part of the state extending directly north from Hillsborough and Polk counties into Madison, Hamilton, and Holmes. Although we have collected carefully in northwestern Florida, we have taken only *parvulum* nymphs. Schneider (1967) recorded the species from the Escambia, Holmes, and Chipola rivers. *P. alachua* is known only from Florida plus a single record from Mississippi (Berner 1977). Florida counties from which specimens have been taken are (map 8): Alachua, Charlotte, DeSoto, Escambia, Hamilton, Hardee, Highlands, Hillsborough, Holmes, Jackson, Lee, Madison, Marion, Pasco, Polk, and Taylor.

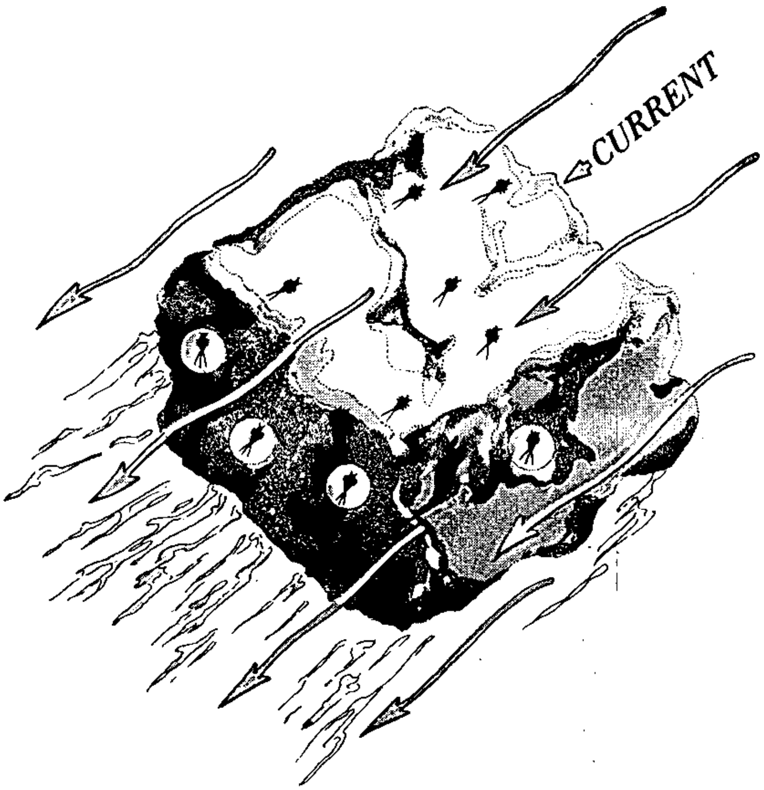


Fig. 170. A diagrammatic representation of the distribution of the nymphs of *Pseudocloeon alachua* and *Baetis propinquus* on a rock in midstream. The two-tailed nymphs on the upper surface are *P. alachua*; the three-tailed forms on the sides of the rock are *B. propinquus*.

ECOLOGY. Ecologically, *P. alachua* nymphs are confined either to streams of the sand-bottomed type or to clear, moderately slow-flowing streams such as Rainbow Springs Run. We have taken nymphs from a creek of the former type (the type locality and now severely polluted) that was not over a foot wide and three to four inches deep, as well as from Hatchet Creek (near Gainesville), a considerably larger stream. The preferred habitats in these streams appear to be the upper sides of rocks or other solid structures in the swiftest current. The nymphs cling with their heads facing upstream and carry on their feeding activities with barely perceptible movements. Figure 170 shows the positions in midstream taken by the nymphs on the surface of a rock that was partially embedded in sand and covered with about one inch of water. Most of the *Pseudocloeon* nymphs on the rock were exposed on the upper surface and seldom moved into the crevices. *Baetis propinquus* nymphs, however, tended to remain in more sheltered areas on the downstream side of the rock, which measured 12 × 6 × 4 inches. The appearance of such a large number of *Pseudocloeon* nymphs on this rock represented the greatest concentration of nymphs of this species we have ever found at one time in such a small area in Florida. One or two nymphs are usually present on each of the smaller stones in the stream where they seem to prefer the downstream side.

Other sand-bottomed streams that lack loose stones have relatively few nymphs in comparison to the *Baetis* represented. In the swiftest water only an occasional specimen is collected from the vegetation, where the nymphs live on the distal parts of the plants swinging freely in the current. Specimens have rarely been collected from submerged logs, but the most productive areas are the small, pebbly riffles that are occasionally exposed in the sand bed.

The population of *P. alachua* nymphs is small in comparison with that of *B. propinquus* in the same stream. In every case where the two species were collected at the same time, there were many more individuals of *propinquus* than of *alachua*, even in the riffles and on the rocks.

The nymphs are more plentiful in the Santa Fe River than they are in the sand-bottomed streams. *P. alachua* nymphs seem to find conditions very suitable not only in that river, but also in the Rainbow Springs Run, the Withlacoochee River (the southern one), the Hillsborough River, and other streams that have rather dense growths of *Vallisneria* in their beds. The nymphs may usually be found on the free ends of the leaves of *Vallisneria*, where it grows in the swiftest current of the streams, though they often inhabit slower waters in smaller numbers.

Acidity or alkalinity that does not range below 6.0 or above 8.0 in pH does not seem to affect nymphs materially. Both these extremes in pH values are rather rare in the streams of the section of Florida in which *P. alachua* occurs; nymphs have, however, been taken from streams with the lower reading and from spring runs that approach the higher pH. Though the immatures appear to thrive equally well in acidic or alkaline waters, they do not occur at the heads of springs—a peculiarity shared in common with all other species of Florida mayflies. The possible explanation for their absence from such habitats has been discussed under the ecology of *Baetis propinquus*.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults of *P. alachua* emerge throughout the year. Although adults were taken or reared only in March, April, May, June, October, and November, nymphs in their last instar were collected in February, November, and December, and other nymphs ranging from very immature to last instar were secured in November. The evidence definitely indicated that disregard for seasonal emergence is characteristic of *P. alachua* in Florida.

We have been unable to rear nymphs through their entire life cycle, but a study of the species in a very small stream on the campus of the University of Florida leads us to believe that *P. alachua* requires about six to eight months to complete its life history. An area near the source of the stream was thoroughly collected until no nymphs except very immature specimens could be found. About six months later the stream was again examined, and it was found that mature as well as very young nymphs were present. Although a few half-grown individuals were also discovered, these might well have been offspring of adults that emerged in other parts of the creek than those examined, and that had flown to the collected area to oviposit during the six-month period.

Emergence of the subimago occurs from about 2:00 P.M. to 5:00 P.M. This emergence time has been noted both in the spring and the late fall, the only two periods during which specimens have been reared or observed emerging in the field. When ready to transform, the nymph swims to the water surface and immediately the subimago bursts free of the nymphal exuviae. It remains quietly resting on the floating skin for a moment and then flies away. In a stream, this is a precarious time for the subimago as it may be swept along at a rather rapid rate. At the slightest disturbance of the floating exuviae, the subimago immediately takes to the wing.

In the laboratory, the subimago molts after 8 to 10 hours, but the period is somewhat variable. The length of adult life, determined only for the female, has been found to be about 40 hours.

The mating flight of *Pseudocloeon* has not been observed for any of the Florida species.

BEHAVIOR. The swimming habits of all members of this genus are similar, but because observations have been made more frequently on *alachua* nymphs than on any of the others they will be described for this species.

When the nymphs are placed in quiet water and stimulated, they move rapidly but very awkwardly. The tails, which merely trail out behind the insect and serve as sensory structures,* have undergone such extensive changes that they are no longer efficient propelling organs like those of *Baetis* or *Callibaetis*. If a resting nymph is incited to move, it may crawl a short distance, then come to rest again. If the stimulus is stronger, the nymph may attempt to swim away from the source of annoyance. This act is accomplished by vigorous abdominal undulations and strong lashing of the almost useless caudal filaments. The whole process is very awkward, and the insect does not move far. As soon as the nymph stops swimming, it usually spreads its legs, separates and raises its tails, arches its abdomen, and settles slowly to the bottom of the pan or dish.

Pseudocloeon nymphs have become highly specialized for living in flowing water. Dodds and Hisaw (1924, pp. 142–143) and Hynes (1970) have discussed such structural modifications as those exhibited by *Pseudocloeon* nymphs, which adapt them to the swiftest water. In their discussion of *Baetis bicaudatus* (this will certainly also apply to *P. alachua*, for it has undergone the same changes as *B. bicaudatus*), Dodds and Hisaw stated:

> The important changes [adaptations for inhabiting very swift streams and torrents] are a great increase in the relative size of thorax and legs, with a corresponding reduction of the abdomen, including an almost entire disappearance of the hairs of the caudal cerci. The decrease in absolute size of the body is probably also of significance, inasmuch as a small body offers less resistance to the current than a large one. Within the genus *Baetis*, as illustrated by our three species, the progressive adaptation to swift water follows the same line as that which differentiates this type from the swimming type, namely: decrease in the size of the body, without a corresponding decrease in the size of the legs; reduction of size of gill lamellae; reduction of middle cercus from a length two-thirds the other two, to a mere rudiment. The reduction of this cercus is, no doubt, of importance in reducing the pull of the water, by reducing the exposed surface in this part of the body, while the remaining two, when held close together, as they commonly are, serve to complete the pointed tip of the tapering body.

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*Peckarsky (1985) has performed experiments demonstrating that cerci serve in defense against stonefly predation.

An examination of the alimentary canal of several nymphs indicated almost nothing concerning the food habits of the species, for in every case the food had been so thoroughly masticated that identification of the fragments was impossible. However, the diatoms and algae, which were abundant on the rocks and plants inhabited by the nymphs, were undoubtedly the food of the insects.

Pseudocloeon bimaculatus Berner

(FIG. 168. MAP 8)

Berner 1950, pp. 252–253; 1977, p. 21.
Schneider 1967, p. 205.

TAXONOMY. *Pseudocloeon bimaculatus* Berner, originally known from three females, one male imago, and numerous nymphs, was described in 1946. The male adult may be distinguished from other species of *Pseudocloeon* by its color pattern, particularly the paired red spots on the abdominal tergites. These spots are also present on the abdomen of the female. Nymphs may be separated from others of the genus by the fact that the seventh pair of gills is deeply colored with reddish brown; moreover, the abdominal maculation is unique, and the banding of the cerci and the length of the vestigial terminal filament in relation to the width of the cerci at their base are distinctive traits. The nymphs are clearly marked and can be selected with the naked eye from unsorted Florida specimens, as it is the only species of *Pseudocloeon* found in this region in which the venter of the terminal abdominal segments is deep red-brown. When additional adult specimens of *bimaculatus* and *punctiventris* become available for a careful study of the two species, they may prove to be the same. Until the problem is resolved, we feel that it is best to leave them in the status quo.

GEOGRAPHIC DISTRIBUTION. Nymphs are known from various streams throughout Florida west of the Apalachicola River and from the Coastal Plain and Piedmont provinces of Alabama. The species is fairly common throughout northwestern Florida and southern Alabama, and nymphs may be found in nearly all permanently flowing streams. The species is also known from streams in the Coastal Plain and Piedmont of Georgia, Mississippi, and South Carolina (Berner 1977). In addition to Schneider's (1967) records of nymphs from the Blackwater, Chipola, Choctawhatchee, Escambia, Perdido, Shoal, and Yellow rivers, we have specimens from the following counties (map 8): Bay, Escambia, Jackson, Okaloosa, Santa Rosa, and Walton.

ECOLOGY. The sand-bottomed streams of the northwestern part of Florida all support populations of *P. bimaculatus*, which is much more common in these streams than its kindred species of the more eastern regions. Particularly abundant in those streams with rather dense growth of eelgrass, the nymphs elsewhere are second in abundance only to *Baetis* species. In the creeks, the nymphs live on the *Vallisneria* where the water is swiftest, but they can also be found in shallower, more slowly flowing water. Some of the streams along the Choctawhatchee Bay region have populations of these nymphs living in *Vallisneria* not more than one hundred yards from the salt water. In other sand-bottomed streams, where there is no eelgrass, the nymphs live close to shore on the vegetation or on any other materials that are permanently anchored in the flowing water. In contradistinction to *P. alachua*, the immatures do not seem to occur as commonly on submerged logs and sticks as they do on the vegetation. In one small creek, about three or four inches in depth, where the bottom was covered with an algal growth, several *P. bimaculatus* nymphs were found in midstream.

The creeks from which nymphs have been collected ranged in pH from 6.0 to 7.6, but the immatures appeared to be more numerous in the acidic streams. This pH relationship may not be significant because vegetation is quite dense in many of the acidic and basic streams of northwestern Florida.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Imagoes are known for June and July. Nymphs in their last instar have been collected in May, June, November, and December, and rather immature nymphs in June. Undoubtedly emergence occurs throughout the year. The nymphs in our collections appear to fall into size groups and indicate that distinct broods form in this northwest Florida species. There are probably at least two winter and three summer broods. From available data it is impossible to estimate the number for the other times of the year.

Because of their high degree of sensitivity to stream conditions, it was almost impossible to keep nymphs of this species alive for more than a couple of hours in quiet water. Owing to this sensitivity and to our inability to remain near one of the streams in which the nymphs live for a sufficient length of time to rear the species, little can be said concerning the life history except that it probably does not differ materially from that of *P. alachua*.

BEHAVIOR. The behavior of the nymphs is like that of *P. punctiventris*.

Pseudocloeon parvulum McDunnough

(FIGS. 116, 169. MAP 8)

Berner 1950, pp. 249–251; 1958, p. 31; 1977, p. 21.
Schneider 1967, p. 205.
Wurtz and Roback 1955, p. 194.

TAXONOMY. In 1950 doubt was expressed concerning the validity of the identification of the Florida specimens as *Pseudocloeon parvulum*. We are still unable to say with certainty that the correct name has been applied to them. A series of nymphs closely resembles Ide's description and drawings of the species, and a single male adult in our collections is much like McDunnough's description of the true *P. parvulum*. The Florida nymphs differ from those of the northern form only slightly in abdominal maculation. The differences in the color patterns of the male adults hardly warrant the erection of a new species.

McDunnough described *P. parvulum* from a series of adults taken at Tillsonburg, Ontario, and from Kazabuzua, Quebec. In his description, he included the male, female, and nymph, and at the same time he indicated that the nymph of *parvulum* is at once distinguishable from all others of the genus by the fact that the caudal filaments are alternately banded with pale and dark colors as in the nymphs of *Stenonema*. Ide (1937) added the maculation of the gills as a distinguishing feature of the nymphs. The Florida specimens all show very clearly the banded cerci, the definitely maculate gills, and mouthparts that are almost identical with those figured by Ide. The banding of the cerci, however, can no longer be considered to be unique because *P. alachua* also shows faintly annulate caudal filaments.

GEOGRAPHIC DISTRIBUTION. *P. parvulum* is known from the southeastern and central United States as well as eastern and western Canada. Our Florida records extend from Alachua County to Liberty County where specimens have been collected from the tributaries of the Apalachicola River on the eastern side of the stream. There the distribution is somewhat spotty and rather difficult to explain, for although the streams on the west side of the Apalachicola do not differ materially from those on the east side, the nymphs do not appear in any of our collections from the western tributaries. Schneider (1967) has taken nymphs from the Chipola, Holmes, and Apalachicola rivers, and Wurtz and Roback (1955) have reported the species from the Escambia River in extreme northwestern Florida. Likewise, our failure to find nymphs in Hillsborough County is frustrating as the conditions in the Hillsborough River are very similar to those in the Santa Fe from which we have many nymphs. County records from Florida include (map 8): Alachua, Escambia, Gilchrist, Holmes, Jackson, Liberty, and Taylor.

ECOLOGY. Nymphs have been found abundantly in the Santa Fe River where they live in the swifter parts of the stream on the *Vallisneria*, which grows very thick there. On the submerged plants the nymphs inhabit the distal portions of the leaves that float freely in the current. Only rarely have the nymphs been found on the rocks strewn here and there over the streambed, but this absence may be explained by the fact that mats of *Fontinalis* entirely cover the upper surfaces of the stones, rendering conditions unsuitable for the nymphs. Occasional immatures may sometimes be found on the undersides or in crevices of the rocks, but they are far more numerous on the plants.

In the Suwannee River, of which the Santa Fe is a tributary, the nymphs must of necessity remain close to shore, as the water becomes deep very rapidly and suitable habitats for the nymphs are rather scarce. The river current is fairly rapid, but the limited aquatic vegetation consists chiefly of *Myriophyllum* and *Polygonum*. Mayflies were not common where our collections were made. Nonetheless, we caught nymphs of several species, among them *P. parvulum*, taken from rocks along the river margin.

Other streams where nymphs were found have sand bottoms, are slightly acidic, and flow at a moderately swift rate. In these streams, the nymphs live on the vegetation and exposed roots of terrestrial plants that project into the water.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Although our collections of *P. parvulum* are not extensive, those at hand indicate that emergence occurs throughout the year. In the northern reaches of its range, the species is seasonal; McDunnough found that in the spring generation the individuals are larger than those of the summer generation, which are extremely minute. Burks (1953), working in Illinois, found adults from early May to mid-June.

Only a single male and one female have been reared by us. These emerged during the afternoon about 3:00 P.M. and remained in the subimaginal stage for about 9 or 10 hours. No other life history data are available.

BEHAVIOR. The behavior of the nymphs is like that of *P. alachua* immatures.

Pseudocloeon punctiventris McDunnough

(MAP 7)

Berner 1950, p. 251; 1958, p. 31; 1977, p. 22.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 205.

TAXONOMY. We have nymphs in our collections that we have referred to as *Pseudocloeon punctiventris*. These immatures differ from Ide's description in that the median pale band on the abdomen is quite distinct and the tracheae in the gills are prominent in our preserved material. McDunnough (1923) described the species from the Rideau River, Ottawa, and since then it has been recorded widely from the southeast (Berner 1977) as well as from Illinois and Ohio by Burks (1953).

The nymphs are distinct from all other Florida species in having a median dark band on each of the cerci and in the absence of color from the seventh pair of gills. The adults, of which we have no Florida specimens, are easily separable from other Florida species of *Pseudocloeon* by the absence of markings on the dorsum of the pale abdominal segments and by the presence of a minute midventral dot at the posterior margin of each abdominal sternite.

GEOGRAPHIC DISTRIBUTION. In Florida the nymphs have the same range as *P. parvulum* and have been taken from the same streams. The species is known to occur in the following counties (map 7): Alachua, Clay, Escambia, Gilchrist, Holmes, Jackson, Liberty, Okaloosa, Putnam, Santa Rosa, and Walton.

ECOLOGY. Ecologically, *P. punctiventris* is indistinguishable from *P. parvulum*.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Nymphs in the last instar have been taken in February, March, May, July, September, October, November, and December. Though we have no Florida adults, these mature nymphs indicate that *punctiventris* emerges throughout the year.

Nothing is known of the life history, but it is probably very similar to that of *P. alachua*.

BEHAVIOR. The behavior of the nymphs is similar to that of *P. alachua*.

METRETOPODIDAE

The status of the family Metretopodidae was reviewed by one of us (Berner) in 1978. In that paper it was pointed out that the small family includes only the two closely related genera *Metretopus* and *Siphloplecton*, the former being widely distributed in the Holarctic region, the latter restricted to the Nearctic. Characteristics separating the adults and nymphs of the two genera were described so that individuals are easily recognized, the adults on the basis of wing venation and the nymphs by the shape of the labial palpus, the labrum, and the presence of spines or setae on the gills. McCafferty and Edmunds (1979, p. 9) derive the family phylogenetically from within the Siphlonurinae. "Because of behavioral and gill structure similarities, its most probable common ancestry was with the *Siphlonurus-Parameletus* cluster." These authors placed the family in their suborder Schistonota.

Siphloplecton Clemens

Berner 1950, pp. 102–103; 1959, p. 51; 1977, p. 15; 1978, pp. 91–106.
Burks 1953, p. 150.
Edmunds, Jensen, and Berner 1976, pp. 149–151.
Unzicker and Carlson 1982, pp. 3.78–3.79.

The history of *Siphloplecton* was reviewed by Berner (1978) and will not be repeated here. It is a small genus, including only seven species, three of which were described in the 1978 paper.

The species are "distributed widely in North America occurring from the northwestern part of the Yukon Territory (Wiens et al. 1975) southward into Alberta, eastward across Canada, and southward through the eastern United States into northern Florida" (Berner 1978, p. 106).

Siphloplecton species can be divided into two groups, *interlineatum* and *basale*. The Florida species are represented in each of the groups with *S. simile, brunneum*, and *speciosum* allied with *basale* and *fuscum* with *interlineatum*.

The adults of *Siphloplecton* are characterized by having two pairs of cubital intercalary veins in the forewings and by having MP_2 strongly divergent from MP_1 at the base. "The crossveins of the stigmatic area are anastomosed and form two rows of cells. The wings of the males of most species are marked with brown at the base and bulla; many of the costal and discal crossveins are infuscated. Compound eyes of the male are large and contiguous dorsally; the first tarsal segment of both the middle and hind legs of the male and all of the legs of the female is fused to the tibia. Two caudal filaments are present" (Berner 1978).

The nymphs of *Siphloplecton*, along with those of *Metretopus*, are unique in having bifid claws on the forelegs. They inhabit slow-flowing streams where the nymphs live among vegetation in shallow water. Unzicker and Carlson (1982) suggest that the nymphs of both *Metretopus* and *Siphloplecton* are probably predators. We do not agree with this supposition as the mouthparts of both genera conform to those of other mayfly genera that are herbivores. The mandibles of nymphs of both genera have well-developed molar areas, structures that are lost or highly modified in predaceous species. Clifford (1976), studying *S. basale*, demonstrated that the nymphs are herbivore-detritivores.

The nymphs of the various *Siphloplecton* species are separable into the *basale* and *interlineatum* groups by a single characteristic, the presence or absence of ventral flaps on the first three gills (Berner 1978). Nymphs of the *interlineatum* group lack the ventral flaps.

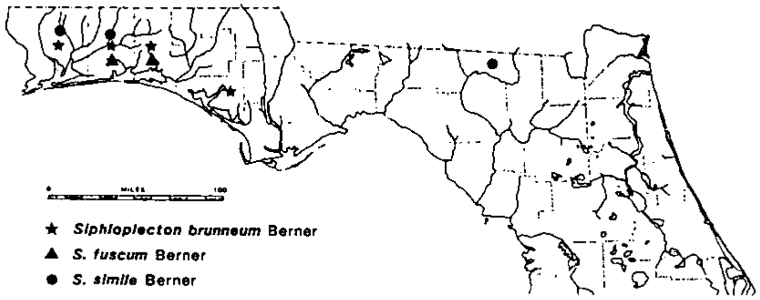
Siphloplecton brunneum Berner

(FIGS. 15, 50, 91. MAP 9)

Berner 1978, pp. 115–116.
Unzicker and Carlson 1982, p. 3.78.

TAXONOMY. *Siphloplecton brunneum* is another species closely related to *S. basale* and *S. simile*. The adult male is easily separated from other species by the distinctive shape of its penes, the coloration of its hind wing veins, and of the uniformly brown caudal filaments. The females resemble the males in having strongly colored wing veins, but they lack the brown basal stains of the male. The adults are a third smaller than those of *S. basale* and are more deeply pigmented. We are unable to distinguish the nymphs of the three Florida species from each other.

GEOGRAPHIC DISTRIBUTION. *S. brunneum* is known to occur only in northwestern Florida. The holotype male and the paratypes were collected at Pine Log Creek in Bay County; the allotype female came from the Blackwater River in Okaloosa County. Additional specimens have also been taken from the Blackwater River in Walton and Santa Rosa counties (map 9).



Map 9. The distribution of *Siphloplecton brunneum*, *S. fuscum*, and *S. simile* in northern Florida.

ECOLOGY. Nymphs from which adults were reared were collected from slowly flowing water where they lived in the vegetation. Both streams from which specimens were taken, Pine Log Creek and the Blackwater River, have brown, slightly acidic water. No other data are available about either immature or adult stages.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Because there have been so few observations, we can only speculate that the species is univoltine, with adults appearing during the winter as early as January 9 and into early April in the spring. We have no information about the life history.

BEHAVIOR. There are no recorded observations of the behavior of *S. brunneum*.

Siphloplecton fuscum Berner

(FIG. 49. MAP 9)

Berner 1978, pp. 125, 127–128.
Unzicker and Carlson 1982, p. 3.78.

TAXONOMY. *Siphloplecton fuscum* was discovered among specimens collected at the Blackwater River in northwestern Florida and was described in the recent review of the Metretopodidae (Berner 1978). The species belongs with the *interlineatum* complex and is easily separated from the three other Florida species by genitalic differences in the males. Colorational differences in the wings, as described in the species key, also help in distinguishing this species.

Although *fuscum* is related to the northern species *interlineatum*, adults differ in the intensity and pattern of color. Adults can be separated from the third species of the complex, *costalense*, by the darker crossveins and lighter main veins of *fuscum*.

GEOGRAPHIC DISTRIBUTION. The species is known positively only from the Blackwater River in Okaloosa County in northwestern Florida (map 9). A nymph collected from a stream in adjacent Walton County has been assigned to *fuscum*, as it is the only one known to possess the characteristics of nymphs of the *interlineatum* group.

ECOLOGY. No information about *S. fuscum*'s ecology is available; however, it is likely to be very similar to that of other Florida species of the genus.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Both type specimens were captured in March. Life history and seasonal distribution are probably identical with those of other Florida species of *Siphloplecton*.

BEHAVIOR. We have no information on the subject.

Siphloplecton simile Berner

(FIG. 51. MAP 9)

Berner 1978, pp. 114–115.
Unzicker and Carlson 1982, p. 3.78.

TAXONOMY. *Siphloplecton simile* was described in 1978 following a careful study of the various species of *Siphloplecton*. Its close affinity to *S. basale* is reflected in the fact that when adults were first collected in southern Georgia, they were identified, questionably, as belonging to that species. A collection of adults from extreme northwestern Florida made by Dr. W. L. Peters included adults of the same species, and it was then concluded that these individuals represented a species distinct from *basale*. *S. simile* is distinguished from *basale* by its size, being only two-thirds as large as the latter and much more intensely colored. Although there is no good evidence to substantiate it, *simile* may represent the terminus of a cline of *basale* extending from western Canada southward to Florida.

GEOGRAPHIC DISTRIBUTION. The species is known to occur only in the Withlacoochee River, Hamilton County, a tributary of the Suwannee River, in southern Georgia and northern Florida, and in the Blackwater River in Okaloosa and Santa Rosa counties in northwestern Florida (map 9).

ECOLOGY. Virtually nothing is known of the ecology of the species other than the fact that the nymphs from which adults were reared were found clinging to vegetation near shore in the more slowly flowing portions of small, brown-water rivers. In the Withlacoochee River, near Valdosta, Georgia, they were in the company of nymphs of *Baetisca obesa*, *Paraleptophlebia volitans*, and *Eurylophella temporalis*. The nymphs from the Florida stream were taken from a similar habitat.

SEASONAL DISTRIBUTION AND LIFE HISTORY. *Siphloplecton simile* adults emerge early in the year. Our first imagoes were collected in southern Georgia on February 1; the latest record of adults is May 3. As we have collected the streams of northwestern Florida extensively during all months of the year but have no records of the species for the warmer period, we surmise that the adults appear during the cool winter and spring seasons, mate, and lay eggs, which do not hatch until the water begins to cool.

Development is apparently arrested in the egg stage during the hot summer months, with hatching beginning in October. Most of the nymphal growth likely occurs in the cool water of the winter and early spring months.

Clifford (1976, p. 269) studying *S. basale* in Alberta, Canada, found adults emerging during daylight hours.

> In the Bigoray River, *S. basale* emerges during full daylight, usually around midday. In Michigan, Lyman (1955) observed a nymph transforming at 1100 hrs and its subimago stage lasting 48 hours. Males have been observed swarming in full daylight of the afternoon and early evening (Clemens 1915; Lyman 1955) and full daylight of the morning (present study). Males swarm above water, usually at a height of 3 to 6 meters. Lyman (1955) gives a description of the male's hovering and darting type flight. Leonard and Leonard (1962) noted that once the female enters the swarm and is seized, the pair rises to tree-top level. Spieth (1940) determined that the *S. basale* pair normally remains coupled for no more than 1½ minutes; however, when captured in a net, the pair might remain *in copula* for up to 7 minutes. I could not confirm Leonard and Leonard's (1962) observation that ovipositing females sometimes drop their eggs while in flight. In the Bigoray River, all ovipositing females appeared to release a few eggs at a time by momentarily resting on the water's surface or less frequently by dipping the abdomen into the water.

BEHAVIOR. We have been unable to observe activities of the nymphs.

Siphloplecton speciosum Traver

(FIG. 141. MAP 11)

Berner 1950, pp. 103–106; 1958, p. 30; 1959, p. 51; 1977, p. 15.
Jones 1977, p. 66.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 204.
Unzicker and Carlson 1982, p. 3.78.

TAXONOMY. The nymph of *Siphloplecton speciosum* was described by Traver in 1932, along with the adult, from streams near Macon, Georgia, and others nearby. Nymphs were collected and reared by P. W. Fattig to enable correct association of adults with the immatures. Both sexes are easily separated from other species by a lack of pigmentation in most of the wing membrane, nonmargined crossveins, and strongly marked bullae in the forewing. Nymphs of *S. speciosum*, differentiated by Traver from others by the presence of a midventral, abdominal brown line and lateral lines, do not show these traits consistently enough to be reliable characteristics for separating them from those of other species. Tarsal length was also used as a differentiating characteristic by Traver; it, too, cannot be used as it does not separate the nymphs of the various species.

GEOGRAPHIC DISTRIBUTION. This species has been reported from northern Florida, southeastern Alabama, and southern and central Georgia. Its known range overlaps that of the two other Florida representatives of the *basale* complex of species, *brunneum* and *simile*. The type locality of *S. speciosum* is very close to the Fall Line, which divides the Coastal Plain and the Piedmont physiographic provinces. Other localities given by Traver in her description of the species also abut the Fall Line. There is as yet no evidence that the species occurs in the Piedmont. The Florida records are from Escambia, Gadsden, Holmes, and Okaloosa counties (map 11).

Though we have searched diligently for *Siphloplecton* nymphs in the more easterly and southern regions of Florida, none has been found in spite of the fact that they were collected from the Withlacoochee River in southern Georgia, a stream that is a tributary of the Suwannee, a Florida river.

ECOLOGY. Nymphs live among submerged vegetation in slowly flowing water, especially where the plant growth is rather dense. Streams in northwestern Florida from which nymphs came, such as the Blackwater River, have a rather strong current and little vegetation. The plants grow in protected places where water movement is slow, and favorable sites available for development of *Siphloplecton* nymphs are scarce. The bed of the Blackwater consists of broad, sandy stretches composed of coarse-grained sand which shifts with the current so that little material becomes lodged in it.

The Withlacoochee River in southern Georgia, where nymphs were collected and from which adults were reared, is a deep, slowly flowing stream bordered by ash, willow, cypress, and blackgum trees. Where the trunks of the trees are submerged, they are usually covered by a densely growing species of moss. Nymphs were found in the moss along with those of *Baetisca obesa*, *Paraleptophlebia volitans*, and *Eurylophella temporalis*.

Other species of mayflies found in the vegetation with nymphs of *S. speciosum* included *Stenacron interpunctatum*, *Leptophlebia bradleyi*, *L. intermedia*, *Callibaetis* sp., *Baetis propinquus*, *Isonychia* sp., *Stenonema smithae*, *Neoephemera compressa*, and *Eurylophella temporalis*.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Mature nymphs of this species have been collected as early as November, and adults were reared on November 11 and 28. Other dates for adults range from February 7 to early May. Emergence appears to be governed by winter and spring water temperatures. It is likely that if there is a prolonged warm period during the winter, a fairly large number of adults may emerge.

As with other Florida species of *Siphloplecton*, we believe that *speciosum* is univoltine. Hatching is delayed over the hot summer months, but as the water cools with the onset of fall and winter, growth is accelerated.

Clifford's excellent study of *S. basale* (1976) was done in western Canada where ecological conditions are so different from those of Florida streams that his observations are not pertinent to our species.

BEHAVIOR. We have no data on the behavior of nymphs or adults of *S. speciosum*.

OLIGONEURIIDAE

The family Oligoneuriidae, distributed worldwide, was broadened in 1979 by McCafferty and Edmunds to include four subfamilies. In their reorganization of familial relationships, the Isonychiinae, formerly included with the Siphlonuridae (Edmunds et al. 1976), were reassigned to the Oligoneuriidae. The association of the Isonychiinae with the other subfamilies was based on nymphal traits that include the presence of a double row of long setae on the prothoracic femora and tibiae, gills on the maxillae, tracheal system without a ventral cephalic branch, and highly setaceous maxillae and labium. McCafferty and Edmunds also indicated that the derived affinities of both the Isonychiinae and the Coloburiscinae are obvious as these characteristics are common to both, and they still retain many siphlonurid adult characteristics. The Oligoneuriidae belong to the suborder Schistonota.

Isonychia Eaton

Berner 1950, pp. 106–108.
Burks 1953, p. 108.
Edmunds, Jensen, and Berner 1976, p. 144.
Kondratieff 1982, pp. 16–18.
Kondratieff and Voshell 1983, pp. 128–138;
1984, pp. 130–138.

Eaton proposed the name *Isonychia* for *manca* Eaton and *ignota* Walker; but in 1881, under the impression that the generic name was preoccupied by *Isonychus* Mannheim, he suggested the name *Chirotenetes* to replace *Isonychia*. McDunnough (1923) reexamined the group and concluded that according to the International Rules of Nomenclature *Isonychia* is available.

The genus has been investigated in depth by Kondratieff and Voshell (1983; 1984), and the taxonomy at the species level carefully studied. As a result of their work there are now 18 recognized species in *Isonychia*, distributed in two subgenera, *Isonychia* and *Prionoides*. The authors further subdivided the subgenus *Isonychia* into four subgroups: *arida*, *bicolor*, *diversa*, and *sicca*. Of these, only species in *arida* and *sicca* are known to occur in Florida.

Isonychia is widely distributed in the Holarctic and Oriental regions. It is also found as far south as Honduras in Central America. It is an abundant and commonly encountered genus in the Nearctic, especially in eastern North America. In Florida, the genus is confined to the northern part of the state and does not occur east of the Suwannee River drainage system. The nymphs are rarely found in Florida streams in the large numbers seen in more northerly areas.

Taxonomically, the nymphs are still poorly known, as suitable characteristics for distinguishing them are not available. Attempts at identification of immatures leave a considerable element of doubt as to correctness, especially since there is such close resemblance among the nymphs of the various species. The length of the tibial spur of the foreleg as compared to the length of the tarsus of this leg is a character used in the past to separate nymphs, and one that we previously employed. We now recognize that it is merely an individual variation related to the instar of the nymph. A nymph in the penultimate instar was kept in the laboratory for several days, during which period it molted once. An examination of the exuviae showed the tibial spur to be long and sturdy, but comparison with the spur on the actual nymph revealed that the spur was now quite short and insignificant. This evidence, later substantiated, indicates that the size of this structure varies from instar to instar. In addition, it has been found that nymphs in the last instar invariably have short tibial spurs, whereas the spurs of those in earlier instars are variable in length, ranging in size from one-half to more than three-fourths the length of the tarsus.

Isonychia (*Isonychia*) *arida* (Say)

(PLATE 6. FIGS. 21, 34, 76. MAP 10)

Berner 1950, pp. 111–114; 1958, p. 30; 1977, p. 13 (*I. pictipes*).
Burks 1953, p. 111.
Edmunds, Jensen, and Berner 1976, p. 147 (*I. pictipes*).
Kondratieff and Voshell 1981, pp. 191–194 (*I. pictipes*); 1983, pp. 135–136 (*I. arida* = *I. pictipes*); 1984, pp. 180, 182–184.
Schneider 1967, p. 204 (*I. pictipes*).

TAXONOMY. Traver described *Isonychia pictipes* from specimens collected by P. W. Fattig at the Apalachee and Alcova rivers in Georgia. She based her species on adult characters that included the bicolored fore tibiae, pale venation, and small size. Our Florida specimens fell clearly within the boundaries of her description, and we assigned the name *pictipes* to them. It was not until Kondratieff and Voshell (1983; 1984) published their studies of *Isonychia* that it became apparent that *arida* and *pictipes* are one and the same species. In their 1983 paper, they designated *pictipes* as a junior synonym of *arida*. They reported (1984) that the only reliable means of identifying nymphs is by slide mounting the forelegs of the mature insects. The characteristic bicolored fore tibiae can then be seen through the nymphal cuticle. Adults of *arida* are characterized by their

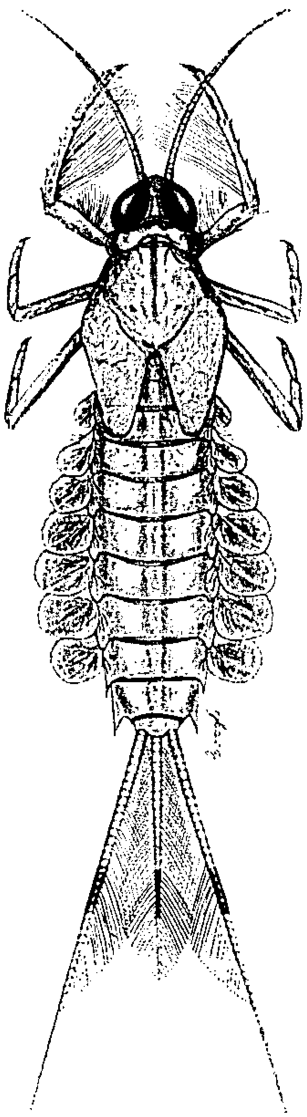
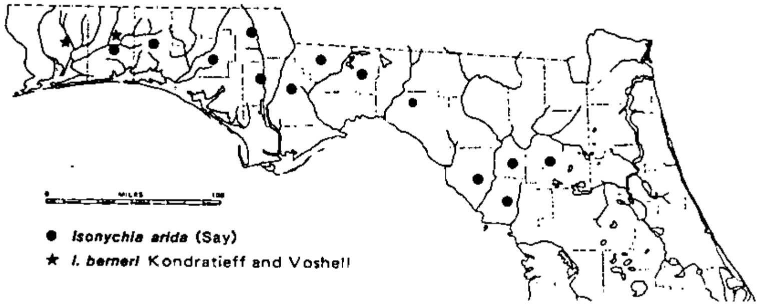


Plate 6. *Isonychia* (*Isonychia*) *arida* (Say), nymph



Map 10. The distribution of *Isonychia arida* and *I. berneri* in northern Florida.

distinctive bicolored fore tibiae, by the structure of the penes, and by the surface sculpturing of the eggs.

GEOGRAPHIC DISTRIBUTION. *I. arida* is a widely distributed species known to occur in Alabama, Georgia, Illinois, Mississippi, and South Carolina as well as in Florida. Florida counties from which the species has been recorded include Alachua, Calhoun, Dixie, Gadsden, Gilchrist, Jackson, Leon, Levy, Liberty, Okaloosa, Walton, and Washington (map 10).

ECOLOGY. Nymphs are found only in flowing water where the current is most rapid. The necessity for their occupying such habitats is evident from an examination of their food-gathering habit of filtering particles from moving water by straining such matter through the double row of long hairs on the fore tibiae and femora (Wallace and O'Hop 1979). Grant and Stewart (1980) observed in their study of *I. sicca* that very early instar nymphs graze on detritus. It is likely that older nymphs rely entirely on filtration for their food supply.

The majority of streams inhabited by this species are of the sand-bottomed type. Rarely were nymphs collected from beds of *Vallisneria* and *Potamogeton*, which form such an important element of many of the streams; however, *arida* nymphs were very frequently found on submerged logs, rocks, and boards that were solidly anchored in the stream. Collections from the few riffles encountered in west Florida creeks included no specimens of *Isonychia*. The most productive situations in the Florida streams are masses of debris caught in the swiftest parts of the current. The debris usually consists of branches, leaves, small sticks, and other trash that may have collected on some permanently fixed obstruction in midstream. Here the nymphs generally cling to the sticks and larger objects; as soon as they are disturbed, the immatures release their hold and thus are easily collected by use of a suitable net.

By far the most productive habitat in the sand-bottomed creek is the tangle of roots of terrestrial plants that are exposed at the banks by the continual washing of the rather swift waters. Many leaves and sticks, as well as much silt and other debris, collect among the exposed roots. Even though there is so much extraneous material present, the nymphs seem to find the conditions excellent, for they occur more plentifully in a situation of this type than on submerged logs where they would seem to be more naturally situated. Where the roots are exposed and the flow of water is reduced, the nymphs are not so frequently encountered as they are in those places where the roots are exposed to the full force of the current. *Isonychia* nymphs have been found to be particularly common in the masses of Spanish moss that often become enmeshed in the roots where the current is strong.

When the nymphs occur on submerged logs or rocks, they select the undersides or more protected areas. Although the full force of the current does not strike them, they are assured a constant, swift flow of water. Clemens (1917), from his experiments on *Isonychia bicolor* (identified as *albomanicata*), claimed that the nymphs cling to the undersurface of stones to avoid the full force of the current. Under the rocks the water moves much less rapidly than nearer the surface, but it still supplies adequate amounts of food and oxygen to the nymphs.

The acidity or alkalinity of the stream appears to have little influence on the presence of the nymphs, as indicated by the fact that specimens have been collected just as frequently from acidic as from basic waters. The current must be permanent and fairly strong, since there is a direct correlation between the rate of flow and the presence of *Isonychia* nymphs. Sweeney (1978, p. 461), studying the effects of thermal variation on *I. bicolor* in a Pennsylvania stream, found that development rate of both eggs and nymphs was "correlated positively with increased magnitude of the diel temperature pulse." He also demonstrated that subimaginal body size and fecundity for winter-generation females were about double those for the summer generation. It is likely that Sweeney's findings for *bicolor* explain the smaller size of the Florida species of *Isonychia* that develop in the warmer streams of the state.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults of *I. arida* emerge throughout most of the year in Florida, as evidenced by the presence in our collections of adults or last-instar nymphs taken in virtually every month of the year (no records available for January, February, or March). Farther north, the species follows the usual pattern of restricted emergence. In Virginia, Kondratieff and Voshell (1981) found adults (identified as *I. pictipes*) in late May, early June, and mid-August at one site; at another, adults appeared from late March to mid-May and from July to early October. At both localities studied by Kondratieff and Voshell, the species was bivoltine. Kondratieff and Voshell (1984) studied adults of this species collected in Florida from April through August and in October and November, but they drew no conclusions regarding *arida*'s pattern of emergence.

The life history of *I. arida* has not been investigated. Subimagoes emerge late in the afternoon or soon after dark, as evidenced by their arrival at lighting sheets in the early evening. They continue to be attracted to light for two or three hours after dark. Predominantly female subimagoes are attracted, but an occasional male imago also comes to light. Subimagoes kept alive until the adult stage was reached required 20–22 hours to complete development. This period is consistent with time required for other species. Kondratieff and Voshell (1984) reported duration of the subimaginal stage of *I. bicolor* in Virginia to be 20–36 hours. Grant and Stewart (1980) found *I. sicca* remained subimagoes from 23 to 29 hours before molting to the adult stage.

Kondratieff and Voshell (1984) found that prior to emerging the nymphs of *I. bicolor* in the Virginia streams crawl 12–15 cm onto objects projecting above the water surface. Kondratieff and Voshell also noted that nymphs that emerged in the spring months crawled farther above the water than those emerging in summer and fall. Where there were few objects reaching above the surface of the water, the nymphs floated in the flowing water, and the subimagoes then burst free. Sometimes the nymphs did not leave the water but merely held to emergent objects until the subimagoes hatched. We have observed the last method of emergence in Florida *I. arida*.

Mating flights of *I. arida* have not been observed by us, nor have others reported seeing them. Kondratieff and Voshell (1984) described the flights of *I. bicolor* in Virginia as lasting from early evening until after dark. They observed large flights of 20–75 males flying from three to six meters above riffles and descending until they almost touched the water's surface. Females oviposited in flight, dropping eggs as subspherical greenish masses.

We are unable to provide any data on growth rate or on length of time required for development from egg to adult.

BEHAVIOR. *Isonychia* nymphs are among the strongest of mayfly immatures. After being liberated in very rapidly moving water, the nymphs were observed swimming against a very strong current and actually moving upstream—an act that most other North American mayfly nymphs cannot perform. The powerful caudal filaments, with their very heavy growth of setae, make an excellent paddle for driving the streamlined insect rapidly through the water. The tails are probably of greatest use to the nymph in moving from place to place in rapid water; movement from place to place is accomplished, in the main, by swimming rather than crawling, which is the chief means of locomotion for the majority of stream-inhabiting species.

The rate of regeneration of caudal filaments is rather rapid. A nymph brought into the laboratory at Gainesville was somewhat damaged in that it lacked half of its right and two-thirds of its middle tail. This condition was noted on March 12, when the nymph was in its penultimate instar. After the molt to the last instar on March 18, the complete tails were again present and were of normal length.

Subimagoes are sensitive to levels of humidity. The mortality rate is high among those kept in captivity. After emergence the adults remain directly over the stream or next to it on fringing vegetation. Specimens are most easily collected either at light at the shore of creeks or from trees or bridges over them. The subimagoes and imagoes are distinctly phototactic, although the latter are less so. At a lighted sheet, the subimagoes tend to alight in a poorly illuminated area. The individuals that are attracted do not all come at once but arrive intermittently.

Isonychia (Isonychia) berneri Kondratieff and Voshell

(FIG. 75. MAP 10)

Kondratieff and Voshell 1984, pp. 149, 184, 186–188.

TAXONOMY. The holotype of *Isonychia (Isonychia) berneri*, described in Kondratieff and Voshell's monograph of the genus *Isonychia* (1984), was among specimens taken at the Blackwater River by Dr. W. L. Peters and others. The authors distinguished the adults based on characteristics that included the shape of the penes lobes, which are narrowly rounded distally, hyaline wings with venation whitish to very light brown, and abdominal terga 1–9 with prominent, anterolateral, purplish black marks. The nymph has not yet been associated with the adult stage. The authors state that the male adult is very distinctive and cannot be confused with any other Nearctic species of *Isonychia.* They point out that some males have an additional thin membranous tissue between the penes lobes, which give the penes a broader appearance medially.

GEOGRAPHIC DISTRIBUTION. Kondratieff and Voshell have examined specimens of *I. berneri* from extreme northwestern Florida, Alabama, and Mississippi. The species appears to be restricted to the Coastal Plain region of these states. In Florida, specimens have been taken from Okaloosa and Santa Rosa counties (map 10).

ECOLOGY. As the immature stage is still unrecognized, we cannot comment about it except to say that it is likely to be very much the same as that of *I. arida.* Kondratieff and Voshell (1984, p. 188) speculated that the species is common in "[t]he Blackwater River, a shifting sand River in northwestern Florida."

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults have been collected in Florida in April and July; in Alabama in May and June; and in Mississippi in April and October. The species is on the wing during the warmer months of the year; it is likely in the egg or nymphal stages during the other months. Nothing is known of the life history of *I. berneri.*

BEHAVIOR. The behavior of *I. berneri* is unknown, but it is probably no different from that of *I. arida* in Florida.

Isonychia (*Prionoides*) *sayi* Burks

(FIG. 73. MAP 11)

Berner 1950, pp. 108–111 (sp. A); pp. 114–115 (sp. B).
Burks 1953, pp. 110–111.
Kondratieff and Voshell 1984, pp. 155, 161, 203, 228–231.

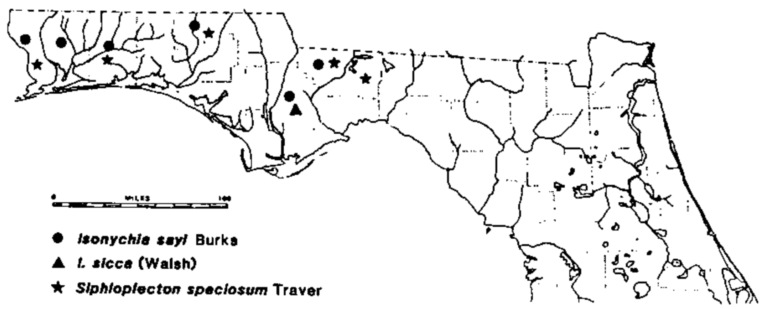
TAXONOMY. The taxonomic history of *I. sayi* was reviewed by Kondratieff and Voshell (1984) and will not be detailed here. The species is the only member of the subgenus *Prionoides* occurring in Florida. One of us (Berner 1950) first reported the species in the state but only in the nymphal stage and referred to it as *Isonychia* sp. A. The adults are very distinctive; the subgenus is distinguished by having hyaline or whitish venation, caudal filaments entirely white, abdominal tergites dark brown with light yellowish anterolateral spots, and males with distinctive genitalia. Females resemble males, but the wing venation is darker, ranging from brownish to purplish. It is very likely that the female adults treated by Berner (1950) as *Isonychia* sp. B are *I. sayi.* These specimens have pale, unbanded caudal filaments and dark wing venation, both characteristics being consistent with those mentioned by Kondratieff and Voshell for female *I. sayi.*

When *I. sayi* (reported as *Isonychia* sp. A) was first recorded from Florida, the adults were recognized as being "[v]ery likely a new species." At the time the species was listed, no traits were found that would separate nymphs from other species. Subsequently, Kondratieff and Voshell, following successful rearing of nymphs to the adult stage by Dr. Harry Savage, found that they are separated from all other *Prionoides* nymphs by having their coxal gills in tufts rather than as a single filament. These authors noted that *sayi* nymphs also seem to lack two characteristic purplish brown spots in the distal margin of the abdominal gill lamellae.

GEOGRAPHIC DISTRIBUTION. *Isonychia sayi* seems to be rare in its northern range but more common farther south. In Florida it is often encountered in the streams of the northwestern part of the state, especially in the well-studied Blackwater River. We believe that the species is distributed from the Ochlockonee River westward in the state. Counties from which specimens have been recorded are (map 11): Bay, Escambia, Gadsden, Holmes, Leon, Liberty, Okaloosa, and Santa Rosa.

ECOLOGY. As these nymphs cannot be separated readily in the field from other species, observations pertaining to their ecology are the same as those given for *I. arida.* Kondratieff and Voshell (1984) summarized the available information and pointed out that Peters and Peters (1977) had recorded temperatures in the Blackwater River, where the species has been taken often, with summer maxima near 30°C and winter minima about 10°C. Peters and Jones (1973) reported that the nymphs live among bank vegetation and leaf litter. Berner (1950) found the nymphs in flowing water where the current was rapid. We have taken them most frequently from among masses of debris lodged in the beds of sand-bottomed streams and from exposed roots of terrestrial plants at undercut banks.

SEASONAL DISTRIBUTION AND LIFE HISTORY. That emergence of adults of *I. sayi* occurs throughout the year in Florida is proved by the presence of



Map 11. The distribution of *Isonychia sayi*, *I. sicca*, and *Siphloplecton speciosum* in northwestern Florida.

nymphs in all stages of development in March, April, June, July, November, and December. Adults have been collected in April, May, and June. The life history of *I. sayi* is unknown, but comments under *I. arida* likely apply to *I. sayi* as well.

BEHAVIOR. The behavior of nymphs and adults is probably the same as that of *I. arida*.

Isonychia (*Isonychia*) *sicca* (Walsh)

(FIG. 74. MAP 11)

Kondratieff and Voshell 1984, pp. 149, 171,
193, 200, 202, 204, 206, 208.

TAXONOMY. *Isonychia sicca*, only recently reported as occurring in Florida by Kondratieff and Voshell, has been known since 1862 when Walsh described the species from Illinois. Kondratieff and Voshell also concluded that, although subspecies of *sicca* had been recognized for many years, they could find no valid reasons for continuing this practice after a careful study of specimens from all parts of its range.

Adults are characterized by their hyaline wings with yellowish brown to black venation; abdominal tergites reddish brown, sometimes tinged with yellow, to dark purplish red, or occasionally dark reddish orange; and males are additionally characterized by the shape of their penes. According to Kondratieff and Voshell, the nymphs are not readily distinguished from other species except by their geographical distribution.

GEOGRAPHIC DISTRIBUTION. *I. sicca* is widely distributed in North America, ranging from Texas to Minnesota, and eastward to Indiana. The Florida population, seemingly disjunct, is more similar to typical midwestern populations than to southwestern ones (Kondratieff and Voshell 1984). All Florida records are from the Apalachicola River in Liberty County in the northwestern part of the state (map 11).*

ECOLOGY. No information is available about the ecology of the species in Florida. Grant and Stewart (1980), in studying the life history of *I. sicca* in an intermittent stream in north-central Texas, reported that their nymphs came from riffles consisting of shallow limestone rubble underlain with packed sand.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Nothing is known about either of these subjects for the Florida form. Grant and Stewart (1980) have studied the species in detail in Texas. They found that fall-hatching nymphs formed a small, overwintering brood that grew slowly through the winter and emerged in late April. In a spring brood that hatched in March, the nymphs grew rapidly, and adults emerged in late May to early June. Adults from the winter and spring broods supplied eggs for a second generation that emerged in late June to early July. These authors noted that subimagoes emerged starting from about 20 minutes after sunset and continuing for about two hours. Emergence was continuous for the period April through July in 1977.

BEHAVIOR. We have no information regarding the behavior of *I. sicca* in Florida. Comments about the behavior of *Isonychia arida* probably apply equally to *I. sicca*.

Homoeoneuria Eaton

Edmunds, Berner, and Traver 1958, p. 376.
Edmunds, Jensen, and Berner 1976, p. 182.
Pescador and Peters 1980, p. 357.

Eaton (1881) established the genus *Homoeoneuria* for the female *H. salviniae* from Duena and Aceytano, Guatemala. Pescador and Peters (1980) recently revised *Homoeoneuria* and discussed the zoogeography and phylogeny.

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* After this book was in press one of us (Pescador) collected several nymphs of *I. sicca* in the Little and Ochlockonee rivers in Gadsden County.

Knowledge of the relationships of *Homoeoneuria* to the other genera of the family Oligoneuriidae is limited. Recent study by one of us (Pescador) of all oligoneuriid genera with known nymphs supports the statement by Edmunds (1979) that *Homoeoneuria* and *Oligoneurisca* are sister groups. In addition to having similar body forms, the nymphs of both genera share the apomorphic characters of reduced tarsi and abdominal posterolateral spines limited to segments 8 and 9.

The adults of *Homoeoneuria* are distinctive and differ from the other oligoneuriid genera by the absence of crossveins in both wings (fig. 26), the lack of male genital forceps, and twisted and vestigial legs of the females. The nymphs have tarsi reduced to papilla-like structures, unhooked and bare meso- and metathoracic claws, a finger-like posteromedian process on abdominal sternum 1, ventral gills on segment 1 large and multibranched, other gills dorsal, small, flat, and slender.

The genus *Homoeoneuria* includes six species, *H. alleni*, *H. ammophila*, *H. cahabensis*, *H. dolani*, *H. fittkaui* and *H. salviniae*, only one of which, *H. dolani*, occurs in Florida.

Homoeoneuria is Nearctic and Neotropic in distribution. Collection records indicate that the genus occurs from Colombia and northern Brazil in South America north to Guatemala and Mexico in Central America, northwestward to New Mexico and Utah, north and southeastward to the central and southeastern United States.

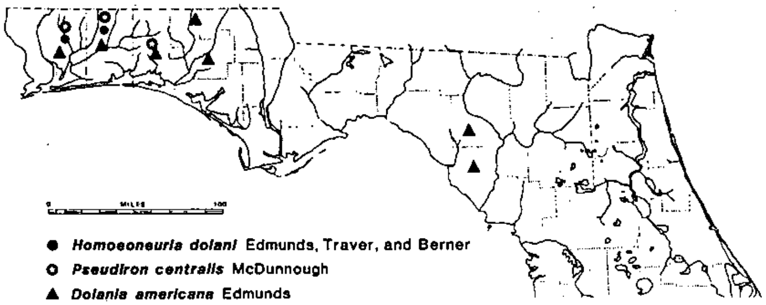
Homoeoneuria dolani Edmunds, Berner, and Traver

(FIGS. 26, 68, 144. MAP 12)

Edmunds, Berner, and Traver 1958, pp. 378, 380.
Pescador and Peters 1980, pp. 373–376.

TAXONOMY. *Homoeoneuria dolani* was described from male and female imagoes and nymphs collected mostly from the Savannah River. Pescador and Peters (1980) recently redefined the species and included discussions of the zoogeography, phylogenetic relationships, and biology along with a treatment of the other species of the genus.

The species appears to be most closely related to *H. cahabensis* from Alabama and differs from the other species of the genus in coloration and markings of the abdomen of both the adults and nymphs, as well as in the shape of the penes of the male. The lack of markings on the vertex, pronotum, and fore coxae of the nymph and the unicolorous pale yellow, nymphal caudal filaments separate *dolani* from other species.



Map 12. The distribution of *Homoeoneuria dolani*, *Pseudiron centralis*, and *Dolania americana* in northwestern Florida.

GEOGRAPHIC DISTRIBUTION. *H. dolani* has been collected from the sandy rivers of Georgia, South Carolina, and Florida. In Florida, the species is known only from the northwestern tier of counties (map 12), including Gadsden, Leon, Okaloosa, and Santa Rosa.

ECOLOGY. The almost transparent nymphs of *H. dolani* occur in the sand-bottom beds of the Blackwater, Shoal, and Ochlockonee rivers in Florida. Nymphs are found burrowing shallowly into the shifting sand, mainly in deep areas of the rivers. The water flows swiftly over the area in which the nymphs live; the bottom is clean-swept, composed mostly of loose, shifting sand with pebbly stretches, and there is no attached vegetation.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults of *H. dolani* are known to be on the wing from early June through late October and exuviae of last-instar nymphs have been found in November. Our collections include nymphs collected from May to October in the Blackwater and Shoal rivers. Whether eggs hatch soon after oviposition is unknown, but we suspect that the species overwinters in the egg stage. We believe that the species is univoltine.

The species appears to have a low level of fecundity. Five dissected mature female nymphs had a mean of 315 eggs (range 270–365) per individual (Pescador and Peters 1980).

BEHAVIOR. *H. dolani* is one of the strictly sand-dwelling mayfly species occurring in the Blackwater River in northwestern Florida. The other two species are *Dolania americana* and *Pseudiron centralis*. Of the three, *H. dolani* is the only nonpredaceous species. The nymphs of *dolani* are shallow burrowers, *D. americana* are deep burrowers, while those of *P. centralis* are surface dwellers.

A unique combination of leg and mouthpart morphology, along with behavioral adaptations, provides an efficient filtering system for the nymphs. Long hairs extending from the legs and mouthparts trap sand and particulate organic materials on which the nymphs browse. An examination of the gut contents revealed that both sand grains and organic matter are ingested as the nymphs feed. The nymphs lie partially buried in the sandy streambed, leaving the head, forelegs, and caudal filaments exposed, which results in a broad, U-shaped appearance. The upstream orientation is accomplished by the scouring motion of the meso- and metathoracic legs digging in a sidewise fashion. As the nymphal position is secured, the prothoracic legs are projected forward with the tibiae almost at a right angle to the femora; the long, plumose, tibial hairs are placed lateroventrally to the mouthparts. This orientation of the prothoracic legs and the placement of the long plumose hairs, along with the setose nature of the mouthparts, provides an efficient food-filtering device for the nymphs.

Adults swarm in midmorning from about 10:00 A.M. to noon, cruising about three feet above the water in full sunlight.

HEPTAGENIIDAE

The family Heptageniidae includes five subfamilies and 29 genera worldwide. The nymphs are easily distinguished from those of other mayfly families by the dorsoventrally flattened head and dorsally located eyes. The adults have five-segmented tarsi and more or less complete wing venation.

The family is widely distributed and very common throughout the Holarctic region. Two subfamilies, Heptageniinae and Pseudironinae, and five genera (*Heptagenia, Macdunnoa, Pseudiron, Stenacron,* and *Stenonema*) occur in Florida, concentrated in the northwestern section of the state.

Pseudiron McDunnough*

Berner 1959, p. 46.
Burks 1953, p. 148.
Edmunds, Allen, and Peters 1963, p. 13.

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*The genus *Pseudiron*, subfamily Pseudironinae, was placed in the Siphlonuridae by Landa and Soldán 1985.

Edmunds, Jensen, and Berner 1976, pp. 208–210.
Jensen 1972, p. 151.
Landa and Soldán 1985, p. 91.
Pescador 1985, pp. 432–438.
Soluk and Clifford 1984, pp. 1534–1539.

McDunnough (1931) established the genus *Pseudiron* for *P. centralis* and based it on female imagoes only. In a recent study of the systematics of *Pseudiron*, Pescador (1985) redescribed the genus and reviewed and discussed its taxonomy. Additionally, the two species *P. centralis* and *P. meridionalis* were synonymized, leaving *Pseudiron* as a monotypic genus.

The genera *Pseudiron* (Pseudironinae) and *Arthroplea* (Arthropleinae) are believed to represent early lineages from plesiomorphic Heptageniidae, as both share the same derived characters of the trachea and the nerve cord (Jensen 1972). *Pseudiron* differs from *Arthroplea* and the other heptageniid genera as follows: *Pseudiron* has three or four cubital intercalaries in the hind wings; the male imagoes have shorter fore tibiae than fore femora; the basal segment of the hind tarsi are fused or partially fused with the tibiae; and the penes lack median titillators. The nymphs of *Pseudiron* have mouthparts adapted for predation with the mandibular incisors modified apically and equipped with sharply pointed spines; the maxillary palpi are four-segmented; and the lamellae of the abdominal gills on segments 2–7 have a slender filament arising from the ventral surface at about midlength. Unique to the long and slender nymphal claws of *Pseudiron* is the presence of a constriction located approximately one-third of the distance from the apex, and within it there is a concentrated mass of nerve cells. A flexible portion of the claw is distal to the constriction.

The genus *Pseudiron*, a Nearctic endemic, has a wide geographic distribution occurring in the central and southeastern United States and west to Utah and Wyoming. It also is known to occur across western and central Canada (Pescador 1985).

Pseudiron centralis McDunnough

(PLATE 7. FIGS. 58, 84, 111, 115, 120, 143. MAP 12)

Berner 1959, p. 46 (*meridionalis*).
Burks 1953, p. 148.
Edmunds, Jensen, and Berner 1976, p. 210.
Pescador 1985, pp. 438–443.

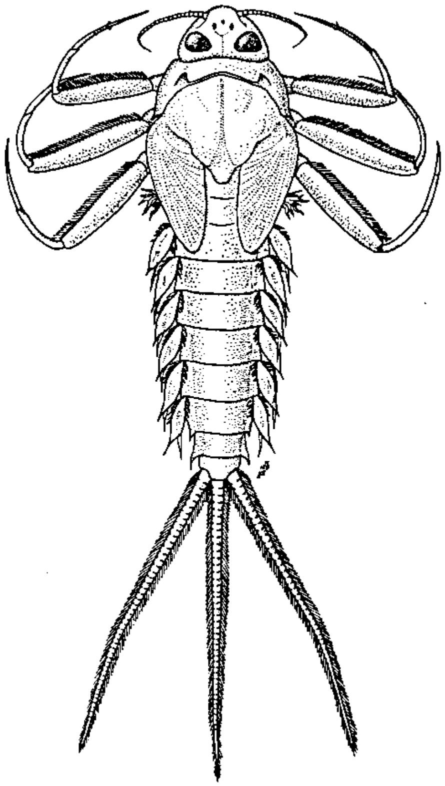


Plate 7. *Pseudiron centralis* McDunnough, nymph

Peters and Jones 1973, p. 246 (*meridionalis*).
Soluk 1983, pp. 8–49.
Soluk and Clifford 1985, pp. 1539–1543.

TAXONOMY. *Pseudiron centralis* was recently redefined by Pescador (1985). The species exhibits an interesting geographic clinal variation of color and pigmentation, with the nymphs and adults from Canada and the northwestern United States being generally darker and more deeply pigmented than specimens from the central and southwestern United States. Specimens from Florida are pale yellow and least pigmented (Pescador 1985).

GEOGRAPHIC DISTRIBUTION. *Pseudiron centralis* is widely distributed throughout North America, mainly east of the Continental Divide and following the Mississippi drainage. In Florida, the species has been collected in the panhandle counties of Okaloosa, Santa Rosa, and Walton (map 12).

ECOLOGY. The nymphs of *Pseudiron centralis* are associated mostly with sandy riverbeds in medium-sized to large rivers over much of North America (Edmunds et al. 1976). In a detailed study of the life history and abundance of *P. centralis*, Soluk and Clifford (1984) observed that in Sand River, Alberta, the nymphs were associated with three types of substrates in the riverbed—shifting sand, marginal sand, and gravelly sand—and exhibited a change in their association with the types of sandy substrates during development. Young nymphs are associated with marginal sand; as they mature, they move to shifting sand. The transfer of the mature nymphs to shifting-sand substrates appears to be a strategy to exploit either the greater prey availability or the lower number of potential predators and competitors in these areas (Soluk 1983). In the Blackwater River of northwest Florida, *P. centralis* has been mostly collected in shifting sand, rarely in gravelly sand (Pescador 1985).

SEASONAL DISTRIBUTION AND LIFE HISTORY. In Canada, *P. centralis* has a univoltine summer life cycle, and the eggs remain dormant for about nine months (Soluk and Clifford 1984). The first-instar nymphs appear in late April and mature in less than eight weeks. Adult emergence occurs from late June to late July. Our collection records over a period of about 10 years indicate that the species appears to have the same emergence period throughout its geographic range, except in Florida where emergence occurs earlier, from mid-March to early May.

Female adults from Florida seem to have higher fecundity levels than females of this species collected from other areas of the geographic range. In Canada, 467 and 626 eggs were counted from two female imagoes (Soluk and Clifford 1984). A single female adult from Tennessee had 692 eggs; while 1553, 1670, and 1724 eggs were found in three dissected female imagoes from Florida (Pescador 1985).

BEHAVIOR. The nymphs of *Pseudiron centralis* are predatory in habit, feeding primarily on chironomid larvae. In the Sand River, Alberta, the nymphs were the only epibenthic predators that occupied areas of actively shifting sand (Soluk and Clifford 1984). In the Blackwater River, two predaceous sand-dwelling species, a mayfly, *Dolania americana*, and a dragonfly, *Progomphus obscurus*, coexist with *P. centralis* nymphs. There is a dietary overlap among these three carnivores, but partitioning of resources and lessening of potential competition is achieved through differential microhabitat utilization (Tsui and Hubbard 1979). Nymphs of *P. centralis* are surface sand-dwellers while *D. americana* and *Progomphus obscurus* are active burrowers, living in their burrows most of the time.

The nymphs lie on top of the sand facing the current with all three pairs of legs laterally directed, spread in a spider-like fashion, with the claws anchored in the sand (Pescador 1985). The functional adaptation of the constriction of the claws, the mass of nerve cells inside them, and the flexible, distal portion of the claws are still unknown.

Heptagenia Walsh

Flowers 1980, p. 93.

Walsh (1863) established the genus *Heptagenia* for the species *Heptagenia flavescens*. The genus has long been suspected by mayfly workers to be polyphyletic, and Traver (1933) previously recognized six species groups for the adults and two species groups for the nymphs. Realizing the taxonomic problems involved in the genus, Bogoescu and Tabacaru (1962) transferred many of the European species of *Heptagenia* to *Ecdyonurus*. Recently Flowers (1980) divided the Nearctic species of *Heptagenia* into three genera: *Heptagenia, Leucrocuta,* and *Nixe*. According to Flowers, the true *Heptagenia* now corresponds to the *flavescens-pulla-elegantula* group of Traver (1933), while *Leucrocuta* and *Nixe* correspond to the *maculipennis* group and *lucidipennis-simplicioides* group, respectively.

The Nearctic *Heptagenia* presently includes 12 species and possibly 3 additional species (*H. bella, H. kennedyi,* and *H. manifesta*). Flowers (1980) cautioned, however, about the need for additional study to confirm the proper generic placement of these 3 species.

Heptagenia is common throughout the Nearctic, extending into Canada and as far south as Florida.

Heptagenia flavescens (Walsh)

(FIGS. 56, 164. MAP 14)

Berner 1953, p. 149; 1958, p. 30; 1959, p. 31;
  1977, p. 25.
Carlson 1980, p. 82.
Flowers 1980, p. 296.
Jones 1977, p. 66.
Schneider 1967, p. 204.
Wurtz and Roback 1955, p. 194.

TAXONOMY. *Heptagenia flavescens* is the only species of the genus that occurs in Florida. The adults are distinguished from the other species of the genus by the fairly large yellowish body and the presence of a brown dorsal stripe that extends almost the entire length of the body. The stripe broadens on the mesothorax and becomes progressively darker and reddish on the posterior abdominal segments. We have found that the dorsal stripe of some adults extends only to abdominal segment 7 and then becomes fragmented into short and narrow median stripes and a pair of submedian stripes on segments 8 and 9 or 10.

The nymphs are recognized by the distinct, dark brown marking on the posterior edge of the ninth abdominal sternite. Burks's excellent description of the nymph in Illinois (1953) applies equally well to the nymphs occurring in Florida. We have found that younger nymphs possess more distinct and pronounced pale yellow markings than mature nymphs.

GEOGRAPHIC DISTRIBUTION. *Heptagenia flavescens* occurs from the central lowlands of Canada to the midwestern and southeastern United States. In Florida, the species had been collected from the following northwestern counties (map 14): Escambia, Gadsden, Holmes, Leon, Okaloosa, Santa Rosa, and Walton.

ECOLOGY. The nymphs of *H. flavescens* have been collected in various habitats. Daggy (1945) found the nymphs under logs in shallow water near the shore at John Latsch State Park, Winona County, Minnesota. Flowers and Hilsenhoff (1975) collected the nymphs in medium-sized to large streams under rocks and debris in deep water in Wisconsin. In northwest Florida, Wurtz and Roback (1955) took nymphs 1.2 miles above the mouth of the Escambia River, which is within the influence of the tides from Escambia Bay. At the time of collection, the river was at high water, with average and maximum depths of 17 and 30 feet, respectively, and had the following bottom chemical and physical readings: alkalinity as $CaCO_3$, 21 ppm; total hardness as $CaCO_3$, 21.9 ppm; Cl, 7.5 ppm; Ca, 6.8 ppm; dissolved oxygen, 7.0 ppm; and turbidity, 0 ppm. Schneider (1967) found the nymphs among leaf detritus, gravel or rock, and vegetation in the Perdido and Shoal rivers. The nymphs have also been collected under submerged rocks and logs in Rocky Comfort Creek, Gadsden County (Jones 1977; Flowers, pers. comm.).

SEASONAL DISTRIBUTION AND LIFE HISTORY. Knowledge of the seasonal distribution and life history of *H. flavescens* is limited. Berner (1959) reported that the eggs take 12 to 49 days to hatch in the laboratory. The nymph probably lives for one year, and the adults from 2 to 4 days. Flowers and Hilsenhoff (1975) observed that the seasonal occurrence of the nymphs in Wisconsin is year-round and the adults emerge in June. The adults emerge in mid-March to early June in North and South Carolina (Unzicker and Carlson 1982). In Florida the nymphs have been collected in March through November, and the adults in March through early May. We believe that the nymphs probably occur year-round and that the emergence period lasts much longer than the collection records indicate.

BEHAVIOR. The nymphs are very active and often scurry to the underside when a stone is lifted from the water. One of us (Berner 1959) noted that when the nymphs are placed in a pan of water with no attachment surface available, they tend to form into balls clinging to one another and tumbling about in the water. When ready to emerge, the nymph comes close to the surface, and the subimago bursts free. The adults are positively phototactic, as most of the adults available to us were collected at light.

Macdunnoa Lehmkuhl

Lehmkuhl 1979, p. 859.
Flowers 1982, p. 25.

Lehmkuhl (1979) established the genus *Macdunnoa* for *Macdunnoa nipawinia* and based his description on the nymph and female imagoes. Flowers (1982) redescribed the nymph and provided the generic description of the male imago, using reared adults of a new species, *M. brunnea*. He also added *Macdunnoa persimplex* to the genus by transferring it from *Heptagenia*. *Macdunnoa* now includes three species, *M. brunnea*, *M. nipawinia*, and *M. persimplex*. Of these, *Macdunnoa brunnea* is the only one found in Florida.

Based on adult and nymphal morphology, *Macdunnoa* belongs to the same phyletic line as *Stenacron* and *Stenonema* (Flowers 1982), and appears to be most closely related to the latter. *Macdunnoa* male adults differ from those of *Stenonema* by having thick median titillators and the absence of spines on the apical lobe of the penes; females lack dark markings on the abdomen; and nymphs of *Macdunnoa* have a vestigial seventh gill.

Macdunnoa occurs from the central lowlands of Canada to the midwestern and southeastern sections of the United States.

Macdunnoa brunnea Flowers

(FIG. 57. MAP 14)

Flowers 1982, p. 25.

TAXONOMY. *Macdunnoa brunnea* was described by Flowers (1982) from reared specimens. The species differs from *M. persimplex* by the absence of lateral minute spines on the penes, and the small crescent-shaped micropyles of the eggs. The nymphs can be distinguished from those of *M. nipawinia* by the absence of a distinct emargination on the front margin of the head capsule.

GEOGRAPHIC DISTRIBUTION. *Macdunnoa brunnea* has only been reported from Florida, South Carolina, and North Carolina. The species has been collected from the following Florida counties (map 14): Escambia, Gadsden, and Okaloosa.

ECOLOGY. Little information is available about the ecology of the species. According to Flowers (1982), the nymphs live on rotting leaves among rocks in deep areas of the streams where the current is swift.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults of *Macdunnoa brunnea* emerge from May to early June at Rocky Comfort Creek, Gadsden County, and are attracted to light (Flowers 1982). The nymphs were collected in March, April, and May in Florida; June in South Carolina; and July in North Carolina.

BEHAVIOR. Except for Flowers' (1982) brief observation, the behavior of *M. brunnea* nymphs is virtually unknown. Flowers noted that when nymphs are placed in still water, they move their gills in a wavelike motion, beginning with the first pair. This behavior is also characteristic of *Stenacron* and *Stenonema* nymphs.

Stenacron Jensen

Berner 1950, p. 57 (*Stenonema*, in part); 1977, p. 28.
Burks 1953, pp. 161–168 (*interpunctatum* group).
Edmunds, Jensen, and Berner 1976, p. 200.
Jensen 1974, pp. 225–228.
Jensen and Edmunds 1973, p. 83 (new genus "A").
Koss 1968, p. 704 (*interpunctatum* group).
Landa 1969, p. 299 (*interpunctatum* group).
Lewis 1974a, p. 9 (*interpunctatum* group).
Unzicker and Carlson 1982, pp. 3.63–3.68, 3.73.

TAXONOMY. Jensen (1974) established the genus *Stenacron* to include the *interpunctatum* group of the genus *Stenonema*. Previous taxonomic accounts of the *interpunctatum* group by other workers (Traver 1933; Spieth 1947; Berner 1950; Koss 1968; Jensen and Edmunds 1973; Lewis 1974a) had also indicated that the group was worthy of either subgeneric or generic rank.

Stenacron apparently originated from a *Heptagenia*-like ancestor, which differentiated into *Stenacron*, *Stenonema*, and *Macdunnoa*. The genera *Heptagenia*, *Stenacron*, and *Stenonema* share a number of similar characters, which show their close relationship. *Stenacron* shares with *Heptagenia* the pectinate spines on the nymphal maxillae as well as similar egg structures. With *Stenonema*, *Stenacron* shares similar structures of the gills and mouthparts, and tarsal segment ratios of the male imagoes.

The adults of *Stenacron* are characterized by the presence of a dark bar below the bullae between veins R_1 and R_2 of the forewings, and the shape of the penes and presence of an unusually well-developed laterosubapical cluster of spines on the penes. The nymphs have pectinate spines on the crown of the maxillae. The lamellate gills on abdominal segments 1–6 end in an acute point. The gills on segment 7 are reduced to slender filaments and lack the fibrilliform portion. The tracheae have a few or no branches.

The genus *Stenacron* presently includes seven species, of which two, *S. floridense* and *S. interpunctatum*, occur in Florida. The former species is apparently endemic in the state. The genus is Nearctic and restricted to eastern and central North America, where it ranges south to Florida and west to Arkansas and Minnesota (Edmunds et al. 1976).

Stenacron floridense (Lewis)

(FIG. 55. MAP 15)

Edmunds, Jensen, and Berner 1976, p. 201.
Jones 1977, p. 66.
Lewis 1974a, pp. 23–24; 1978, p. 23 (as *Stenonema*).

TAXONOMY. Lewis (1974b) described *Stenacron floridense* (as *Stenonema floridense*) from male and female imagoes and nymphs collected at the Blackwater River near Holt, Florida. *Stenacron floridense* superficially resembles *S. interpunctatum*, but the armature of the male genitalia, in which the penis lobes have two or more axial spines, is distinctive. Very few adults have light brown pleural streaks on either tergum 8 or 9; otherwise most specimens show no trace of pleural streaks or spiracular spots on the abdomen. The nymphs have 8 pectinate spines on the crown of the maxillae (rather than 9 or 10 as in *S. interpunctatum*); rarely do 9 spines occur. The nymphs of *S. floridense* also have 7 teeth on the inner margin of the outer canine, 4 teeth on the inner margin of the inner canine, fewer than 25 lateral setae on the ventral surface of the galea-lacinia of each maxilla, and a dorsal pattern of interrupted elongate pale spots.

GEOGRAPHIC DISTRIBUTION. *Stenacron floridense* is known only from northwestern Florida and has been collected from the following counties (map 15): Gadsden, Holmes, Jackson, Liberty, Okaloosa, Santa Rosa, Taylor, Wakulla, and Walton.

ECOLOGY. The nymphs of *Stenacron floridense* are very common in the sand-bottom streams in northwest Florida. Streams in the Blackwater River drainage, where most of the specimens were collected, are mainly spring fed, and the water is extremely soft and low in minerals and nutrients. Beck (1973) reported the chemical data of the Blackwater River system as follows: pH varying from 5.0 to 6.3; total dissolved solids 15–17 mg/l; and dissolved oxygen 6.8–9.7 mg/l.

Lewis (1974a) has suggested that *S. floridense* is restricted to the naturally acid streams of the southeast that have not been affected by pollution.

We collected several nymphs and adults of this species in Bear Creek and Rocky Comfort Creek, Gadsden County. The nymphs were found in various habitats that included thick growths of filamentous algae and water moss (*Spirogyra* sp. and *Leptodictyum riparium*), submerged logs, and leaf litter trapped between tree stumps or fallen branches of trees. Pescador and Peters (1974) gave the following chemical data pertaining to Bear Creek and Rocky Comfort Creek: CO_2 (free carbon dioxide) varying from 1.0 to 2.5 mg/l; $CaCO_3$ (calcium carbonate) 11.0–16.5 mg/l; and dissolved oxygen 5.0–7.5 mg/l.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The nymphs and adults of *S. floridense* have been collected throughout the year. Although no detailed study on the life history of the species has been done, we surmise that it probably has the same life history as *S. interpunctatum*, which also emerges throughout the year; and the nymphs of both species generally occupy the same kinds of habitats.

BEHAVIOR. The nymphs of *S. floridense*, like the other species of *Stenacron* and *Stenonema*, are negatively phototactic. The nymphs immediately crawl under logs, stones, or leaf litter when exposed to light. The nymphs are gatherers, as revealed by dissected gut contents where we found a mixture of particulate organic material and occasional sand particles. Adults were collected mostly by the use of light traps.

Stenacron interpunctatum (Say)

(Figs. 24, 54, 114, 166. Map 15)

Berner 1950, pp. 73–78 (*proximum*); 1958, p. 30; 1977, p. 27.
Cowell and Carew 1976, pp. 590–591.
Lanquist 1953, p. 40 (*proximum*).
Lewis 1974a, pp. 26–27.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 204.

TAXONOMY. Much apparent intraspecific variation in *Stenacron interpunctatum* has created confusion in trying to define the species. Spieth (1947) examined the problem in depth and attempted to resolve it by erecting four subspecies. The problem with the Florida species, identified as *S. proximum*, was recognized long ago (Berner 1950) when it was suggested that, as more data became available, the species might well be *Stenacron interpunctatum*. In a 1958 paper (Berner), *interpunctatum* was assigned as the name of the Florida form. The pattern of variation in this species does not fit the normal subspecies concept, and, until the biological nature of the variations is understood, attempts to apply names below the species level seem premature, according to Lewis (1974a) and Edmunds et al. (1976). A recent study by McCafferty and Pereira (1984) on the effects of temperature on the development of *S. interpunctatum* and their taxonomic interpretations has indeed indicated that the subspecific classification of this species is no longer tenable. According to McCafferty and Pereira, there are no clear geographic isolates; variants of the species appear to be, for the most part, the result of developmental responses to thermal conditions that can be no more sharply delineated than their spatially and temporally variable causative factors. Specimens of *interpunctatum* reared in different thermal regimes generated the several phenotypic differences previously thought to be taxonomically significant for subspecies classification.

The nymphs of this species are characterized by having 7 to 10 spinelike setae on the crowns of their maxillae and continuous or nearly continuous middorsal pale streaks on the abdominal terga. Often these streaks are obscured on Florida nymphs from the northern part of the state; however, some mature nymphs show the trait clearly. The male adults have terminal or subterminal spines on the penes lobes. The abdominal terga are usually pale, although sometimes there is a dark mark at the posterior margin of some of the segments. The adults are often yellowish, and the abdomen of females may appear to be orange because of the color of the eggs contained within.

GEOGRAPHIC DISTRIBUTION. *Stenacron interpunctatum* is widely distributed and basically has the same geographic range as the genus. The species has been found to be distributed generally throughout Florida wherever there are permanently flowing waters. Adults and nymphs have been taken in Hillsborough County in the west-central part of Florida, and Cantrell has found it to be common throughout southwest Florida to Lee County. The species is known to extend from Nassau County in the east to the western boundary of the state (map 15).

ECOLOGY. *Stenacron interpunctatum* is often abundant in streams and rivers in the eastern half of North America (McCafferty and Huff 1978). Flowers and Hilsenhoff (1979) collected the nymphs in great numbers in small eutrophic streams in southern Wisconsin, where at times they were the only heptageniid to be found. Lewis (1974a) collected the nymphs from a stream in southern Ohio that received moderate amounts of organic pollutants from an overloaded sewage treatment plant; however, the current was swift and the dissolved oxygen was near saturation. He found very few nymphs in the Ohio River downstream from Cincinnati where the dissolved oxygen often falls below 4.0 ppm during the summer, but nymphs were abundant in the unaffected reaches upstream of the city.

In Florida, *S. interpunctatum* in many respects resembles *Stenonema smithae* ecologically, but its ecological valence seems to be less than that of the latter species. A chief inhabitant of the larger streams of north-central Florida, *interpunctatum* is very rarely found in the smaller streams that support large populations of *smithae*. Its habitat in these streams is identical with that of *smithae*—submerged logs, rocks, sticks, and boards in almost any part of the stream. The species seems to flourish to a much greater extent in alkaline creeks of moderate dimensions, varying from the size of Hatchet Creek near Gainesville to that of the Santa Fe River.

Nymphs of *S. interpunctatum,* also inhabitants of sand-bottomed lakes, are confined to the shore region where they can be found on the undersides of boards, logs, sticks, or any other predominantly submerged object that might give a good foothold and furnish a continuous food supply. In the lakes, the insects confine themselves to that part entirely free of silt and characterized by a cleanly washed sand shore and beach. There is little wave action or deposition of silt in this region. Vegetation is almost lacking, and suitable situations for the nymphs are not plentiful. Consequently, when a board is located on which there are nymphs, it will usually have quite a number of individuals on it.

The stream associates of *S. interpunctatum* are the same as those of *Stenonema smithae*; the lake associates are *Eurylophella temporalis, Choroterpes hubbelli,* and occasionally *Stenonema exiguum.* In the lake from which *interpunctatum* was taken most commonly, other animals present were indicative of a stream association. The mayflies listed above are typical stream forms, and we have found such normal stream inhabitants as sponges, caddisflies, and parnid beetles living with *S. interpunctatum.* The associations have been observed infrequently in the sand-bottomed lakes of Florida, although they are probably widespread. The finding of a lakeshore fauna that so closely resembles a stream fauna is reminiscent of the conditions found along some of the rocky beaches of northern lakes where the mayfly fauna is quite abundant. However, it seems apparent that only very tolerant forms can withstand the conditions prevailing along the lake margins in Florida. This situation is somewhat understandable when one considers the slight wave action, the scant debris along the shore, the complete absence of rocks or pebbles, and the small amount of vegetation.

SEASONAL DISTRIBUTION AND LIFE HISTORY. In a study of the life cycle of *S. interpunctatum* in a small stream in Indiana, McCafferty and Huff (1978) found three broods at different degrees of maturation at any one time of year. These broods emerge in early spring, midsummer, and late summer–early fall, respectively: the former two overwintering in different stages of larval development, and the latter completing development in one growing season in warm temperatures and maturing at relatively smaller sizes. The population possessed a complex life cycle ranging from one generation per year to three generations every two years.

In Wisconsin, Flowers and Hilsenhoff (1978) observed that *S. interpunctatum* may have separate flight periods when they noted that adults were present in June and August. The nymphs maturing in August were distinctly smaller than those maturing in June. It is possible, according to Flowers and Hilsenhoff, that the August nymphs were offspring of the June-emerging adults.

Unzicker and Carlson (1982) have indicated that *S. interpunctatum* probably emerges in late April through September in North Carolina and South Carolina.

In Florida, adults of *S. interpunctatum* have been collected throughout the year.

BEHAVIOR. The habits of this species are much the same as those of *smithae.* The nymphs are very tolerant and have been kept alive in aquaria in the laboratory for more than two months, during which time many specimens emerged. There is some difference, however, in the size of adults that emerged when the nymphs were first brought into the laboratory and those that emerged after one or two months under these conditions. The latter are somewhat smaller, having been dwarfed by confinement or by food that was not conducive to a full growth.

The subimago emerges in late afternoon after sunset, flies to a nearby support where, after 18 to 22 hours, the final molt takes place, and the adult is soon ready for mating.

The mating flight begins just after the sun has set and continues until darkness has fallen. We lost sight of the individuals in the swarm as darkness fell and, therefore, could not determine how long the flight lasted. The following description of swarming is taken from notes of April 1, 1939 (Berner):

> At 7:00 P.M. while standing on the bridge over Hatchet Creek, I noted several *S. smithae* females flying up and down the stream in the act of oviposition but could see no mating flight

> of this species. . . . While the *S. smithae* females were ovipositing, I suddenly noticed below me a bit of activity, which rapidly began to increase. It was becoming rather dark, but by shifting my position, I could see that this activity was caused by a group of *S. proximum* [*S. interpunctatum*] males in their mating flight. The swarm was small, composed of not more than twenty males. These insects flew up and down continuously; the upward flight was rapid, the downward slower, as though the insects were drifting. I paced off the horizontal distance covered by the swarm and found it to be almost negligible, not more than five feet, and this was not varied during the fifteen minutes which I observed the insects. At 7:15 it became so dark that further observation was impossible.
>
> Now and then, I saw a female that approached the swarm, entered it and coupled with a male, after which the two seemed to drift from the swarm and settle to the ground where I lost sight of them. The female could easily be distinguished by the brilliant orange eggs which showed clearly through the translucent abdomen. I swept my net through the swarm once and captured seven males and two females. The latter were probably in copulation with two of the males when they were interrupted, for as I lifted the females from the net, there remained behind two clumps of orange-colored eggs dropped by them as they came in contact with the cloth. The dropping of eggs is very likely correlated with mating, because females that have not mated will retain the ova. Yet if copulation is in progress or has been completed, the eggs are released on contact. All during the flight, the strong breeze which was blowing did not seem to disturb the flight of the imagoes.
>
> The minimum height of the flight of the swarm was between six and eight feet above the stream. The rise and fall of the males was between five and six feet. The females seldom rose as high as the males.

The pronounced difference in the flight of *interpunctatum* and *smithae* is in the great rise and fall of the males of the former species. The flight of other species of *Stenacron* has not been described; however, Smith (*in* Needham et al. 1935, pp. 72–73) has described the method of oviposition of one of the species, and since this has not been observed in *interpunctatum*, we repeat his observations:

> This individual, when I first saw her, was flying straight upstream, about five feet above the water, and was barely making headway against the evening breeze. On the underside of the abdomen she was carrying a fairly large mass of eggs, just as *Ephemerella* does. The eggs were of an orange or reddish color. Finally she settled down to the water and was carried downstream about a foot. She then flew up again but without the eggs. The individual was captured. She was spent, and the tip of the abdomen was still curved down, where it was fitted over the egg mass.
>
> Unfortunately no other females carrying eggs were captured; so I could not find out what happens to the mass when it is laid in water, but the eggs were equipped with two very long coiled threads, which probably adhere to the bottom and to other eggs.
>
> Mayflies belonging to this group are seldom seen in the early evening, but they may often be found later at lights. It therefore seems likely that oviposition usually occurs after dark.

On April 19, while living material that had been collected on April 6 was being examined, we found several *Stenacron* nymphs that were in either the first or the second instar. Although we are by no means certain of the identification, we believe that they were the young of *S. interpunctatum.* Because so few specimens were available, we will not attempt to describe the development. The eggs from which these nymphs hatched were probably brought into the laboratory attached to vegetation that was used as aquarium plants. The vegetation was not examined when first brought in, and it was not until two weeks later that we discovered young mayfly nymphs on a leaf. Even after such a short period of time in the laboratory, the aquarium was literally teeming with organisms, especially dipterous larvae, a few caddisfly larvae, and young snails, most of which had apparently hatched in the laboratory. The mayflies had been hatched long enough so that some had entered the second instar, as demonstrated by the presence of gills. These nymphs differed from the first instar of *Stenonema smithae* in that they were reddish brown, while the *smithae* nymphs were white. For three more weeks some of the nymphs remained alive; but very shortly after this, all had disappeared. Growth during these three weeks was rapid: the nymphs developed additional gills and more spines on the femora; the caudal filaments elongated; and the thorax became much more robust.

Stenonema Traver

Bednarik 1979, pp. 190–191.
Bednarik and McCafferty 1979, pp. 1–7.
Berner 1950, pp. 57, 59; 1959, pp. 52–53; 1977, p. 28.
Burks 1953, pp. 154–155.
Edmunds, Jensen, and Berner 1976, pp. 202–205.
Koss and Edmunds 1974, pp. 317–318.
Lewis 1974 (1978), pp. 1–11.

In 1933 Traver reviewed the Heptageniidae of North America and erected *Stenonema* to include those species that were formerly placed in *Ecdyonurus* and some that were formerly considered to be *Heptagenia*. After studying the type species of *Ecdyonurus*, she decided that this genus did not occur in North America but was confined to the "Old World."

In general, male adults are easily distinguished from other Heptageniidae; but the difficulties involved in generic placement of females are much greater because there is much overlapping of characters. Generally, it is easiest to identify females generically by associating them with males collected at the same time. The threadlike seventh gills of the nymphs easily set them apart from the nymphs of other mayfly genera, except for *Stenacron*. Color differences and color patterns of adults are highly variable in some species, and individuals collected from the same place and at different times may appear to be different species, although they are in reality nothing more than variants of the typical form. Recent studies by Bednarik and McCafferty (1979) have demonstrated that in many cases nymphs can be identified to species either morphologically or by color patterns.

Traver divided *Stenonema* into two groups on the basis of genitalia and by the use of wing venation; nymphs of the two groups were separated by gill structure. Jensen (1974) decided that differences were significant enough to separate them into two genera, *Stenonema* and his new genus, *Stenacron*.

Stenonema is one of the largest genera of mayflies in North America. According to the review of the genus by Bednarik and McCafferty (1979), only one species, *S. terminatum*, is known to occur in the western part of North America, where it is "found primarily in the Snake River drainage and also known from Wyoming, Utah, and northeastern Nevada." Many species of *Stenonema* occupy almost all available situations in the Ap-

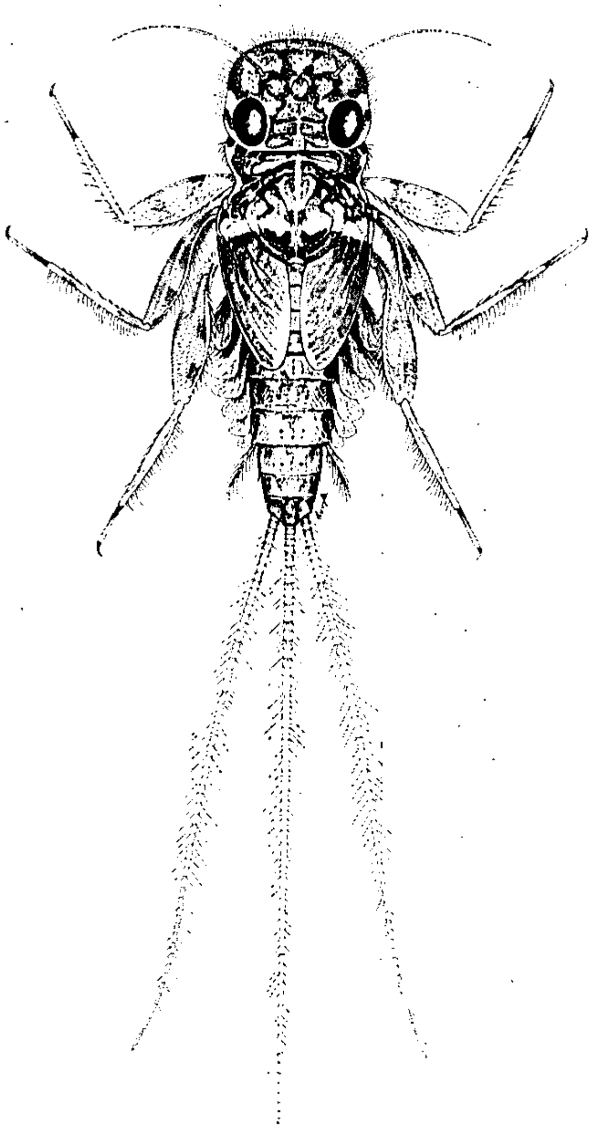


Plate 8. *Stenonema exiguum* Traver, nymph

palachian Province, which is the ideal region for their development. Although other heptageniid mayflies occur in the mountains, *Stenonema* is the one most frequently found. The ecological adaptability of the species in this genus has contributed greatly to its successful invasion of the streams and lakes of the Coastal Plain.

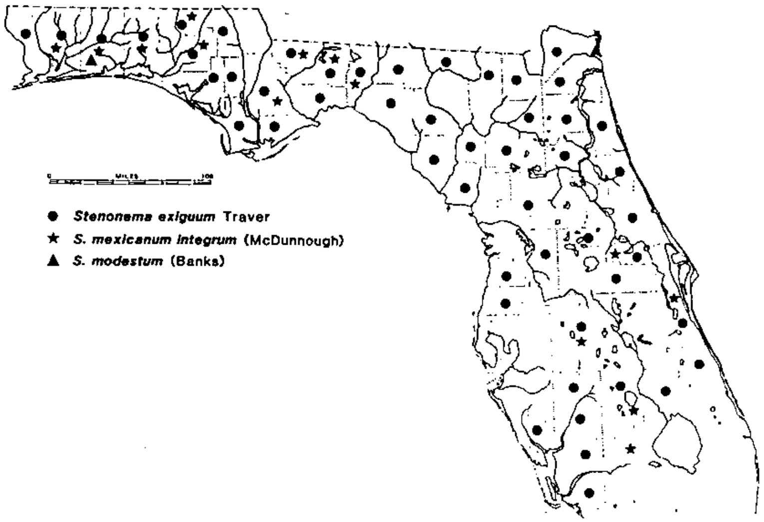
Stenonema exiguum Traver

(PLATE 8. FIGS. 53, 102. MAP 13)

Berner 1950, pp. 70–73; 1958, p. 30; 1977, p. 29.
Cowell and Carew 1976, pp. 589–591.
Jones 1977, p. 66.
Lanquist 1953, pp. 24, 27, 40, 42, 53, 62, 63, 66.
Lewis 1974 (1978), p. 22.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 204.
Schneider and Beck 1963, p. 110.

TAXONOMY. *Stenonema exiguum* can easily be distinguished from the other Florida species *S. smithae*, *S. modestum*, and *S. mexicanum integrum* by the characters set forth in the key. In her description, Dr. Traver suggested that *exiguum* is close to *S. mexicanum integrum*; however, Bednarik and McCafferty (1979) show that the two species are easily separated on the basis of the presence of the longitudinal middorsal lines on abdominal terga 3 and 6 of *S. m. integrum*. The original description of *exiguum* included only the male and female adults. The nymphal stage was described by Daggy (1945) from specimens collected from the Mississippi River in Minnesota. The type specimens were collected near Woodlawn, North Carolina, at the Chattahoochee River, Atlanta, Georgia, and the Etowah River at Rome, Georgia.

GEOGRAPHIC DISTRIBUTION. In Florida *S. exiguum* is known to occur from Lee County in the south to as far north and west as the Georgia and Alabama state lines; eastward, the species has been found in Clay County (map 13). Records from Mobile County, Alabama, and the Satilla River in southeastern Georgia are also at hand. The distribution of *S. exiguum* parallels that of *S. smithae* and is almost identical with it except south of Alachua County. The close resemblance of the nymphs of the two species makes determination of very young specimens rather difficult, unless mouthparts are removed from each one. For this reason some of the individuals we have referred to *exiguum* may possibly be *smithae* or *modestum*. We have a series of adult *Stenonema* from Hillsborough County, but none is identifiable as *S. smithae* or *modestum*—a circumstance that leads us to believe that *exiguum* and *mexicanum integrum* are the only *Stenonema* in the southern part of the peninsula. We have been unable to confirm Cowell and Carew's finding (1976) of nymphs of *S. smithae* during their stream drift studies in Hillsborough County.



Map 13. The distribution of *Stenonema exiguum*, *S. mexicanum integrum*, and *S. modestum* in Florida.

The distribution of *exiguum* is interesting because the species is known from so broad an area of North America, ranging over the central part of the United States and into southern Canada (Bednarik and McCafferty 1979). Its distribution suggests that it originated in the Mississippi River drainage and then spread outward from there.

ECOLOGY. Ecologically, the species is very similar to *S. smithae* and *S. modestum* except in two respects. In the first place, nymphs in west-central and north-central Florida are very seldom found in smaller streams, but they are very numerous—probably outnumbering *smithae* and *modestum*—in the larger creeks and rivers. The sites occupied within the inhabited streams are, however, identical with those of *smithae* and *modestum*. Second, nymphs have been collected from sand-bottomed lakes, a habitat in which *smithae* and *modestum* have never been found. One specimen was brought from a depth of 15 feet by means of an Ekmann dredge, but it was dead when collected. However, it was in a very good state of preservation; so death must have occurred either just before collection or during collection because of an injury suffered in the dredge, although there were no external manifestations of such injury. Generally in upper peninsular Florida nymphs are not found in lakes; but as there is a small, slow-flowing stream entering the lake it is possible that the nymph was washed in shortly after death.

Mr. Richard W. Cantrell of the Florida Department of Environmental Regulation has made some very interesting observations regarding the occurrence of *S. exiguum* and *S. m. integrum* in south Florida. He speculates that there is a mutual exclusion existing between the two species as he and his colleagues have not found a site in which both species occur. In a letter (to Berner, dated April 4, 1980) he commented, "As an example, Lake Arbuckle and Lake Istokpoga are connected via Arbuckle Creek; *S. integrum* inhabits the Cypress lined shores of both lakes but has not been collected in the stream, *S. exiguum* on the other hand is found in the stream but not on the lake shores." In a subsequent letter (dated August 1, 1980), Cantrell stated, "I would be most interested in your thoughts as to what I might look for regarding the apparent mutually exclusive distribution of *Stenonema exiguum* and *S. integrum*. . . . Routine water chemistry and physical parameters apparently are not the entire answer based on the data which I have collected. The lack of perennial flow I believe accounts for the absence of *S. exiguum* at the sites from which *S. integrum* is routinely collected. What I can not adequately explain is the absence of *S. integrum* from streams supporting *S. exiguum* especially since Phil Lewis has informed me that these two species frequently coexist in Ohio River basin streams. Could *S. exiguum* out compete *S. integrum* by some mechanism for the limited Heptageniid habitat available in our South Florida Streams?" We still have no satisfactory answer to the enigma of apparent mutual exclusion.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Emergence of *S. exiguum* is year-round, based on collection of adults or mature nymphs. This year-round emergence occurs both in peninsular Florida and in the panhandle.

The life history of the species does not differ essentially from that of

S. smithae except that we have found the subimaginal period to be somewhat shorter, lasting from 17 to 20 hours. We have observed no mating flights of *S. exiguum*.

BEHAVIOR. The behavior of *S. exiguum* nymphs appears to be no different from that of *S. smithae* and *modestum*. In the field, mature *exiguum* nymphs can be differentiated from other Florida species of *Stenonema* by the presence of a rather broad yellowish brown band across the mesonotum.

Stenonema mexicanum integrum (McDunnough)

(MAP 13)

Allen and Cohen 1977, p. 411.
Bednarik and McCafferty 1979, p. 19.
Berner 1959, p. 52.
Burks 1953, p. 176.
Flowers and Peters 1981, p. 152.
Lewis 1973, p. 68; 1974, p. 25.
McCafferty 1984b, p. 125.

TAXONOMY. Lewis (1974a) and Bednarik and McCafferty (1979) comprehensively discussed the taxonomic history of *Stenonema mexicanum* (as *Stenonema integrum*). In a recent paper on the relationships between North and Middle American *Stenonema*, McCafferty (1984) synonymized *S. integrum* (McDunnough) with *S. mexicanum* (Ulmer) and designated subspecific status for Nearctic and Neotropical populations of this species as *S. m. integrum* and *S. m. mexicanum* respectively.

Stenonema mexicanum is classified under the subgenus *Maccaffertium*, and the adults are characterized by their distinctively small and rounded penes, similar to those of *S. exiguum*, prominent middorsal longitudinal lines on abdominal terga 3 and 6, and somewhat elongate cells distal to the bulla region of the forewings. The pale, V-shaped, dorsal pattern on the abdomen, the low number of spinelike setae, and the high number of hair setae on the maxillary crown are diagnostic for the nymph.

The two subspecies, besides being geographically disjunct, can provisionally be separated in the adults by the presence of dark brown pleural stripes in *S. m. mexicanum* which are absent in *S. m. integrum*. We agree with McCafferty that no consistent morphological characteristics have been found to allow us confidently to separate the nymphs of the subspecies.

GEOGRAPHIC DISTRIBUTION. According to McCafferty (1984), *S. mexicanum integrum* evidently originated in the Appalachian area relatively recently (probably no older than Pleistocene). The species is widespread in the midwestern and southern United States southward to the Central American Neotropics. In Florida, the species has been collected in the following counties (map 13): Gadsden, Glades, Highlands, Leon, Liberty, Okaloosa, Polk, Santa Rosa, Walton, and Washington.

ECOLOGY. The nymphs of *S. mexicanum integrum* are relatively pollution tolerant and seem to prefer large, deep rivers (Lewis 1974). Lewis collected the nymphs in great abundance below sewage outfalls of the Ohio and Mississippi rivers. The species belongs to that category of widely adapted species ranging through most humid regions (McCafferty and Provonsha 1978).

In Florida, although the nymphs of the species have been sporadically collected in the peninsular and northern sections of the state, they are found in greater numbers in the Apalachicola and Blackwater rivers. The nymphs occur in a wide variety of habitats, which include gravel, rubble, slabs, and leaf litter trapped between rocks, submerged logs, and roots of vegetation along river banks in north Florida. In south Florida, as reported to us by Mr. Richard Cantrell, they live on debris of the cypress tree–lined shores of lakes (see *S. exiguum* for a fuller discussion).

SEASONAL DISTRIBUTION AND LIFE HISTORY. In Wisconsin, Flowers (1978) occasionally collected the nymphs in the Wisconsin River until late June when large numbers of mature specimens ready to emerge suddenly appeared at the water's edge. Emergence of the species in North and South Carolina occurs in late March through September (Unzicker and Carlson 1982), with peak emergence in the South Carolina Piedmont area from April through mid-May (Carlson 1971). Carlson observed that emergence took place from late morning to late afternoon, and oviposition from early afternoon until after sunset. Except for reared adults which emerge anytime of the day and individuals collected at light traps, the emergence pattern of *S. mexicanum integrum* has never been observed in Florida. Collection records indicate that both the nymphs and the adults of the species occur throughout the year in the state. The number of generations per year remains to be investigated.

BEHAVIOR. The adults of *S. mexicanum integrum* are positively phototactic, as hundreds of individuals had been collected at light traps operated at the Blackwater River. Like other *Stenonema* species, the nymphs of *S. m.*

integrum are collectors (gatherers). Dissected nymphs revealed the gut contents as being composed of fine particulate organic materials and a few sand grains.

Stenonema modestum (Banks)

(MAP 13)

Bednarik and McCafferty 1979, p. 29.
Berner 1959, p. 52.
Burks 1953, p. 52.
Koss 1968, p. 706.
Leonard and Leonard 1962, p. 111.
Lewis 1974a, p. 30.

TAXONOMY. The recent revisions of the genus *Stenonema* by Lewis (1974a), and Bednarik and McCafferty (1979) include excellent taxonomic reviews of *Stenonema modestum* (Banks). Occurrence of this species in Florida is still quite dubious because through all the years of collecting in the state only three male imagoes have been recorded, and there are, as yet, no nymphal collections. Nevertheless, we are including a discussion of the bionomics of the species in the event the record is confirmed.

Stenonema modestum is a member of the subgenus *Maccaffertium.* The male imagoes are characterized by the following combination of characters: (1) presence of two or three crossveins in each of the first three bulla interspaces in the forewings, and (2) abdominal tergum 8 has a median, longitudinal, pinkish brown shading. The nymphs have more than 30 crown hair setae on each maxilla; and abdominal sternum 8, and occasionally 7, has an anteromedian brown area, sometimes expanded to a crescent-shaped, dark brown maculation.

GEOGRAPHIC DISTRIBUTION. *Stenonema modestum* has a wide geographic range occurring from the Midwest to the eastern United States and northward to southeastern Canada. In Florida, the species has been collected only in Aedes Creek, a small tributary of the Blackwater River in Okaloosa County (map 13).

ECOLOGY. The nymphs of *S. modestum* are found in shallow streams of various sizes with moderate to swift current. In Michigan, the nymphs have been collected in shallow water on gravel, bedrock, and rubble substrate (Leonard and Leonard 1962; Bell 1969). The nymphs have never been collected in Florida.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Except for the three imagoes that were collected in mid-March, knowledge of the seasonal distribution and life history of the species in Florida is unknown. In two streams in the Coweeta Experimental Forest in the mountains of western North Carolina, Tebo and Hassler (1961) found that the nymphs of *Stenonema modestum* (Banks) (as *S. annexum*) along with *Stenacron carolina* (Banks) and *Stenonema pudicum* (Hagen) reached peak numbers during September, October, and November. Collection records indicate that the emergence period of the species in its northern geographic range occurs in April through August. In its southern range emergence apparently is not as seasonal, because adults have been collected in Georgia during March, June, July, September, and November.

BEHAVIOR. Knowledge of the behavior of the species is limited. The three male imagoes were collected from a small swarm in Aedes Creek at 7:00 P.M.

Stenonema smithae Traver

(PLATE 9. FIGS. 23, 52, 90, 101, 113, 165. MAP 14)

Bednarik and McCafferty 1979, pp. 38–39.
Berner 1950, pp. 58–70; 1958, p. 30; 1977, p. 31.
Cowell and Carew 1976, p. 590.
Jones 1977, p. 66.
Landa 1969, p. 291.
Lewis 1974a, p. 34.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 204.

TAXONOMY. While she was on a short collecting trip through several states in the southeast, Dr. Traver discovered *Stenonema smithae* in west-central Alabama near Tuscaloosa. She described the male, the female, and the nymph. We have found that the Florida insects agree fairly well with the description except that in the adults there is often an orange coloration on the vertex in the majority of specimens. Traver failed to mention the condition of the mouthparts of the nymphs, but it has been found that the structure of the maxillae is one of the easiest characters to use in separating *S. smithae* nymphs from those of *S. exiguum* and *S. mexicanum integrum*. Adult *smithae* are easily distinguished from other Florida species—except for *modestum*—by the presence of stigmatic spots or the lack of

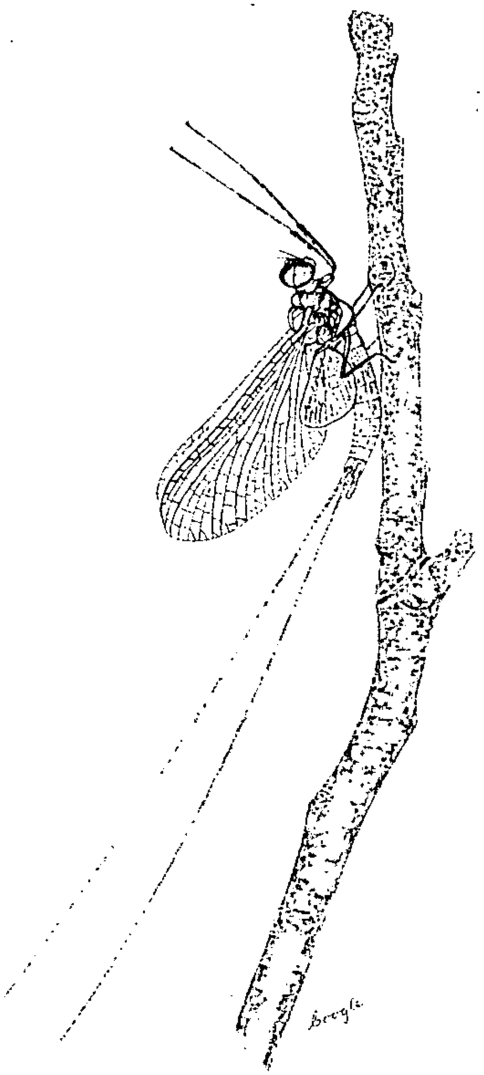


Plate 9. *Stenonema smithae* Traver, male imago

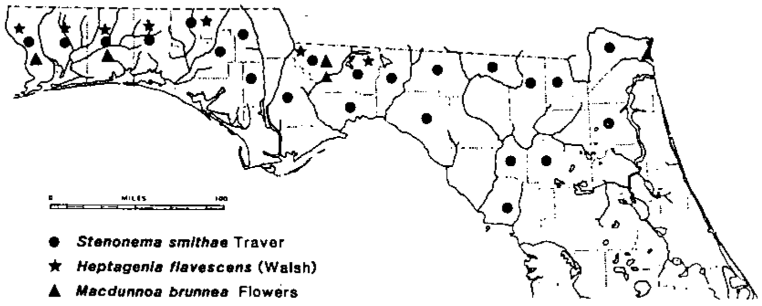
middorsal abdominal stripes, by the shape of male genitalia, and by the pattern of crossveins in the forewings.

Bednarik and McCafferty (1979) consider *S. smithae* to be closely related to *S. modestum*, and they speculated that it may represent a species in "statu nascendi." For some time we debated the desirability of treating the species separately or synonymizing them; however, we concluded that until additional specimens of those we are calling *modestum* are available, we would not take the latter action.

GEOGRAPHIC DISTRIBUTION. *S. smithae* is one of the commonest stream mayflies in Florida, but it appears not to be distributed south of Alachua County, although we have Cowell and Carew's (1976) record of the species being taken in stream drift in Blackwater Creek, Hillsborough County (map 14). We have been unable to confirm their identification, but as no specimens of *smithae* have been collected by us in the region, we are assuming that the species is restricted to northern Florida, where all flowing waters we have examined have populations of *S. smithae* nymphs. Although Bednarik and McCafferty's map (1974, p. 39) shows *S. smithae*'s range extending into south-central Florida, our records do not substantiate such a distribution.

The species is known only from the Coastal Plain, although it is possible that it passes beyond the Fall Line into the Piedmont. Winged insects such as mayflies could easily surmount such an obstacle and enter the streams of the Piedmont (at least in the lower region), provided they are ecologically suitable. We have specimens from the following Florida counties: Alachua, Baker, Bay, Calhoun, Clay, Columbia, Escambia, Gadsden, Gilchrist, Hamilton, Holmes, Jackson, Jefferson, Leon, Levy, Liberty, Madison, Nassau, Okaloosa, Santa Rosa, Taylor, Wakulla, Walton, and Washington.

ECOLOGY. In the parts of Florida where *S. smithae* occurs, almost any constantly flowing brooklet, creek, or river will have nymphs in it. The insects can be found on various submerged objects that are at least partially anchored in the streambed, including submerged logs, sticks, leaves, rocks, pebbles, and even aluminum cans. In the sand-bottomed creeks where there are broad expanses of almost barren sands, no nymphs are found; but if there is, by chance, a log in midstream, the underside is almost certain to have these nymphs on it. A board partially buried in the sand where the current slackens may harbor as many as 15 to 20 nymphs, the majority being rather young. Stones, likewise, will support a fair number on the darkened, protected undersurfaces. Many immatures can also be



Map 14. The distribution of *Stenonema smithae*, *Heptagenia flavescens*, and *Macdunnoa brunnea* in northern Florida.

found among leaf drift that accumulates in the slowly flowing water or becomes entangled in submerged branches and vegetation. Frequently, but in no wise so commonly as on more solid supports, nymphs occur on vegetation; however, the immatures are not well suited to such a situation and apparently shun it whenever a better place is offered.

Size of the stream offers no obstacle to *smithae* nymphs, as is indicated by their presence in permanently flowing water that is no more than two inches deep and one foot across (at low water), as well as in large rivers such as the Suwannee. Rate of flow is likewise not of particular importance, for in Florida the nymphs occur in waterways that are almost stagnant as well as in the most rapidly flowing streams, of which the Santa Fe River is one of the swiftest. In the Santa Fe the nymphs are numerous on the undersides of the rocks that are strewn over the streambed, but they are much less numerous on *Vallisneria* and other vegetation that form huge mats. At Poe Springs, the current of the Santa Fe is very rapid. Nevertheless, the nymphs are very common even in the swiftest water; at the shore, where the flow becomes negligible, immatures are almost as numerous as in the rapids. Depths to which the nymphs descend, as far as we have been able to determine, are somewhat limited by the materials available for support and the amount of flow, but it is likely that the nymphs do enter deep water in the larger rivers.

We have found on many occasions that nymphs had occupied areas where the current was rather strong at high water; but as the level of the stream fell and the movement of the water became less vigorous, the nymphs did not migrate into the swifter parts but remained in the almost stagnant portions left behind by the receding flood. In some cases nymphs were even found to be isolated in small pools cut off from the main stream, and here they lived on leaf drift and other debris that accumulated in the bottom of the pool.

Because of wide limits of tolerance, *smithae* nymphs adapt to many and varied conditions, allowing them to become the most frequently encountered mayfly nymphs in the streams of northern Florida. The nymphs are very little, or not at all, affected by pH: we have found them inhabiting a swampy, slow-flowing body of murky water with a pH somewhat below 4.0, as well as in a clear, sand-bottomed spring run with a pH of 7.8. Even though this is not as wide a range as that occupied by *Callibaetis floridanus*, it is certainly far beyond that of most mayfly species. Likewise, temperature does not seem of great importance: nymphs are known to inhabit water with a temperature of 30°C as well as water where ice forms at times in the quieter portions. Because of the wide ecological valence of *smithae*, it does not appear logical that the species should stop its southward range at Alachua County, but that seems to be the case. One can readily see that stream mayflies could not normally inhabit the canals of southern Florida; however, the clean, sand-bottomed creeks of Hillsborough County are not essentially different from those of north-central Florida, yet we have no confirmed reports of the species occurring there.

The small, pebbly riffles in the sand-bottomed creeks of north-central Florida, and to some extent in northwestern Florida, also afford an excellent collecting place for nymphs of *smithae*. The nymphs tend to congregate in such places because conditions, from the standpoint of food, are excellent, the current is as swift as can be found in the stream, and although predators are rather numerous, the nymphs are still well protected. Young nymphs seem to predominate in the riffles, but this is not always the case and frequently older specimens will be the only ones taken.

At one time or another almost every Florida species of mayfly has been collected in the same streams as *S. smithae* except *Hexagenia orlando* and *Callibaetis floridanus* (south Florida form). In its favored haunt on submerged logs and boards only a few species are present along with *S. smithae*. These include *Stenacron interpunctatum, Stenonema exiguum, Baetis propinquus, B. pygmaeus, Pseudocloeon alachua*, and *Tricorythodes albilineatus*. The *Stenonema* and *Stenacron* nymphs are the only ones that occupy the undersurfaces of the supports to any extent; the others tend to remain on the sides or on the upper surface. In leaf drift, the leptophlebine mayflies are found in addition to *Baetis* species.

SEASONAL DISTRIBUTION AND LIFE HISTORY. We have collected or have records of adults for each month of the year in some part of Florida. With its year-round emergence there is actually no period that reflects seasonality in this species. Dr. Peter Grant, while studying mayflies in northwestern Florida, kept records of adult collections at Burnt Mill Creek in Jefferson County. During 1980 when he sampled throughout the year, he took adults from April through November. He also worked at this stream in 1979 from June through December and found adults in each of the months except December. He collected no adults during his sampling period of January through June in 1981. We believe that a greater preponderance of adults may occur during the summer months. Emergence slows down during cold snaps; as soon as warm weather returns, the adults begin to appear once more. Nymphs of all ages can be collected from any one stream at any time of the year, and there is no tendency toward forming broods. Of course, since temperatures are slightly more uniform and higher in north-central than in northwestern Florida, there is a greater amount of emergence in the former section during the winter months because of the longer warm spells. The specimens collected in Alabama by Traver were taken during July and offer no indication of seasonal range in the more northerly part of the geographic area occupied by *smithae*.

We have attempted to rear this species from the egg several times, but in every case the nymphs died a few days after hatching. To get the eggs to hatch was simple; to go much beyond this stage was another matter. The crux of the problem is probably the food supply. Introduction of food invariably introduces other organisms, and once these are present they seem to multiply at such a rapid rate that the competition offered by them was too much for the delicate mayfly nymphs under our laboratory conditions.

The surest method of securing *S. smithae* eggs that are reasonably certain to hatch is to capture ovipositing females and force them to continue oviposition in dishes containing small amounts of water. The eggs are liberated in small masses as the female dips her abdomen and lightly touches the surface of the stream. After liberation, the ova settle to the bottom where they absorb water which causes a jellylike substance to swell about each ovum, forming a transparent protective covering that is also adhesive. It may be of some significance that unfertilized eggs take anywhere from a few minutes to several hours to form this jellylike covering, but if the eggs are fertilized, the covering forms within five minutes of deposition of the ova.

The eggs, either aerated or not and kept in shallow dishes of water, hatched in the laboratory over a period varying from 11 to 15 days. These figures include the earliest and latest hatchings observed in the eggs of three females. Because the eggs were accidentally mixed when collected, we were unable to determine to which female the earlier- and later-hatching eggs belonged. Our first attempt at hatching eggs of this species was fairly successful, although the females we secured were nearly spent and contained only a few eggs in the anterior portion of the body; however, these were fertilized and a number of nymphs hatched within approximately 14 days. Later we collected females that had just begun oviposition and were completely filled with eggs, from which hundreds of nymphs hatched.

These last eggs were deposited on October 5. They were examined on October 15, and it was found that nearly every one contained an almost fully developed nymph coiled within. The first hatching was noted exactly 270 hours and 13 minutes after oviposition. Hatching continued for 4 more days, with a peak occurring at about 12 to 13 days after laying.

The movements of the nymph within the chorion as it tries to escape are very clear and easily observed. There is a forward, backward, and sideways motion of the head as though the insect were scraping the egg burster against the eggshell; however, very little action occurs in the tightly coiled, more posterior portions of the body. We observed this movement within individual eggs lasting as long as two days, with the final liberation of the immature after this period.

Finally, the egg ruptures along its longitudinal axis, and the nymph emerges. The exit is rather slow and arduous. The first part of the body to pass from the shell is, of course, the head. As it is pulled, or rather pushed, the chitin of the insect yields in the median region much as cellophane does when it is stretched. As the head is pushed out, the thorax gradually squeezes through, giving here and there to accommodate the narrow opening in the chorion. It is rather surprising that the opening is so small, because it provides quite an obstacle to the rapid hatching of the nymphs, which would seem to be a prerequisite of the habitat in which the insects dwell. However, this slow hatching may be a condition peculiar to laboratory-reared individuals. Information gleaned from other authors indicates that this slowness is not confined to *smithae* nymphs. Soon after the thorax—or at least the anterior two-thirds—is freed, the antennae pop out and are immediately extended. The wriggling motion increases, and the body begins to swing from side to side as sufficient mass is freed to give some force to the movement. At the same time, a series of waves, created by intense muscular exertions, passes along the body. The abdomen is soon entirely free of the shell, the middle legs are suddenly released, and the caudal filaments are drawn out. The other two pairs of legs are then withdrawn. The legs appear to be held together by some sort of adhesive; it is only by the greatest effort on the part of the nymph that the legs are separated from each other. They are extended straight out from the body, but the insect is still unable to bend them. Soon a tremor passes through the nymph, and all the legs are flexed simultaneously. The nymph immediately becomes active and scrambles away from the shell, pulling the remainder of its tails free. The time required for hatching in the specimens observed varied from 3 to 10 minutes from the time the head appeared through the slit in the chorion until the caudal filaments were entirely free. Laboratory hatching occurred just as frequently during any part of the day or night.

The newly hatched nymph is very similar in appearance to that of *Stenacron interpunctatum canadense* illustrated by Ide (1935). The anterior part of the alimentary tract is filled with yolk, and the nymph can survive on this material for as long as two days. The most noticeable part of the insect is its enormous head with the five eyes, the only really dark part of the body.

Thigmotactic and phototactic responses are present when the nymphs are hatched, and the immatures can be seen both running about seeking darkened places and clinging tightly to the objects on which they are situated. The young nymphs, like the more mature insects, move readily backward, sideways, or forward, according to the direction of the stimulus.

Mayfly nymphs, immediately after molting, are very pale, almost white. Molting was observed in *smithae* nymphs at 1:45 P.M. By 4:00 P.M. melanization had occurred to such a great extent that the nymph was almost back to its normal brown color. By 5:30 P.M. full coloration was achieved.

We have observed the mating flight of this species on many occasions, and each time it was essentially the same. Just before dusk, a small band of approximately 10 to 20 males gather directly over a stream—whether it be small or large makes no difference. The characteristic flight is then begun about 12 to 15 feet above the water. The horizontal flight is slight; the vertical rise and fall is about two feet. A flight was observed in May at 7:00 P.M. and in early July at 8:00 P.M.; in early spring we watched one begin at 6:15 P.M. (all times were EST). There seems to be an intimate correlation between amount of light and the time at which the swarming takes place. The length of time that the flight lasts was not determined because the insects were still flying when darkness fell. Since the females begin to oviposit while it is still light, it would seem that mating ceases either very shortly before dark or soon thereafter.

The forward flight of the males was not much over 8 to 10 feet, with a rapid return to the original position. Occasionally a female would fly into the swarm and be immediately seized by a male. These two then separated from the swarm and were usually lost to sight; some were seen settling to the ground where they soon separated, the male returning to the swarm, the female flying off to oviposit. H. G. Cooke (1940, p. 13) made an interesting observation on the copulatory approach of the sexes of *S. vicarium* during flight:

> Females showed very little tendency to take part in the flights. The captures of two complete companies of imagoes and the greater portion of a third yielded only one female, which was taken with the second group. It is probable that this female had just entered the swarm from beneath, because when a single female was seen passing below a company of males it was seldom disturbed; on the other hand, when it passed a few feet above or directly through the swarm, it was instantly attacked by them. The large eyes of the males are situated on the dorsolateral regions of the head . . . , a location which perhaps enables this sex to see females above them better than below. All attempts to mate were made by the male flying up beneath the female placing his forelegs over her prothorax and head. With upcurved abdomen he grasped the body of the female with forceps near her seventh abdominal segment . . . and mating thus became effective.

Observations on the oviposition of the females were made often by us. The insect flies low over the water, about 6 to 12 inches above the surface. At intervals, the abdomen is touched to the surface where the current is rather noticeable. The action resembles that of a dragonfly or damselfly. The ovipositing flight, for the most part up and down but occasionally cross-stream, is not composed of pronounced risings and fallings such as take place during the mating flights but is in a straightforward direction. The eggs are released, a few at a time, until the female is spent, when she flies to some low-hanging bush. The horizontal flight may cover a distance varying between 20 and 50 feet, oviposition occurring both on the downstream and return flights. We did not determine the entire time required for release of the ova, but it must not take much more than 5 to 10 minutes, because spent females were collected before darkness had fallen completely.

The urge to oviposit is very great. During a heavy downpour we observed, and later captured, a female in oviposition flight. Seemingly she dodged between the raindrops. Certainly, if one had struck her, the flight would have immediately ended.

An interesting note concerning the manner of oviposition of other mayflies related to *smithae* was given by Dr. Osgood Smith (*in* Needham et al. 1935) when he observed that stream forms have an oviposition flight which is not greatly different from the mating flight; however, in the lake species "there was no up and down dance, but there were occasional pauses and then sudden starts, somewhat after the manner of a dragonfly. Once in a while a female would slow up a bit and dip her abdomen in the water without actually alighting, and sometimes she would alight on the water for just a moment." From this habit there would seem to be a close relationship between the lake-dwelling *Stenonema* species and the stream forms of the Coastal Plain, but if one refers to the morphological characters, such a relationship is not so evident.

Emergence of *S. smithae* subimagoes occurs in the late afternoon at approximately the same time as the mating flight. We have often taken subimagoes rising from the stream at the same time that mating flights were in progress. The nymph, when preparing for transformation, floats freely at the surface of the water. The thoracic skin then splits suddenly and the subimago appears. The actual emergence takes only a few seconds. With almost no rest, the insect rises and flies upward until out of sight (unless there is some support nearby); the flight is never horizontal but always upward at a moderate incline. After 20 to 24 hours, the imaginal molt occurs. Female imagoes may live for about 2½ days.

An interesting point concerning the eyes of *S. smithae* relates to mating males, that is, those taken during a mating flight, when the eyes are black. Laboratory-reared males kept in the dark will have black eyes; when they are exposed to light for a short while, the eyes become pale, but this change is gradual and, in laboratory-reared insects, may take as long as 40 minutes. Lyman observed similar color changes in *Stenonema* in 1943.

BEHAVIOR. *Stenonema* nymphs can be identified at a glance among Florida specimens. Their flattened bodies, broad, flat heads, and spreading legs are characteristics shared by no other genera in the state, except *Stenacron* and *Heptagenia*. However, the habitude of the nymphs does not easily separate *smithae* from other Florida species of the genus. When morphology and coloration are employed, *exiguum*, *m. integrum*, and *smithae* are easily differentiated, but *modestum* and *smithae* are not.

If a board, rock, or other object on which the nymphs are living is rapidly lifted from the water and the underside examined, a mad scrambling will be observed as the nymphs of *Stenonema* seek to return to the seclusion of their underwater home. The draining of the water from the support causes the nymphs to cease moving, and detection of the immatures then becomes rather difficult. If a little water is dashed over the object, the nymphs again begin to run about. Very few of them actually reach the rim of the support and drop off, although some do successfully escape in this manner.

Swimming motions are very awkward, and it is obvious immediately that *Stenonema* nymphs are certainly not adapted to a free-ranging existence. Though they can swim only forward, the nymphs can walk in almost any direction with equal ease—forward, backward, and sideways. An undulating motion is the driving force in swimming—the head is first depressed and the wave travels along the abdomen to the caudal filaments, which lash out with little effect because they are almost devoid of long hairs such as those that make other nymphs such efficient swimmers. The swimming act never carries the insect very far, and after a few strokes the nymphs settle on any object that comes within reach, whether it is animate or inanimate. The swimming speed of *smithae* nymphs cannot compare with the rapidity of its crawling movements when underwater. It is almost impossible to seize the nymphs with forceps without injuring them when they are attached under water. It is obvious that the ability to crawl rapidly should naturally be greatly accentuated over the ability to swim as an adaptation for a clinging life.

One of the most characteristic behaviors of a *Stenonema* nymph is its strong thigmotactic response. The slightest contact with an object in the water will cause the nymphs to fasten their claws immediately and to hold on "for dear life." Of course, such tenacity is necessary when the nymphs are exposed to the strong currents that, at times, must sweep under rocks in midstream, disturbing both the boundary layer and the relatively quiet zone beneath the rocks. Even though the nymphs may be taken from almost stagnant water, thigmotactic responses are as strongly developed in them as in nymphs living in the swiftest water. The reaction is so strongly developed that if several nymphs are placed together in a dish of water with nothing to which they may cling, they will form a clump and remain clumped until some more attractive object is placed with them. The tenacity of the nymphs is shown by their reluctance to release their hold when the object to which they are clinging is lifted from the water. An inexperienced collector frequently injures the nymphs by attempting to pull rather than lift the insects from the support to which they are holding.

Wodsedalek (1912a, p. 35) found in experimenting with nymphs of *Stenacron interpunctatum* that the desire for contact is so strong that they are not fully satisfied until even the dorsum is in contact with some object. To quote him directly:

> Two long bricks were placed one over the other in a basin of water and between them small pebbles varying in size so that the space gradually varied in thickness from one end to the other. Then a large number of nymphs were put in the water, and after a short time it was found that nearly all of the specimens were attached to the lower surface of the upper brick with their dorsal side downward, and a large majority of the specimens were in that portion of the wedge-shaped space where their backs came in contact with the brick below.

The same author showed that the taxis is so strong that only when the water in which the nymphs live was heated to 45°C did the insects leave the stones to which they were clinging; and this happened only after the nymphs had been overcome by the heat.

Reaction to light is very strong in the nymphs of *Stenonema;* they readily react to changes in intensity, moving away from light. In a simple experiment, a stone was placed on a white background in a dish of water and another on a dark background; the nymphs were released on the former stone. After a few hours, nearly all the nymphs had migrated to the darkened area, where they remained; none returned to the stone with the white background.

Wodsedalek (1912b, p. 260), during his research on Palmen's organ, found that the supposed reaction to light is in part a result of orientation, and he concluded:

> In their natural habitat they are always found clinging to the under surfaces of small rocks, and this same position is regularly assumed by all normal ones in the aquaria of the laboratory. When a stone, to which the specimens are attached is inverted in the water, the insects soon make for its under side, many of them doing this as the stone is being turned over. This is also true of normal specimens in the dark-room, and

> hence it is obvious that this tendency of the nymphs to cling to the lower surfaces of rocks, with their dorsal side downward, is not due entirely to their negative reaction to light. It is unquestionably due, in part, to a definite power of orientation independent of phototaxis.

The imagoes are slightly phototactic, more so in the subimaginal stage. The amount of reaction to light seems also to be linked with temperature, for on cool nights none were attracted to our lighting sheets, although adults were known to be on the wing. On mild nights in midsummer when temperatures are high and adults are active, many are attracted to lights.

As might be expected, the nymphs' food consists almost entirely of multicellular plants. There are a few diatoms scattered among the materials in the alimentary tract, but filamentous algae, epidermis of living and dead plants, and various unidentifiable substances predominate. We have been able to keep nymphs alive and in apparent good health in aquaria in which *Vallisneria* leaves were placed. These were covered with diatoms and small algae; on the other hand, aquaria in which only decaying leaves were put also contained a sufficient food supply for the developing nymphs, and they reached adulthood without difficulty and were of normal size.

Spinadis Edmunds and Jensen

Berner 1977, p. 33.
Edmunds and Jensen 1974, pp. 495–497.
Edmunds, Jensen, and Berner 1976, pp. 212–213.
Lager 1985, pp. 255–256.
McCafferty and Provonsha 1984, pp. 173–179.
Unzicker and Carlson 1982, p. 3.68.

TAXONOMY. Edmunds and Jensen (1974) established the genus *Spinadis* based upon nymphs collected in Georgia, Wisconsin, and Indiana, and designated *S. wallacei* as the type species. The nymphs are sufficiently distinctive from other heptageniids so that Edmunds and Jensen (1974) proposed a new subfamily, Spinadinae, for *Spinadis*. This monotypic genus is known only from the nymphs and one female adult (McCafferty and Provonsha 1984). The carnivorous nymph is characterized by the lack of a terminal filament and the presence of prominent dorsal tubercles on the head, thorax, and abdomen.

The nymphs are very much alike throughout the geographic range, except for differences in the shape of tubercles and the intensity of color pattern. Whether the nymphs from the different localities all belong to *S. wallacei* remains to be investigated.

GEOGRAPHIC DISTRIBUTION. Representatives of the genus have never been collected in Florida, but we believe there is a good possibility that it occurs in the state. Edmunds and Jensen (1974) reported that nymphs were taken from the Altamaha River, Toombs County, Georgia, near the Florida-Georgia line. The genus also occurs in Arkansas, Indiana, and Wisconsin. Recently, a small nymph was collected in the Savannah River, Burke County, on the Georgia–South Carolina state line (J. Morse and B. Painer, pers. comm.).

ECOLOGY. According to Edmunds and Jensen (1974), nymphs have been collected from large rivers in rather swift current. The specimens from Georgia were collected by drift nets in water 10 feet deep. The specimens from Wisconsin were taken from water about 5 feet deep after the river level had dropped, and the Indiana specimens were collected from a log at a 2-foot depth in White River. The nymph from the Savannah River was collected in the deep part of the river by the use of a Hester-Dendy sampler. Lager (1985) collected the nymphs in the midportion of the Arkansas River; at the collection site, the river is 500 meters wide and 6 meters deep, with a boulder and gravel bottom. The current varied from 0.7 m/sec to 0.9 m/sec.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The nymphs were collected in May and June. The adults probably emerge in late June and early July (Edmunds and Jensen 1974); the single reared adult was collected on July 26.

BEHAVIOR. The nymphs are carnivorous, feeding on chironomids.

LEPTOPHLEBIIDAE

Leptophlebiidae is a very widespread family occurring worldwide but with its greatest diversity in the southern hemisphere. Peters and Edmunds (1970) reviewed the history of the family and gave its limiting characteristics. Edmunds et al. (1976) placed the family in the Leptophlebioidea, commenting that it is relatively isolated and retains a number of primitive characteristics. McCafferty and Edmunds (1979), in their treatment of the higher classification of the Ephemeroptera, reconsidered Edmunds's earlier conclusions (1972) as to lineages and decided that the Ephemerellidae and Tricorythidae should no longer be considered in the same superfamily as the Leptophlebiidae. Of these authors' two suborders, the family clearly falls into the Schistonota along with the Baetoidea and Ephemeroidea.

Florida genera included in the family are *Leptophlebia, Paraleptophlebia, Choroterpes, Habrophlebia,* and *Habrophlebiodes.*

Choroterpes Eaton

Allen 1974, p. 161.
Berner 1950, p. 140; 1975, p. 138.
Burks 1953, p. 95.
Edmunds, Jensen, and Berner 1976, pp. 214–217.

In the nymphal stage, *Choroterpes* is quite distinctive by virtue of the morphology of its gills. The adults are easily separated from other mayflies by the structure of the male genitalia and the venation of the metathoracic wings. Eaton erected this genus in 1881 to include the one species that he knew, *C. picteti* of Europe.

Even though the genus is easily distinguished, the species within the genus are difficult to separate. For the most part the species are separated by color pattern and by the shape of the basal segment of the forceps of the males.

Choroterpes, with two subgenera (Allen 1974), is a Neotropical, Holarctic, Ethiopian, and Oriental genus, which is widespread in both North and Central America.

Choroterpes hubbelli Berner

(PLATE 10. FIGS. 18, 42, 61, 133. MAP 15)

Berner 1950, pp. 140–145; 1975, p. 138; 1977, p. 37.
Lanquist 1953, p. 20.
Lyman 1956, p. 573.
Schneider 1967, p. 203.

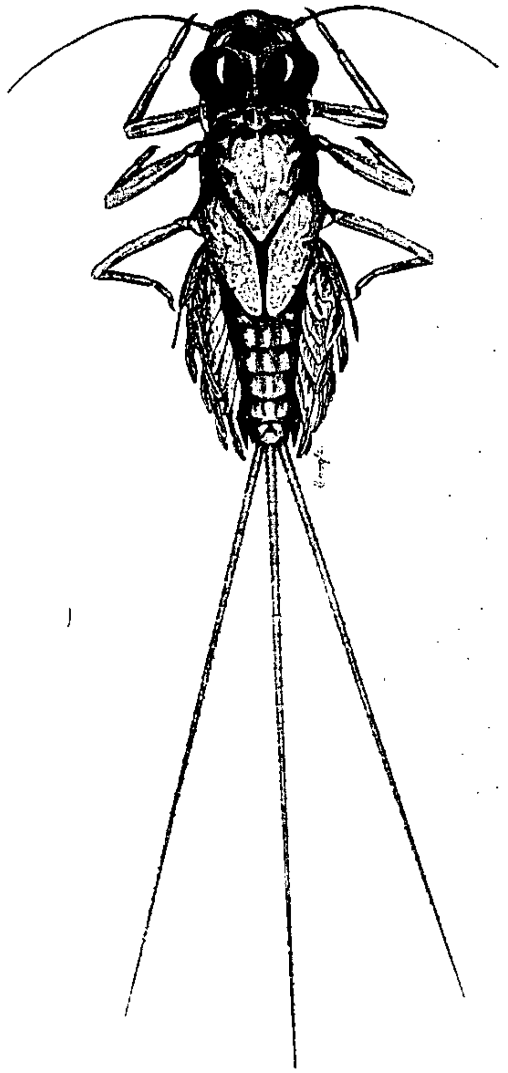


Plate 10. *Choroterpes hubbelli* Berner, nymph

TAXONOMY. *Choroterpes hubbelli* can be distinguished from all other species in the genus by its dark abdomen and pale, unbanded caudal filaments. The species was described in 1946 in the nymphal and adult stages. Of the North American species, only the nymphs of *C. basalis* and *C. hubbelli* have so far been recognized.

GEOGRAPHIC DISTRIBUTION. The species is widely distributed in Florida (map 15). Its range extends from the western part of Duval County to the northeastern part of Hillsborough County and to south-central Glades County, with the greater concentration in the north-central part of the state; *C. hubbelli* has also been found in Bay and Walton counties in the panhandle of northwestern Florida.* Nymphs have also been taken in Thomas County, Georgia, adjacent to Jefferson and Leon counties in Florida. We also have nymphs, or nymphs and adults, from Toombs County, Georgia, southeastern Alabama, southern Mississippi, and eastern Louisiana. It is most likely that *C. hubbelli* occurs in the streams between Alachua and Bay counties, even though the species has not appeared in collections made between the two regions. We believe the species is confined to the streams of the Coastal Plain.

ECOLOGY. Among the unexpected places in which *hubbelli* nymphs have appeared, the most spectacular is Jerome Sink, located approximately two miles north of the town of Newberry in a perennially arid region. Drainage in this part of Florida is subterranean. The nearest surface stream is the Santa Fe River, about 12 miles distant. Underlying the Newberry region are many subsurface streams, but very few are exposed at the surface. Of those exposed, only a small portion of the water is in evidence. The openings to these subterranean waters are usually steep-sided, sometimes even well-like, sinkholes, the sides of which may be covered with various types of ferns. Water flow is not evident in any of the sinkholes we have observed, though the various underground channels do seem to connect, as indicated by the distribution of the white cave crayfish. The walls of Jerome Sink extend 30 feet downward to the surface of the water, and thence an unknown distance to the bottom of the sink. That part of the open east wall lying below the surface of the water probably connects the sink water with the subterranean drainage. Along the west shore of the sink, the bottom drops off rapidly, but there is sufficient shore to allow the accumulation of dead leaves and other debris. It is here that *Choroterpes* nymphs occur, along with *Epiaeschina heros*, a dragonfly that Byers (1930) says "lives clinging to debris caught in moving water." Other insects are rare, but *Erimystax* sp., one of the small, stream-inhabiting minnows, is rather common.

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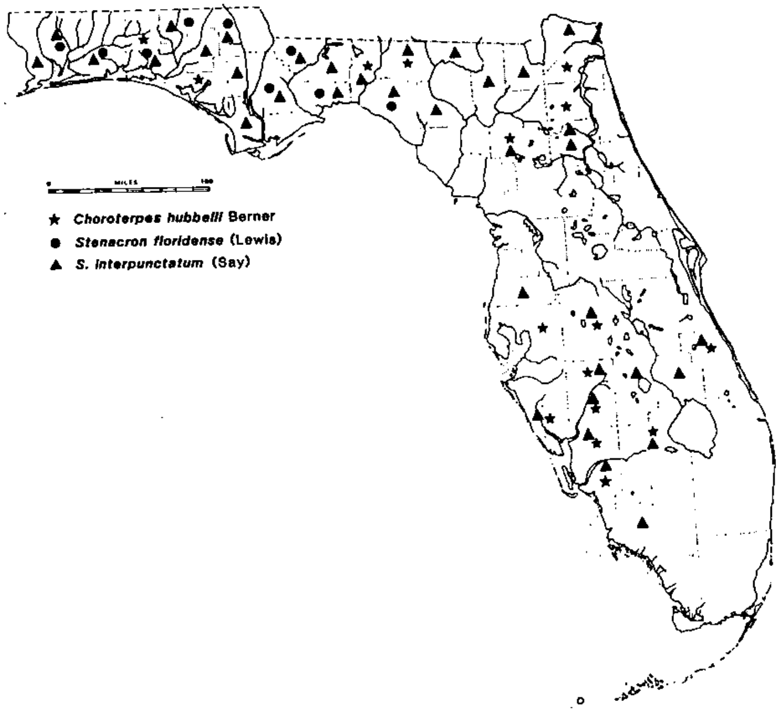
*Cantrell has taken nymphs from the Peace, Manatee, and Myakka river drainages as well as from the Imperial River in extreme southern Lee County and from Indian River County on the east coast.



Map 15. The distribution of *Choroterpes hubbelli*, *Stenacron floridense*, and *S. interpunctatum* in Florida.

Very few species of mayflies inhabit the shores of sand-bottomed lakes in Florida. Partially buried sticks, logs, and boards usually appear on the bare sand in shallow water, and their underside crevices sometimes provide habitats for three species of ephemerids—*C. hubbelli, Eurylophella temporalis*, and *Stenacron interpunctatum*—of which *Choroterpes* is the scarcest.

C. hubbelli nymphs apparently prefer streams where they may inhabit the leaf drift in the slow-flowing reaches. One of the richest *Choroterpes* streams that we have examined is located in Walton County. At the time the collections were made, the stream coursed over a bed of silt varying in thickness from one to three or more feet; to reach the main channel, two smaller branches, each with its own bed of soft silt, had to be traversed. In several places it was only by holding to the pilings of the bridge over the stream that it was possible to reach a site suitable for collecting nymphs. The floor of the creek was paved with many layers of leaves intermingled with silt, and the margins of the bed were bordered with dense growths of *Ludwigia* and *Pontederia*, which were absent from the main flow. Among the silt-imbedded leaves there were numerous mayfly nymphs, the majority of which were *C. hubbelli*.

The nymphs frequently show up in unusual places. In a small, sand-bottomed creek emptying into the Choctawhatchee Bay, the underside of a large log lying not more than 12 feet from the salt water of the bay was literally covered with mayfly nymphs, chiefly *C. hubbelli*. The water around the log was perfectly fresh, there being a continuous flow unaffected by the tides. The tidal fluctuation in the Choctawhatchee Bay amounts to only a few inches, hardly sufficient either to overflow the sandbar separating the fresh from the salt water or to cause the salt water to back up into the creek.

The streams in which nymphs of *C. hubbelli* live are either slightly acidic or circumneutral. Red Water Lake, one of the two lakes from which specimens have been taken, derives its name from the color of its water, which is clearly acidic. As can be seen from the distribution of this species, the nymphs shun the stagnant waters of the eastern and southern parts of Florida.

SEASONAL DISTRIBUTION AND LIFE HISTORY. We have taken or reared adults during March, April, May, June, July, August, and October. Though we have no records of nymphs or adults from other months, we believe that emergence occurs throughout the year, reaching its peak during the spring and early summer. Emergence records for other species show that the northern forms emerge from July to the early part of September. *C. nanita* from Texas was described from specimens taken in June; the types of *C. oklahoma* were collected on March 20.

Nymphal data indicate that underwater life may occupy a period of from six to eight months. So few adults have been reared that the length of life of the imago has not been determined, but it appears likely that death takes place within 15 to 24 hours after the final molt. Transformation in the laboratory, which occurs after dark, has taken place as late as 9:30 P.M.

When the subimago is ready to emerge, the nymph, like *Leptophlebia*, swims vigorously; however, it does not crawl from the water but bursts free at the surface, floats for a moment on the exuviae as a subimago, and then flies to a nearby support. Transformation is over in a few seconds. The whole process, after the swimming movements have been completed, takes no more than 30 seconds. Once emergence has taken place, the subimago quietly awaits the final molt—an event which almost never happens in the laboratory under normal room conditions. We were successful in obtaining one male and one female imago by placing subimagoes in paper sacks with wet blotters in the bottom. Two other adults molted when we used the bell-jar method discussed under *Leptophlebia intermedia*. Subimaginal life lasts 8 to 10 hours, and in some cases it may be even shorter. The female of this species, as is true of most other mayfly species, molts with greater ease than the male does.

The mating flights of *Choroterpes hubbelli* have never been observed. A search of the literature revealed that the only published observations of this phenomenon in other North American species are those of Needham (1905) and Morgan (1913). Needham has described the flight of *C. basalis* as occurring in small swarms in early afternoon. The insects flew high above the water, seldom descending to low levels. Morgan, who has observed the mating flight of the same species, noted a swarm of 300–400 individuals of *C. basalis* flying over Fall Creek at about 4:00 P.M. The swarm included both males and females.

BEHAVIOR. As with other species of the subfamily, *C. hubbelli* nymphs are negatively phototactic and strongly thigmotactic. The adult, particularly during the subimaginal stage, shows a strong positive reaction to light, and this phototactic response has been demonstrated frequently in the laboratory.

Food substances eaten by nymphs are much the same as those utilized by *Habrophlebiodes brunneipennis*, that is, chiefly plant materials. When nymphs are kept in an aquarium with only dead leaves, they seem to grow perfectly well on a diet of scrapings from the surface of these leaves. They have been kept alive almost two months on such food.

Though body movements of nymphs are similar to those of *Habrophlebiodes*, the nymphs are easily distinguished from other Leptophlebiinae by the fact that the gills, which are not spread when the insect is submerged, are held above and close to the abdomen, where they are frequently vibrated.

Habrophlebia Eaton

Berner 1950, p. 145; 1975, p. 138; 1977, p. 37.
Burks 1953, p. 94.
Edmunds, Jensen, and Berner 1976, p. 218.
Peters 1979, pp. 51–56.
Peters and Edmunds 1970, pp. 182–183.
Peters and Jones 1973, p. 246.

The genus *Habrophlebia* is a somewhat more diversified genus in Europe than in North America, several species having been recorded from the former, whereas only one is known from the latter.

The nymphs are most easily distinguished from other leptophlebiids by the structure of the abdominal gills, which consist of two clusters of slender filaments. Likewise, the adults are easily identified by the shape of the male genitalia and by the venation of the metathoracic wings.

Habrophlebia is known in North America only from the east and the southeast, ranging from Canada and New York to Florida, Alabama, Georgia, North Carolina, South Carolina, and Tennessee.

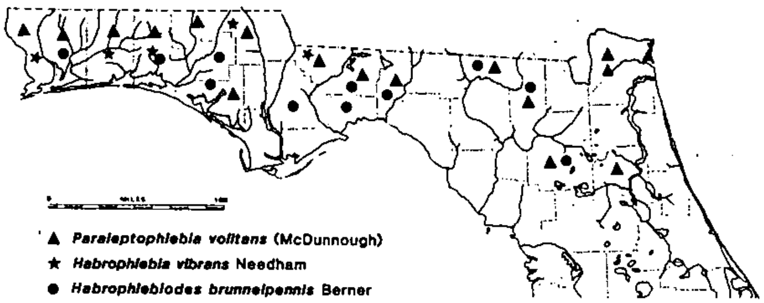
Peters (1979) established a new subgenus, *Hesperaphlebia*, for the North American species of *Habrophlebia*.

Habrophlebia (*Hesperaphlebia*) *vibrans* Needham

(FIGS. 17, 43, 59, 136. MAP 16)

Berner 1950, p. 145; 1975, p. 138; 1977, p. 37.
Burks 1953, p. 94.
Edmunds, Jensen, and Berner 1976, p. 218.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 203.

TAXONOMY. *Habrophlebia vibrans*, the only known species in the genus occurring in North America, was described from New York by J. G. Needham in 1907 and recorded from the Black Mountains of North Carolina by Banks in 1914 as *H. jocosa* (synonymized with *vibrans* by McDunnough in 1925). In 1932 Traver described *H. pusilla* as a new species based on a male subimago she had reared. Later she identified a male adult from South Carolina as *pusilla*. A review of the genus *Habrophlebia* (Berner 1975) resulted in *pusilla* being synonymized with *vibrans*.



Map 16. The distribution of *Paraleptophlebia volitans*, *Habrophlebia vibrans*, and *Habrophlebiodes brunneipennis* in northern Florida.

GEOGRAPHIC DISTRIBUTION. *H. vibrans*, a species that is only rarely collected, is known to occur over the eastern part of the United States and Canada southward into northern Florida. While one of us (Berner) was working in the smaller mountain streams of Macon County, North Carolina, nymphs and adults of *H. vibrans* were often collected during July and early August. In Florida, we have records from Jackson and Okaloosa counties, and Schneider (1967) recorded the species from Escambia, Gadsden, and Walton counties as well. All records of its occurrence in Florida are from the panhandle (map 16).

ECOLOGY. Little has been written concerning the ecology of *H. vibrans*, and we can add only slightly to it as we have made very few observations about the species.* Our first immature was collected in December from leaf debris that accumulated in a small, sand-bottomed stream in the northwestern part of the state. The bottom of this creek, which was heavily covered in places with leaf drift, was quite silty, and the water was slightly acidic, with a pH of 6.2. Another nymph was collected from a

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* The paper "Life history and production of the stream-dwelling mayfly *Habrophlebia vibrans* Needham (Ephemeroptera; Leptophlebiidae)," by M. Lauzon and P. P. Harper, 1986, Canadian Journal of Zoology, 64: 2038–2045, came to our attention after our manuscript was in press. Significant information about the ecology and life history of the species in Quebec is included in this paper.

swift-flowing, sand-bottomed stream, and a third, which we collected in February, came from the same stream from which the first was taken.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The nymphs collected in December and February were more than half grown; the second specimen, collected in April, was in its last instar. With such scanty data, no conclusions can be drawn as to the life history of the species in Florida, but it is clear from the April specimen that emergence takes place in the spring months. In Quebec, McDunnough found adults to be common in late June; in the mountains of North Carolina, adults are out in July and early August. Carlson (1971) collected large numbers of adults from Pickens County, South Carolina, from April 20 through August 28. He found the period of greatest abundance to be from April 28 through July 2, and his largest collection was made on May 2, when he took 513 adults.

BEHAVIOR. We have been unable to observe the behavior of Florida nymphs, but we have seen them in North Carolina and assume that there would be no difference. They resemble *Habrophlebiodes brunneipennis* in their movements while swimming and in following receding water when placed in a white-enameled pan as they are collected. Needham et al. (1935) commented on their mating flights only briefly, describing them as small, compact swarms in forest openings beside brooks.

Habrophlebiodes Ulmer

Berner 1950, pp. 130–131; 1975, p. 141.
Burks 1953, pp. 95–96.
Edmunds, Jensen, and Berner 1976, pp. 218–221.
Peters 1980, pp. 33–39.

Ulmer established *Habrophlebiodes* in 1919—including *betteni* (now synonymized with *americana*) and *americana*—chiefly on genitalial characteristics and peculiarities in the shape and venation of the metathoracic wings. At present, the genus is known to include four species that can be placed in two groups: *annulata*; and *americana*, *brunneipennis*, and *celeteria*.

The species of *Habrophlebiodes* are widely distributed over eastern North America. *H. americana* is known from Quebec to Georgia; *celeteria* has been taken only in Tennessee; *annulata* is an Oklahoma species; and our collecting has produced specimens of *brunneipennis* in Alabama, Florida, Georgia, and South Carolina. The Appalachians constitute the region of greatest apparent abundance for the species of the genus, but future collecting may well show that species of *Habrophlebiodes* are common throughout the midportion of the continent.

Peters's review (1980) of the phylogeny of the family Leptophlebiidae resulted in his establishing two subfamilies, Atalophlebiinae and Leptophlebiinae. *Habrophlebiodes* is included in the Leptophlebiinae.

Habrophlebiodes brunneipennis Berner

(PLATES 11, 12. FIGS. 20, 41, 67, 93, 171. MAP 16)

Berner 1950, pp. 131–139; 1958, p. 30; 1975, p. 142; 1977, p. 37.
Jones 1977, p. 66.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 203.
Unzicker and Carlson 1982, p. 3.56.

TAXONOMY. *Habrophlebiodes brunneipennis* is a close relative of *H. americana*. The most obvious differences between them are in the wings: those of *brunneipennis* are deep amber, with strong, dark venation, while those of *americana* are colorless, or almost so, with weaker, paler venation. The genitalia of the two species are similar.

Nymphs of *H. brunneipennis* differ from those of the other species of the genus in having spinules on tergite 6, as well as on 7 through 10. It was earlier thought that the absence of spinules from tergites 1 through 6 and their presence on 7 through 10 constituted one of the generic traits of *Habrophlebiodes*.

GEOGRAPHIC DISTRIBUTION. In Florida, *H. brunneipennis* is confined to the northern part of the state, the southeasternmost limit of the known range being Alachua County. As is usual with most stream forms—even very tolerant ones—*brunneipennis* is absent from the more or less stagnant waters in the lowlands of southern Florida. We have collected the species in the following counties of Florida (map 16): Alachua, Bay, Columbia, Gadsden, Hamilton, Jefferson, Leon, Liberty, Santa Rosa, Wakulla, Walton, and Washington.

ECOLOGY. *H. brunneipennis* is found commonly in slow to moderately swift-flowing streams, where the nymphs dwell in the leaf debris. These streams are usually of the sand-bottomed type, but occasionally the nymphs can be taken from slow-flowing, silt-bottomed streams. If leaf debris is scarce, the nymphs tend to gather on vegetation near shore where they are fairly well protected. *H. brunneipennis* nymphs inhabit any portion of the stream

Plate 11. *Habrophlebiodes brunneipennis* Berner, male imago

where the current is moderate to slow and in which there is either vegetation or leaf drift. Nymphs have never been taken from rivers or large streams, but occasionally they occur in medium-sized creeks and are most common in small brooks. The small brooks flowing through the ravines of the Tallahassee Hills have a mayfly fauna consisting almost entirely of *brunneipennis*, but the species is much less frequently encountered in the larger streams of this area.

The well-tracheated gills allow these nymphs a great deal of freedom in moving from one part of the stream to another. We have studied this species most thoroughly in a small, sand-bottomed creek about 2½ miles west of Gainesville. The nymphs were exceedingly common here, particularly in the leaf drift along the margin of the stream and in quiet pools. Roots of terrestrial plants are exposed over large areas in the bottom of this brook, forming a dense mat where the nymphs are easily located. Among the roots, the immatures become clingers rather than sprawlers, because the current is much swifter over these root beds than in the leaf drift. *H. brunneipennis* nymphs, in the earlier instars, may often be found among the pebbles in riffles, but they are less numerous in this situation than in quieter, more silty zones.

The streams inhabited by this species drain heavily wooded areas, and in consequence are usually somewhat acidic and tinged with brown. Temperatures in the streams rarely fall to freezing, and then only in the almost stagnant areas. The temperature of the water seldom varies more than 15°C.

Common associates of the nymphs of *brunneipennis* include other species of mayflies and Odonata. Large numbers of chironomids and caddis fly larvae, occasional stone flies, larvae of the very large crane fly *Tipula abdominalis*, various other dipterous larvae, and, very commonly, the snail *Physella* are also in the leaf drift. These associates make up the principal macroscopic inhabitants of the leaf drift and riffle communities of small Florida streams.

SEASONAL DISTRIBUTION AND LIFE HISTORY. *H. brunneipennis* is not limited to a seasonal reproductive period, and nymphs of all ages are found in Florida streams throughout the year. Adults have been taken in 10 months of the year with no records of their occurrence for May and December, probably because of the lack of collecting during those periods. There seems to be no peak of emergence, for examination of the nymphal fauna indicates that the distribution of immatures of all ages is approximately the same throughout the year.

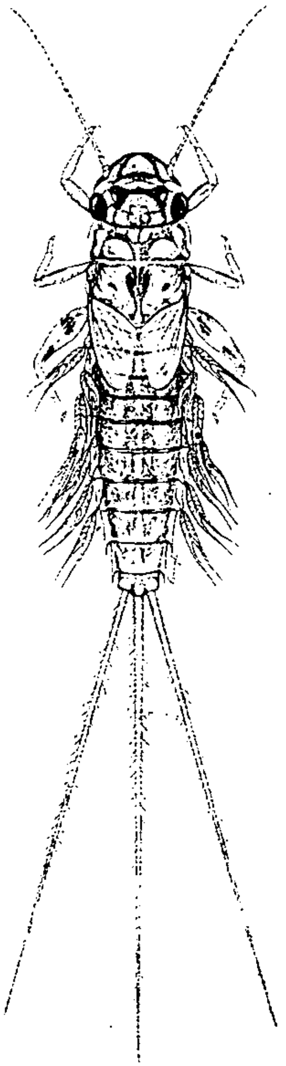


Plate 12. *Habrophlebiodes brunneipennis* Berner, nymph

Development of nymphs from egg to adult probably takes only a few months; however, there are no data available to make possible a more exact estimate. Numerous attempts to hatch eggs have failed. We have repeatedly tried without success to induce artificial fertilization and parthenogenetic development. In addition, eggs that were stripped from apparently impregnated females were placed in small dishes, some of which were aerated, others not. At the end of three weeks no development could be seen in any of the eggs. The eggs are elongated, with the sides parallel, and the ends are rounded. Those of *H. americana* were described in detail by Koss (1968) and are in all likelihood like those of *brunneipennis*. Upon deposition the eggs immediately settle to the bottom where they adhere to any solid object. These eggs do not send out tenacious threads as do the eggs of many other species, but Koss observed suckerlike plates, which he suspected act as suckers, aided by an adhesive substance coating the egg.

The oviposition of *americana* (as *betteni*) was briefly mentioned by Morrison (1919) in a discussion of the mayfly ovipositor, a structure peculiar to the leptophlebiid mayflies. Of all North American genera, *Habrophlebiodes* has the best developed ovipositor.

The oviposition of *H. brunneipennis* was observed under artificial conditions in the laboratory. A female, which was believed to have mated, was held firmly by the wings; the body was raised and lowered, and then touched to the water surface rhythmically; the female soon began to release her eggs upon each contact. They came out usually two at a time, but occasionally singly, passing between the egg valve and the ovipositor, slipping out as though in a greased trough. As oviposition occurred, the forward end of the abdomen was depressed, the posterior portion (segments 8 through 10 and the caudal filaments) was elevated. At first the eggs were ejected in a continuous stream, but as the female became spent, the flow of eggs grew slower until an egg only occasionally left the body (fig. 171). The abdomen of another female treated in the same way became somewhat transparent as she released her eggs, and the release of the eggs into the posterior part of the oviducts could be easily observed. The eggs literally popped into place with machine-like regularity and precision. As they were freed from her body, the female would twitch her abdomen, apparently to disseminate them. Oviposition continued uninterruptedly, eggs passing from the body even when the female was not in contact with the water. They accumulated around the ovipositor, but as soon as the female touched the surface, the eggs were dispersed.

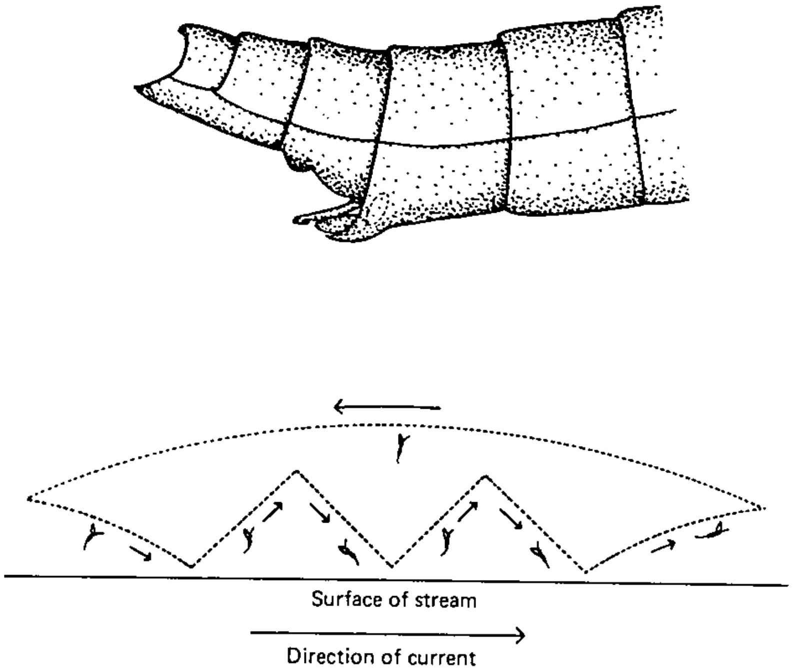


Fig. 171. Upper figure: The terminal abdominal segments of a female *Habrophlebiodes brunneipennis* showing the ovipositor and the passage of an egg from the body. Lower figure: A diagrammatic representation of the characteristic movements of the males of *H. brunneipennis* during the mating flight.

Transformation usually occurs in the early afternoon from noon to about 3:00 P.M., depending on the season, but it has been known to take place as early as 10:30 A.M. The process has been observed only in the laboratory. When ready to transform, the mature nymph slowly crawls from the water, sometimes as far as an inch above the surface. After a few moments, the thorax begins to pulsate, the nymphal skin splits, and the adult thorax and abdomen are gradually drawn forth, followed by the wings, legs, and tails. The subimago slowly crawls away from the exuviae for a short distance, then flies to a nearby support. Along the banks of streams, subimagoes can be found on the undersides of leaves about four or five feet above the water. The shaded sides of bridges are also favorite

resting places. Subimaginal life lasts only 12 to 14 hours. In captivity, this species has little difficulty in undergoing its ultimate molt so long as the environment is not too dry.

Life as an adult is little more than a day. Two males were collected as subimagoes at 3:00 P.M. on November 11; by 9:20 P.M. on November 12 one male was dead, and the other showed only slight movements. Other tests of longevity of adults have confirmed that *H. brunneipennis* is typically a very short-lived species.

Mating flights occur in early afternoon, and as with emergence, the time depends on the season. One flight observed in March was sighted at 2:15 P.M. The small insects were flying about six inches above the water and the swarm consisted of males only. The flight took place in an open area bathed in sunlight. The swarms appear to consist of only a few individuals, five or six members, all males. On one occasion, almost the entire swarm was captured, with only two individuals left, and these continued flying for about 10 minutes, when two other males joined them. Two females then flew into the small male swarm and began rising and falling with the males in a typical swarming pattern. The males then approached the females from below, and, as soon as they were coupled, the two pairs flew to shore and were lost in the shadows of the vegetation. Twenty minutes later the third male paired with another female that had entered the scene. Within a few minutes another male joined the remaining one that was still flying. These flew in unison, and then the first male approached the new arrival to assume the copulatory position, but he seemed to be repulsed, as the two separated immediately and began flying in unison again. Once more copulation was attempted, the attempt lasting not more than two or three seconds. The new arrival finally withdrew and was lost to sight. After 50 minutes, a female approached the remaining male and coupled with him. The two flew slowly toward shore and parted after about 10 seconds, the male returning to midstream, the female becoming lost in the shadows. Exactly one hour after our observations began, the last male ceased its flight.

The insects did not at any time rise more than 12 inches above the stream surface, and the horizontal distance covered did not exceed three feet. The flight was fairly rapid and took place in bright sunlight except toward the last. As the sun shifted, trees began to cast shadows over the area in which the remaining single male was dancing, but the shadows had little effect on his position. The flight was usually in a downstream direction against the wind, but occasionally it became transverse and, once or twice, the insect was headed upstream. The male seemed to fly backward, forward, sideways, or obliquely with equal ease. When directed downstream, the flight of the insect was forward and backward, but when crosswise, the flight was from side to side. During the flight the abdomen drooped considerably, being held at an angle of about 60° or more with the horizontal, and sometimes becoming almost perpendicular. The tails could sometimes be seen if the light happened to strike them at the correct angle.

The insect markedly resembled a mechanical toy attached to an invisible string. Running the length of the string, the toy is suddenly jerked backwards, then immediately runs out again. The movement during the mating flight is diagramed in figure 171.

Almost never during the period of swarming did the insect do an about-face to move upstream. Now and then, the mayfly seemed to touch the surface of the water and then to rise immediately.

Spiderwebs are common along the small streams of Florida, especially so at the stream where most of the swarming flights have been observed. These webs are often spun approximately six to eight inches above the water. Numerous *H. brunneipennis* adults have been taken from the webs and in March and April, when most of our observations were made, between the hours of 2:00 and 3:00 P.M., all entrapped individuals were still alive; apparently the spiders were not yet ready to immobilize their catches. These adults had undoubtedly come from mating swarms.

Other observations of swarming behavior were made in May at the same stream where the flights described above were seen. Numerous flights were seen occurring simultaneously. The flights resembled those of March but were much larger, each being composed of 7 to 10 males. The bodies of the flying insects were usually held in a perpendicular position and now and then seemed even to be leaning over backwards. No copulating pairs were seen at this time. After the males flew for a considerable time, the flights dispersed. Seemingly, there was no reason for this breaking up of the swarms, as no mating was observed taking place. The males flew in unison, but frequently they would "get out of step." The insects were so insensitive to outside influences that one was able virtually to enter the swarms without disturbing them. At this time males were very common. After the flights had ended, we swept the vegetation along the stream and collected a large number of them without finding any females. Perhaps the explanation for the absence of the females is that they fly away from the stream after mating. The male flights took place most often in the shade, but frequently they moved into the sunlight. Even though subimagoes emerge early in the afternoon in the laboratory, our experience has shown them to be scarce or absent from the vegetation lining the stream banks.

Another series of flights was observed in January. At this time two distinct types of swarming behavior were exhibited. In a distance of about 250 yards, 21 separate swarms were counted, each in a sunlit area. The swarms varied in size from those with only two males to those with nearly 100 in them. Two pairs of copulating adults were also observed but only for a moment as they were almost immediately lost in the shadows. At this time there seemed to be a clear correlation between size of swarm and height of flight. The very small groups flew 6 to 12 inches above the water, whereas the large swarms of 20 to 100 males flew from two to five feet above the water. The manner of flight in large swarms did not differ from that of small swarms except in the height above the stream.

BEHAVIOR. The feeding habits of the nymphs of *H. brunneipennis* are not known with certainty, but we believe they do not differ significantly from those of most other mayflies. The well-developed molar area of the mandibles proves that grinding of food materials must be habitual. When a nymph is placed in an aquarium with only plant materials, it flourishes and does not seem to lack sufficient food for normal growth. Examination of the nymphal gut indicates that the food materials are obtained by scraping the surface of dead leaves. Organic substances as well as small grains of sand were found in the enteron.

Although the gills are highly tracheated, single, and exposed fully, the nymphs keep them in constant motion. When the nymphs are at rest, the gills are held stiffly out from the body at a 45° angle to the plane of the dorsum and are slowly waved forward and backward. In swimming, the nymphs avoid the interference of the gills by appressing them against the abdomen.

Like all leptophlebiids, these nymphs are rather awkward swimmers that usually move most efficiently by crawling. Swimming requires a great amount of exertion and is not at all natural in members of this genus; the swimming movements can in no way compare in gracefulness with the darting of the Baetidae. The nymphs swim by a series of undulatory motions; the wave begins cephalically and travels to the tails, which are depressed or raised as a unit. The caudal filaments aid very little in propelling the insect; almost naked, they are little more than long hairs trailing behind.

Leptophlebiid nymphs can be recognized immediately by their movements on the surface of a white-enameled pan. When the water is drained away from them, the insects follow in the wake of the liquid, vigorously wriggling their abdomens and tails from side to side in a sort of scrambling effort to hide themselves beneath any convenient object.

As in many of the Ephemeroptera, *brunneipennis* nymphs exhibit a definite negative phototactic reaction. There is a reversal of this condition in the subimaginal and imaginal stages. The nymphs also display rheotaxis when they are placed in any sort of current.

H. brunneipennis adults orient to wind currents, as can be demonstrated by blowing gently on the insect. They react by turning in the direction of the air movement, and they will remain attached to their footholds until the strength of the wind becomes excessive. They will then fly away. These observations are consistent with those of Krecker (1915), who observed that orientation with the head turned to the wind is the result of tension exerted on the leg and wing muscles.

Leptophlebia Westwood

Berner 1950, pp. 115–116 (*Blasturus*); 1975, pp. 144, 146.
Burks 1953, pp. 84–85 (*Leptophlebia* = *Blasturus*).
Edmunds, Jensen, and Berner 1976, pp. 226–230.
Peters 1980, pp. 33–39.

TAXONOMY. Prior to Burks's study (1953) of Illinois mayflies, many North American species, now recognized as belonging to the genus *Leptophlebia*, were assigned to *Blasturus*. The genus *Blasturus* was described by Eaton in 1881 and redefined in his monograph on the Ephemeridae in 1884. In 1932, Traver discussed the genus as it occurs in North Carolina and described five new species. In her paper, she included the description of *Blasturus gracillis*, but she subsequently removed this species to the genus *Leptophlebia*, after first shifting all the North America species formerly placed in that genus to *Paraleptophlebia*. Ide (1935) suggested that *Leptophlebia johnsoni* might be intermediate between *Blasturus* and other *Leptophlebia* species, and that it would be well to drop entirely the generic name *Blasturus*. Spieth (1938) followed Ide's suggestion, and, in his discussion of coloration in relation to seasonal emergence, he used the generic name *Leptophlebia* to refer to species placed in *Blasturus* and *Paraleptophlebia* by Traver.

Traver (1932, p. 123) wrote, "Both as to nymphs and imagoes, the genus *Blasturus* is a difficult one to separate into its component species. Structural differences are minor and difficult to recognize until some time is spent in studying the group as a whole. Color differences exist, but they are likewise minor and relative, and are an unsatisfactory basis for the separation of species." To date additional information has not changed the situation; more than 50 years later we have still not resolved the problems inherent in distinguishing North American species. It is likely that many of Traver's species will ultimately be synonymized.

Leptophlebia bradleyi Needham

(FIGS. 62, 134. MAP 17)

Berner 1950, pp. 128–130; 1958, p. 30; 1975, 146–150; 1977, p. 38.
Edmunds, Jensen, and Berner 1976, pp. 230, 233.
Henry and Kondratieff 1982, pp. 125–126.
Jones 1977, p. 66.
Kondratieff and Voshell 1981, p. 193.
Schneider 1962, p. 132; 1967, p. 203.

TAXONOMY. Described by Needham in 1932, eighteen years after the specimens were collected in the Okefenokee Swamp in southern Georgia by Dr. J. C. Bradley, *Leptophlebia bradleyi* was thought to be unique, especially in the nymphal stage, among North American members of the genus. The male imago can be separated from the other species by the morphology of its genitalia, its lack of pale abdominal segments, and its tinted wings. Because of its distinctiveness, it is rather difficult to say in which direction its affinities lie.

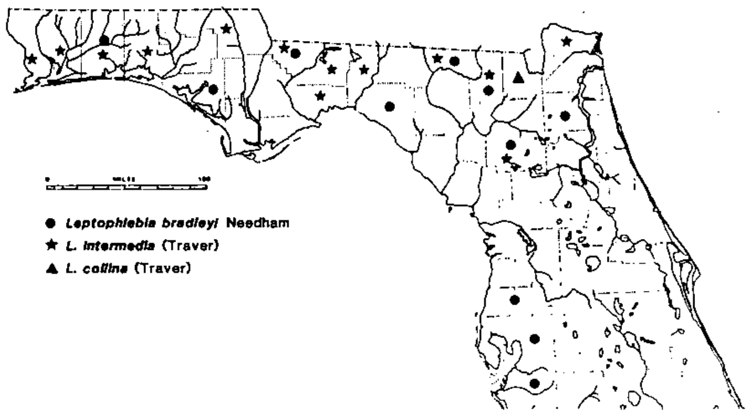
The nymphs of *L. bradleyi* cannot be easily confused with those of any other eastern North American species. The uniqueness of the nymphs lies in the structure of their gills, which resulted in the species being assigned to *Paraleptophlebia* for many years. In *L. bradleyi* each gill is composed of two plates like those of other species of *Leptophlebia;* each lamella has distinct and prominent main tracheae provided with numerous lateral branches. In other North American *Leptophlebia* species, the gill lamellae are shaped into one or two blunt lobes at the base of the terminal filament; in *bradleyi,* on the other hand, the gill lamellae are rounded. Edmunds et al. (1976) illustrated gills of nymphs collected in Texas that are like those of Florida nymphs. Subsequently, Henry and Kondratieff (1982) studied adults of *bradleyi* collected in New York, Oklahoma, Texas (nymphs also), and Virginia.

Realizing that Traver's assignment of *bradleyi* to *Paraleptophlebia* would more appropriately have been to *Leptophlebia*, one of us (Berner 1975) reassigned the species and gave reasons for the transfer. In the same paper the female imago and the nymph were described.

GEOGRAPHIC DISTRIBUTION. Individuals of *L. bradleyi* seem to be scarce and are not frequently encountered in collections. The initial discovery in the Okefenokee Swamp was followed by locating populations of the species in tributaries of the Suwannee River, which drains the swamp southwestward into Florida. For many years we believed that the species was restricted to the southeastern United States; however, Henry and Kondratieff (1982) have now demonstrated that it is a wide-ranging species, distributed from New York to Texas. In Florida, we have records of the species from the following counties (map 17): Alachua, Bay, Liberty, Holmes, Clay, Columbia, Gadsden, Hamilton, Manatee, Okaloosa, Pasco, and Taylor.

ECOLOGY. The nymphs prefer slow-flowing streams with silty bottoms, where they dwell amid the leaf drift, on submergent vegetation, sticks, and almost any other available support, where they may be found in cracks or crevices, as well as on the protected sides of these objects. All streams from which the species has been collected are of the brown-water type with the pH in the acid range. As a rule, the nymphs shun the center of the stream and live where there is little movement of the water. The nymphs were collected from the middle of the Fenholloway River, now badly polluted, where the flow was almost negligible. The Styx River in Alachua County presented a picture of stagnation with vegetation typical of this type of habitat; yet *L. bradleyi* nymphs were found here in association with other mayflies, some of which are typical inhabitants of standing bodies of water. On another occasion, a nymph was found on submerged wood in the littoral zone of Santa Fe Lake, which is also part of the Suwannee River drainage system.

SEASONAL DISTRIBUTION AND LIFE HISTORY. *L. bradleyi* appears to have a seasonal distribution similar to that of *L. intermedia*, with the adults being "on the wing" during the cooler months. All of our Florida adults were collected in November, January, and February. Henry and Kondratieff (1982) have adults collected or reared in Texas during December, January, and February; from Oklahoma in March; from Virginia in March; and from New York in April. The appearance of the adults during these cooler months leads us to the conclusion that emergence is strictly limited and that it is temperature related. Furthermore, we believe that the species, like *L. intermedia*, is univoltine.



Map 17. The distribution of *Leptophlebia bradleyi*, *L. intermedia*, and *L. collina* in Florida.

Growth during the cooler months is rapid, as we have specimens that are only one-third grown collected in October, while those taken in November were half grown. All of our February specimens from Florida were in their last instar or at least in the penultimate. Bradley captured his adults on December 21, 27, 28, and 29.

BEHAVIOR. Because of the rarity of encounters with nymphs, few observations have been made. They act much as do other members of the family, moving with a sideways wriggling and twisting of the body. Generally, when dead leaves and other detritus are removed from a stream, placed in a white-enameled pan, and the water drained away, the nymphs will leave their hiding places among the decaying leaves and follow the receding water. Their characteristic movements soon reveal them against the white background, and they are easily collected. They apparently feed on detritus and decaying vegetation for the most part.

Adult swarms have been noted on a few occasions. The first time we observed them was on January 8 when we saw a small flight in late afternoon. The air temperature was 64°F, the wind was moving only slightly, and the sky was clear and bright. The swarm, consisting of from 5 to 10 males, was flying low—at a height of from four to six inches—over the water of Hatchet Creek, a small stream near Gainesville.The flight occurred in shaded but open areas. Only a single female was taken at this time. Our next observation of flights was at Black Creek in Clay County on January 25. We observed the swarm of about 10–15 males flying about one foot above the water surface in bright sunlight. Our observations extended from about 4:00 to 5:00 P.M., and the temperature was rather cool but the air still. At another location, also in late January, a swarm was seen flying very close to the water surface. Females were caught by net as they dipped their abdomens to the water to oviposit. They were not seen entering the swarm. On still another occasion in late January males flying very close to the water were seen touching their abdomens to the surface two or three times and then resuming their normal up-and-down mating-flight behavior. These flights all occurred in late afternoon after 4:00 P.M. and continued until the sky was nearly dark.

Leptophlebia collina (Traver)

(FIG. 64. MAP 17)

Berner 1975, p. 150; 1977, p. 38.

TAXONOMY. The sole record of *L. collina* from Florida was the result of the capture of adult males in the northern part of the state at Glen St. Mary on March 11, 1958. The species, described by Traver in 1932, is very similar to *L. austrina* and *L. intermedia.* Males of *collina* are separated from those of the related Florida species, *L. intermedia,* by the length of their decurrent appendages of the penes. Also, the median caudal filament of *collina* is significantly shorter than that of *intermedia.* We have been unable to find characters that will allow us to separate females and nymphs from the other two similar species with any degree of reliability.

Whether *L. collina* is a valid species is not clear. We lean toward the opinion that it is synonymous with *austrina* and *intermedia,* but much additional study is required before a conclusion can be reached with any degree of certainty. Our inability to separate the species with confidence reinforces the obvious need for an in-depth study of all North American *Leptophlebia.*

GEOGRAPHIC DISTRIBUTION. The species is known only from North Carolina, South Carolina, Georgia, and Florida. Our single collection of three male adults and three male subimagoes is from Glen St. Mary in Baker County (map 17). We have also reared adults from nymphs collected at the Withlacoochee River in Lowndes County, Georgia. Both streams from which specimens came are in the Suwannee River drainage system. As *L. intermedia* has been taken from the same river system, the collection of both species in this drainage lends credence to the supposition that we are dealing with a single species.

ECOLOGY, SEASONAL DISTRIBUTION, LIFE HISTORY, AND BEHAVIOR. We have no information on these subjects for this species, but we surmise that they would be similar to the biology of *L. intermedia.*

Leptophlebia intermedia (Traver)

(PLATE 13. FIGS. 16, 35, 63, 132. MAP 17)

Berner 1950, pp. 116–123; 1958, p. 30; 1975, pp. 151–152; 1977, p. 39.
Jones 1977, p. 66.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 203.
Wurtz and Roback 1955, p. 193.

TAXONOMY. Since Eaton's work (1883–88), very few ephemerids have been described from the subimago; unless the species is quite distinct from all others, subimaginal descriptions may tend to be misleading and may frequently cause misinterpretations. However, Traver (1932) broke with custom and set up a subimago as the holotype of *L. intermedia,* figuring the genitalia and various nymphal structures. By 1935, male imagoes had been reared, and *intermedia* was then found to be distinct on the basis of genital differences from all others in the genus, except *L. grandis.* Dr. Traver designated the genitalia of this complex as the "distinctive 'scarf' type" of penes; in her key to the species she separated *intermedia* and *grandis* from *austrina* and *collina* (bearing the "hooded type" penes) by the relative length of the reflexed spurs. In the former group, these spurs extend anteriorly from the distal end of the penes to the base of the notch between the paired penes, while in the latter, the spurs are relatively shorter. The length of the decurrent appendage of the penes is often difficult to determine, and the terms "scarf type" or "hooded type" to describe the appearance of the penes can be misleading. Absence of a brown cloud in the forewing or presence or absence of a brown stain in the stigmatic area of this wing was used by Traver to distinguish *intermedia* and *grandis* from the remaining species of the genus. We have found the in-

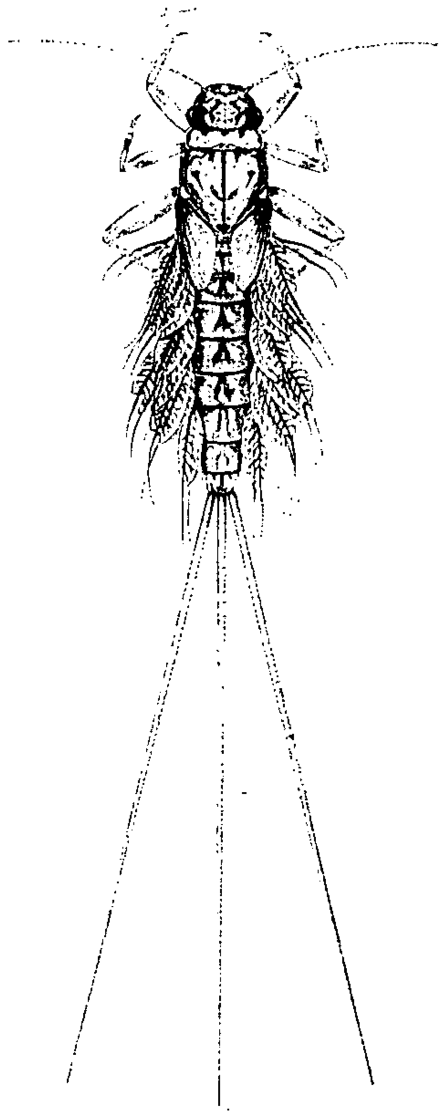


Plate 13. *Leptophlebia intermedia* (Traver), nymph

tensity of color in the stigmatic area to be a very unreliable trait for separating *intermedia* from other species. *L. grandis* is separated from *intermedia* by its larger size and by its short middle caudal filament. The median tail in *grandis* is only one-half the length of the laterals, while in *intermedia* the middle filament is two-thirds the length of the outer ones. Nymphs and females must be identified with utmost caution as the differentiating characteristics are not all clearly defined.

GEOGRAPHIC DISTRIBUTION. On the basis of genitalia, *intermedia* is seen to be most closely related to *grandis*. The distribution of these two species bears out this conclusion as to their relationship, both having been recorded from North Carolina, *grandis* from the Piedmont region and *intermedia* from the Coastal Plain. Since Traver's record of *grandis* in 1932, there have been no other reports of the species having been collected. Circumstantial evidence points to synonymy of the two species; however, we are not yet taking the action of equating them.

In Florida, *L. intermedia* is rather widely distributed over the state; in fact, in the continental area it is found from the eastern portion to the western borders. In the peninsular region, the species is much more sporadic in occurrence, but this "spotty" distribution is entirely the result of ecological factors. We have recorded the species from the following Florida counties (map 17): Alachua, Bay, Columbia, Gadsden, Hamilton, Jackson, Jefferson, Leon, Liberty, Okaloosa, Santa Rosa, Wakulla, and Walton. Wurtz and Roback (1955) have also taken the species in Escambia County.

ECOLOGY. Florida nymphs of *Leptophlebia intermedia* are limited to slow streams, preferably small to medium-sized creeks. The range of this species in the state is probably limited by physiological as well as physical barriers. Flowing water is relatively scarce in most of the regions from which no specimens have been taken. From the standpoint of mayflies, the unproductive southeastern regions and the flat pinelands and palmetto-scrub area of the East Coast prohibit the existence of *Leptophlebia intermedia* in this geologically newly arisen area.

With their enormous expanse of gills, *L. intermedia* nymphs are poorly adapted for swift water, and one seldom finds them elsewhere than in the quieter parts of the streams or pools recently cut off from streams. Even though highly tolerant of standing water and conditions where there is little oxygen and much silt, the nymphs occur only in streams or associated waters, and the size of the streams is no criterion for the occupancy of their bed. The presence of the nymphs seems only to demand a permanently flowing stream with quiet areas near the banks, pools where dead leaves may accumulate, or submerged mossy banks where the nymphs crawl amid the bases of the plants. In those parts of the stream where there is submergent vegetation unlike that described above, the nymphs are usually absent. If both conditions obtain in a stream, that is, if mossy banks and leaf debris are present, the chances are fairly good that *L. intermedia* nymphs will be there. A small creek near Gainesville yielded more than 200 nymphs in their last instar from an area not more than two feet long, three feet wide, and six inches deep. This was a slough of the main stream and connected with it over a shallow sandbank. In this puddle, dead leaves were piled several layers deep, the lower layers partially buried in silt; the first dip with a coffee strainer yielded 23 nymphs. Subsequent dips produced an average of 15 nymphs until most of the leaves had been cleared out, and only then did the catch fall off to four or five nymphs per haul. Downstream a hundred yards, another pool, in the lee of the root of a moderate-sized tree, yielded 100 more nymphs without clearing out more than half the debris. The latter pool was smaller than the former yet seemed just as rich in mayflies.

Dr. Ferris Neave (1930) studied the migratory habits of *L. cupidus* nymphs in Manitoba. During the spring, this species migrates into and up the temporary streams formed by melting snow, even leaving the water and crawling along the banks in its urgency to move upstream. The nymph may migrate as much as 300–400 yards per day, which is remarkable in the instance of so small an insect that must walk this distance and especially remarkable in an aquatic and normally slow-moving type. Clifford et al. (1979, pp. 1027–1028) reported on the spring migration of the same species in an Alberta stream. They wrote:

> In April, during and shortly after the ice goes out, nymphs move to the shore and then start following the shoreline upstream. All sizes of nymphs participate in the migration. The nymphs follow the main stream's shoreline upstream until it bends in towards a tributary, usually small vernal tributaries. This leads the nymphs out of the main stream and into the tributaries and subsequently into the marshy regions drained by the tributaries. Most tributaries have about the same water temperature as does the main stream. The nymphs move up all tributaries with seemingly no preference. Usually by 1 June, most of the population is extensively dispersed in the marshy areas drained by the tributaries. However a residual population remains in (and emerges from) the main stream. . . .

> . . . The immediate adaptive value of the movements would seem to allow the nymphs to escape from the springtime turbulence of the main stream. Other workers have suggested that the springtime movements into the marshes allow the nymphs to exploit a more plentiful food supply or expose the nymphs to warmer water and hence accelerate development . . . there was no evidence that marsh nymphs ingested greater amounts of detritus and diatoms than did nymphs of the main stream.

In Florida, we have noted no such migrations and rather doubt that they occur here, but there may be smaller migrations of the nymphs from the streambed proper into pools of the type from which so many specimens have been collected. The concentration of mature nymphs seems to indicate something of the sort, particularly since younger nymphs are more frequently encountered in the leaf drift along creek margins than in the pools, while the reverse is true of the mature nymphs.

Connecting with Hatchet Creek, near Gainesville, there is a fairly large, stagnant canal from which water disappears during the dry season. The canal passes through a rich mesophytic hammock, and its floor is covered with leaves partially buried in silt. Numerous nymphs in their last instar were collected here in February; a visit to the canal in April produced none. Prior to their emergence the mature nymphs must certainly have migrated into the canal, since no mature nymphs were found here on other occasions; this migration probably is not comparable to that studied by Neave and by Clifford and others as their nymphs migrated upstream against swift-flowing water and were not all mature. We believe that quiet water is essential for the emergence of *L. intermedia* and that maturation of the gonads acts as a stimulus, forcing the nymphs to find this ideal situation. The young nymphs, often found in small numbers with the more abundant mature ones in quiet water, have probably wandered there accidentally.

The adults are less tolerant of desiccation than many mayflies and are confined to mesophytic conditions where the humidity is rather high. If the subimagoes are removed from this moist environment, the final molt to the adult stage is almost impossible.

Most common associates of *L. intermedia* nymphs in the leaf drift are other genera of ephemerids, nymphal Odonata, chironomid larvae, and the small snail *Physella*. Mayfly nymphs, however, far outnumber their insect coinhabitants of these detritus drifts.

SEASONAL DISTRIBUTION AND LIFE HISTORY. In general, seasonal changes appear to have no great effect on mayfly life histories in Florida, but *Leptophlebia* seems to be one of the exceptions. This genus is the earliest of those mayflies of Florida that are seasonal. Its sexual activity gradually increases to a maximum in February and March, and then gradually declines. *L. intermedia* appears to be univoltine.

There is much overlapping of mature forms with immatures. In February we collected numerous nymphs of *L. intermedia* from a small creek near Gainesville; here, mature nymphs outnumbered very young and half-grown nymphs almost 10 to 1. This would seem to indicate that in Florida this species, unlike the majority of mayflies, has a definite maximum emergence period, with most of the individuals maturing in February to March but with limited emergences occurring later in the spring.

The duration of egg development and nymphal life of *L. intermedia* is unknown but seems to be one year. This assumption is based on the concentration of mature nymphs during one definite period and has resulted in our conclusion that the species is univoltine. Many mature specimens have been reared to the adult stage in the laboratory, but we have found it rather difficult to keep younger nymphs alive for more than two months. Clifford et al. (1979) reported that they observed cleaving eggs of *L. cupida* within three days after fertilization. At 20°C hatching started between 10 and 14 days after oviposition, with hatching continuing for at least 43 days. These authors found that in the laboratory when the temperature was maintained at 20°C there were 34 nymphal instars. They stated, "Probably, however, there is no fixed number of nymphal instars for *L. cupida*, the 34th being just one of several instars in which the nymphs, given the proper environmental cues, might transform." We believe that it is likely that *L. intermedia* requires approximately the same number of instars in Florida waters as *L. cupida* required in the laboratory.

Just prior to metamorphosis, the mature nymph moves to the surface, still slowly vibrating its expansive gills. With its mesothorax projecting from the water, it begins to strain, the effects of which are soon evident, for a longitudinal split appears down the thorax. Pulling mightily by bracing itself against the nymphal skin, the subimago gradually extricates the wings from their sacs, all the time moving its abdomen from side to side, a movement apparently caused by the tremendous exertion necessary to free the body from the nymphal exuviae. As the wings are pulled free, it can be seen that they are inverted, that is, the costal border faces ventrally. The sudden release of the wings causes them to snap into place and at the same time to twist into their normal position. Immediately after emerging, the subimago is a dull gray with rather translucent wings, but after a short time the animal begins to darken until it is quite blackish. The time consumed between exposure of the split mesothorax and removal of the wings varies from one to three minutes. Once the wings are freed the animal rests, supported partially by the surface film and partially by the floating nymphal skin. During this resting period the wings are frequently vibrated. Having regained its strength, the subimago begins to walk away from its exuviae and slowly pulls its three caudal filaments from their sheaths. Its tails, when freed, are slightly raised above the surface of the water. After resting again for a short time, the winged insect flies or crawls to some nearby support to await the bodily changes that will force it either to undergo a final molt or to perish.

To undergo its imaginal molt, the subimago establishes itself firmly on its support and begins to strain at the mesothorax. The straining is probably localized in this part of the body because of the tremendous wing muscles located in the synthorax. The contraction of these muscles forces the wings to spread outward until they touch the support. As the adult pulls itself from its subimaginal skin, the wings are gradually drawn in toward the body until they lie alongside the abdomen and are folded fanwise. The withdrawal is slow. When the wings are almost freed, the creature releases its adult legs from the attached skin, fastens its claws to some object, and pulls the wings free. Immediately, the wings are raised, but only to about a 60° angle with the horizontal. The adult rests a moment, flexes its wings, approximates them in the usual manner, and then slowly walks away, pulling its tails out as it moves. The subimaginal exuviae are left behind as a gray skin with crumpled sacs, the sole remaining evidence of the subimaginal wings.

We have not been able to observe mating flights of this species, but male adults kept in the laboratory became very restless in the afternoon between 2:00 and 4:00. In regard to *L. cupida* Dr. Traver (1925, p. 217) observed that:

> The "stag" flights usually begin at about 3:00 P.M. and last intermittently till nearly 7:00 P.M. At no time were more than a dozen insects seen flying at once, and none of these swarms were directly over the water. One favorite location for this dance was a small grassy plateau about six feet from the water's edge, upon which the last lingering rays of sunlight fell. Here, in the sun's departing beams, the dance went on and on. Often the insects were rising not more than 7 or 8 feet and then with

> the undulating downward sweep, coming within a few inches of the grass. The wings glistened brightly in the light and were a better guide to the location of the imago than the tails, which could barely be seen a few feet away. The downward movement is apparently a mere falling with the force of gravity, the tails and forelegs serving to increase resistance. Then the insect slowly but surely rises again to repeat the performance. There is a rhythmic swing to the dance, though each dancer keeps his own time.

Leonard and Leonard (1962) observed mating flights of the same species taking place from late afternoon to dark in Michigan. They noted that females deposit their eggs by repeatedly tapping the surface with the tips of their abdomens as they fly low over the water. Clifford et al. (1979) claimed that females always returned to the main stream to oviposit rather than remaining in the marshes or other lentic habitats from which they had emerged. They estimated that oviposition by *L. cupida* required less than five minutes, and they observed that the process occurred during daylight hours, in the morning and in the afternoon.

Two female subimagoes reared in the laboratory failed to undergo their final molt. Kept under a bell jar, one of these lived as a subadult for approximately 50 hours and 30 minutes; the second for 95 hours. Tests for longevity of adults kept under bell jars showed that males remain alive for about 35 or 40 hours after the subimaginal molt; females live 80 to 90 hours after this molt. Traver's study of *L. cupida* showed that the length of adult life when the insects were kept in captivity at room temperature was 24 hours or less. Clifford et al. (1979) concluded that in Alberta the subimago and imago stages together lasted about 48 hours.

BEHAVIOR. The nymphs of *L. intermedia* feed on detritus, diatoms, and algae, scraping the surface of the decaying leaves and indiscriminately eating the animal, vegetable, or mineral material on the leaves. Only particles that are too large are not eaten. Feeding is an almost continuous process. Clifford et al. (1979) found that insofar as nymphs of *L. cupida* are concerned, on a yearly basis, nymphs ingested 95.6% detritus and 3.9% diatoms. They concluded that it is unlikely that nymphs select detritus over diatoms but that the relative amounts of detritus and diatoms in the gut cavities simply reflect the relative amounts of these small particle food items available to the nymphs.

Nymphs are more or less negatively phototactic, while the reverse is true of the subimago and imago. In the laboratory, nymphs seek the dark underside of any materials in their container during the day and whenever artificial light is cast on them. If left in a dark room, they soon find their way to the upper surface of the leaves, but as soon as a light is turned on, they again scurry away into some dark crevice. Nymphs about to emerge undergo a phototactic reversal and crawl to the upper side of leaves or onto sticks, logs, or any other available support that is near the surface of the water.

Paraleptophlebia Lestage

Berner 1950, pp. 123–124; 1975, pp. 39–40; 1977, p. 152.
Burks 1953, pp. 87–90.
Edmunds, Jensen, and Berner 1976, pp. 230–233.
Peters and Edmunds 1970, pp. 175–176.
Unzicker and Carlson 1982, pp. 3.58–3.60.

Paraleptophlebia was described in 1917 to receive certain European mayfly species which Lestage felt should not be retained in *Leptophlebia*. His genus was not recognized by American students until 1934, when Traver transferred to it all the North American species (except *gracilis* and *johnsoni*) that had formerly been placed in *Leptophlebia*.

For a time the status of the genus *Paraleptophlebia* was in question, at least insofar as the North American species were concerned. Ide (1935; 1937; and 1940) and Ide and Spieth (1939) disregarded the name, but at present the genus is recognized as a valid category for those species from North America that can be separated from *Leptophlebia*. *Paraleptophlebia* adults may be differentiated from those of *Leptophlebia* by the length of the terminal (median) caudal filament, which is shorter and thinner than the cerci (outer filaments) in *Leptophlebia* (except for *L. johnsoni*), while in *Paraleptophlebia* the filaments are subequal in length. The male genitalia of the two genera are different in shape and in their decurrent appendages. The nymphs can be separated by the form of their gills.

Paraleptophlebia volitans (McDunnough)

(FIGS. 19, 40, 60, 94, 135. MAP 16)

Berner 1950, pp. 124–128; 1958, p. 30; 1975, pp. 153–155; 1977, p. 40.

Burks 1953, p. 93.
Carlson 1980, p. 82.
Jones 1977, p. 66.
Peters and Jones 1973, p. 246.
Schneider 1962, p. 132; 1967, p. 203.
Unzicker and Carlson 1982, p. 3.57.
Wurtz and Roback 1955, p. 193.

TAXONOMY. *Paraleptophlebia volitans* was described by McDunnough in 1924 from Quebec. On the basis of genital structure, it stands alone. The earlier descriptions of the penes given by Traver (1935) and Burks (1953) were misleading as they represented the decurrent appendages as slender, anteriorly directed rods that are U-shaped at their free ends. A subsequent study of the genitalia (Berner 1975) showed that the decurrent appendage is expanded at its anterior end and appears to open cornucopia-like. The anterolaterally directed opening is edged inwardly on the ventral surface with a row of fine teeth. Several other species of *Paraleptophlebia* also have reflexed appendages on their penes, but in *volitans* the shape of these structures is unique. On the basis of the presence and shape of the appendages, *volitans* may be closely related to *P. guttata*.

The nymphs from northwest Florida are fundamentally like those of the north-central part of the state but differ in having a brownish tinge to the gills; however, adults from the two regions are identical. Some years ago, Dr. F. P. Ide kindly compared Florida nymphs with those from Canada. He wrote that the Florida species is "very close to our *P. volitans*, which occurs all over the Lauretian Shield region of Ontario. The legs are somewhat hairier and the abdominal markings more prominent than in *P. volitans*." By rearing and thus correlating nymphs and adults, Dr. Ide's identification was fully verified.

The nymphs of *P. volitans* and *Habrophlebiodes* are very similar and are easily confused unless carefully examined. The easiest method of distinguishing between them is by means of gill structure. In *volitans*, the gills each bear a bifurcate trachea which has no lateral branches. Although the gills of *Habrophlebiodes brunneipennis* also have bifurcate tracheae, there are prominent lateral branches from the main trunks. Unzicker and Carlson (1982) also differentiate *Paraleptophlebia* and *Habrophlebiodes* using the depth of an emargination of the labrum as a criterion: that of *Habrophlebiodes* is moderately deep, that of *Paraleptophlebia* shallow.

GEOGRAPHIC DISTRIBUTION. There is nothing in the appearance of *P. volitans* to suggest that it is an unusually vagile form, yet it has been taken in an area stretching from Ontario to Florida. The species has been recorded from Alabama, Florida, Georgia, Louisiana, Mississippi, and South and North Carolina.

In Florida, *P. volitans*, *Leptophlebia intermedia*, and *Habrophlebiodes brunneipennis* have an almost identical distribution over the northern portion of the state. *P. volitans* extends southward only to the area around Gainesville; eastward, it has been taken in the western part of Nassau County; westward, it is distributed to the state border. We have records from the following Florida counties (map 16): Alachua, Bay, Columbia, Escambia, Gadsden, Hamilton, Holmes, Jackson, Jefferson, Leon, Liberty, Nassau, Okaloosa, Putnam, Santa Rosa, and Walton.

ECOLOGY. The ecological distribution of *volitans* is almost identical with that of *Habrophlebiodes brunneipennis*. Ide (1930) and Gordon (1933) allotted a few brief sentences to a discussion of the environment of *volitans*. Ide (1935, pp. 64–65) studied the effects of temperature on the distribution of mayflies in a stream, and, although *volitans* is present in the area in which Ide worked, he did not mention its occurrence in any of the streams he examined. However, his conclusions, drawn in part from a study of other species of *Paraleptophlebia*, are very interesting, particularly the following:

> The facts brought out by this study appear to throw some light on the subject of the geographical distribution of mayflies. A spring stream, especially near its source, supplies a remarkably uniform environment for mayfly nymphs, wherever the stream occurs—in warm climes, at high elevations on mountains, or in the north. This uniform environment provides a pathway by which organisms may extend their range wherever this environment is present. As one goes north, however, the warm-season forms will be eliminated and the forms of the source, or near it, will still be accommodated further downstream, and, provided the source becomes colder, there is an opportunity for new forms to appear at the source. The forms near the source are those with a northern distribution in general, and those lower down have a more southerly distribution.
>
> It is probably safe to say that a spring stream in its fauna, taken from the warmer reaches to the source, recapitulates south to north distribution, in the way that a mountain in the

> torrid zone gives in its fauna and flora, taken from the foot to the top, roughly a vertical section of geographical distribution from torrid to frigid zone.

In Florida, the nymphs of *P. volitans* live amid the leaf debris in streams where the current is slow to moderately swift. Though most commonly found in these situations, they may also be taken from riffles, submerged sticks, logs, and vegetation, but they seldom venture into swifter waters. The creeks supporting populations of *volitans* are not more than three to four feet at the deepest point, and the nymphs tend to remain in the shallower areas. The small streams draining the ravines of the Tallahassee Hills region, although heavily populated with *Habrophlebiodes brunneipennis*, have no *P. volitans*. Just west of the region, the latter species is found in the larger streams emptying into the Apalachicola River. In these larger, but shallow, streams the nymphs can commonly be found near the banks among the roots of terrestrial plants that project into the water.

The sand-bottomed streams from which nymphs have been taken are mostly circumneutral or acidic, and they usually drain flatwoods. The water is often tinted, the tint ranging anywhere from almost colorless to the color of strong tea.

Subimagoes are confined to moist, heavily shaded areas along the creek banks or to any other shaded area above the stream where the humidity is very high. The subimago molts only with great difficulty in the laboratory; in fact, it is rare for a male under such conditions to complete its final ecdysis successfully. Even specimens placed under bell jars in high humidity failed to shed, and attempts made in a dry atmosphere failed as well.

Dr. B. D. Burks, while studying Ephemeroptera at the Illinois Natural History Survey, found that subimagoes of the species do not experience any difficulties in molting. He discovered that the subimagoes must be kept in fairly dry jars in cool, dark places, because they need to lose moisture. We tried his method, but on the morning following emergence, as usual, the insects lay dead and withered on the bottom of the container. Of all species of mayflies with which we have dealt, *volitans* has the most difficulty in completing the last molt in the laboratory.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Available records for Florida adults indicate that in this region the species emerges throughout the year; however, in Canada (Algonquin Park, Ontario), Ide (1940) reported that emergence takes place in the latter half of July and in August. Traver, in recording the species from the South, did not give the date of collection. Among the Florida specimens, there are imagoes taken during the following months: January, February, March, April, May, June, July, September, October, and November. The peak of emergence is probably during April and May. As might be inferred from these data, nymphs of all ages can be taken during any month of the year. There is some evidence that nymphs in a particular stream may have a tendency toward transformation during a definite period, but there is so much overlapping of instars that this tendency is usually obscured.

Little work has been done on the life history of *Paraleptophlebia* except for the description of last-instar nymphs for taxonomic reasons. The eggs of the genus have been described by Koss (1968).

From Ide's data on the emergence of *P. volitans* in Canada, it is obvious that the life history in that northern region requires a full year. We doubt strongly that the same length of time is needed in the warm Florida waters. Several attempts to hatch eggs have been unsuccessful, perhaps because the females from which the eggs were taken may not have mated. Emergence records and rate of growth of nymphs in the laboratory lead us to suspect that six to eight months may be more than sufficient for nymphal development.

Emergence, as observed outdoors, occurs normally in late afternoon, about two hours before sunset. In the laboratory, most subimagoes appeared at about the same hour, but in some instances individuals have transformed as late as 7:30 P.M. during April, while in October transformation occurred between 6:20 and 7:00 P.M. Subimaginal life lasts 12 to 14 hours; the male imago lives a day longer, and the female may sometimes survive as long as two or three days after this last molt.

We have never observed mating flights of this species, but that of another is briefly treated by Morgan (1913, p. 392), who stated, "Mating flights of *Leptophlebia* [*Paraleptophlebia*] *praepedita* have been seen in the middle of a sunny afternoon, and at two, four and five o'clock of bright afternoons in May and June. None of these rose higher than 15 feet and two of the swarms did not fly more than six feet above the ground. One entire swarm which was captured contained forty males and one female." We have observed swarms of *P. guttata* near Highlands, North Carolina, flying at a height of about 15 feet directly over a stream in bright sunlight in the middle of the afternoon. The swarms consisted entirely of males.

BEHAVIOR. Plant matter in one form or another probably constitutes the bulk of the food of *P. volitans* nymphs. When they are placed in a pan with only dead leaves that have been submerged long enough to become softened, they do quite well and have been kept alive in the laboratory for as long as six weeks. Since they are commonly found in leaf drift, it might be presumed that they are detritus feeders. They have also been taken from places where algae were quite abundant, and these likewise must play an important part in the nymphal diet.

Discussion of peculiarities of movement among the Leptophlebiidae may be found in the section dealing with *Habrophlebiodes brunneipennis.* The leptophlebiids, when placed in a dish of water, spread their gills and are frequently caught in the surface film where they float helplessly.

As with most other ephemerids, the nymphs are negatively phototactic; the adults are the reverse. This characteristic is not pronounced in adults and subimagoes. We have "lighted" at stream banks where we knew *volitans* was emerging from the stream, but not a specimen was attracted to the lighting sheet; on the other hand, when adults are brought into the laboratory, there is a definite orientation to light, and subimagoes emerging in cages are immediately attracted to the most strongly illuminated side.

BEHNINGIIDAE

The family Behningiidae consists of three interesting but rare and little-known genera of mayflies. Taxonomic reviews of the family are found in Edmunds and Traver (1959) and Peters and Peters (1977).

The behningiid nymphs are unique among the Ephemeroidea in that the mandibles lack tusks and the forelegs are not adapted for digging. The setose meso- and metathoracic legs are modified to serve as protective devices for the gills. The gills are ventral; those on segment I are single and are longer than those on the other segments. The male adults have long cylindrical penes that are longer than the forceps. The legs of both sexes are feeble and twisted.

The eggs are by far the largest known of any mayfly. The eggs, as described by Koss and Edmunds (1974), lack polar caps and have a weakly developed large-mesh reticulation and funnelform micropyles. The suprachorionic sperm guides are funnel-shaped excavations.

The family is Holarctic in distribution, ranging from Poland to Siberia and in North America.

Dolania Edmunds and Traver

(PLATE 14. FIG. 14)

Berner 1977, p. 48.
Edmunds, Jensen, and Berner 1976, p. 274.
Edmunds and Traver 1959, p. 43.
Koss and Edmunds 1974, p. 267.
McCafferty 1975, pp. 451–452.
Peters and Peters 1977, p. 409.

Edmunds and Traver (1959) established *Dolania* for *D. americana* found in the Savannah River and its tributaries in South Carolina. The adults were briefly described by Edmunds et al. (1976).

Typical of the bizarre behningiid nymphs, *Dolania* lacks mandibular tusks and the anterolateral margins of the head and pronotum are crowned with short, densely packed spines. The prothoracic legs are short and resemble the labial palpi. The legs lack tarsal claws and the gills are ventrally oriented. Legs of adults of both sexes are feeble and more or less twisted. The penes of males are at least twice as long as the genital forceps. The eggs have adhesive material only along the equatorial zone, and the walls of the sperm guide are gradually sloping (Koss and Edmunds 1974).

Dolania is known from northwestern Florida, southwestern Louisiana, Georgia, and South Carolina.

Dolania americana Edmunds and Traver

(PLATE 14. FIG. 14. MAP 12)

Benke et al. 1984, p. 62.
Berner 1977, p. 48.
Edmunds, Jensen, and Berner 1976, pp. 275–276.
Edmunds and Traver 1959, p. 46.
Harvey, Vannote, and Sweeney 1980, pp. 211–230.
Peters and Jones 1973, p. 267.
Peters and Peters 1977, pp. 409–438.
Soldán 1979, pp. 636–641.
Sweeney and Vannote 1982, pp. 810–821.
Tsui and Hubbard 1979, pp. 119–123.

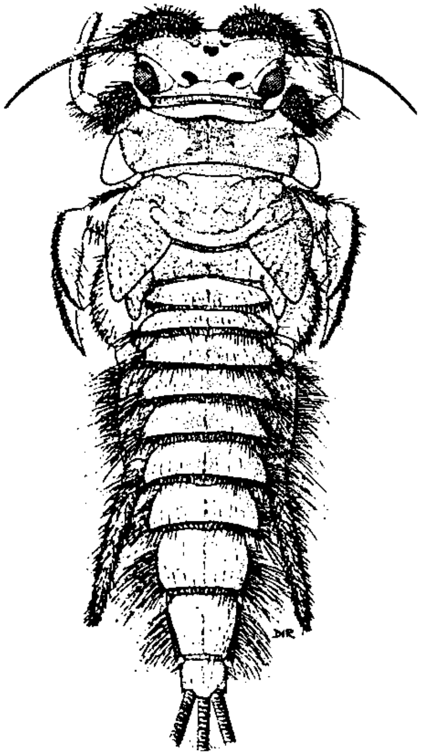


Plate 14. *Dolania americana* Edmunds and Traver, nymph (from Edmunds and Traver 1959)

TAXONOMY. *Dolania americana* was originally described from nymphs collected from the Savannah River drainage system during a study conducted by the Academy of Natural Sciences of Philadelphia. The adult taxonomy of the species has never been treated formally.

The unique nymphs, which cannot be confused with any other North American species, are generally light yellowish dorsally and pale yellow ventrally and are covered with numerous dark golden hairs and spines. The head is crowned with dark, golden brown spines, and the legs are thickly adorned with long, light brown or dark golden brown setae.

The females, which never molt to imaginal state, are polymorphic. The dark female morph has a dark brown head and an almost black thorax. The light female morph generally has a whitish head and thorax. The legs of the dark female are brownish, but those of the light morph are whitish. The wings of both morphs are white, but the basal sclerotized portions are darker in the dark female. Occasionally, intermediate color forms between the morphs do occur (Peters and Peters 1977). The males, which do molt, have the same general body color as the light female morphs except that their wings are purplish and the thoracic nota are slightly darker. The long cylindrical penes are washed with purple, becoming progressively darker distally. Soldán (1979) has described the internal anatomy of both nymphs and adults.

GEOGRAPHIC DISTRIBUTION. *Dolania americana* has a limited distribution, having been recorded only from the Savannah River drainage system in South Carolina and Georgia (the river is the boundary between the two states), the Satilla River in Georgia, and from various streams in northern and northwestern Florida. We have records of the species occurring in the following Florida counties (map 12): Dixie, Holmes, Lafayette, Okaloosa, Santa Rosa, Walton, and Washington.

ECOLOGY. The nymphs of *D. americana* live in relatively clean, circumneutral to slightly acidic, sand-bottomed, intermediate-sized streams and rivers. Morphologically, the nymph is well adapted for burrowing in loose and continuously shifting sand, as it possesses various protective structures to counteract the abrasive actions of the sand grains. The burrows generally occur in the top two inches of the sandy substrates. In the Blackwater River of the Florida panhandle, the nymphs occur abundantly in the submarginal and midstream areas, with mature nymphs being more common in the latter. The nymphs feed chiefly on chironomid larvae (95%); other foods are microcrustacea, ceratopogonid larvae, nematodes, and a rarely taken tardigrade (Tsui and Hubbard 1979).

SEASONAL DISTRIBUTION AND LIFE HISTORY. The nymphs of *D. americana* occur throughout the year in the Blackwater and Shoal rivers. The species has previously been reported to have a univoltine life cycle (Edmunds et al. 1976; Tsui and Hubbard 1979). A detailed study of the life history and development of *D. americana* from the Upper Three Runs River in South Carolina by Harvey et al. (1980), however, revealed that the species has a two year life cycle. Eggs deposited in early June hatched the following spring. Nymphal growth occurs continuously throughout the year although there are seasonal differences in the amount of growth, which is greatest in nonwinter months, when stream temperatures exceeded 15°C. Females generally grow more efficiently and faster than males during all seasons (Harvey et al. 1980). In the Upper Three Runs, the nymphs require 12–14 months to mature.

In the Blackwater River, adult emergence generally occurs over a two- to three-week period that begins between the end of April and the middle of May (Peters and Peters 1977). Emergence may stretch into early June, with a few adult stragglers seen in the flight patrol. In the Upper Three Runs, *D. americana* emerges over a one-week period that generally takes place within the first two weeks of June (Harvey et al. 1980).

Emergence of *D. americana* has been suggested by Peters and Peters (1977) to be photoperiodically entrained, with temperature the phase setter and light intensity the synchronizer. More experiments are presently being conducted by both workers on environmental parameters relative to the emergence pattern of the species.

Adult fecundity of *D. americana* is low, probably the lowest in all the mayflies. Harvey et al. (1980) counted an average of 77 eggs per female adult, with a range from 44 to 148 eggs from 18 dissected female subimagoes. Peters and Peters recorded a mean average of 91 eggs from a total of 82 female adults. Although *D. americana* produces fewer eggs per female than has been reported for any other mayfly species, the individual egg is at least 10 times heavier than reported for any other mayfly. Harvey et al. (1980) suggested that the low fecundity–large egg reproductive strategy of *D. americana* may be related to the species' trophic habit (that it is a predator). Soldán (1979), however, attributed the low fecundity–large egg trait of the species to the unique ontogeny of its ovaries: only a single egg matures in an ovariole, and some ovarioles disintegrate in older and mature nymphs.

The incubation period of eggs is about 10 months. Eggs dissected in June, fertilized, and kept in a constant temperature water bath simulating the temperature regime of the Upper Three Runs, started hatching in April and continued through May of the following year (Harvey et al. 1980).

BEHAVIOR. As previously mentioned, the nymphs of *D. americana* lack specialized structures (i.e., modified forelegs, mandibular tasks) for burrowing, which most ephemeroids possess. Such structures for digging are not very useful in the loose, continuously shifting sand that is the habitat of *Dolania* nymphs. Instead, the nymphs have tremendously long spinous hairs over their bodies to protect them from the abrasive actions of the sand grains. Edmunds et al. (1976, p. 274) discussed the nymphal habits of *D. americana* as follows:

> When burrowing, the nymphs have no dorsal-ventral orientation. Forward motion is effected by the burrowing action of the forelegs and the elongated labial and maxillary palpi. The head functions as a bulldozer blade and also protects the mouthparts and the eyes. The thoracic prolongations and the drawn up, chelipodlike middle legs box in the bulky ventral anterior half of the nymph, thus increasing its efficiency as a burrower. The trailing hind tibiae and tarsi lie just below the ventral rows of gills and the elongate first gill is held motionless at the sides, thus the gills are free of sand at all times. Gills 2–7 move rhythmically to produce a constant current.

The nymphs are predaceous, feeding mainly on psammophilous chironomid larvae. The nymphal population of *D. americana* in the Blackwater River consists of individuals of various sizes year-round. Nymphs of all sizes consume small chironomid larvae; the larger nymphs, however, eat an increasingly wider range of chironomid sizes. Such size variability within the nymphal (predator) population might be an important adaptive resource strategy, as the feeding habits of the nymphs appear to a certain extent prey-size dependent, allowing better partitioning of the available food resources (Tsui and Hubbard 1979).

Peters and Peters (1977) discussed in detail the adult habits of *D. americana* in the Blackwater River. They observed that the adults usually fly at low speed in a back-and-forth horizontal pattern some three to six feet above the river. After mating, female subimagoes display a separate oviposition activity. The female faces upstream when ovipositing and deposits her eggs in areas of strong current. Oviposition is accomplished in a matter of seconds. Unmated females continue flying until they die. Male imagoes exhibit two types of flight patterns, the horizontal patrol flight and a vertical swarming flight. In the horizontal patrol flight, which is similar to the "Type C" of Brodskii (1973), the males simply fly upstream and downstream in a horizontal fashion. In flight, the body is horizontal, and the prothoracic legs are pointed straight forward; the caudal filaments flow backwards and are slightly raised and spread. In the vertical swarming flight, which is similar to "Type A" of Brodskii (1973), the males fly up vertically and then drop straight down.

In mating flights of *D. americana*, as observed by Peters and Peters (1977), the male imago flies up behind a female, assumes a nearly horizontal position under her, bends the tip of his abdomen up and recurves his genitalia forward over his body in alignment with the female abdomen. Copulation is accomplished within 1–6 seconds.

Adult emergence of *D. americana* is highly synchronous. The adaptive significance of synchronous emergence among aquatic insects is in the forefront of subjects being considered by aquatic ecologists. It has been suggested that emergence synchrony increases the probability of finding a mate (Corbet 1964), and maximizes the species chance for reproduction (Sweeney and Vannote 1982). Sweeney and Vannote suggested the predator satiation hypothesis as a possible explanation of the adaptive value of emergence synchrony in *D. americana*. According to this hypothesis predator satiation occurs when the quantity of a particular prey item at a given time far exceeds the potential number that can be taken by fixed density of local predators. The predators are satiated, and the remaining prey survive to reproduce, providing prey densities remain above the level necessary for satiation. Hence, the hypothesis predicts an inverse relationship between prey mortality due to predation and prey availability above the level needed to satiate as long as the number of predators remains more or less fixed for a given time interval. In *D. americana*, Sweeney and Vannote (1982, pp. 820–821) found that during emergence "[t]he percentage of adults that succumb to predators, aerial and/or aquatic, on a given day is inversely related to the total number of adults available as prey each day. This inverse relationship supports a predator satiation hypothesis concerning the adaptive significance of reproductive synchrony in this species. Thus an individual adult *D. americana* maximizes its chance for successful reproduction by emerging synchronously with other members of its own cohort."

POLYMITARCYIDAE

The widespread family Polymitarcyidae is well represented in the Americas, especially in South America where the subfamily Campsurinae has speciated extensively. The New World species of Campsurinae adults are characterized by the degenerative condition of the middle and hind legs to the point that they have become nonfunctional. Most species appear to have mass emergences and very short mating flights, which are crepuscular or nocturnal. The nymphs are specialized for burrowing.

Tortopus Needham and Murphy

Berner 1950, pp. 96–97 (*Campsurus*); 1959, p. 54; 1977, p. 52.
Burks 1953, p. 28.
Edmunds, Jensen, and Berner 1976, p. 300.
Ide 1955, pp. 15–16.
McCafferty 1975, p. 489.
Peters and Jones 1973, p. 246.
Scott, Berner, and Hirsch 1959, pp. 205–213.
Traver 1950, pp. 596–604.
Unzicker and Carlson 1982, pp. 3.31–3.35.

When *The Mayflies of Florida* was published in 1950, Traver's paper (1950) concerned with *Campsurus* and *Tortopus* was not yet available. The Florida species was, at that time on the basis of current information, assigned to the genus *Campsurus*. With the clarification of generic assignment of North American species, it is now obvious that the Florida form is a member of *Tortopus* because both middle and hind legs have all segments, even though they are vestigial, and the male genitalia possess a pair of clawlike appendages extending laterally from the forceps base.

Tortopus was described by Needham and Murphy in 1924 from Peruvian specimens. When Traver studied the South American species and those of Central and North America and reviewed Dr. Ulmer's paper (1942), she realized that it was necessary to assign four of the species to *Tortopus*. No further studies of the taxonomy of the genus in depth have been made since Traver's, although McCafferty is in the process of reviewing the Nearctic species (pers. comm.).

The various species of this New World genus are distributed in the southeastern and central parts of the United States, north into central

Canada, and southward through Central America into several countries of South America.

Tortopus incertus (Traver)

(FIGS. 13, 36, 172, 173. MAP 18)

Berner 1950, p. 97; 1958, p. 29; 1977, p. 52.
McCafferty 1975, p. 491.
Peters and Jones 1973, p. 246 (*Tortopus* sp.).
Scott, Berner, and Hirsch 1959, pp. 205–213.
Tsui and Peters 1974, pp. 349–356.
Unzicker and Carlson 1982, pp. 3.31–3.34.

TAXONOMY. When Traver described *Tortopus incertus*, she stated that it might be synonymous with *puella* (Pictet), described in 1843 from New Orleans but not since reported. Edmunds et al. (1976) in Appendix 1 concluded that the name is "not applicable with confidence to any known species." We are, therefore, accepting this conclusion and considering Traver's name of *incertus* to be the acceptable one for the Florida species.

Traver's adults were collected at Spring Creek, Georgia, a tributary of the Flint River now drowned in Lake Seminole, which was formed by the impounding of the Flint and Chattahoochee rivers. Other specimens she studied were taken at Eufaula, Alabama, on the west shore of the Chattahoochee River in a section also now impounded to form Lake Eufaula. The Flint and Chattahoochee rivers join at the Florida-Georgia state line to form the Apalachicola River, which flows southward through Florida to the Gulf of Mexico. Traver's third lot of specimens from Macon, Georgia, was apparently from the Ocmulgee River, which flows southeastward to the Atlantic Ocean.

She differentiated the adults from other North American species on the basis of color differences on the pronotum and the abdominal dorsum. Burks (1953) concluded that these color differences were not sufficient to support Traver's separation, and he synonymized *incertus* and *manitobensis* with *primus* and further suggested that all might be synonyms of *T. puella*. Edmunds et al. (1976) agreed that *manitobensis* was a synonym of *primus* but not *incertus*. The status of *incertus* has still not been resolved satisfactorily, but we will continue to recognize it as a valid species for now.

After the description of the adult by Traver, the nymph of *Tortopus* remained unknown until it was collected during a biological survey of the Savannah River by the Academy of Natural Sciences of Philadelphia (1953). Later, adults and nymphs collected at the Savannah River proved to be *incertus*, and the nymphs were differentiated from those of *Campsurus* and described by one of us (Berner) in a paper by Scott et al. (1959). McCafferty (1975) summarized the traits that separate *Tortopus* nymphs from those of *Campsurus*, and Unzicker and Carlson (1982) characterized the distinguishing features of *incertus* nymphs based on the 1959 description. The latter authors stressed the importance of differences in color pattern and the heavily sclerotized bilobed gills on abdominal segments 2–7. As *incertus* is the only species known in the nymphal stage, it remains to be seen what other characteristics can be used to separate it from the others.

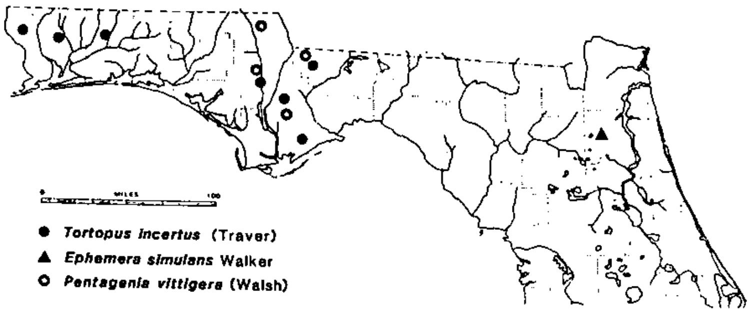
GEOGRAPHIC DISTRIBUTION. *T. incertus* has been collected from Alabama, Florida, Georgia, Louisiana, Mississippi, and South Carolina (Berner 1977). All collections of the species are from the Coastal Plain except that of Traver taken at Macon, Georgia, a city located on the Fall Line between the Coastal Plain and the Piedmont physiographic provinces.

In Florida, the species has been collected only in the northwestern part of the state from the Apalachicola River westward (map 18). Numerous efforts were made to find the nymphs in the Apalachicola River in 1965 by dredging in this large—and very difficult to work—stream; but no nymphs were found. Burrows in the riverbank were spotted, but no nymphs were collected from them; apparently, the burrows were all empty. Several nymphs have been collected in the Choctawhatchee River by Paul Carlson (1971).

Counties from which *T. incertus* has been recorded include Calhoun, Escambia, Franklin, Gadsden, Liberty, Okaloosa, and Santa Rosa.

ECOLOGY. Prior to the discovery of the nymphs in the Savannah River in 1951, nothing was known of the ecology of the species. Subsequent studies by Scott et al. (1959, p. 205) have conclusively demonstrated that they burrow in clay banks of medium-sized to large rivers (figs. 172, 173). These banks support a community of organisms dominated by *T. incertus* nymphs, whose burrows perforate them at almost every bend of the river. "The clay substrate inhabited by *Tortopus* is always firm, nearly always vertical, and usually exposed to swift water."

The nymphs burrow into the bank at right angles to the surface and produce U-shaped tubes with parallel arms. "Apparently, a burrow is enlarged in length and diameter as the size of the occupant increases. This is accomplished by the nymph digging straight back from the end of the burrow and piling some of the clay in the center of the tunnel to form a septum separating the two arms. This method of construction allows the



Map 18. The distribution of *Tortopus incertus*, *Ephemera simulans*, and *Pentagenia vittigera* in northern Florida.

nymphs to keep a current of water flowing through the burrow as it is enlarged."

An interesting feature of the clay bank community is its apparently migratory nature, clearly indicating the vertical movement of the insect with the rise and fall of the water level.

Sometimes nymphs were found in bottom samples, but it is likely that they were washed from the steep clay banks because of the erosive action of the swiftly flowing water. Rarely nymphs were seen tunneling in rotten wood, and some have been taken from sandy clay, peat, and unconsolidated sandstone.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Available data indicate that *T. incertus* generally emerges during the warmer months in Florida. Adults have been collected from the last week in June to as late as October 24. Edmunds et al. (1976) reported that adults emerge in Florida from June 6 through November 14, with the beginning and ending dates varying by less than one week. Our collections reveal that peak emergences occur from early July through late August. McCafferty (1975) stated that the species might require two years to reach maturity; however, all information available to us suggests that there may be a one-year period of development. Scott et al. (1959) found three size groups among a series of 600 nymphs collected from the Savannah River in July—those about to emerge, those nearing maturity, and those that were half the size of the mature forms. They concluded that the species emerges in two broods, one in July or early August, the second in late August or early September. That they found half-grown nymphs indicated to them that the species requires two

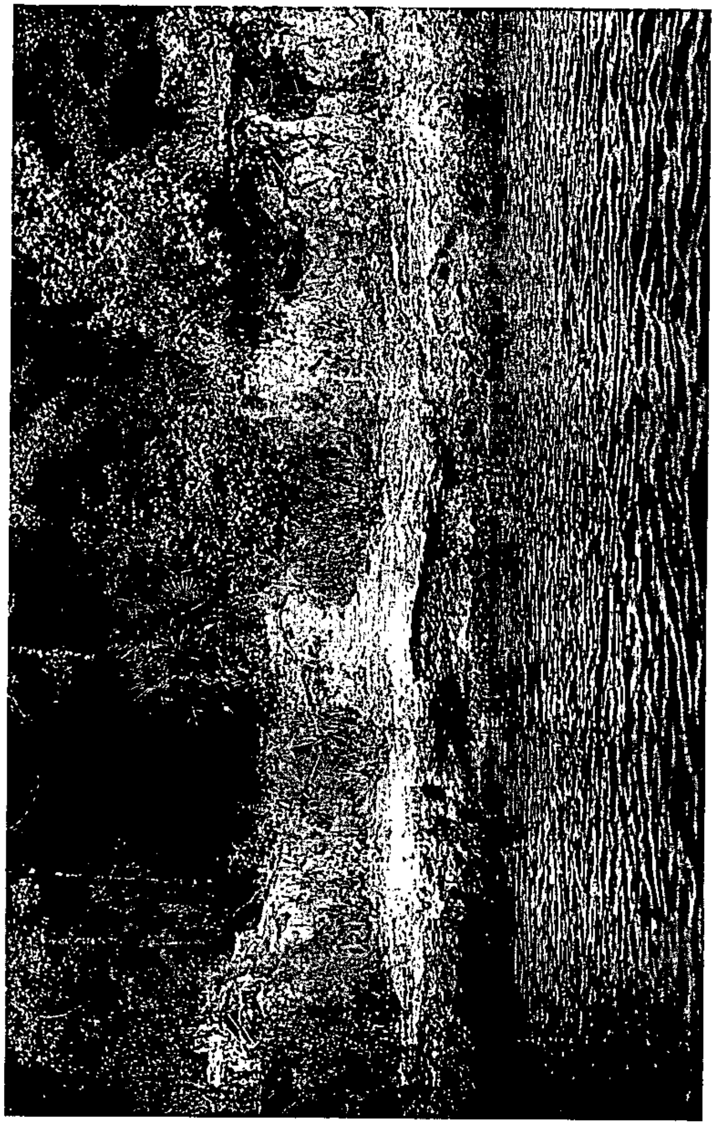


Fig. 172. East bank of the Savannah River near Ebenezer Church, Effingham County, Georgia. Empty burrows of *Tortopus incertus* are exposed (July 1954)

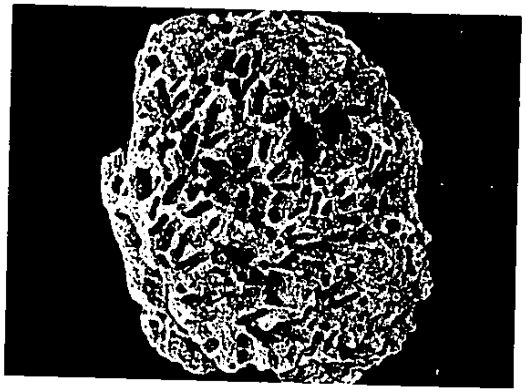


Fig. 173. A mass of clay from the banks of the Savannah River showing the perforations produced by *Tortopus* nymphs

years to mature, with the half-grown nymphs destined to emerge the year following their collection. This interpretation may be incorrect as, under high temperature conditions and with an abundance of food, development may be so rapid that the small nymphs might emerge during late August or early September, thus demonstrating that only one year may be required for the life history. The small nymphs may have developed from eggs that had undergone diapause.

Tsui and Peters (1974) studied embryonic development and early instar morphology of this species, obtaining eggs from gravid females on August 21 and 28. They kept the eggs at three different temperatures, 13.65°C ± 1°C, 19.45°C ± 1°C, and 23.0°C ± 1°C. Successful hatching occurred under the latter two temperatures but with the ova showing a highly variable rate of development. At 19.45°C the eggs began to hatch on the 33d day and at 23.0°C after 41 days. These authors described the eggs, embryonic stages, and the first- and second-instar nymphs.

It is obvious that there must be close synchronization of emergence if mating is to be successful. As the legs of the adult female are nonfunctional, and all except the forelegs of the male are likewise vestigial, the entire adult life must be aerial. During this brief period, mating, fertilization of the eggs, and oviposition must occur. Mating flights have never been observed by us; however, Edmunds et al. (1976) reported that mass flights have been sighted over rivers from just after sunset to as late as 2:00 A.M. Females do not molt to the imaginal stage, although males do, probably while on the wing, in much the same way as *Ephoron*, another member of the family Polymitarcyidae.

BEHAVIOR. Virtually nothing is known of the behavior of adult *T. incertus* other than the fact that females appear to be attracted to lights more readily than males.

Nymphal behavior was reported by Scott et al. These authors noted that the burrowing activities of the nymphs seem to be similar to those of the related genus *Povilla*, which tunnels in silt, wood, or freshwater sponges in lakes and rivers in tropical Africa and Asia. Feeding also seems to be similar to that of *Povilla* (Hartland-Rowe 1953), which filters organic food particles from water passing through the long hairs on its forelegs and head and by using the hairy mouthparts as well.

It is likely that the nymphs seldom leave their burrows except to migrate vertically with the fall or rise of river water level. At the time of emergence when the nymphs must, of necessity, leave their burrows, they are obviously subject to heavy predation by fish.

EPHEMERIDAE

When McCafferty and Edmunds (1979) reviewed the higher classification of Ephemeroptera, they concluded that the family Ephemeridae should be more restrictive than previously considered by others. The North American genera now remaining in the family after the 1979 review include only *Ephemera*, *Hexagenia*, and *Litobrancha*.

All are characterized by the venation of the forewing, in which MP_2 and CuA are strongly divergent from vein MP_1 basally, and vein A_1 is not forked and is attached to the hind wing margin by two to many veinlets. The nymphs are burrowers in sand, silt, or mud in streams and lakes. They are characterized by having projecting mandibular tusks and fossorial front legs. The family occurs worldwide, except in Australia.

Ephemera Linnaeus

Berner 1950, p. 94; 1959, pp. 23–24; 1977, p. 49.
Burks 1953, pp. 35–36.
Edmunds, Jensen, and Berner 1976, pp. 282–284.

McCafferty 1975, pp. 461, 463.
McCafferty and Edmunds 1973, pp. 300–307.

Ephemera was named by Linnaeus in 1758 and has been adequately characterized many times since then. The systematics of the genus was reviewed by McCafferty and Edmunds in 1973, at which time they established three subgenera, *Ephemera, Dicrephemera,* and *Aethephemera,* of which only *Ephemera* s.s. occurs in North America. Nymphs normally burrow in sand or silt in streams and lakes. Species of the genus *Ephemera* occur in the Ethiopian, Oriental, and Holarctic regions, and representatives are widely distributed over much of North America.

Ephemera (*Ephemera*) *simulans* Walker

(FIG. 12. MAP 18)

Berner 1950, pp. 94–95; 1977, p. 49.
Britt 1962, pp. 47–64.
Burks 1953, pp. 36–37.
Cobb and Flannagan 1980, p. 163.
Eriksen 1963, pp. 447–453; 1964, pp. 506–510; 1968, pp. 93–103.
Ide 1935, pp. 436–446.
McCafferty 1975, p. 465.
Unzicker and Carlson 1982, pp. 3.28–3.29.

TAXONOMY. Approximately 60 nymphs of a species of *Ephemera* were presumably collected by the late Professor J. Speed Rogers from Kingsley Lake in May 1935; subsequent efforts to obtain additional material have been unsuccessful. Some of the nymphs were sent many years ago to Dr. Hermann Spieth, who tentatively identified them as *Ephemera simulans* Walker. Because no additional specimens of *Ephemera* have been taken in Florida in the more than 50 years since the "Kingsley Lake" collection, we are including this record with "tongue in cheek."

GEOGRAPHIC DISTRIBUTION. McCafferty (1975) pointed out that *E. simulans* is found throughout most of the United States except in the southwest and possible extreme southeast. However, Edmunds et al. (1976) reported the occurrence of the species in the southwest. If the dubious record from Florida is ultimately substantiated, then the range of the species would clearly be extended into the extreme southeast. The only record for a species of *Ephemera* from the southeastern Coastal Plain was given by Berner (1977) on the basis of a single, very young nymph collected by Dr. Donald Scott in a bottom sample dredged from the Savannah River at mile 141.0, Screven County, Georgia. All other southeastern records are from higher elevations. Unzicker and Carlson (1982) found no species of *Ephemera* in the Coastal Plain areas of North and South Carolina. There is a single record of *Ephemera* sp. taken in an airplane towing at Tallulah, Louisiana, at a height of 2000 feet (Glick 1939). Other species of the genus are often found in the streams of the southern Appalachians. If the Florida record is correct, the species occurs in Clay County (map 18).

ECOLOGY. Although nothing is known of the ecology of the Florida *Ephemera* nymphs, much has been published concerning *E. simulans* as it occurs elsewhere in North America (Britt 1962; Eriksen 1963, 1964, 1968). Needham (1920) summarized its ecological habits as follows: "The 'mackrels' are lacustrine rather than fluviatile in habitat, especially *E. simulans.*" The Florida nymphs were supposedly taken in an Ekmann dredge from the lake bottom, but whether from sand or silt is unknown. If *E. simulans* occurs in Kingsley Lake, we believe that the nymphs inhabit the sandier bottom areas. Edmunds informs us that *E. simulans* nymphs occur in rivers—and even in fast-flowing trout streams—in the West.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The Florida nymphs we have are nearly full grown, approximately in the tertultimate instar. Emergence is probably limited to a short period during the summer, for these nearly mature nymphs, collected during May, are almost all of the same size.

Spieth (1936) found that in Lake Wawasee, Indiana, *E. simulans* is a burrowing form restricted to the littoral zone; he concluded that it takes one year to complete its life cycle. Britt's study (1962) led him to the same conclusion. Ide (1935) described the first 13 and the last 7 instars of Canadian nymphs, but he did not determine the total number of instars required for development. Ide's estimate of about 30 instars has still not been confirmed or refuted.

Mating flights were described by Needham in 1908 and 1920. In 1913 Clemens also described the flight as well as the copulatory act, which does not differ essentially from that of other mayflies. Clemens did, however, notice an interesting peculiarity, namely, "that the male *Ephemera* frequently attempted copulation with the male *Hexagenia,* apparently being deceived by color." Britt also treated emergence of the subimago, molting, and mating activities of the adults.

BEHAVIOR. Nothing is known of the behavior of *E. simulans* in Florida, although the species has been studied extensively elsewhere.

Hexagenia Walsh

Berner 1950, pp. 78–79; 1959, pp. 33–35; 1977, pp. 49–51.
Burks 1953, pp. 38–39.
Edmunds, Jensen, and Berner 1976, pp. 284–291.
Koss and Edmunds 1974, p. 333.
McCafferty 1975, p. 469; 1984, p. 789.
Unzicker and Carlson 1982, pp. 3.27–3.30.

Hexagenia, described by Benjamin Walsh in 1863, was one of the first North American genera to be considered new. Needham, as late as 1920, recognized only two "good and distinct species" in the eastern United States—a lowland form, *H. bilineata*, from lakes and rivers, and an upland bog-stream species, *H. recurvata*. McDunnough (1927, p. 117) commented as follows concerning Needham's paper:

> With the above conclusions I must emphatically disagree; from a study of a large number of dried specimens and further from personal observations on living material (both subimagoes and imagoes) during the annual "swarming" period at Sparrow Lake, Ont., in the latter half of June 1925, I am convinced that there are a number of good species in this genus, closely related, it is true, but well separable, partially on male genital characters and also on color pattern of the abdomen, size of the eyes, etc.; none of these features varies to any appreciable extent in any given species and Needham's so-called intergradients are in reality good species.

Traver described seven additional species in 1931, another in 1935, and a ninth in 1937. After studying Walker's types in the British Museum, Spieth (1940) reduced *occulta* and *viridescens* to the status of subspecies of *limbata*. In 1941, Spieth revised the genus and listed 14 species and subspecies of *Hexagenia* occurring in North America north of Mexico. Burks (1953), although agreeing in general with Spieth's interpretation of species limits, did not follow him in recognizing subspecies within *limbata* and *munda*. McCafferty (1975) likewise did not utilize subspecific categories for these two *Hexagenia* species. Edmunds et al. (1976) did, however, use the subspecific designations, as did Berner (1977) and Unzicker and Carlson (1982). McCafferty (1984, p. 789) concluded that there was no valid reason for continuing the use of subspecific designations within *H. munda* or *H. limbata*, and, in fact, concluded that *munda* represents nothing more than variants of *limbata*. As a result of his study, he stated that "[f]ourteen specific epithets are now referable to *H. limbata*, including seven that have been synonymized with *H. munda*."

Species of *Hexagenia* occur over much of North America, ranging from Canada to Mexico.

Earlier ideas about the phylogeny of the Ephemeridae (Spieth 1933) have been substantially reordered by Edmunds and others. Edmunds (1972), in his review of the biogeography and evolution of Ephemeroptera, suggests that the "burrowers" evolved from a proto-Leptophlebiidae line, although other relationships are suggested. His diagram (*in* Edmunds et al. 1976) of the probable phylogeny of the subfamilies of Ephemeroptera shows the Ephemerinae, including *Hexagenia*, arising from prepotamanthids. In 1979 McCafferty and Edmunds, when establishing the two suborders Schistonota and Pannota, assigned the genus to the Schistonota in which the ancestral condition of the nymphal thorax has been retained and mature nymphs have the forewing pads free from notal fusion for one-half or more of their length.

Hexagenia bilineata (Say)

(FIGS. 46, 151. MAP 19)

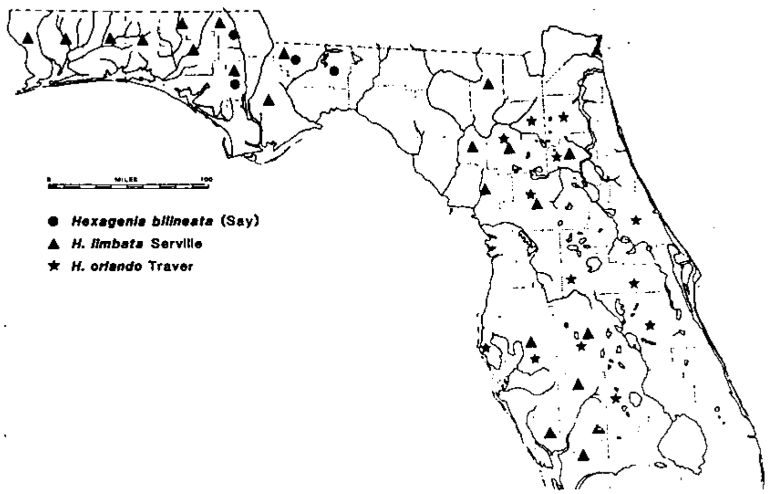
Berner 1950, pp. 93–94; 1958, p. 29; 1977, p. 49.
Burks 1953, p. 39.
Edmunds 1953, p. 45.
Fremling 1960, pp. 842–852; 1967, pp. 407–410; 1973b, pp. 15–16; 1973a, pp. 1521–1526.
Gooch 1967, pp. 101–103.
McCafferty 1975, pp. 470–471.
Schneider 1967, p. 202.
Tennessen, Miller, and Price 1982, pp. 133–137.
Unzicker and Carlson 1982, pp. 3.28–3.31.

TAXONOMY. *Hexagenia bilineata* adults are more easily recognized than the majority of other species of *Hexagenia,* but the nymphs are not so readily separated from others of the genus. McCafferty (1975), in a footnote, reported that Fremling, in many instances, was unable to separate morphologically *bilineata* nymphs from those of *limbata* taken from the Mississippi River. Gooch (1967) has shown that nymphs over 16 mm in length can be separated from those of *limbata* by examining the claws, which are consistently swollen basally in *bilineata,* while those of *limbata* are long and slender. McCafferty cautions that this trait must be used only with mature nymphs and therefore is of limited value. Thus far, we have no nymphs collected in Florida that can be assigned to *bilineata* although we have many adult specimens, both male and female.

In 1920, Needham decided to apply the name *bilineata* to "all variants of the species that occupies the beds of our larger lakes and streams." McDunnough (1927) strongly disagreed with Needham and restored the species names that the latter had synonymized. Although many of the present species of *Hexagenia* were considered by Spieth (1941) to be subspecies of *limbata* and *munda* (now *H. limbata*), *bilineata* is so distinct that there can be no doubt as to its specific status. Subsequent to Spieth's work, other ephemeropterists have accepted the conclusion that *bilineata* is distinct from all other species of *Hexagenia,* and the name is now firmly established. Both male genitalia and abdominal color pattern provide means for identification of the species.

Many years ago while collecting mayflies at a light in front of an icehouse facing the dammed-up part of Blue Springs Creek near Marianna, one of us (Berner) noted a large mayfly circling about the lights. Upon its capture, the insect was immediately recognized as being a species new to Florida. Before the evening was over, nine individuals, all females, were taken. Collections from other localities included males and females that enabled us to identify the species clearly as *bilineata.*

GEOGRAPHIC DISTRIBUTION. The species was originally described from Minnesota by Thomas Say in 1824 (Edmunds 1953). Walsh recorded *bilineata* from Illinois; Eaton, from Louisiana and Texas; and McDunnough mentioned that the species seems to be confined to the Mississippi and its tributaries. Spieth (1941) established the range of *bilineata* as being along the eastern Piedmont area and McCafferty (1975) reported that the species is known generally throughout the United States except in the West and Northwest. The species has not yet been reported from the extreme northeastern tier of states nor from Canada, but it is known from northern Mexico (Edmunds et al. 1976), and Daggy (1941) lists its occurrence in New Mexico.



Map 19. The distribution of *Hexagenia bilineata, H. limbata,* and *H. orlando* in Florida.

The first Florida specimens taken were from a tributary of the Chipola River, which in turn flows into the Apalachicola River. The Chattahoochee River, which flows through Atlanta, is listed as a locality for *H. bilineata,* and, as this river serves as a major tributary of the Apalachicola, it appears to have been the highway the species followed in entering Florida. All records of *bilineata* in Florida are from streams flowing into the Apalachicola or those not far distant from it.

The species has been recorded from the following counties in Florida (map 19): Calhoun, Gadsden, Jackson, Leon, and Liberty.

ECOLOGY. The nymphs are known to be burrowers in the silt and muds of larger streams. Ecologically, the nymphs are well known because of Dr. C. R. Fremling's careful and detailed studies of the species as it occurs in the upper Mississippi River (1960, 1973). He found the burrows of the nymphs in the river bottom to be most abundant in impounded areas where there was little or no current and where the bottom was silty.

In the Mississippi, Fremling located nymphs at depths ranging from 1 to 25 feet, principally in soft mud. Occasionally, large numbers of immatures were seen in other bottom types where there was a mixture of sand and silt made up of an equal volume of leaf fragments, small sticks, bark, and pebbles.

The nymphs, like others of the genus, build U-shaped burrows with the insect oriented so that it faces upward. Water passes over the gills because of their undulating movements and brings in a constantly renewed supply of oxygen. The nymphs obtain their nourishment from the organic materials in the mud on which they feed. There is no evidence that they are filter feeders.

Tennessen et al. (1982) experimented with eggs of *H. bilineata* to determine the effects of a brief thermal shock on hatching success. Their aim was to learn whether such exposure to above-ambient temperatures—similar to what those eggs would experience if oviposition took place in a thermal plume and the eggs then sank to an ambient lake bottom—would affect hatching success. They concluded that some delayed lethal effects can occur from the brief exposure to temperature increases.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Fremling (1960) reported finding adults emerging from the Mississippi River as early as May and as late as August with the seasonal peak being reached in mid-July. The life history, emergence of the subimago, and mating behavior were also described by Fremling. In 1973, he discussed environmental synchronization of mass emergences of this species in the Mississippi River, and he attributed this effect to the more uniform temperature, light, and substrate in an aquatic environment than in a terrestrial one. He suggested that these factors are the synchronizing features in the part of the river in which he worked. He also postulated that long-distance, downstream drift of eggs during their incubation period would allow for increased population sizes in localized areas of the river where pools are formed.

BEHAVIOR. We have not observed the behavior of the Florida nymphs of this species; however, we believe that there would be little or no difference between it and that described by Fremling for the Mississippi River insects.

Hexagenia limbata (Serville)

(PLATE 15. FIGS. 47, 152, 154, 159. MAP 19)

Berner 1950, pp. 86–93 (*marilandica* and *elegans*); 1958, p. 29 (*marilandica* and *elegans*);

1959, p. 33 (*marilandica* and *elegans*); 1977 (*marilandica* and *elegans*).
Carlson 1980, p. 82.
Jones 1977, p. 65 (*marilandica*).
McCafferty 1975, p. 472 (*marilandica*); 1984, p. 789 (*limbata* = *marilandica* and *elegans*).
Peters and Jones 1973, p. 246 (*marilandica*).
Schneider 1962, p. 132 (*marilandica*); 1967, p. 202 (*marilandica* and *elegans*).
Schneider and Beck 1963, p. 110 (*marilandica*).
Walker and Burbank 1973, pp. 1527–1533 (*marilandica* and *elegans* intergrades).
Wurtz and Roback 1955, p. 193 (*elegans*).

TAXONOMY. McCafferty's 1984 note was published soon after we had made a careful reexamination of all adult *Hexagenia* specimens in our collections that we had previously identified as either *H. munda elegans* or *H. munda marilandica* and after we had concluded there was no valid reason for distinguishing between the two subspecies in Florida. In his note McCafferty contended that there was no reason to continue recognizing *munda* as distinct from *limbata* and that all seven subspecies of *munda* should be regarded as *limbata*. We maintain, however, that *orlando* (formerly *H. munda orlando*) is separable from *limbata* for reasons that have been given under the species.

Prior to the publication of his 1984 paper, McCafferty (1975) had reached the conclusion, because of the ever-increasing frequency of capturing intergrades, that the practicality of using subspecific names for *munda* and *limbata* had become questionable. His synonymizing the two helps to clarify this taxonomic jungle in an important genus of mayflies.

GEOGRAPHIC DISTRIBUTION. Now that all of Spieth's (1941) subspecies of *limbata* and *munda* have been incorporated under the single name *limbata* (excluding *orlando*), it is clear that the species occupies virtually all of North America from the East Coast to the West Coast and from Florida into Canada. In Florida we have recorded the species from as far south as Hillsborough County and as far west as the Escambia River in the extreme northwestern part of the state. It is very likely that the species entered Florida through the headwaters of the Apalachicola River and spread widely from this source wherever suitable habitats were available.

H. limbata has been recorded from the following counties in Florida

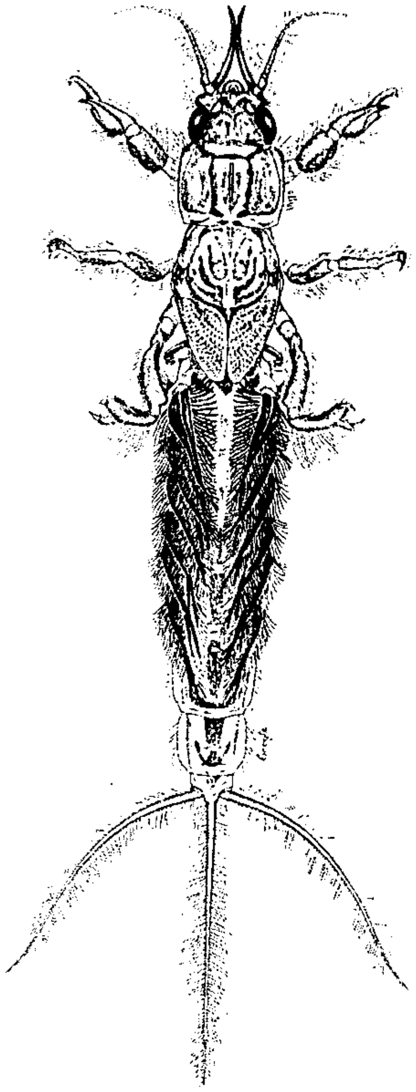


Plate 15. *Hexagenia limbata* (Serville), nymph

(map 19): Alachua, Calhoun, Charlotte, Columbia, DeSoto, Escambia, Gadsden, Gilchrist, Hardee, Hillsborough, Holmes, Jackson, Levy, Liberty, Marion, Okaloosa, Putnam, Santa Rosa, Walton, and Washington.

ECOLOGY. The immatures burrow in the silt of the shallow stream margins. It is easy to locate the nymphs because they leave small, round openings leading into their burrows, which can be seen in the shallow water. If there is a rather large deposit of silt in quiet water, there may be many of these opening over a comparatively small area. Holmes Creek, in northwestern Florida, offers ideal conditions for the development of the nymphs, and it was at this stream that we found them to be more common than at any other locality from which the insects have been collected. Here the water flows slowly over a very silty bottom. Vegetation grows profusely in the streambed; but in places where the current is slightly more rapid, the floor is bare except for the silt. At the time collections were taken, the water was quite low, not more than a few inches in depth, and burrows were located without trouble from the bridge over the stream. The nymphs build burrows that descend only a very short distance so that a shallow scoop with a scraper easily removed the insects.

The nymphs were found burrowing in large numbers in the banks of sand-bottomed streams in Gadsden and Liberty counties. The beds of these streams are composed mostly of clean-swept yellow sand. At the edges, however, are deposits of reddish clay mixed with silt, in which the nymphs burrow.

Stream size is probably not a limiting factor because in the Tallahassee Hills region nymphs were taken from a small stream not more than three feet across; yet the immatures must be present in prodigious numbers in the Apalachicola River if the reports of emergences that have reached us bear any semblance of truth.

We have been told that when the "willow flies" come out, they cover everything, forming huge piles under lights and making pests of themselves. When the adults are out in numbers along the Apalachicola, they cover the willow trees that line the banks of the river; hence the name "willow flies." We have also learned from fishermen that the bass lie in wait under the willows, and as the insects accidentally fall from their perches onto the water surface, the fish immediately seize them. At this time all that one needs to do to catch "a mess of bass" is to cast under the willows: the bait is sure to be taken. The people of this region look forward eagerly to the arrival of the flies for their best fishing.

Professor J. G. Needham's description of these insects is well worth repeating. Traver (1931, p. 607) quotes from Dr. Needham's field notes:

> The capture of *Hexagenia weewa* [*H. limbata*] occurred on this wise. Prof. C. R. Crosby and I were passengers on the Apalachicola River steamboat *John C. Callahan, Jr.* On the evening of the eighth of April, this big boat ventured up the Chipola River above Dead Lake to Cotton Bluff to take on some barrels of turpentine. Near Cotton Bluff the boat got stuck in one of the bends of that crooked little stream just at nightfall. The searchlight was turned on, and in the beam of light that it cast upstream the mayflies rose above the black waters by thousands. Along with multitudes of midges and a few other mayflies of the genus Ephemerella [probably *Eurylophella temporalis*], the big yellow female Hexagenias came fluttering up to the light. They settled all over the front of the boat, two or three layers deep wherever there was support. They flew in our faces and clung to our clothing. One could gather them up by barrelsful. But among the many thousands of females, only two or three males were seen.

The nymphs are very hardy. One of us (Berner) brought 12 of them a distance of 300 miles in two small vials filled with moist silt, and these individuals were not removed from the bottles during a period of more than 24 hours. "Upon my return to Gainesville, every nymph was found to be alive and apparently in good health. Moreover, while I was away from Gainesville for two weeks, the water evaporated from the pans containing the nymphs until the surface of the mud was completely dry. When water was added to the mud and it was stirred, out swam the nymphs none the worse for the desiccation." The hardiness of these nymphs in surviving drying is consistent with Fremling's experiences (1960) with the nymphs of *Hexagenia bilineata*, which were found to be alive and well in clods of mud dried on the surface but still moist inside.

We have also found nymphs burrowing in the much-abused and polluted Hogtown Creek that traverses the city of Gainesville. The nymphs have never been found to be abundant in this stream, but over a period of about three hours, with much effort, we were able to collect 45 specimens. From time to time phenolic pollutants released into the headwaters of one of the tributaries have virtually eradicated the population in the creek only to have it recover again from small residual pockets well downstream.

The 45 nymphs referred to were confined in a rather small pan; at the end of one month mortality was found to be very low: only five specimens died. This low mortality rate continued, with scattered emergences of adults, until summer, when nearly all of the remaining nymphs reached the last instar. For some unknown reason these were unable to transform. Under these stress conditions all of the nymphs were undersized.

A detailed study of *limbata* (as the *munda* complex) from an ecological standpoint was conducted by Walker and Burbank (1973) in Stone Mountain Lake, Georgia. The lake is formed from an impoundment of Stone Mountain Creek and Little Stone Mountain Creek. The population with which Walker and Burbank worked consisted of what were considered by them to be intergrades between *marilandica* and *elegans* and very likely was similar to the population that occurs in northwestern Florida. They concluded that the chief factor regulating distribution of the nymphs is substratum type, a finding consistent with that of others who have studied *H. limbata*. Their work demonstrated that the nymphs selected a mud or sandy mud substratum with particles having a diameter of 0.05 to 2.0 mm. "In no case were nymphs, neither experimentally nor in the field, found in a substratum containing more than 55% sand by weight. . . . Ninety per cent of the nymphs, both large and small, burrowed to depths of 10 cm, but only large nymphs, with an average length of 29.25 mm, burrowed to depths of 15 cm."

Some burrowing dragonfly nymphs are associated with *limbata* in the silt of the streambed; the most commonly found mayfly species include *Caenis hilaris*, *C. diminuta*, and *Brachycercus berneri*, which do not burrow but frequently live on top of the silt or sandy silt.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The specimens Dr. Needham collected were taken on April 8, 1927. We have adults captured from March through August and laboratory-reared specimens that emerged in September and October. Inconclusive data point to an early summer emergence or to an August period as the major times for the adult stages to be on the wing. We have little doubt that *limbata* is a seasonal species emerging over a period of about six or seven months. Nymphs collected at various times of the year fall into distinct size groups, and there is much overlapping of young with old nymphs. Fremling (1967) has demonstrated that *H. bilineata* may develop rapidly during the summer months, and he suggested that there is a summer brood that grows from egg to adult in a few months. He was able to rear newly hatched nymphs to the adult stage in only 79 days in a tank in which the water temperature was maintained between 24°C and 27°C.

Some indication of the rate of growth under rigorous conditions is shown in table 2, which is based on measurements of laboratory-reared

TABLE 2
GROWTH OF NYMPHS OF *Hexagenia limbata*

Date Measured	No. of Specimens Measured	Smallest Nymph	Largest Nymph	Average
February 2	32	6.5 mm	25.0 mm	13.6 mm
May 1	31	9.5 mm	23.0 mm	16.3 mm
June 19	19	9.0 mm	22.0 mm	17.5 mm

nymphs collected from Hogtown Creek. An attempt to rear nymphs was made in the stream as a control, but because of contamination with phenols, the check failed owing to the death of the nymphs.

The male nymphs just before transformation ranged from 17.5 mm to 19 mm in length. The larger nymphs were female.

Subimagoes, in the laboratory and in the field, emerge in late afternoon, just about dusk, but we have observed a single female emerge in the field about 10:00 A.M. After a resting period of 14 to 20 hours, the final molt occurs; this is followed by mating if conditions are propitious.

We have observed several small mating flights of this species composed of from 30 to 75 males. The flights took place just at dusk and on succeeding nights could be timed to within five minutes of its occurrence. The males flew at a height of about 20 to 25 feet above the ground and usually over vegetation consisting chiefly of willow trees. As the flights began, one or two males moved up and down in the manner typical of mayflies, and almost immediately they were joined by others until the swarm soon reached its maximum size. The up-and-down flight varied considerably but as a rule appeared to be about five or six feet. The upsweep was accomplished with the caudal filaments depressed and held close together and with the wings beating rapidly. On the downsweep, the filaments were raised and separated; the wings, which were outspread, did not beat; and the insect merely floated downward on opened wings. Each male appeared to choose its place in the swarm and maintained its position until it left the flight to mate. We have not seen females enter the group of swarming males, but we have observed the coupled pairs flying at about the same height as the swarm and off to one side. In every case where we could follow the flight, the pair separated after a few seconds: the male returned to the swarm, and the female disappeared into the vegetation. The flight of males lasted about 15 minutes and gradually dispersed just about dark.

At the same time that the males were flying, females could be observed flying in swarms about equal in size to those of the males. Instead of being an up-and-down flight, theirs was horizontal back and forth, and they flew about 10 feet below, and away from, the males. The flight of females continued until after dark. It was interesting to note that on two successive evenings, while we stood on a bridge and watched flights of females below us, three or four at a time would leave the swarm and fly over the bridge at precisely the same spot. For some reason, they chose the southwest corner of the bridge, just over a projecting willow branch. We stood at this point and collected a large number of the females as they left the swarm. The flight of the females was crosswise to the flow of the stream, while that of the males was parallel to the flow. Females leaving the swarm had evidently not oviposited for they frequently deposited their ova into the net when captured. Sometimes two large clusters of orange-colored eggs were protruding from the abdomen, also indicating that oviposition had not yet occurred.

BEHAVIOR. The behavior of the *limbata* nymphs is similar to that of *orlando*.

Hexagenia orlando Traver

(FIGS. 11, 37, 45, 112, 160. MAP 19)

Berner 1950, pp. 79–86; 1959, p. 33; 1977, p. 51.
Frost 1967, p. 281.
McCafferty 1975, pp. 472–473 (*munda*).

TAXONOMY. Spieth (1941), after studying a series of mayflies from Florida, concluded that *H. orlando*, described by Traver, should be considered a subspecies of *H. munda*. He considered that specimens from High Springs (obviously the Santa Fe River) and from Rock Bluff (on the Apalachicola River) to be intergrades of *orlando* and *elegans*. Other specimens before him at the time of his work were apparently typical *orlando* from lakes. Our specimens from localities near those from which he recorded intergrades are not intergrades but true *limbata*. Numerous subsequent collections of adults from lakes in peninsular Florida are clearly *H. orlando*.

H. orlando can be separated from other Florida species of *Hexagenia* by its color pattern, its smaller size, and the fact that it is confined to the sand-bottomed lakes of the Central Highlands of Florida. For the preceding reasons, and because it is ecologically isolated from *H. limbata* of streams, we are retaining the name *H. orlando* for the lake form of *Hexagenia*.

GEOGRAPHIC DISTRIBUTION. *H. orlando*, which is endemic to the Central Highlands of Florida, is found only in lakes. Lake Harney, from which Eaton's specimens of "*variabilis*"* came, is on the edge of the lake region; it is one of the chain of lakes of the St. Johns River not far from its headwaters. Florida counties from which the species is known are (map 19): Alachua, Bradford, Clay, Highlands, Hillsborough, Lake, Marion, Orange, Osceola, Polk, Putnam, and Volusia.

ECOLOGY. *H. orlando* is one of the most ecologically limited species found in Florida. The nymphs burrow in the sand and silt of lake bottoms. The only method by which the nymphs have been taken has been by the use of a dredge, because they live in water ranging from 9 to 30 feet in depth. The heaviest concentration of the immatures apparently lies in the region from 18 to 30 feet deep, but a few nymphs have been collected from the deepest parts of most of the lakes that were sampled. One exceptional specimen was even taken at a depth of 45 feet, the deepest spot that could be located in Kingsley Lake. There was some evidence of thermal stratification in the deeper parts of this lake during August, and no nymphs could be found below this zone; however, immatures were taken closer to shore. That part of the lake bottom in which *Hexagenia* nymphs are most common is sandy, but it is usually overlain with a very thin layer of silt and has *Utricularia* scattered over it. In the deeper portions of some of the shallow, sand-bottomed lakes, there is a deposit of rather slimy, but firm, black mud covering the sand bottom. Nymphs are frequently collected from this mud. Along with them many *Chaoborus* larvae, a few annelids, and an occasional amphipod may be brought up.

Although such large Florida lakes as Newnan's and Orange are very interesting in themselves, they are notable for the absence of burrowing mayfly nymphs. Only the more tolerant insects, such as the chironomids and chaoborids, thrive in them. Newnan's Lake, near Gainesville, has a bottom deposit of silt which is thick, loose, and fluffy, and in which very few organisms exist. The tremendous amount of silt apparently makes it impossible for those bottom organisms requiring a moderate supply of free oxygen to remain alive. In the past when the lake margins were covered with dense growths of water hyacinth, *Eichhornia crassipes*, the bottom received a continuous and large supply of dead vegetation. Lakes of this type may have many floating plants—water hyacinths, and to a lesser extent water lettuce, which drift about at the mercy of the winds—and sometimes there is an abundance of spatterdock extending out to a depth of as much as seven feet.

Immatures have not been collected from the lakes of the southern part of the Central Highlands, but adults from these lakes are like those of the northern part of this region. A superficial examination of the southern lakes indicates that they are similar to the sand-bottomed type of the more northern area.

The lake bottoms must constitute an ideal habitat, because enormous numbers of individuals live in them as burrowers. Various people have reported that when *H. orlando* is emerging, the adults become pests, as they they pile up under lights and have to be swept from the streets. We have seen them congregating in such numbers that the sides of a bathhouse were almost hidden by the insects—nearly every blade of grass supported several individuals. The mayflies, when disturbed, fluttered upward in great masses to settle on the nearest support, and even clung to body and clothing. In every depression on the sandy beach, dead mayflies were accumulated several layers deep. Along the edge of the water, there was a row, five to six inches wide, of dead adults and nymphal exuviae, which had been washed up on the shore. Many nymphal skins, as well as dead adults, were found floating on the surface of the lake. Persons who have observed the emergences of the Florida species and the dramatic past emergences of *Hexagenia limbata* and *H. rigida* from the Great Lakes, prior to their extensive pollution, say that the actual number of individuals emerging from the Florida lakes is considerably smaller per unit area.

Ephemera simulans is the only species of mayfly that may be associated with *H. orlando* as a burrower in the lakes of Florida.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The greater part of the emergence of this species takes place during the summer months, particularly in June, July, and August; however, we have adults taken from March through December. It seems likely that the species emerges during the spring, summer, and autumn, but that winter temperatures are sufficiently low so that emergence does not occur during the coldest months. It is also

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*Eaton described *H. variabilis* from adults taken at Utah Lake; Texas; Florida; St. Louis, Mo.; Galena and Rock Island, Ill.; Detroit, Mich.; New England; Philadelphia, Pa.; and Washington, D.C. Eaton's specimens must have included a broad range of forms of the highly variable *H. limbata* as well as the Florida species, *H. orlando*.

very likely that in the southern part of the state, the species transforms over most of the year with sporadic emergences even in the cold months of January and February to make the species a year-round emerger. The major emergence period is more restricted and occurs during the warm months of summer.

We have not determined the length of time required for nymphal development, but from emergence data it would seem to be approximately one year, although during the summer months development is probably accelerated. On the basis of statistical measurements, Neave (1932) estimated that *H. limbata* took two years to go through its life history in Lake Winnipeg. After studying *Ephemera simulans* and *H. limbata* in Lake Wawasee, Indiana, Spieth (1936 and 1938) concluded, also on the basis of measurements, that both species take only one year for development. He subsequently revised his opinion and thought a two-year period to be more likely. He noted (1938, p. 214) that there is "no reason why a species in the northern part of its range might not take two years to mature, while in the southern parts of its range one year would be sufficient." Other studies (Hunt 1953; Lyman 1955; Hudson and Swanson 1972) demonstrated that in Michigan and South Dakota, where low temperatures depress developmental rates, *H. limbata* may require one or two years for the entire life cycle.

Since temperatures in the lakes of Florida seldom or never become low enough to stop growth completely, it would not be surprising to find that *H. orlando* completes its development within one year or less. Collections made in early spring include rather small, half-grown, and almost mature nymphs, as well as intermediates. Since growth rate is a function of temperature, it would certainly be reasonable to expect that all of these nymphs, in the warm Florida waters, would have emerged sometime during the same year. Nymphs collected in autumn ranged in age from very young to two-thirds grown individuals. No mature specimens were taken. The larger individuals of autumn would probably have emerged in spring or early summer of the following year; the half-grown specimens would appear as adults in summer, and the very young nymphs would have emerged in late summer or early autumn. Edmunds et al. (1976) reported that in Utah *H. limbata* emerged from canal channels that were dry 17 weeks earlier and, under laboratory conditions where high temperatures prevailed, *H. bilineata* was reared from eggs in as brief a period as 13 weeks, although most required six months.

There is a definite brooding of *H. orlando*. During the summer, the broods may sometimes be separated by not more than a week or 10 days; at other times, the intervening period may be much longer. In the spring and early summer the emerging broods are smaller, on an average, than they are during July and August, and they decrease in size in September and early fall until emergence probably stops completely in the very cold months. There may be a few isolated individuals on the wing between emergence periods, but they are scarce and difficult to find.

Just prior to emergence, the nymph, ordinarily negatively phototactic and positively geotactic, reverses these responses and swims from the lake bottom to the surface, where it breaks through the surface film, and the adult immediately bursts free. The winged insect rests a moment, and, if not taken by a fish or bird, flies to shore where it alights on the nearest available support. At the time of emergence, the predators become extremely active and gorge themselves on nymphs and subimagoes. We have observed subimagoes "popping" out of their nymphal skins at the surface, and many bass and other fish voraciously striking at them before they had an opportunity to fly away. At the same time, birds were sitting on the trees and bushes along the lakeshore eagerly awaiting the advent of the insects, and whenever one approached a bird immediately seized it.

Subimagoes emerge during the night or in the very early morning. Mr. Richard Franz found subimagoes rising from a lake in north-central Florida (September 1983) about 11:00 P.M. By 3:00 p.m. of the following day, they had all transformed to the adult stage. At other times subimagoes taken into the laboratory molted by the next evening after a resting period of about 24 hours. We have not observed the mating flight of *H. orlando*, but on one occasion we did notice restlessness on the part of a large group of these insects about 30 minutes before sunset. We have been told that the species forms large swarms that fly out over the lakes just about sunset, all at about the same height of approximately 30 feet.

Duration of the egg stage has not been determined for *H. orlando*. According to Clemens (1922), eggs of *H. recurvata* hatched in the laboratory 14 days after oviposition; Wiebe (1926) found that artificially inseminated eggs hatched in the laboratory in 9 days. Spieth (1938) hatched eggs of *H. limbata* by placing them in jars that were immersed in a small stream. These eggs took 20 days to develop. At the same time, another group of eggs kept in the laboratory hatched in only 15 days. Edmunds et al. (1976) indicate that the time required for hatching depends on temperature. Nymphs hatched from eggs in the laboratory in from 11 to 26 days, some requiring much longer. These authors estimated that in lakes under natural conditions eggs hatch in about two weeks. Whether this time frame is true for *H. orlando* remains to be determined.

BEHAVIOR. The burrowing habit is very strongly developed in the nymphs, and all bodily structure is adapted to suit the immatures to a hypogeic existence. The gills present an enormous aerating surface, the legs are modified for digging and casting out the soil as it is passed back, and the incisors of the mandibles are elongated into tusks as accessory digging organs and for lifting the roof of the burrow. Lyman (1943), Hunt (1953), Fremling (1960), and others have described at length the adaptations and behavior of *Hexagenia* nymphs in their subterranean habitats. Those of *H. orlando* are consistent with the northern species described by the cited authors.

The gill movements of *H. orlando* are like those of *Litobrancha recurvata* (formerly *Hexagenia recurvata*), which Morgan and Grierson (1932, p. 233) described as follows:

> Waves of motion pass backward over the gills sometimes too rapidly for the eye to follow but at other times in listless ripples. The gills may cease moving altogether, usually for a few seconds or for 1 or 2 minutes, though at times they may be quiet for half an hour. The motions vary with those of the nymph's body and also with the temperature and chemical content of the water. When resting, the gills are held almost upright or bent slightly backward. When waving, each pair bends backward, the filaments of the opposite gills touch each other, instantly separating as the gills are pulled upward, the whole performance resembling the rapid opening and closing of a V. So far as observed, the gills move whenever the nymph is active, especially when it burrows. While digging, the nymph holds its front legs closely against its wedge-shaped head, then lunges forward, at the same time pushing these legs outward. Almost synchronously with this, its middle legs are pushed outward and backward and the hind legs backward. As its body wedges forward, the nymph fans the silt with its gills, opening and closing them in the V-shaped angle. Thus, their surfaces are cleared of the mud thrown back by the hind legs, the water is continually circulated about them.

Hexagenia orlando nymphs are rather adept swimmers. When they are placed in a dish of water in which there is no silt or sand for burrowing, they will swim vigorously, attempting to escape, and will continually butt their heads against the sides of the container. The burrowing habit is so strongly developed that, under these conditions, small nymphs will seek larger individuals and attempt to burrow under them. Swimming is accomplished by wavelike motions of the abdomen and up-and-down sweeps of the caudal filaments. The gills seem to play little or no part in this activity. Morgan and Grierson, experimenting with *Hexagenia* nymphs from which the gills had been removed, found that the gill-less individuals swam almost as well as, but more slowly than, those with gills.

The method of feeding is analogous to that of an earthworm in that the nymphs feed as they burrow. Examination of the digestive tract of immatures showed the presence of a few diatoms and some cells that seemed to be algae, but for the most part the contents were not determinable. Surprisingly, there were no sand grains in any of the digestive tracts examined. Hunt (1953) reported that *H. limbata* nymphs appear to be mud eaters, deriving nourishment from organic material and perhaps bacteria ingested with the mud. He also found fragments of higher plants, filamentous algae, and diatoms along with the usual large quantity of marl-mud or silt. On several occasions in the laboratory in the daytime, he observed nymphs at the mouths of burrows, apparently feeding.

PALINGENIIDAE

With the publication of their paper on the Palingeniidae, McCafferty and Edmunds (1976) showed that the genus *Pentagenia* should be assigned to that family, thus clarifying an enigmatic situation that had puzzled ephemeropterists for many years. The members of this widespread family share in common reduced forelegs in the male adults; nymphs are relatively homogeneous and are clearly delimited from those of other families. Representatives of the Palingeniidae occur in Eurasia, New Guinea, Madagascar, Sumatra, and North America, with *Pentagenia* the only North American representative. All of the nymphs are burrowers.

Pentagenia Walsh

Berner 1950, p. 96.
Edmunds, Jensen, and Berner 1976, pp. 292–294.
McCafferty 1972, pp. 50–56; 1975, p. 479; 1979, p. 48.
McCafferty and Edmunds 1976, pp. 486–489.

This genus is the sole member of the subfamily Pentageniinae, a subfamily discussed and described by McCafferty and Edmunds in 1976. Only two species are recognized in the genus. One, *robusta* McDunnough, is known only from the type specimens. The other species, *vittigera*, is discussed below.

Pentagenia vittigera (Walsh)

(FIG. 48. MAP 18)

Berner 1950, p. 96; 1958, p. 29; 1977, p. 52.
Burks 1953, pp. 37–38.
Fremling 1970, pp. 20–21; 1973, pp. 17–19.
Hamilton 1959, p. 451.
Ide 1955, pp. 15–16.
McCafferty 1975, p. 479.
Schneider 1967, p. 202.
Unzicker and Carlson 1982, pp. 3.26–3.27.

TAXONOMY. Adults of the rather large *Pentagenia vittigera* are recognized by the presence of four dark spots, actually bullae, in veins Sc, R_2, R_{4+5}, and MP_1; males have tubelike penes. The nymphs are separated from those of other genera by the crenulated outer upper margin of the mandibular tusks as well as other characteristics described in the key.

GEOGRAPHIC DISTRIBUTION. In common with the riverine *Hexagenia bilineata*, this species is widely distributed over central and southeastern North America. *P. vittigera* has been collected from Manitoba southward to the Gulf coastal states, but it is still not known from the eastern tier of states nor from Canada east of Manitoba. It seems reasonable to assume that the species is most closely associated with the Mississippi River drainage system and that it has spread from that source into larger rivers of neighboring regions. The species has been recorded from the Tennessee River and has also become established in the Chattahoochee, which flows southward between Georgia and Alabama, joining the Flint River to form the Apalachicola in Florida (map 18), the only locality in the state where *vittigera* has been found.

ECOLOGY. The ecology of *Pentagenia* nymphs is still poorly known even though the species was described in 1863. The first report of finding nymphs is that of Needham (1920), who recorded cast nymphal skins from the Mississippi River. Using these exuviae and a single nymph from the Mississippi at Keokuk, Iowa, he described the immature. McCafferty (1975, p. 479) stated, "Although these mayflies can be abundant around large rivers, the larvae are most difficult to collect and are taken most commonly in drift samples."

Fremling (1970, 1973) has provided a little ecological information on *Pentagenia*. He reported that the nymphs apparently live in faster-flowing water than *Hexagenia* nymphs and are difficult to find. In his studies he discovered that the *Pentagenia* nymphs in the Mississippi River are highly susceptible to the effects of pollutants as water temperature rises in summer. Organic enrichment at higher temperatures results in oxygen depletion, clearly affecting the ability of these nymphs to inhabit parts of the river. He assumed that early summer and late summer emergences result from nymphs drifting far from the zone of pollution into more protected areas where dissolved oxygen levels are higher. McCafferty (1975) collected nymphs in hard clay banks approximately three feet below the water surface in the Wabash River in Indiana. He found the clay banks to be honeycombed by *Pentagenia* nymphs in the same manner that the banks of the Savannah River are honeycombed by *Tortopus*. McCafferty observed the *Pentagenia* nymphs using their mandibular tusks to dig the burrows.

SEASONAL DISTRIBUTION AND LIFE HISTORY. So little is known about *Pentagenia* that we can only record the dates of adult collections to reflect known times of maturity. In Florida, the adults were taken on May 3, 1941, and June 3, 1953. Traver (1937) collected an adult in northern Alabama on July 4, and Ide (1955) recorded his adults from Manitoba on July 12. Berner (1977) recorded adult collections from Alabama in May and June; Louisiana in September; Mississippi in August; and Tennessee in June. McCafferty (1975) lists collections from Georgia in July, Louisiana in early September, and Mississippi in mid-August. Fremling (1973) charted the seasonal distribution along the Mississippi River, with adults appearing at Keokuk, Iowa, as early as May 15 and as late as September 20. No further information is available relating to seasonal distribution or life history, although Unzicker and Carlson (1982) speculate that there is a one-year life cycle for *P. vittigera*.

BEHAVIOR. No observations have been published describing behavior of adults or nymphs. The lack of available nymphs and adults in Florida has precluded studies of this species.

EPHEMERELLIDAE

The widespread family Ephemerellidae has been the subject of numerous studies and of disagreements about the generic divisions within it. In North America, the family included only *Ephemerella* until Allen (1980) took the long-needed action of raising former subgenera to generic status. The North American genera he included within the subfamily Ephemerellinae are: *Attenella,* Caudatella, Dannella,* Drunella, Ephemerella,* Eurylophella,* Serratella,** and *Timpanoga*. The asterisks indicate the genera that occur in Florida.

Prior to Allen's action of raising the subgenera to generic status, Edmunds (1959, p. 543) wrote:

> There is considerable difference of opinion among Ephemeropterists concerning the number of generic or subgeneric categories to be recognized within the Holarctic Ephemerellidae. Generally the specialists in Western Europe have placed a small number of species in three or four genera, while workers in North America and Asia have generally included a much larger number of species within the single genus *Ephemerella*. The nymphs of the complex show great diversity and the adults a moderate diversity of characters, so it is not difficult to find large morphological gaps between a small number of species within any geographic area. It is only when the world fauna is examined that there is great difficulty in recognizing gaps between groups of species.

The family Ephemerellidae was assigned to the suborder Pannota by McCafferty and Edmunds (1979) and placed by them in the superfamily Ephemerelloidea along with the Tricorythidae.

Attenella Edmunds

Allen 1980, p. 84 (subgenus *Attenella* = genus *Attenella*).
Allen and Edmunds 1961, pp. 161–163 (subgenus *Attenella*).
Edmunds 1959, p. 546 (subgenus *Attenuatella*).
Edmunds 1971, p. 152 (*Attenuatella* = *Attenella*).

Attenella was described by Edmunds in 1959 as a subgenus of *Ephemerella* under the name *Attenuatella*, which he later found to be a homonym. He corrected the oversight in 1971, renaming the subgenus *Attenella*.

The males are separated from those of other genera of the family chiefly by genitalial differences. Females can be identified by their association with males or by rearing them from known nymphs. The nymphs are characterized by gills on abdominal segments 4–7 and rudimentary gills usually present on segment 1; abdominal segments 8 and 9 are subequal in size; the abdomen has moderately well-developed, paired submedian tubercles on terga 2–9, 3–9, or 3–8; and the tarsal claws possess denticles.

The members of this genus appear to be confined to North America.

Attenella attenuata (McDunnough)

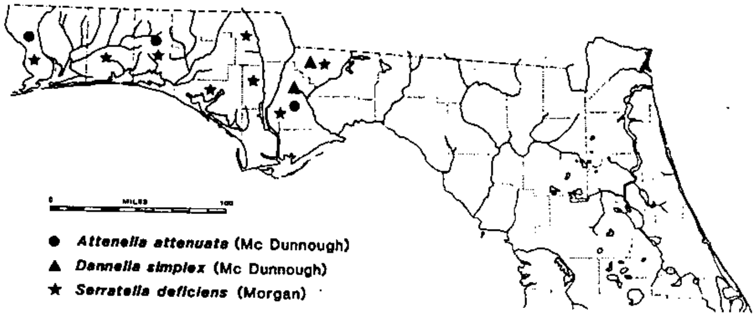
(FIGS. 69, 158. MAP 20)

Allen and Edmunds 1961, p. 162 (*A. attenuata* McDunnough = *A. hirsuta* Berner), pp. 163–164.
Berner 1950, pp. 165–166 (*A. hirsuta*); 1958, p. 30 (*A. hirsuta*); 1977, p. 41.
Cowell and Carew 1976, p. 590 (*A. hirsuta*).
Edmunds 1959, p. 546 (*A. hirsuta*).
Peters and Jones 1973, p. 246.
Schneider 1967, p. 203 (*A. hirsuta*).
Wurtz and Roback 1955, p. 193 (*A. hirsuta*).

TAXONOMY. In 1946, *Ephemerella hirsuta* Berner was described from two nymphs collected from Perdido Creek less than one mile north of the Florida state line in Alabama. The nymphs fell clearly into Traver's (1935) distinctive *simplex* group. Later, two adult males were taken at Sandy Creek in Walton County, Florida, that also belonged to the same group and consequently were assigned to *hirsuta*.

Allen and Edmunds (1961), after comparing some of McDunnough's specimens of *Ephemerella attenuata* from the Canadian National Collections, concluded that *hirsuta* fitted well within the limits of variability of the former species. Other collections they studied bridged the distributional gap between the Canadian and the southern forms. As a result, these authors synonymized the two names.

The males of *attenuata*, the only species of the genus occurring in Flor-



Map 20. The distribution of *Attenella attenuata*, *Dannella simplex*, and *Serratella deficiens* in northwestern Florida.

ida, are easily separated from others of the genus by genital differences, according to Allen and Edmunds. The nymphs are variable in both morphological and color characteristics, and so separation is more difficult than with the males. As the geographic distribution of the other species of *Attenella* is so different from *attenuata*, there is little likelihood that any of the other species would be sympatric in the Southeast.

GEOGRAPHIC DISTRIBUTION. *A. attenuata* has been found on a few occasions in Florida, chiefly in the northwestern part. Only a few nymphs are taken from a stream where the species occurs. The single record of the occurrence of *attenuata* from peninsular Florida is that of Cowell and Carew (1976), who collected their specimens while they were conducting a study of drift organisms in a Hillsborough County stream. We have not had an opportunity to verify Dr. Cowell's identification of his specimens as *attenuata*.

The species has been recorded from Alabama, Georgia, North and South Carolina, as well as from Florida in the southeast. Other reports of the species are from Nova Scotia, New Brunswick, and Quebec in Canada and from Massachusetts, Pennsylvania, and Virginia (Allen and Edmunds 1961). Those Florida counties from which specimens have been recorded are (map 20): Escambia, Hillsborough, Liberty, and Walton.

ECOLOGY. The rarely collected nymphs of *attenuata* live mainly in algal mats or among leaf drift and silty matter deposited about the bases of

Polygonum stems near stream shores where water movement is almost negligible. The slowly moving nymphs are covered on the dorsum of the thorax and head with long, somewhat matted hairs. Similar hairs also cover the femora and anterior part of the abdomen, acting as a protection from the debris that might otherwise collect on the insects.

SEASONAL DISTRIBUTION AND LIFE HISTORY. We have so few data about these subjects that we are unable to estimate time required for development of this species. We do have the adults collected in May at Sandy Creek in Walton County and a record of adults, also taken in May, in South Carolina but no other information on which to speculate about these matters.

BEHAVIOR. We have no observations relating to this species.

Dannella Edmunds

Allen and Edmunds 1962a, pp. 333–334.
Edmunds 1959, p. 546.
Edmunds, Jensen, and Berner 1976, p. 244.
McCafferty 1977, pp. 881–889.

Allen raised Edmunds's subgenus *Dannella* of *Ephemerella* to generic status in 1980 in his article on reclassification of the subfamily Ephemerellinae.

Dannella is a small genus consisting of four known species, only one of which occurs in Florida. According to McCafferty (1977), adult males may be recognized by the relatively generalized condition of the male genitalia. Allen and Edmunds (1962, pp. 333–334) characterized the male by "(1) the third segment of the genital forceps scarcely longer than wide . . . , (2) second segment of genital forceps thin, (3) the penes swollen apically and without subapical projection or dorsal or ventral spines . . . , (4) tibiae of foreleg shorter than tarsi and third tarsal segment longer than second." These authors distinguished nymphs by the presence of semioperculate gills on segments 4–7 and a pair of rudimentary gills on the first abdominal segment; the abdominal terga lack paired tubercles; and the claws are without teeth.

The genus is distributed widely over eastern and north-central North America from Manitoba and New Brunswick in Canada southward to Alabama and Florida.

Dannella simplex (McDunnough)

(FIGS. 66, 155. MAP 20)

Berner 1958, p. 30; 1977, p. 45.
Jones 1977, p. 65.
McCafferty 1977, pp. 885, 887–888.

TAXONOMY. The adults of only two species of *Dannella* are known, *D. lita* (Burks) and *D. simplex* (McDunnough). McCafferty's key (1977) to distinguish males is based on the shape of posterolateral processes of the ninth abdominal segment and vestigial nymphal abdominal processes retained by the adult. However, the nymphal stage is the one that is the most easily used in identification of the species. The characteristic separating *simplex* from the three other species is the shape of the posterolateral abdominal processes of segment 3. The posterolateral processes of the other segments are also significant in differentiating *simplex*. Regardless of the traits used to separate the species, they are still not readily identified. As *simplex* is the only Florida species, the problems inherent in separating it from the others do not arise so long as only the Florida fauna is considered.

GEOGRAPHIC DISTRIBUTION. *D. simplex* is distributed throughout eastern and north-central North America and ranges southward to northwestern Florida, where it has been recorded from Gadsden and Liberty counties (map 20).

ECOLOGY. Nymphs of *D. simplex* are so rarely taken that we have few observations about their ecological requirements. The nymphs occur only in streams, where they dwell in the quieter sections under conditions similar to those of *Attenuata attenella*.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Only the nymphal stage has been found in Florida. Those in the final instar have been collected in April; and a single individual in the penultimate instar as well as one that was about a third the size of a mature nymph was taken in February. We believe that the species is univoltine, with emergence occurring in April or May.

BEHAVIOR. We have no information about the behavior of nymphs except that they are found in places that are silt laden; so the hairy nymphs with their burden of silt lodged among the setae are extremely inconspicuous. They are seen as they begin to move slowly when water is drained away from them in a collecting pan.

Ephemerella Walsh

Allen 1980, pp. 74–75.
Allen and Edmunds 1965, pp. 245–253.
Edmunds 1959, p. 544.
Edmunds, Jensen, and Berner 1976, pp. 247–248.

Until Allen (1980) subdivided the old genus *Ephemerella* into 14 genera, the old concept of its components resulted in a rather unwieldy unit, which was the largest in the order Ephemeroptera. There had been several attempts to recognize the diversity within the genus prior to Allen's action, the most recent being those of Edmunds (1959) and Allen and Edmunds (1965).

Ephemerella, as now restricted, can be separated from the other Ephemerellinae only by examining male adults or nymphs; unassociated females cannot be identified to genus. The terminal segment of the male adult's genital forceps is less than twice as long as broad; the lateral margins of the penes project apically as distinct processes or lobes; and dorsal and/or ventral spines are usually present on the penes. Characters differentiating the nymphs are imbricated gills on abdominal segments 3–7; lack of tubercles on the leading margin of the fore femora; no well-developed paired tubercles on the head and thorax; numerous denticles (3–14, generally more than 6) on the tarsal claws; presence of well-developed, three-segmented maxillary palpi; and caudal filaments that are subequal in length (Allen and Edmunds 1965).

The genus *Ephemerella*, in its present context, has a Holarctic distribution. The species occurs over much of North America.

Ephemerella choctawhatchee Berner

(FIGS. 99, 146. MAP 21)

Allen and Edmunds 1965, p. 264.
Berner 1950, pp. 164–165; 1958, p. 30; 1977, p. 41.
Jones 1977, p. 65.
Schneider 1967, p. 203.

TAXONOMY. This rather rare species is represented in collections by only a small number of nymphs and adults. *E. choctawhatchee*, described from the nymphal stage, is a small insect, the nymphs being only 5–6 mm in length. The nymphal tibiae have a pale band at the apex; the tarsi are banded with brown in the proximal third; the lateral extensions of the abdomen are moderately developed; and small, paired, dorsal abdominal spines are present. The male adult has not yet been described, although four specimens are available in collections. It can be distinguished from other *Ephemerella* species on the basis of its genitalia. These differ from those of *catawba* in the shape of the penes, and they are quite distinct from those of *invaria*, with which Allen and Edmunds (1965) postulated synonymy.

GEOGRAPHIC DISTRIBUTION. *E. choctawhatchee* is one of two species of the genus occurring in the Coastal Plain. Eleven species of *Ephemerella* have been recorded from southeastern states, but most of them are from the Piedmont or mountainous regions. Although the distribution of the species appears to be closely related to the Apalachicola River and its tributaries, it seems to have spread westward in the panhandle of Florida. We have records of its occurrence in the following counties (map 21): Gadsden, Liberty, Okaloosa, Santa Rosa, and Walton. Schneider (1967) collected nymphs in Escambia and Calhoun counties.

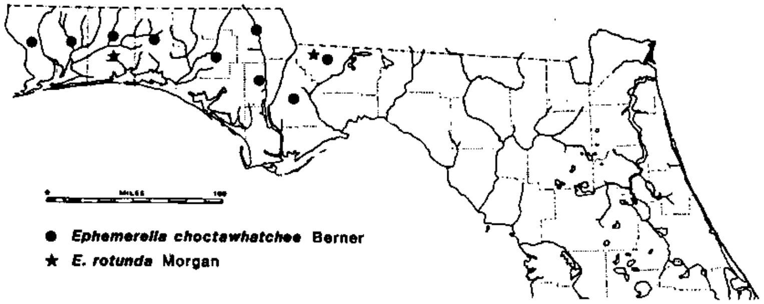
ECOLOGY. Clear, sand-bottomed streams with a rather strong flow provide an ideal habitat for the majority of the stream forms of Florida. *E. choctawhatchee* is no exception. In Sweetwater Creek, the nymphs inhabit the same root beds from which *Serratella deficiens* was taken. In other streams they live either in the vegetation in more rapidly flowing water or near the shore amid the projecting roots.

SEASONAL DISTRIBUTION AND LIFE HISTORY. With so few nymphs and adults available, we hesitate to draw conclusions about these subjects. We have nymphs taken from December and into May, with the largest number (six) collected in March. Adults have been reared in March and April. It seems, based on the scanty data available, that the species is in the adult stage only during the spring months, eggs are laid that do not hatch until fall, and the nymphs grow during the cooler months of the year.

BEHAVIOR. We have no information about this aspect of the species' biology, but we believe it to be similar to others of the genus.

Ephemerella dorothea Needham

Berner 1977, p. 43.
Schneider 1967, p. 204.



Map 21. The distribution of *Ephemerella choctawhatchee* and *E. rotunda* in northwestern Florida.

Schneider (1967) recorded this species from the Choctawhatchee River and Holmes Creek in northwestern Florida, and his findings were included in the paper "Distributional patterns of southeastern mayflies (Ephemeroptera)" (Berner 1977). As we have no specimens of this species, we are reluctant to say that it occurs in Florida. Reviewing our correspondence with Mr. Schneider, we have found that in a letter of October 28, 1965, we (Berner) wrote, "The nymphs of *Ephemerella* which you have designated simply by the letters sp. are probably *dorothea*." A handwritten note appended to the identifications states, "*Ephemerella dorothea* Needham? (May be *choctawhatchee* but without abdominal spines)." At this point, we prefer to consider that these nymphs of Schneider's are merely variants of *E. choctawhatchee*.

Ephemerella rotunda Morgan

(MAP 21)

Berner 1958, p. 30; 1977, p. 44.
Schneider 1967, p. 204.

TAXONOMY. We have a few nymphs that have been designated as *Ephemerella rotunda* even though they do not conform to the size range given by Allen and Edmunds (1965) for the species. Mature Florida nymphs measure about 5 mm, while the more typical nymphs have a body length of 10–11 mm. In other respects the Florida nymphs are not distinguishable from typical *rotunda*. We also have two adult males, and the genitalia of both appear to be those of *rotunda*. The similarities existing among *ro-*

tunda, invaria, and *choctawhatchee* may be sufficiently great so that when many more specimens of these species are available for study the three may prove to be synonymous. At this writing we prefer to adhere to their present status.

Morgan described *rotunda* from specimens collected in New York. Subsequently, other names were given to the species as a result of collections made in other parts of the eastern United States. Allen and Edmunds (1965) have reviewed the taxonomic history of the species; we will not repeat it here.

E. rotunda males have penes with numerous dorsal spines, while the adult male of *choctawhatchee,* not yet described, has none to three or four. Nymphs of the two species are very similar in appearance, but *rotunda* has vestiges of paired submedian tubercles on tergites 2 and 9, which *choctawhatchee* lacks.

GEOGRAPHIC DISTRIBUTION. *Ephemerella rotunda* is widely distributed over eastern North America and is known from northern Ontario to Nova Scotia and southward to northern Florida. The species has been found in the following northwestern counties (map 21): Gadsden, Liberty, and Okaloosa.

ECOLOGY. We have no information about the specific ecological needs of *rotunda,* but we surmise that they are no different from those of *E. choctawhatchee.*

SEASONAL DISTRIBUTION AND LIFE HISTORY. We have mature nymphs collected in January and March and adults taken in March and April. These scanty data lead us to suggest a springtime emergence for the species, a long dormant period for the egg, hatching in cooler weather, and development during the winter months.

BEHAVIOR. The behavior of nymphs and adults is probably similar to that of other species of *Ephemerella.*

Eurylophella Tiensuu

Allen 1980, pp. 84–85.
Allen and Edmunds 1963b, pp. 597–603.
Edmunds 1959, p. 546.
Edmunds, Jensen, and Berner 1976, pp. 248–250.

Eurylophella includes some of the best known, as well as some of the most difficult to separate, species of the family Ephemerellidae. The subgenus *Eurylophella* was raised to generic status by Allen when he concluded that the genus *Ephemerella* was too inclusive and too unwieldy to be used effectively. The nymphs may be separated from those of the other genera of the family by the presence of operculate gills on abdominal segments 4–7, with rudimentary gills on segment 1, and by the presence of paired submedian tubercles on abdominal segments 1–9 or 1–10. Adult males are differentiated specifically from each other by the shape of their genitalia; females cannot be separated.

The genus is Holarctic. In North America it occurs predominantly in the east, but species are known from western Canada and the western part of the United States.

Eurylophella temporalis (McDunnough)

(PLATES 16, 17. FIGS. 25, 44, 65, 98. MAP 23)

Allen and Edmunds 1963b, pp. 614–617 (*E. trilineata*).
Berner 1950, pp. 154–160 (*E. trilineata*); 1958, p. 30 (*E. trilineata*); 1977, p. 46 (*E. trilineata*); 1984, p. 567 (*E. temporalis* = *E. trilineata*).
Cowell and Carew 1976, p. 590 (*E. hirsuta*).
Jones 1977, p. 65 (*E. trilineata*).
Landa 1969, p. 291 (*E. trilineata*).
Lanquist 1953, p. 34 (*E. trilineata*).
Peters and Jones 1973, p. 246 (*E. trilineata*).
Schneider 1962, p. 132 (*E. trilineata*; 1967, p. 204 (*E. trilineata*).
Schneider and Beck 1963, p. 110 (*E. trilineata*).
Wurtz and Roback 1955, p. 193 (*E. trilineata*).

TAXONOMY. The Florida specimens of *E. temporalis* were identified for many years as *Ephemerella trilineata* Berner until both *Ephemerella doris* Traver and *E. trilineata* were reevaluated with the conclusion reached (Berner 1984) that both are really synonyms of *Eurylophella temporalis* (McD.). The synonymizing of the three species has cleared an enigma that has troubled the taxonomy of this genus for years. As long ago as 1963,

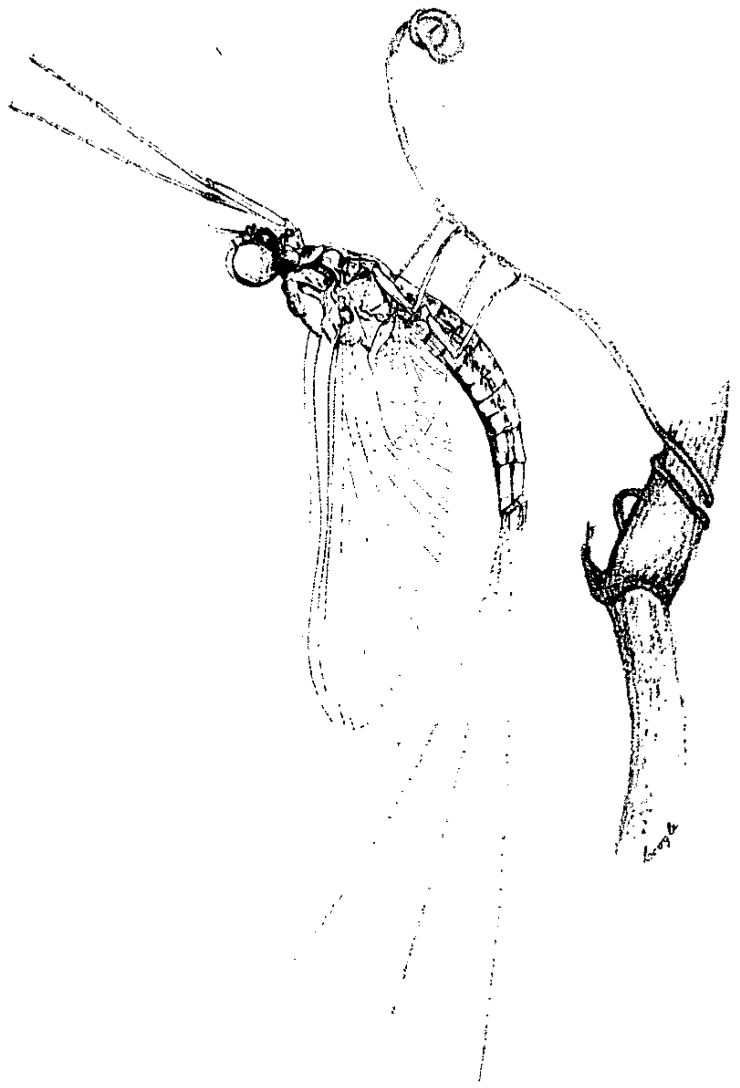


Plate 16. *Eurlyophella temporalis* (McDunnough), male imago

Allen and Edmunds wanted to take this action, but they refrained because of their lack of sufficient specimens from the Southeast.

Allen and Edmunds (1963b) claimed that *E. temporalis* is one of the most easily recognized species in *Eurylophella*, both as a nymph and male adult. The male has characteristic genitalia; the nymph has occipital and abdominal tubercles. Females can be identified only by association with males or by rearing from identifiable nymphs. There is some variation among nymphs in the thickness and degree of erectness of the abdominal spines and much variation in color patterns, but the differences do not appear to have any taxonomic significance.

GEOGRAPHIC DISTRIBUTION. *E. temporalis* is a widely distributed species, ranging from Saskatchewan to New Brunswick and southward into Florida. It is found in many Florida streams and lakes and has been recorded from the following Florida counties (map 23): Alachua, Baker, Calhoun, Clay, Columbia, Escambia, Gadsden, Gulf, Hamilton, Hardee, Highlands, Hillsborough, Holmes, Jackson, Jefferson, Lake, Liberty, Madison, Manatee, Marion, Okaloosa, Putnam, Santa Rosa, Taylor, Walton, and Washington.

ECOLOGY. Ecologically the nymphs are confined either to flowing water or lake margins where there is sufficient stirring of the water to supply conditions suitable for development. Both silt-bottomed and sand-bottomed creeks support populations of nymphs equally well, and in them the immatures favor vegetation where the flow is not too rapid and where there may be thick algal mats. We have found many specimens entangled in masses of *Spirogyra*, where they seemed to be thriving. Another favored habitat for more mature nymphs is among large masses of leaf drift in slow water. Submerged logs, boards, sticks, and other rather solid materials, where the nymphs hide in cracks and crevices, beneath the bark, or in any other protected place, provide a third important habitat. Nymphs have been found abundantly at Hatchet Creek near Gainesville. This stream is a moderately swift-flowing, sand-bottomed, acid creek that drains flatwoods. That part of the stream most thoroughly examined was dredged some years ago, and became rather deep and slow flowing. Near the shore of the dredged area, in shallow water where the flow of water is negligible, there are dense growths of parrot's feather, *Myriophyllum*. *Eurylophella* nymphs are quite common during the fall and spring on the submerged stems and leaves of *Myriophyllum*, but they are also frequently found on other vegetation near shore where the water is not too swift.

Seldom venturing beyond depths of three feet, small populations of *Eurylophella temporalis* nymphs inhabit lakes with sandy shores. They are

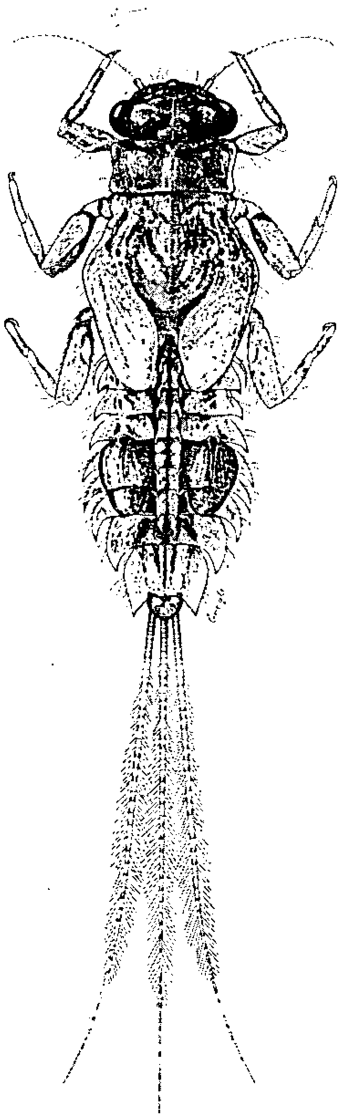


Plate 17. *Eurylophella temporalis* (McDunnough), nymph

not found on vegetation or among the smaller debris, as in streams, but are confined to submerged sticks, boards, logs, and other large objects partially buried in the sand. The immatures live only on the undersurfaces in company with nymphs of *Stenacron interpunctatum* and *Choroterpes hubbelli.*

The streams inhabited by nymphs of this species drain flatwoods and are usually acidic or circumneutral, and the water is nearly always tinted.

SEASONAL DISTRIBUTION AND LIFE HISTORY. *E. temporalis* is a late winter, spring, and early summer species. The period of principal emergence is restricted to spring, chiefly in April, but scattered emergences occur from early February through late June. Traver recorded the emergence of her specimens (as *E. doris*) on March 21 and 22, May 6 and 30, and July 4; the latter collection dates are from mountainous regions where, because of lower water temperatures, transformation would be expected to occur later in the year than in the lowlands.

A study of the material in our collections indicates clearly that *temporalis* requires approximately one year to pass through its life history. Last-instar nymphs have been taken from January through the middle and latter part of June, but during July, August, September, and October there are no records, although we have collected from streams in which nymphs are plentiful during the remaining months of the year. Since we collected very young nymphs in November, it seems reasonable to suppose that the eggs were hatching and nymphs developing during the late summer and early fall seasons. Nymphs one-third to two-thirds grown were found in December, and some were even in the penultimate instar. In March, rather immature specimens, which were obviously the summer brood, were taken in Hillsborough County.

We have not observed transformation in the field, but in the laboratory the nymphs, just before emergence, swim vigorously and then float freely at the water surface for a few moments. Soon the thorax splits, and the subimago appears on the floating skin where it rests quietly. After recovering from the exertions necessary for its emergence, the subimago flies away to the nearest shaded support where it remains until the imaginal molt. We have noted that when partially submerged sticks were placed in the aquarium the nymphs tended to crawl onto them until a portion of the thorax was above the water; in this position they transformed.

On one occasion in February, we saw an *E. temporalis* female begin to emerge at 6:25 P.M., just at dark. The female nymph came to the surface of the water and remained in the quieter portion of the aquarium away from the air bubbles that were rising from the air hose. Now and then it swam vigorously for a short distance and again came to rest. The nymph was stimulated to move; it then submerged, swam into the region where the water was agitated, and immediately returned to the quiet water at the surface. There it strained so intensely that its head and mesothorax broke through the surface film. It repeated the straining after each spurt of swimming, but for the most part it lay quietly at the surface. At 6:35 P.M. it reared its thorax almost completely out of the water and, by the count of 10, the wings were free. The subimago did not move after freeing its abdomen, but sat quite still, partially on the surface film and partially on the exuviae; after two minutes, it became active again, crawled up the side of the aquarium, rested briefly and then flew to the wall of the cage.

Emergence, which normally takes place in late afternoon, sometimes occurs after dark in the laboratory. Life as a subimago extends from late in the afternoon of the emergence date until late afternoon of the following day, the number of hours varying from 22 to 25 in both sexes. The mating flight of *temporalis* has not been observed.

BEHAVIOR. *E. temporalis* nymphs blend perfectly with their backgrounds when lifted from the water while they are attached to sticks, boards, or other dark objects. It is only when they begin moving about that they become discernible. Their movements are slow and deliberate; each step seems to be measured. When out of water, the nymphs flick their tails forward over the abdomen and then straighten them, repeating the act continually. The movement is very reminiscent of that of *Caenis*, *Brachycercus*, and *Neoephemera*. When they are placed in water, the nymphs, like the others mentioned, swim awkwardly with undulatory movements of the abdomen. They then head for some submerged object to which they can cling and, once attached, become difficult to see. The nymphs are easily identified by their actions on the surface of a white-enameled pan. Characteristically, they move forward slowly—not wriggling as the leptophlebiids do—and occasionally flick their tails as described above. The movement may be confused with that of *Caenis*, but the nymphs can be separated from this group by the easily seen, sawlike margins of the abdomen and the widely separated gill elytra.

We have been able to keep nymphs alive in the laboratory for as long as two months, and during this period have fed them only dead leaves. Examination of the enteron of freshly caught nymphs indicates that they, too, eat the epidermis of decaying vegetation, as well as that of living plants, for the alimentary canal was packed with plant fibers and other cellulose materials.

Nymphs of *Eurylophella* are characterized by the absence of gills from segments 2 and 3 and by the modifications of the fourth gills into gill covers. When they respire, water is circulated about the gills by the lifting of the operculate covers and the rapid vibrations of the fifth, sixth, and seventh pairs. Normally, both gill covers are raised at the same time, but we have observed on numerous occasions that one gill cover may remain tightly closed while the other is raised and the gills under it rapidly vibrated.

Serratella Edmunds

Allen 1980, pp. 75–76.
Allen and Edmunds 1963a, pp. 583–587.
Berner and Allen 1961, p. 149.
Edmunds 1959, pp. 544–546.

In 1959 Edmunds established the subgenus *Serratella*, which he postulated might be inseparable from the European *Torleya*. Allen (1980) concluded that *Serratella* should have generic status and that *Torleya* was distinct from it. He pointed out that the penes of the male imago of *Serratella* resemble those of *Torleya* except for two species that show slight differences.

Serratella males are characterized by having the three caudal filaments subequal; the terminal segment of the genital forceps is less than twice as long as broad; the penes lack dorsal or ventral spines, and the penes lobes generally have a lateral subapical projection; and the third fore tarsal segment is shorter than the second (Allen and Edmunds 1963a).

Nymphs have imbricated gills on segments 3 through 7; the ventral margin of the fore femora lacks tubercles; the maxillary palpi may be absent or much reduced in size; and the caudal filaments are subequal and have whorls of apical segmental spines and usually lack intersegmental setae.

Serratella has a Holarctic distribution. In North America the species are found mostly in eastern Canada and southward into Baja California, New Mexico, and Florida, with the largest concentrations in the southeastern United States.

Serratella deficiens (Morgan)

(PLATE 18. FIGS. 70, 100. MAP 20)

Allen and Edmunds 1963a, pp. 587–589.

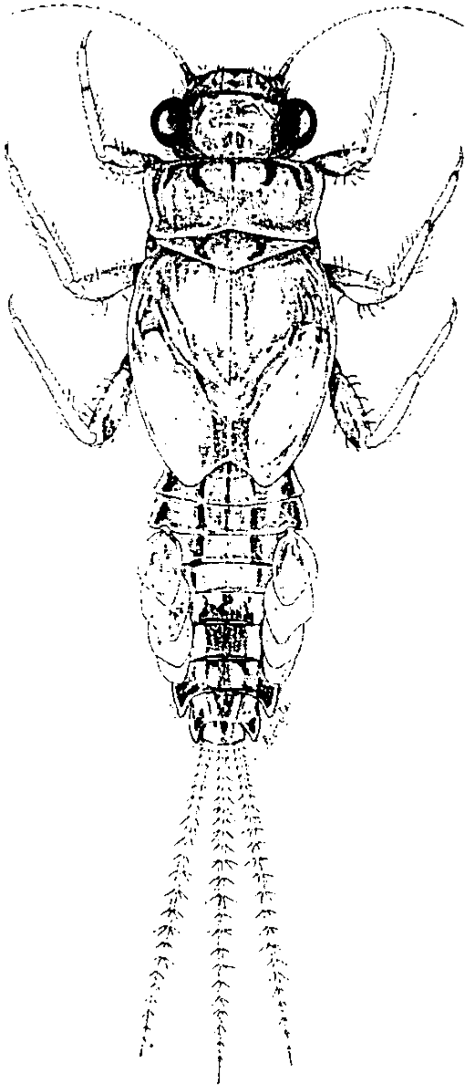


Plate 18. *Serratella deficiens* (Morgan), nymph

Berner 1950, pp. 160–163 (sp. A); 1958, p. 30 (sp. A); 1977, p. 42.
Berner and Allen 1961, pp. 156–158 (sp. A = *deficiens*).
Peters and Jones 1973, p. 246.
Schneider 1967, p. 204.

TAXONOMY. Until the name designation was resolved in 1961 (Berner and Allen), *Serratella deficiens* specimens collected in Florida were referred to as *Ephemerella* sp. A. At the time the species was first reported from the state (Berner 1950), the nymphs were recognized as being closely related to *deficiens*, but because of slight differences from the nymphs described by Morgan (1911), that name was not assigned to them. One of the traits that appeared to be different was claw shape and size. It was supposed that Morgan's specimens lived in swift water and as an adaptation to that habitat the tarsal claws were short and thick. The Florida nymphs, in most respects agreeing with Morgan's description, have proportionately longer and thinner claws, the structure of which appears to be correlated with the slower water flow in Florida streams.

Adult males are separated from the closely related *S. serrata* by genitalial and color differences. The nymphs are similar to other species in the genus; however, as this species is the only one occurring in Florida, it is easily identified by its lack of a maxillary palpus, no paired submedian tubercles on the abdominal terga, and denticulate tarsal claws. The nymphs are often marked with a pale, median-dorsal stripe that extends over the entire body.

GEOGRAPHIC DISTRIBUTION. *S. deficiens* has been collected only in the panhandle section of Florida from the Apalachicola River drainage westward. The species ranges over a vast territory extending from central Canada eastward and southward through Michigan in the west and in the east from Maine to Alabama, Georgia, Mississippi, and Florida. It is known to occur in mountain streams as well as those of the Coastal Plain. Specimens have been collected in the following Florida counties (map 20): Bay, Calhoun, Escambia, Gadsden, Jackson, Liberty, Okaloosa, and Walton.

ECOLOGY. We have collected nymphs of *S. deficiens* from Florida streams of both moderate and fairly swift rates of flow. In Sweetwater Creek, one of the westward-flowing tributaries of the Apalachicola, the nymphs are not especially abundant. In this stream, there are no rocks and very few logs or other footholds for clinging forms like *Serratella*. Nymphs that inhabit the creek usually live on the roots of terrestrial plants that project into the water. The roots are numerous, for the banks of the stream are being continually undercut, and these root masses form silty mats where frequently dead leaves, Spanish moss, and other detritus are caught. Many mayfly nymphs of several species live in this mass of debris; included among them are *S. deficiens.*

Farther west, in Walton and Okaloosa counties, the nymphs have been taken in swifter water on the masses of vegetation that choke the streams. In none of these creeks, however, have we found *deficiens* nymphs in large numbers. We collected from a stream in Escambia County in which root masses like those of Sweetwater Creek and dense growths of aquatic vegetation similar to those of the Walton and Okaloosa county streams were present. There the nymphs were found to be a more conspicuous element of the ephemerid fauna than in any other Florida stream that we have examined. The nymphs were most common in the dense mats of *Potamogeton* in the more gently flowing water, but they were also present on the roots projecting from the undercut banks. The species was also found along the undercut banks of a small, moderately swift-flowing stream.

The streams in which this species lives vary from being strongly to moderately acidic and drain the red-clay hills of the Citronelle Formation or the flatwoods and swamps of the lowlands. All the streams are permanent and have a moderate to rather swift flow; none is normally more than three feet nor less than six inches in depth.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Our collections include nymphs taken as early as March and as late as mid-July. Our April and May nymphs were all in their last instar, and the June records include nymphs of all ages, ranging from those less than one-third the length of mature individuals to those in the last instar. This size range would lead one to conclude that the species emerges year-round; however, we do not believe this to be so. Rather, the data point more clearly to an emergence beginning in spring and extending through midsummer with a long egg period. The gradation in size of nymphs may be explained by there being a very rapid growth period allowing for the production of several broods each year. From the small amount of material at hand, it is impossible to draw conclusions regarding the peak of emergence. No nymphs have been found in any of the streams of northwestern Florida, which we have studied during the fall and winter months.

Coleman and Hynes (1970, p. 1337), investigating the life histories of some Ontario mayflies, stated about *S. deficiens,* "Morgan showed a peak emergence in mid-May but some adults could still be found until mid-July. The occurrence of nymphs in our samples was irregular, possibly because they don't occur mainly in midstream where most of our samples were taken. It seems, however, that this species may have a long egg-diapause and hatch and grow only during the coldest season." Perhaps the same situation pertains to the Florida population.

BEHAVIOR. As much of the rearing for this study was conducted at the University of Florida in Gainesville, difficulties of transporting live nymphs from northwestern Florida to the peninsular portion were very great, and while nymphs of some species have been carried successfully, no nymphs of *S. deficiens* survived the trip.

The nymphs, which live in well-protected places where there is usually some accumulation of silt, are very difficult to see when mingled with debris. In streams in Alabama, Georgia, and North Carolina, specimens have been collected from moss covering the upper side of larger rocks. Traver (1937) described the habits of *deficiens* in North Carolina and stated that she found the nymphs among the moss and other plant growth that grew thickly on the upper side of all the larger rocks where they could be seen only after the rock had been left out of the water for some time. Our observations are consistent with those of Traver, but we should add that as the water drains away from the rocks after they have been taken from the water, the nymphs move upwards and can then be seen as they attempt to wriggle free of their previous haven.

In the field, young *S. deficiens* nymphs may easily be confused with those of *Neoephemera* or *Tricorythodes.* When taken from the water, members of all three genera walk slowly about, flicking the caudal filaments over the dorsum. *S. deficiens* nymphs are easily distinguished from both *Neoephemera* and *Tricorythodes* as they lack operculate gill covers on abdominal segment 2.

TRICORYTHIDAE*

When McCafferty and Edmunds (1979) divided the Ephemeroptera into two suborders, the Tricorythidae clearly fulfilled the criteria established for the Pannota, in which the nymphal wing pads are fused along the mesonotum, and at the same time there is general enlargement of this body segment. Gills of pannote nymphs tend to be reduced and pro-

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*Landa and Soldán (1985) split the family Tricorythidae of Edmunds and Traver into Leptohyphidae and Tricorythidae. Our North American genera, *Leptohyphes* and *Tricorythodes*, are thus assigned to Leptohyphidae. As we are using the McCafferty and Edmunds (1979) phylogeny throughout this book, we are not changing the family assignment.

tected. In the Tricorythidae there are specialized operculate gills which serve to protect those posterior to them.

The family is distributed over much of the world, reaching its greatest diversity in Africa. The only subfamily represented in the New World is the Leptohyphinae and of the two North American genera in the subfamily, only *Tricorythodes* is known to occur widely in Florida. Nymphs of the other genus, *Leptohyphes,* have been collected from the Savannah River at a distance of only 150 miles north of Florida, and recently Lager (1985) reported that he collected nymphs from the Withlacoochee River in Florida, just south of the Georgia-Florida state line.

Leptohyphes Eaton

Allen 1967, p. 350; 1978, p. 537.
Burks 1953, p. 55.
Edmunds, Allen, and Peters 1963, p. 17 (= *Bruchella*).
Edmunds, Jensen, and Berner 1976, p. 254.
Traver 1958a, p. 496 (= *Bruchella*); 1958b, p. 81.

Previous taxonomic accounts of the genus *Leptohyphes* have been comprehensively reviewed by Allen (1978). *Leptohyphes, Tricorythodes,* and *Haplohyphes* belong to the subfamily Leptohyphinae. The leptohyphine nymph is generally small and has a robust body, large metathorax, and relatively short abdomen; the gills on segment 2 are operculate or semioperculate, with their shapes varying from oval to triangular. Like the nymph, the adult also has a massive mesothorax, and the hind wings are either absent or greatly reduced, but when present they have a long and straight or recurved costal projection.

The adults of *Leptohyphes* are distinguished from the other genera of Leptohyphinae in that veins CuP and A of the forewing are not convergent or are only slightly convergent at the wing margin; hind wings are present in males but absent in females; and eyes of both sexes are relatively small and well separated. The nymphs are characterized by having sprawling, stout bodies with thickset legs; their operculate second gills are elongate-oval to oval; and the fore femora have a median transverse row of short or long heavy spines. The nymphs of *Leptohyphes* are often confused with those of *Tricorythodes*, but are distinguished from them by the shape of their operculate gills and the spines of the fore femora.

According to Allen (1978) *Leptohyphes* is a dominant element in the mayfly fauna of the southwestern United States, Mexico, and Central America. There are 35 species described in the genus from North and Central America. *Leptohyphes* occurs in the Neotropic and Nearctic, and presumably has an Austral-Lower North Temperate origin (Allen and Brusca 1973). Edmunds (1982) included *Leptohyphes* among mayfly genera of Gondwanian origin that underwent a dispersal pattern from South America to Central and North America. The Nearctic range of the genus includes the southwestern United States and eastward to Maryland, into the Piedmont and Coastal Provinces of the Southeast.

Leptohyphes dolani Allen

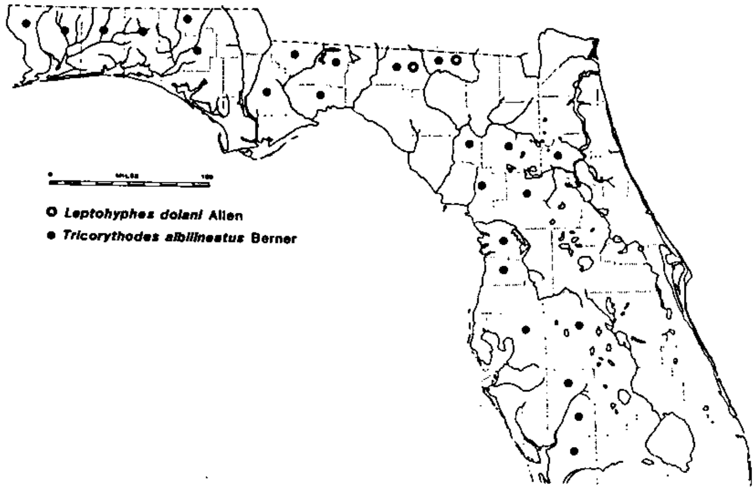
(FIG. 142. MAP 22)

Allen 1967, p. 351; 1978, p. 547.
Allen and Roback 1969, p. 376.
Berner 1977, p. 46.
Edmunds, Jensen, and Berner 1976, p. 256.
Lager 1985, p. 255.
Unzicker and Carlson 1982, p. 3.52.

TAXONOMY. Allen (1967) described *L. dolani* from nymphs collected from the Savannah River at the South Carolina–Georgia line. This species and *L. robacki* are the only two in the genus known to occur in eastern North America. The former was discovered in extreme northern Florida by Lager (1985). Allen (1978) included *L. dolani* in the *apache* group of the genus because of the lack of an elevated carina on the middle abdominal segments and the presence of submarginal denticles on the tarsal claws of the nymphs, which are distinctive for the group. The adults of *L. dolani* are still unknown.

GEOGRAPHIC DISTRIBUTION. *Leptohyphes dolani* has been collected from Texas eastward to the northeast and southeast. Most of the available specimens were collected in the Savannah River drainage along the South Carolina–Georgia line by a team from the Academy of Natural Sciences of Philadelphia while they were evaluating the stream for the Atomic Energy Commission. In Florida, the nymphs were collected only from the Withlacoochee River near Pinetta (map 22), at the Hamilton-Madison County line (Lager 1985).

ECOLOGY. Lager found the nymphs of *L. dolani* living on wood and calcareous rocks in a slow current in the Withlacoochee River; most of the surface was shaded by a dense tree canopy. Unzicker and Carlson (1982)



Map 22. The distribution of *Leptohyphes dolani* and *Tricorythodes albilineatus* in Florida.

reported that the microhabitats of *Leptohyphes* nymphs include submerged logs, sticks, branches, vegetation, and rocks found in slow current of medium to large rivers.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Except for the nymphal collection records, the seasonal distribution and life history of *L. dolani* is unknown. The nymphs from Florida were collected in September, and those from the Savannah River in August, September, and October. The nymphs from the Guadalupe River, Texas, were collected in August and September.

BEHAVIOR. Like the other tricorythid mayflies, the nymphs of *Leptohyphes dolani* are crawlers. The nymphs tend to remain motionless for a while on a hand-screen or collecting pan and, with their general body color camouflaged to match the substrate, they are easily overlooked by collectors.

Tricorythodes Ulmer

Allen 1977, p. 431.
Allen and Brusca 1973, pp. 55, 58–59.

Allen and Murvosh 1983, p. 433.
Berner 1950, p. 166; 1977, p. 47.
Unzicker and Carlson 1982, pp. 3.52–3.54.
Wurtz and Roback 1955, p. 193.

Until Ulmer established the genus *Tricorythodes* in 1920, the North American forms were included under *Tricorythus*. The males of species of these two genera may be separated by the length of the foreleg, which, in the African *Tricorythus*, is half the length of the body; in the American *Tricorythodes*, it is almost, if not fully, as long as the body.

McDunnough in 1931 summarized the knowledge of the North American species of *Tricorythodes* and described four, one of which was new. In 1935 Traver limited *T. explicatus* (Eaton) to a Texas form and described four additional species. McDunnough (1939) described another new species and also agreed with Traver's limitation of *explicatus*. A tenth species of *Tricorythodes* was described in 1946. Subsequently, four more species were found in various sections of North America north of Mexico, with the result that 14 species are now recorded. Allen's taxonomic studies of *Tricorythodes* nymphs have contributed substantially to our knowledge of the genus in the New World.

Tricorythodes is a widely distributed genus occurring in both the Neotropical and Nearctic areas. Allen and Brusca (1973, p. 58) postulate an austral origin for the genus because of the "great concentration of described species in the southern hemisphere." The authors state further that "[a]n austral origin of *Tricorythodes* is also supported by the fact that the great concentration of the species known to occur in the Neartcic [*sic*] Region is in the southern United States from Southern California to Florida."

In recent years greater attention has been given to Needham's "snowflake mayfly," which has been observed in miles-long flights (Needham and Christenson 1927). Newell (1976) and Newell and Minshall (1978) studied the effects of temperature on growth and development of *T. minutus* in Idaho. In Minnesota, Hall (1975; and with others 1975, 1980) investigated in depth the life history, drift, and production rate of *T. atratus*. Because of the work of Hall and Newell in particular, as well as that of other ecologists, much is known of the biology of at least these two species of *Tricorythodes*.

Spieth (1933) placed the genus in the same family with *Ephemerella*, removing it from its classical position in the Caenidae. Traver (1935) disagreed with this view, considering *Tricorythodes* to be an aberrant member of the Caeninae, but she presented no evidence, merely stating that the venation of the imago is much nearer to the other members of the Caeninae than to *Ephemerella*. Edmunds et al. (1976, p. 28) in a general discussion of classification systems pointed out that

> Increases in knowledge of the mayflies lead to many changes in classification, and it is important to realize that such knowledge is not equally available or known to all persons who decide on what classification to use. An example of changes brought about by increased knowledge is seen in the mayflies that we place in the families Tricorythidae and Caenidae. These were long regarded as one family, Caenidae (or as the subfamily Caeninae). Studies of the characteristics of these and other mayflies have shown in a very convincing manner that these two families are distantly related. The obvious similarities of *Tricorythodes* (Tricorythidae) and *Caenis* (Caenidae) resulted from convergent evolution caused by similar natural selection pressures on the two groups. In Africa, some of the Tricorythidae are similar to the Ephemerellidae, their true close relatives. The Caenidae are now known to be most closely related to the family Neoephemeridae. Since 1920 additional knowledge has made it increasingly clear that the Tricorythidae are distantly related to the Caenidae and cannot be correctly grouped with them.

Tricorythodes albilineatus Berner

(PLATE 19. FIGS. 4, 79, 145. MAP 22)

Allen 1977, p. 431.
Berner 1946, p. 72; 1950, p. 168; 1958, p. 30; 1977, p. 47.
Jones 1977, p. 66.
Landa 1969, p. 292.
Lanquist 1953, pp. 50, 53, 62.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 204.
Sloan 1956, p. 92.

TAXONOMY. *Tricorythodes albilineatus*, described in 1946, can be distinguished from other species of the genus by differences in color pattern.

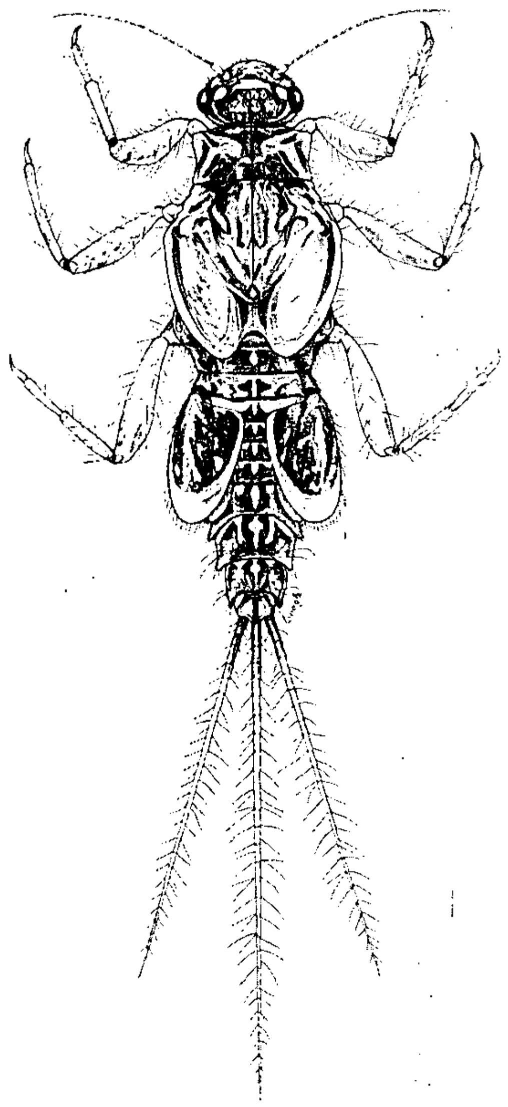


Plate 19. *Tricorythodes albilineatus* Berner, nymph

The sprinkling of numerous black dots on the femora, a characteristic given by Traver (1935) as diagnostic, would place the Florida specimens as *atratus*. Judging from McDunnough's description of *atratus* and our study of adult specimens from Minnesota, *albilineatus* has more limited dark markings on the abdomen than does *atratus*, and it is characterized by a pale median line on the dorsum of the abdomen. There is also a slight difference in the leg measurements of the males of the two species. The colorational characters are quite constant in *albilineatus*, particularly the pale line, even in series from widely separated localities.

GEOGRAPHIC DISTRIBUTION. *T. albilineatus* is generally distributed over Florida wherever there is permanently flowing water. Nymphs or adults are known from as far south as Charlotte County and as far north and west as Escambia County. The species occurs in an almost continuous belt, starting in DeSoto County and extending westward to Alabama and north into Georgia. The geographic distribution is probably limited by the ecologic factors of flowing water and the acidity of the water.

The species has been collected from streams in the following Florida counties (map 22): Alachua, Bay, Charlotte, Citrus, DeSoto, Escambia, Gadsden, Gilchrist, Hamilton, Hernando, Hillsborough, Jackson, Leon, Levy, Liberty, Madison, Marion, Okaloosa, Polk, Putnam, Santa Rosa, Wakulla, Walton, and Washington.

ECOLOGY. Ecologically, the nymphs are confined to streams with at least a perceptible current. They are moss and silt dwellers, occurring occasionally on vegetation in more swiftly flowing water. The Santa Fe River is an ideal stream for the rheotactic *T. albilineatus*. There, below a dam (destroyed in the 1970s) where the river spread out and became shallow, the streambed was strewn with pebbles and rocks. The upper surfaces of the larger stones were covered with dense mats of *Fontinalis*, one of the mosses which grows profusely when completely submerged. The flow of water over these rocks was quite rapid; nevertheless, silt became lodged between the closely packed moss "leaves." When one of the rocks was removed from the water and allowed to dry for a few minutes, *Tricorythodes albilineatus* nymphs began to crawl slowly about, flicking their tails over the abdomen just as many other nymphs that possess operculate gills do. If the moss is examined while it is wet, the nymphs are very difficult to see, their movements being slight until the drying action begins to take effect.

Below the destroyed dam, and to some extent above it, the Santa Fe River is normally choked with the plants *Vallisneria*, *Sagittaria*, and *Najas*. Frequently, when a dip net is run through these tangles of submerged vegetation in swift-moving water, *Tricorythodes* nymphs will be found along with the usual inhabitants of this biotope.

In smaller streams, predominantly of the sand-bottomed type, nymphs can be found clinging to vegetation, occasionally on detritus, and most frequently among roots of terrestrial vegetation that project into the stream. Silt and various other detrital elements accumulate among these roots. The nymphs of *Tricorythodes* tend to congregate in this mass of roots but are much less numerous than they are in the Santa Fe River.

Many sand-bottomed streams in Florida have dense growths of *Vallisneria* and *Sagittaria* like those in the Santa Fe River but without the exposed rock surfaces. In these streams, which include the runs of most of the springs in Florida, the nymphs are commonly found clinging to the vegetation, sometimes very close to the base of the plants, but they are not limited to this situation. Frequently, they occur near shore among leaf drift and on other debris.

The nymphs, which are found more often and in greater numbers in alkaline waters, are also fairly common in circumneutral or slightly acid streams. *T. albilineatus* is one of the representative species of mayflies of the spring runs and has been collected from many of them. The nymphs become noticeable about one-fourth of a mile below the head of the springs where the water has been exposed for a time to surface conditions and has become well aerated (Sloan 1956).

T. albilineatus is normally the only mayfly living on the upper side of the moss-covered rocks; on the underside occur species of *Stenonema* and *Stenacron*. Also associated with the nymphs in the moss but most commonly found on the underside of the rocks are *Corydalis cornutus* larvae, caddisfly larvae, sometimes crane fly and various other dipterous larvae, as well as snails. In the eelgrass are *Baetis propinquus*, *B. intercalaris*, *Pseudocloeon parvulum*, *P. punctiventris*, *Centroptilum viridocularis*, *C. hobbsi*, *Stenonema smithae*, *S. exiguum*, and *Stenacron interpunctatum*, together with the snail *Elimia*, one of the most numerous and characteristic animals of the basic streams in Florida. Many other aquatic animals are also found in the eelgrass association.

We have never found nymphs in the very small permanent streams but have taken them from slightly larger streams that are one to two feet deep and at least 10 feet in width. The limiting factors involved in stream size are unknown, but they may be linked with the relative rate of flow and the type of vegetation present. *Vallisneria* is seldom present in very shallow streams. Where the detritus and silt are markedly subject to drying at low water, the nymphs cannot withstand such great changes and consequently are not found.

Although the ecology of *T. albilineatus* has not been investigated in depth, very likely the species is an important component of stream drift just as *T. atratus* was demonstrated to be by Hall et al. (1975; 1980) in Minnesota. Cowell and Carew's (1976) drift collections in a tributary of the Hillsborough River in Florida did not produce specimens even though *albilineatus* has been collected from the main river. Further studies of drift in other Florida streams will likely confirm the similarity of *albilineatus* to *atratus* in this important means of dispersal.

That adults are very sensitive to humidity levels is demonstrated by the difficulty of obtaining imagoes from laboratory-reared specimens. Nevertheless, in the field it appears that the majority of subimagoes molt successfully.

SEASONAL DISTRIBUTION AND LIFE HISTORY. From a study of our specimens, it seems clear that *T. albilineatus* emerges in most of Florida throughout the year. For that portion of the state east and south of Leon County, we have records of adults taken from early February, March, April, June, August, and October, and mature nymphs collected in Levy County in November. Our records of adults from northwestern Florida include adults from Escambia County collected in late October. We also have adults from that part of the state taken in April, May, and June, and mature nymphs in July. The northwestern collections also include very young nymphs in May, June, July, and November. It is likely that growth of the nymphs is continuous in warmer streams of peninsular Florida, but it may be slowed by the lower water temperatures in streams in the panhandle. Jacobi and Benke (1985), studying growth rates of mayflies during the summer months in east-central Georgia, found that the species with which they were working (probably *albilineatus*) completed its development in about 52 days in an artificial stream using water from the Ogeechee River. Emergence of adults, then, appears to be continuous so long as low water temperatures do not inhibit growth and so imagoes appear on the wing in the warmer parts of the state throughout the year. Interestingly, Newell and Minshall (1978) found in Idaho that under favorable conditions (below a large spring with a constant temperature of 18°C) *T. minutus* emerged throughout the year, with dead adults being observed on the snow during the winter months.

Just as in more northern species, large numbers of adults emerge at the same time, and we have seen literally thousands of adults floating on the surface of the Santa Fe River. They were present in such numbers that they might be scooped up by the handful, but most of them were in a somewhat advanced state of decomposition. Emergence probably occurs after dark. We could not find a single adult before dusk, but when our light was turned on just after dark, the lighting sheet was very soon covered with the predominantly male subimagoes.

Many of the subimagoes seem to experience difficulties in molting even under natural conditions. In the Santa Fe River, there are many large boulders projecting one to two feet above the surface of the stream. Upon emergence large numbers of *Tricorythodes* subimagoes alight on them and remain to shed; however, sprinkled among the many shed skins, we found a considerable number of exuviae still retaining the partially freed imagoes—males and females in approximately equal numbers. These were dead but not yet dried when discovered. All of them seemed to have experienced great difficulty in freeing the wings, for it was by these structures that they were held.

We have witnessed the mating flight of this species only once at the Escambia River on October 23. A swarm of male *Tricorythodes* was discovered on our arrival at the stream at 9:15 A.M. on a warm (72°F), clear, calm day. They were flying at the edge of the river in bright sunlight at a height of 8–12 feet. The swarm was small, consisting of about a dozen individuals. Seven males were collected, and this disrupted the flight, the other males dispersing at the river shore.

Needham (1908) reported that *T. allectus* swarmed in great numbers at midday over an open area above a bridge. The same author (with Christenson 1927, p. 13) described the flight of *T. minutus* (as *T. explicatus*):

> They fly by day, the swarms being thickest in the forenoon. The males fly highest, up to 50 feet or more, in vertical lines, up and down incessantly. The females, after mating, fly low over the rippled surface of the stream, each carrying her little bunch of eggs extended at the tip of the abdomen and ready to let fall into the water. On sweeping the wet hand-screen thru the swarm, it was covered at one stroke with hundreds of females and their loosened egg masses.

Hall et al. (1975) described the mating flight of *T. atratus* in northern Minnesota. Males and females showed divergent flight patterns. In mid-July as the sun rose, large swarms of males were sighted at a height of 25–30 feet. Some observations revealed thousands of males flying in a jerky, up-and-down pattern at tree-top level. Females in groups of three or four would join the male swarms so that there was a constant stream of them entering. After entry of a large number of females, the flight continued for another 20–30 minutes and then began to disperse. After leaving the swarm, females descended to the stream to oviposit.

Leonard and Leonard (1962) observed large mating flights of *T. stygiatus* in Michigan during the early morning hours from 4:30 to 10:00 A.M., with death following soon after mating and oviposition.

Our first attempts to rear the nymphs in the laboratory in still water resulted in the death of the insects within one or two days after collecting. After installation of an aerator, the immatures were kept for as long as a month after collection, and many of these emerged.

Emergence was not seen in the field; in the laboratory, there seemed to be no set time for the event to occur. All our observations were made in February, during which the hours of emergence ranged from 9:15 A.M. to 7:30 P.M., with most taking place in the morning. The subimaginal and imaginal life spans were not determined because the subimagoes died before molting in every case.

Hall (1975) noted that emergence of the subimago of *T. atratus* occurs under water. In quiet water, the nymph first attached to a fixed object, the thoracic notum split, and the subimago, with wings still folded, swam to emergent vegetation, crawled out of the water, remained quiescent, and then expanded its wings to their full extent. When the water was flowing, the subimago simply swam to the surface of the stream, opened its wings, and then flew to a nearby resting place.

Hall discovered that the emergence pattern of the male differed from that of the female. Males began emerging at dusk and continued the process throughout the night. Females emerged at dawn and for about two hours after. The male subimaginal stage lasted from five to seven hours. As females emerge at dawn and the mating flights begin soon after, the female molts almost immediately after emergence; however, some females were observed to take up to two hours for the molt to occur. Hall also found that when humidity was high, subimagoes did not molt until sunlight struck them; when humidity was low, subimagoes molted much faster—usually within two or three minutes after emergence.

At the same time that Hall was working with *T. atratus* in Minnesota, Newell (1976) was studying *T. minutus* in Idaho. The pattern of emergence he observed showed the subimago emerging at the stream surface. The subimaginal stage lasted less than 30 minutes. He observed large swarms flying from one to eight meters over the stream. Mating flights occurred during midday in the spring and fall, and about two hours after sunrise and two to three hours before sunset in the summer.

Newell and Minshall (1978), after a careful study of exuviae, suggested that their data indicated that *T. minutus* males require about 19 instars and females 23 to complete their nymphal development.

BEHAVIOR. Examination of the alimentary canal of the nymphs showed that the specimens that are root inhabitants feed on epidermis of dead leaves, other debris, and occasionally diatoms; the nymphs living among water grasses feed on the epidermis of these plants, as well as on the diatoms covering them, although the latter are not eaten in great numbers. The moss-dwelling individuals also feed to a large extent on plant epidermis, but the diatoms form a more important element in their diet than in that of the two other groups.

The nymphs are awkward swimmers, using an undulating action of the abdomen for propulsion. The nymphs seldom swim, moving about almost entirely by crawling. The operculate gills are more or less rhythmically raised to allow aeration of the lower or posterior pairs. In the lowered position, the operculate gills cover rather completely all others behind them, though not so well as do those of *Eurylophella temporalis*.

NEOEPHEMERIDAE

Representatives of the family Neoephemeridae occur in the Holarctic and Oriental regions. The family, first named by Burks (1953), has been assigned by McCafferty and Edmunds (1979) to the superfamily Caenoidea along with the Caenidae, following its placement there in 1963 by Edmunds, Allen, and Peters. These latter authors discussed the basis of their placement of these two families together in spite of the very striking differences in the wing venations of the adults. The venation of *Neoephemera* led Needham, Traver, and Hsu (1935) to associate the genus with the Ephemeridae. Edmunds et al. arrived at the relationship of the Neoephemeridae and the Caenidae because of the nymphal similarities that they concluded are the result of common ancestry. The family, as presently recognized, includes three genera of which only one, *Neoephemera*, occurs in North America.

Neoephemera McDunnough

Berner 1950, p. 98 (*Orieanthus*); 1953, p. 145;
1956, pp. 33–34; 1959, pp. 41–42; 1977,
p. 33.

Burks 1953, pp. 42–43.
Demoulin 1961, pp. 63–68.
Edmunds 1972, p. 33.
Edmunds, Allen, Peters 1963, pp. 20–21.
Jazdzewska 1975, p. 227.
Unzicker and Carlson 1982, p. 3.35.

The unique nymphs belonging to this genus were described by Traver in 1931, 1935, and 1937 as *Oreianthus purpureus* and *Oreianthus* species no. 1. A third species, described by Joly as *Caenis maximus* in 1871, from nymphs collected at the Garonne River in France, was also assigned tentatively to *Oreianthus* by Traver (1931). Traver's assignment was subsequently confirmed, and the range of the species extended in Europe (Jazdzewska 1975), although the species is now known as *Neoephemera maxima.* The relationships of *Neoephemera* are particularly interesting, for while the wing venation of the adult is similar to some of the Ephemeroidea, the nymphal characters very closely parallel those of the Caenidae. For many years it was considered that the nymphal characters were secondary adaptations, and that the wing venation, which is fundamentally that of the Ephemeridae type, indicated the true relationships. Edmunds et al. (1963) stated that the similarities of the nymphs of the Neoephemeridae and the Caenidae result from common ancestry and are not the result of convergent evolution. Edmunds (1972, p. 32) concluded that as the immatures of the "Neoephemeridae share so few apomorphic characters with the Ephemeroidea that the venational similarities are almost certainly a result of parallel evolution."

McDunnough (1925) described *Neoephemera* from eight males collected at Laprairie, Quebec, but he gave no information relative to phylogenetic relationships of the genus or any other information about the insects. Burks (1953) concluded that those insects Traver had named *Oreianthus* were not sufficiently distinct from *Neoephemera* to warrant generic rank, and he synonymized the two names.

With the discovery of a new species of *Neoephemera* occurring in southern Georgia and northern Florida and the rearing of Traver's "*Oreianthus* sp. no. 1," Berner (1956) reviewed the North American species of the genus and prepared a key to the adult and immature stages. Demoulin (1961) reviewed the status of *Neoephemera maxima*, established three subgenera of *Neoephemera,* and provided a key for identifying them. Two of the three, *Neoephemera* (including *bicolor, compressa,* and *youngi*) and *Oreianthus* (*purpureus*), are North American; the third, *Caenomera* (including *Neoephemera maxima*), is European.

North American species of *Neoephemera* are found from southeastern Canada southward through the Appalachians to Florida (map 23). Westward, the genus is known from Michigan. Nymphs and adults are rarely found in collections, and records of the occurrence of the genus are sparse.

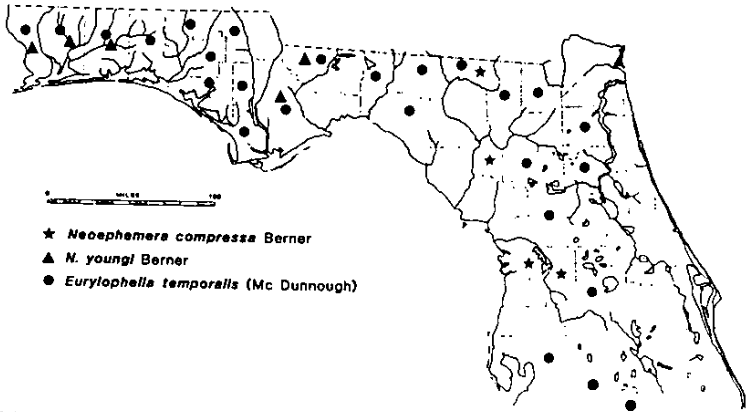
Neoephemera (Neoephemera) compressa Berner

(FIG. 156. MAP 23)

Berner 1956, pp. 34–40; 1959, p. 41; 1977, p. 33.
Demoulin 1961, p. 68.
Jones 1977, pp. 19, 20.
Schneider 1967, p. 202.

TAXONOMY. *Neoephemera compressa,* the most recently discovered species in the genus, was described in a taxonomic review of the North American species (Berner 1956). The adults of this species can be separated from others of the genus by size, venational characters, or color differences. It is easily distinguished from *N. bicolor* and *N. youngi* by differences in coloration of its legs and by the absence of annulations on its caudal filaments. The adults of *N. compressa* lack the small, dorsally projecting, median spine on tergite 2 which is found in *N. youngi* adults. Younger nymphs are particularly striking in appearance and show a pronounced dorsoventral flattening of the thorax. The tubercles of the anteromedian margin of the pronotum are very conspicuous as is another pair at the anterior margin of the mesonotum. As the nymphs mature, the thorax swells in size so that it assumes a more normal shape and the anterior tubercles are almost obliterated.

GEOGRAPHIC DISTRIBUTION. *N. compressa* has a limited distribution, being known only from extreme western and north-central Florida and central and southwestern Georgia. A single record of young nymphs from the Escambia River represents the farthest west that the species has been recorded in Florida. With the large number of collections made in northwestern Florida in recent years, it is surprising that there have been no additional specimens taken. The southwestern Georgia specimen was collected from a tributary of the Flint River, which is a tributary of the Apalachicola. The other collections are from the Withlacoochee and the Santa Fe rivers, both of which flow into the Suwannee. Florida counties from which the species is known are (map 23): Alachua, Columbia, Escambia, and Hamilton.



Map 23. The distribution of *Neoephemera compressa*, *N. youngi*, and *Eurylophella temporalis* in Florida.

ECOLOGY. The nymphs of *N. compressa* occur in streams of slow to moderate flow.

> The Withlacoochee River, where the nymphs were found in some abundance, is a deep, slow-flowing stream bordered by ash, willow, cypress and black-gum trees. Where the trunks of these trees are submerged, they are usually covered by a densely growing species of moss. It was in this moss that the nymphs were found, usually after a careful examination. They are slowly moving insects which are sometimes difficult to see in the dark vegetation and it is only by removing large clumps of the plant and shaking them that the nymphs are dislodged. Many were removed by picking them from the moss after it was taken from the water. The nymphs were associated with those of *Baetisca obesa*, which were very common in the moss. Amphipods and isopods were also numerous in this association. Nymphs were often found in some abundance by running a dip net through debris anchored in flowing water. (Berner 1956, p. 38)

At another stream, nymphs were found among the submerged but exposed and well-washed roots of terrestrial plants in much the same situation where *N. youngi* nymphs occur in other streams. A few nymphs were also taken from long-submerged logs. No nymphs have been found in rapidly flowing water. We surmise that by and large the ecological relationships of *N. compressa* are much like those of *N. youngi*.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Little is known about the seasonal distribution and life history other than that adults were reared from mature nymphs collected in January and March. The earliest emergence occurred in late February and the latest in early April. Nymphs collected in late November were half grown and would likely have emerged sometime between late February and early April. We assume that the life history and seasonal distribution of *N. compressa* must be very similar to that of *N. youngi*.

BEHAVIOR. Observed behavior of nymphs of this species was identical to that of *N. youngi*.

Neoephemera (Neoephemera) youngi Berner

(PLATE 20. FIG. 157. MAP 23)

Berner 1950, pp. 99–102; 1953, pp. 145–148; 1956, pp. 41–42; 1959, p. 41; 1977, p. 33.
Carlson 1980, p. 83.
Demoulin 1961, pp. 65–68.
Edmunds, Jensen, and Berner 1976, p. 263.
Jones 1977, pp. 1–145.
Peters and Jones 1973, p. 246.
Schneider 1967, p. 202.

TAXONOMY. The nymphs of *Neoephemera youngi* were first described by Traver in 1937 as *Oreianthus* sp. no. 1 and illustrated by Berner (1950), who described additional details in 1956. The species was transferred to *Neoephemera*, named, and the adults described in 1953. When Traver treated the Florida nymphs collected by Dr. J. G. Needham in 1927 from Sweetwater Creek in Liberty County, she suggested that the differences between the Florida nymphs and those of *Oreianthus purpureus* from North Carolina might be generic rather than specific. However, the examination of reared adults of both species clearly shows that they are members of the same genus but fall into different subgenera, *purpureus* in *Oreianthus* and *youngi* in *Neoephemera*.

At first glance, one is likely to confuse young nymphs with those of *Caenis*, but closer examination immediately distinguishes the two, for *Neo-*

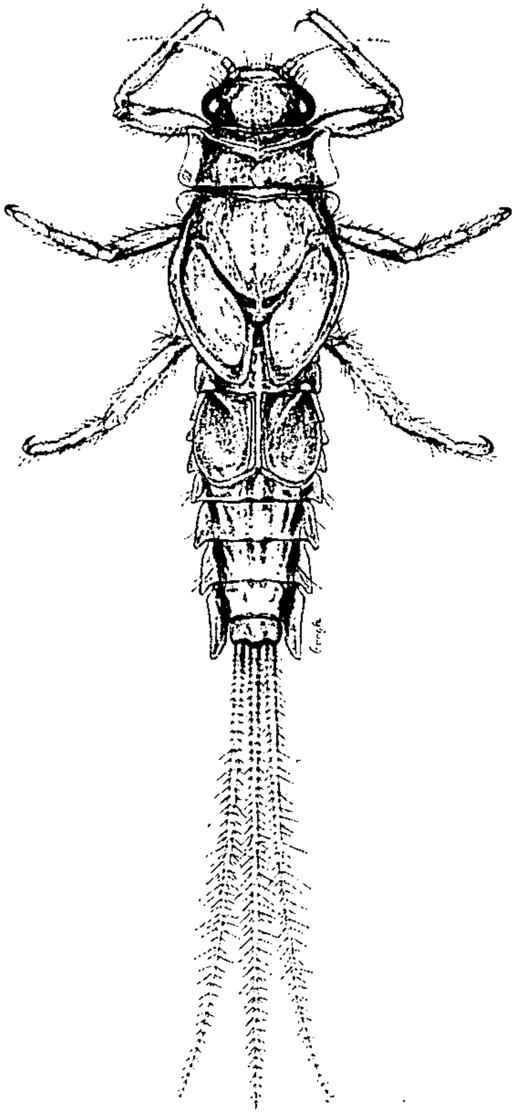


Plate 20. *Neoephemera youngi* Berner, nymph

ephemera has prominent metathoracic wing pads. In later instars *Neoephemera* nymphs are much larger than are those of *Caenis* and are very different in gross appearance as well as in structural details.

Jones (1977) has reviewed comprehensively the taxonomy of *Neoephemera youngi* in his excellent study of the ecology and life history of the species.

GEOGRAPHIC DISTRIBUTION. *N. youngi* is known to occur in the Coastal Plain of Alabama, Georgia, and Florida and in the extreme southern parts of the Piedmont of Alabama, Georgia, and South Carolina. In Florida, specimens have been collected over much of the northwestern panhandle from tributaries of the Ochlockonee River in the east to the Yellow River in the western part of the state. In spite of the distributional range of *N. youngi* specimens are only rarely taken in general collecting, and records of its occurrence are not frequent. The species has been recorded from the following Florida counties (map 23): Escambia, Gadsden, Liberty, Okaloosa, and Santa Rosa.

ECOLOGY. Jones (1977) has discussed the ecology of the various instars in his study of the life history of *N. youngi*. His findings are consistent with those earlier described for the species. The nymphs are confined to those parts of streams where flow is continuous, although not necessarily rapid; most frequently they live among the roots of terrestrial plants that project into the water. Debris and silt accumulate among the tangle of the roots, which together furnish an apparently ideal situation for the development of the nymphs. Only rarely do the insects appear in collections made from cleanly washed roots in the swifter waters where *Isonychia* is so common.

Although not as numerous as in the root habitat, the nymphs can be found in leaf drift and among branches that become anchored rather permanently in the streambed. However, these nymphs seem to be marginal forms and do not appear to be adapted to swifter waters. Jones found nymphs of the first eight instars almost exclusively in a water moss, *Leptodictyum riparium*, confined to an exposed flat, concrete spillway at the mouth of culverts. He concluded that silt and debris that accumulate in the tangle of the moss offer a uniquely ideal situation for the development of the younger stages. Older nymphs were found living among the roots of terrestrial vegetation.

The spindly legs of the immatures and the presence of gill covers indicate that the Florida nymphs find their natural habitat in the silty places where they have been taken rather than on the undersides of cleanly swept rocks in midstream where Traver first collected the nymphs of *Neoephemera purpurea.* Frequently, large, submerged and well-anchored logs were found in the streambed, yet no *Neoephemera* nymphs were on them. It is apparent that other habitats must be more acceptable to the immatures, but even in them they are not especially numerous, although Jones reported that he collected 50 nymphs from among exposed roots. That this root habitat is the preferred one for nymphs of *Neoephemera* is apparent from our finding specimens of *N. purpurea* among the roots in a mountain stream in North Carolina rather than under large stones in midstream, the habitat described for them by Traver.

The nymphs have a high degree of tolerance to certain kinds of disturbances. Traver had one nymph of *N. purpurea* that survived a three-day automobile trip, during which the water was changed infrequently each day. Several nymphs of *N. youngi,* confined in a half-pint jar in which the water was not changed, were brought by car to Gainesville from Sweetwater Creek, a distance of about 250 miles. They were removed overnight to an open pan but the following day were replaced in the jar for the remainder of the trip. In Gainesville they were kept in a pan of shallow water, where they lived for a time, but, for some undetermined reason, none lived longer than 20 days in captivity. Two nymphs reached the point of emergence but died before transformation was accomplished.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Jones's (1977) study of the life history of *N. youngi* revealed that the species is strictly seasonal and univoltine. He noted the production of a single generation per year in the two populations he studied. In the field imagoes were seen first emerging in early April, with the process extending into early May. The peak of emergence was in mid-April, with the latest field observation occurring on May 9. Adults were reared in the laboratory as early as mid-March. *Neoephemera* is among those few Florida mayflies that have a highly restricted seasonal range. This fact is in accord with other evidence suggesting a southern origin for the species.

Jones found mature eggs to be ellipsoid and without sculpturing or polar caps. Attachment structures included an adhesive layer and a few short filaments on the egg surface. Incubation required 66 to 82 days in the laboratory. He observed hatching over a period of 30 to 40 days. His records of the earliest dates of adult emergence and the earliest appearance of nymphs in field collections led him to suggest an egg stage of about three months. Females produced from 958 to 2101 eggs, with an average of 1461 per individual.

Careful observations led Jones to conclude that the species requires 15 nymphal instars to complete development. In his study, he described the salient changes occurring in each instar. As usual in mayfly nymphs in the first instar, gills are absent, but they do appear by the fifth instar. Jones was unable to obtain nymphs in the third and fourth instars but was successful in obtaining the remaining stages. The first-instar nymphs molted three to five days after hatching. He was unsuccessful in rearing second-instar nymphs, as all died two to six days following their last molt. Fifth-instar nymphs, obtained from field collections, molted 4 to 10 days after capture. The sixth instar required 14–17 days, and the seventh-instar nymphs died before molting to the next stage. Eighth-instar nymphs molted over a period of 7–16 days after field capture. Ninth-instar nymphs, now growing rapidly, required an average of 20 days to complete development to the 10th instar, which lasted an average of 23 days. At the 11th instar the nymphs measured as much as 6.2 mm, but Jones was not able to determine the length of time required for development. Twelfth-instar nymphs were obtained from field collections and molted from 4 to 15 days after capture. Thirteenth-instar nymphs were as large as 8.2 mm and required about 19 days to develop to the 14th instar, which averaged 22 days. Nymphs in the 15th, and last, instar reached a length of about 10 mm and emerged as subimagoes from 21 to 25 days after attaining this instar.

Subimagoes emerged for the most part during the period extending from 30 minutes before sunrise to 30 minutes after. Additional evidence indicated to Jones that subimaginal emergence actually occurs over a four-hour period extending from one hour before to about three hours after sunrise. Emergence occurs at the surface of the stream in 40–60 seconds. The newly emerged insects then fly directly upward to a resting site.

Jones was able to determine the length of subimaginal life in the laboratory and found it to range from 12 to 16 hours. He found no relationship of temperature and humidity in the laboratory to length of subimaginal stage. Molting of the subimago to the adult stage required from 5 to 12 minutes.

Although Jones was not able to observe mating swarms of *N. youngi,* he did observe a possible form of preswarming, stream-orientation behavior on several occasions. He noted a single male imago descend to the surface of the stream, touch the water with the tip of its abdomen, then fly quickly up and out of sight. He observed this same behavior in a total of 10 males in April, beginning about two hours before sunset and lasting for about an hour. About an hour before sunset, he noted a single female fly into the same area of the stream and release her eggs from about three feet over the water. Ten other females followed the first and displayed the same type of ovipositing behavior. Once eggs were released, some of the females fell to the surface of the stream and were soon eaten by fish.

Jones observed similar flight activities on other occasions in late April, but there were no further sightings of flying imagoes after May 9. During the time the adults were flying, the air temperatures ranged from 21°C to 31°C; water temperature was 17°C to 22°C. Most of the activity was seen in a quiet, riffle-free part of the stream. There was little wind, and the sky was clear to partly cloudy.

Jones was led to believe that the imagoes mate early in the evening just before sunset and that swarming must occur high in the air out of sight of the observer. He suggests that the dipping of the abdomen in the water assists the males in orienting themselves with reference to the stream flow.

Adults were kept alive for about 24 hours. In the laboratory the adults lived from 20 to almost 29 hours. Slight variations in temperature and humidity in the laboratory apparently had little effect on longevity of the adults.

Jones's earliest collection of very young nymphs was on June 29, and he estimated that they were already in their second instar. He believes that hatching occurred three to four days before these second-instar nymphs were collected. He found the first nine instars to be relatively abundant from July to November. Fully mature nymphs were seen in late February. The first with black wing pads were not taken until mid-March, but at the same time small nymphs were also observed, indicating an extended hatching period. The last nymphs were taken on May 2.

BEHAVIOR. The nymphs swim very little, and their motions are extremely awkward when they do. The tails are bent over the abdomen and suddenly lash out so that the movement of the abdomen, assisted by the beating of the almost bare caudal filaments, drives the insect slowly and with much difficulty through the water.

The attitude of the nymphs when taken from the water is much the same as that characterizing all those species of mayflies which have operculate gill covers. A slow, deliberate movement is coupled with an occasional flicking motion of the caudal filaments as the insect brings the filaments completely back over its dorsum until they point anteriorly, and then lashes out with them as though it were using them for propulsion. The nymphs' coloration and choice of habitat doubtless act as protection against the many predators infesting the streams.

According to Jones, the nymphs are detritivores, which eat plant fragments and filamentous algae. He found detritus, derived mostly from leaves that had fallen into the streams, to be the choice food of the nymphs he examined. Sand particles were found to be thoroughly intermixed with the materials in the digestive tract, and he suggested that the nymphs may be attracted to the film of fungi and bacteria that is usually present on or among the particles.

Nymphs were observed by Jones to feed mostly at night and were found usually on the upper surfaces of the leaves when feeding. He found on one occasion in the laboratory that a fully mature nymph had completely skeletonized a whole maple leaf in a period of four days.

CAENIDAE

The family Caenidae includes some of the smallest species of mayflies, representatives of which occur virtually worldwide. They are absent only from New Zealand and most Oceanic Islands; but with increased shipping in recent years, *Caenis nigropunctata* Klapalek, known from Java, Sumatra, Bali, and the Philippines, has been introduced into the Hawaiian Islands (Zimmerman 1957). The adults of the two North American genera have only a single pair of wings with a greatly expanded anal area and with the hind margin bordered with setae. The three caudal filaments are very long in males but very short in females. The body of the female is robust; that of the male slender.

Nymphs have more or less flattened bodies and lack hind wing pads; the gills on the second abdominal segment are operculate but not fused along the midline. There are three caudal filaments.

Along with the Neoephemeridae, the Caenidae have been assigned to the suborder Pannota and superfamily Caenoidea by McCafferty and Edmunds (1979). The North American genera of the Caenidae are easily separated from all other Ephemeroptera both in the adult and nymphal stages.

Caenis Stephens

Berner 1950, pp. 173–174; 1959, pp. 13–15; 1977, pp. 34–35.
Burks 1953, pp. 50–51.
Edmunds, Jensen, and Berner 1976, pp. 266–269.
Leonard and Leonard 1962, pp. 39–40.

The genus *Caenis* was described in 1835 by Stephens, who made the European *Caenis macrura* the genotype. At the time of publication of Eaton's monograph, only two species of *Caenis* were known from North America, seven from Europe (he included *Brachycercus harrisella*), one from Asia, and two from Africa. Hagen (1861) listed three species in his *Neuroptera of North America,* but Eaton synonymized *diminuta* and *amica* (the latter now recognized as a valid species). The next general review of the genus in North America was that of McDunnough (1931) in his paper on the subfamily Caeninae, in which he treated 10 species, of which 5 were described as new. Traver (1935), in *The Biology of Mayflies,* again treated the North American species of *Caenis,* describing two new ones, and redescribing the 10 that had been discussed and described by McDunnough. Burks (1953) found still another new species, *C. gigas,* in Illinois, and Harper and Harper (1981) named *candida* from Quebec. Presently, Arwin Provonsha is preparing an in-depth revision of *Caenis.*

Campion (1923) discussed in full the synonymy of the generic name *Caenis* and erected the genus *Ordella* to include part of *Caenis*; the remainder was placed under the name *Brachycercus.* Lestage (1924) followed Campion and suggested that the family name be changed from Caenidae to Brachycercidae; however, McDunnough, without stating a reason, restored the American species to *Caenis* and used Caenidae to include *Brachycercus, Tricorythodes,* and *Caenis.* Subsequently, *Tricorythodes* has been recognized as belonging to the Tricorythidae, not Caenidae (Edmunds and Traver 1954).

No detailed studies have been made of the ecology of North American species of *Caenis,* although Rodgers (1982) has investigated the effects of elevated water temperatures on nymphal development and emergence patterns. Needham et al. (1935, p. 180) characterized the nymphs as "the sprawlers amid the silt in still water."

The species of this genus are generally distributed throughout North America, although there are relatively few published records from the west.

The high state of development of *Caenis* is indicated by the complete absence of hind wings. Diminution in size leading to loss of the hind wings began in the Jurassic. Reduction of the number of segments in the forceps of the male to a single segment further bears out the idea that the genus is an advanced one. *Caenis, Brachycercus,* and *Cercobrachys* are similar in the adult stage, but *Caenis* can be separated from the other genera by its much longer prosternum, causing the fore coxae to be brought close together on the ventral side of the body. Nymphs are readily differentiated: *Caenis* nymphs have no ocellar tubercles, whereas the other two genera have three prominent ones. *Caenis* has three-segmented maxillary and labial palpi as compared with two-segmented ones in the others. Finally, the body is much less flattened in *Caenis* than in *Brachycercus* and *Cercobrachys.*

Caenis diminuta Walker

(PLATES 21, 22. FIGS. 5, 78, 107. MAP 24)

Berner 1950, pp. 174–185; 1958, p. 29; 1977, p. 34.
Burks 1953, p. 51.
Frost 1967, p. 281.
Jones 1977, p. 65.
Lanquist 1953, pp. 23, 24, 27, 31, 34, 40, 41, 44, 62, 66.
Needham 1949, p. 455 (*C. amica*), p. 457 (*C. diminuta*).
Peters and Jones 1973, p. 247.
Schneider 1967, p. 202.
Sloan 1956, p. 92.

TAXONOMY. Francis Walker described this minute mayfly in 1853 from specimens collected at St. Johns Bluff, Florida, a point on the south side of the St. Johns River about six miles from the ocean. Since then the species has been redescribed by Hagen (1861), who related it to *C. lactea* of Europe; by Eaton (1871; 1881); by McDunnough (1931); and by Traver (1935). Spieth (1940) supplemented the description. All these authors agreed that the species is quite distinct, but McDunnough and Traver have shown that in addition to the true *diminuta,* the material of earlier

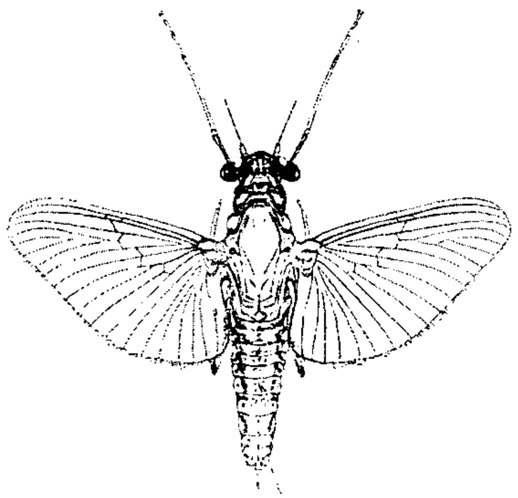


Plate 21. *Caenis diminuta* Walker, male imago

writers also included five other species. The adults of *C. diminuta* may be distinguished from all other North American species of *Caenis* by the dark stigmatic streaks present on the anterior abdominal tergites, by the presence of a dark apical band on the hind femora, and by the absence of black dots from the femora. At the present state of our knowledge nymphs of *Caenis* are almost impossible to separate; but if only the two Florida species are considered, the problem is somewhat simplified. In general, *diminuta* nymphs in their last instar range from 3.9 mm to 6.7 mm and usually have numerous yellowish spots scattered over the pro- and mesonota; in *hilaris*, the other Florida species, the size range is from 2.2 mm to 3.8 mm. Yellowish spots are usually absent from the pronotum of *hilaris*; the mesonotum has one pair of submedian spots and yellowish spots at the bases of the wing pads. The difference in size between the two species is the significant feature, the smaller measurements given above being those of mature male nymphs, the larger those of mature females.

GEOGRAPHIC DISTRIBUTION. *Caenis diminuta* is one of the most widely distributed species of mayflies occurring in Florida. McDunnough recorded specimens taken near Gravenhurst, Ontario, and from Stuart, Florida, and the species is now known from many localities in Florida. It has been reported from Alabama, Georgia, Louisiana, and Tennessee (Berner 1977). In Florida, the species is known to occur from the southernmost county and throughout the state. We have recorded *C. diminuta* from 43 of Florida's 67 counties, and we believe that it can be found in the other 24. Those counties from which we have specimens are (map 24): Alachua, Bay, Broward, Calhoun, Citrus, Clay, Collier, Columbia, Dade, DeSoto, Escambia, Flagler, Franklin, Gadsden, Glades, Gulf, Hamilton, Hernando, Highlands, Hillsborough, Holmes, Jackson, Jefferson, Lake, Lee, Leon, Levy, Liberty, Madison, Marion, Monroe, Nassau, Okaloosa, Orange, Pasco, Putnam, St. Johns, Santa Rosa, Sarasota, Taylor, Volusia, Walton, and Washington.

ECOLOGY. Even very small bodies of fresh water serve as habitats for *Caenis* nymphs. The smallest biotope in which we have found nymphs was a pool about a foot wide, which had been produced by the recession of a creek that had overflowed. The species is most successful in standing bodies of water of pond size or smaller. In lakes of the silt-bottomed type, represented by Lake Wauberg near Gainesville, the species is very common, but in such sand-bottomed lakes as Lake Geneva in Clay County, they are much scarcer or may even be absent. The nymphs are sprawlers

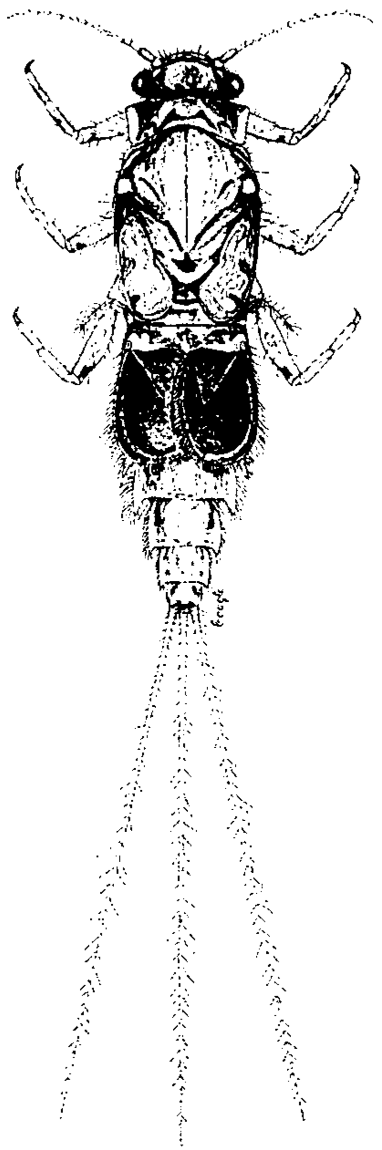
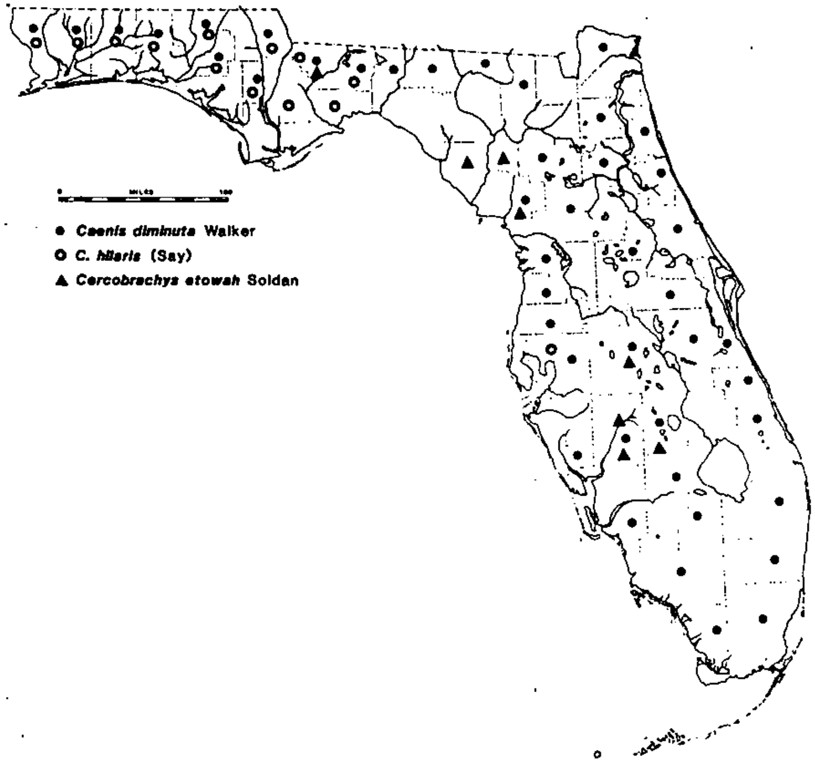


Plate 22. *Caenis diminuta* Walker, nymph



Map 24. The distribution of *Caenis diminuta*, *C. hilaris*, and *Cercobrachys etowah* in Florida.

in the mud and silt of the pond bed. Here they crawl slowly over the plant stems, where they are more or less protected from predators. Occasionally, they leave the bottom to climb a short distance up the plants, but they are more frequently found clinging to the bottom of the stems. Leaf debris and other trash accumulating in shallow water also harbor *Caenis* nymphs, but they do not seem to be as numerous here as in the plant association. The margin of the vegetation also appears to limit the distribution of the nymphs, and, even though there may be debris beyond this shore zone, the insects seldom venture into the deeper water.

Caenis nymphs do not commonly live in ponds and lake edges that are covered with water hyacinths because there is usually an inadequate supply of oxygen and not enough bottom vegetation to support even these rather tolerant nymphs. However, Lanquist (1953) often found them along with bloodworms and tubificid worms in the decaying hyacinth detritus and debris on the bottom of the tributaries and canals connected with the Peace River in southwestern Florida. Likewise, sinkhole ponds covered with duckweed and *Wolffia brasiliensis* seldom have populations of this species, as in most of these waters attached vegetation is lacking and there is much decaying material. The combination of these factors may be sufficient to render the bottom of these ponds unsuitable for habitation. Two sinkhole ponds, approximately one-fourth of a mile apart on the University of Florida campus, exemplify this phenomenon. One of these ponds was completely covered with duckweed; the other was entirely free of the plant but had a luxuriant growth of *Riccia fluitans*. In the former there were no mayfly nymphs; in the latter there was an abundance of *C. diminuta* immatures. Mayflies are not the only animals affected by the paucity of oxygen in the duckweed-covered pond, for the usual pond associates of *C. diminuta* are also either entirely absent or extremely rare.

Roadside ditches are among the most fruitful places for finding *C. diminuta* nymphs because comparatively few predators inhabit them, submergent vegetation is plentiful, and oxygen and food are abundant. Cypress swamps and marshes in which there is vegetation or leaf debris also maintain populations of nymphs. Even streams may be inhabited by the nymphs of this species. In flowing water, they live in shallow regions among the rooted aquatic plants, on the roots of terrestrial plants projecting into the water, on submerged logs, sticks, or other trash, and even on rocks in moderately swift water. When in the flowing parts of the stream, they must cling more closely than in the quiet areas, and the current limits their ability to move about easily. In still or slowly flowing water they move more freely.

The nymphs have surprisingly wide limits of tolerance; they withstand not only marked variations in acidity and alkalinity but also marked fluctuations in temperature and in the amount of decomposition taking place in the water. The lowest pH recorded in water from which nymphs were taken was somewhat less than 4.0, the highest well above 8.0. *C. diminuta* nymphs must also be able to withstand great temperature variations, as is indicated by the fact that they thrive in shallow pools continually exposed to southern Florida sunlight and yet apparently flourish in the very cold waters of Canada. Nymphs in all stages of development have been collected from odorous, stagnating water along with larvae of the rat-tailed maggot; apparently, the nymphs have remarkable powers of resistance to putrefaction. In fact, Lanquist (1953) stated, "Berner (1950) recognized *Callibaetis* as being the most tolerant mayfly in Florida; but after taking *Caenis* with the pollution indicators at so many of my stations and after finding *Callibaetis* usually at the shore or in hyacinths near the surface, I would give *Caenis diminuta* the honor of being the most tolerant form." Further, Sloan (1956, p. 92) remarked about *C. diminuta*, "It is apparently fairly tolerant as a species although its populations are seen to be quite small in areas of environmental extremes such as the pool and estuary [of spring runs]."

SEASONAL DISTRIBUTION AND LIFE HISTORY. There is no definite season for emergence of *C. diminuta* in Florida. Adults have been collected in all months of the year, and there are no clear-cut broods. McDunnough (1931) recorded the species from adults taken on August 20 at Gravenhurst, Ontario. In the northern parts of its range, the species must certainly be seasonal; it could not be otherwise, for the ponds in which it lives are probably frozen over during the winter months. Though in Florida emergence occurs throughout the year, the species is limited to some extent by temperature; during cold spells emergence comes to a standstill, but as soon as there is a change in the weather and the shore zone warms sufficiently, subimagoes begin rising.

Collections of adults at a light on warm nights during the winter indicate that the rate of emergence is somewhat less than during the summer months. Nevertheless, the number of emerging adults is large. Collecting at lights in a particular area on consecutive nights frequently does not yield the same results, although lighting conditions may be about the same. This may be due to emergence of different broods from the same pond, but as there is so much overlapping in generations, the existence of distinct broods is somewhat doubtful. Rodgers (1982), working in northern Alabama with *Caenis* n. sp. near *amica*, suggested that her evidence implied two asynchronous generations of the species per year.

One of us (Berner) had limited success in rearing *C. diminuta* from egg to adult. Many nymphs were hatched, but only two were successfully reared, the others having died during some preadult stage. The entire period of development was approximately 124 days. The number of instars could not be determined, but some data have been obtained on growth rate, hatching, and other features of life history. These are presented in table 3.

On October 23 at 6:40 P.M. 15 female adults of *Caenis diminuta* were collected at light. These specimens were taken within 10 minutes, even though it was not yet dark and there was a bright moon. Each of the females was placed on the surface of a bowl of water, and each began to oviposit immediately. The process was completed by 7:20 P.M. Most of the individuals voluntarily completed oviposition, but those that did not were aided by having their abdomens squeezed with forceps. The females, once placed on the water surface, showed no inclination to leave even after emptying the abdomen of eggs. Each dish was numbered, as well as each female, which was then preserved in alcohol.

In some of the bowls all the eggs had hatched by 7:15 P.M. on October 30, a week after oviposition; in the remainder of the bowls, hatching had begun. By December 4 all nymphs were healthy and apparently growing rapidly. Two of the nymphs, though, were very immature, hardly larger than a normal week-old individual; the immaturity may have been due to delayed hatching.

While the bowls were being prepared for the *C. diminuta* eggs on October 23, a few of the ova adhered to the vial in which the females were brought to the laboratory. The bottle had been filled with water and a pinch of dried organic matter added; the bottle was put to one side and forgotten. On February 7 the vial was discovered—the water was almost gone, but there were seven *Caenis* nymphs still alive and active in it. The individuals were all dwarfed. Two of the nymphs had not even developed gills—only a pair of tubular outpocketings on abdominal segment 1. The stunting was evidently the result of an insufficiency of food. The small mass of organic material that had been added to the vial originally was still hard-packed and apparently had only been nibbled at by the nymphs. It is quite possible that hatching had been long delayed, which might account for the size of the nymphs and their lack of development.

Of those nymphs that hatched on October 30, only four remained alive by February 19. Three of the four were in the last instar, and one of them measured 4.5 mm. Finally, on February 24 the wing pads of one of these last instar-nymphs began to blacken, and on March 3 the subimago was ready to emerge.

The first of the laboratory-reared adults emerged during the late afternoon or early evening of March 3, and on the morning of March 4 it was found floating on the surface of the water in the bowl in which it had been reared. The shed nymphal exuviae of another specimen was also found in the rearing dish, but the imago had escaped.

Table 3, together with the observations, gives a partial picture of the development of *C. diminuta* from egg to adult. Many difficulties beset the rearing of the nymphs. The eggs are easily hatched; but rotifers, flatworms, and small oligochaetes, accidentally introduced with food mate-

TABLE 3
RATE OF GROWTH OF *Caenis diminuta* NYMPHS
(Average measurements covering about one-fourth of early life)

Date Specimen Killed	Body Length	Antennal Length	No. of Antennal Segments	Length of Lateral Cerci	No. Segments in Lateral Cerci	Length of Median Filament	No. Segments in Median Filament	Length of Fore Tibio-tarsus	Length of Foreclaw	Gills Present
Oct. 30	0.42 mm	0.20 mm	5	0.35 mm	3	0.36 mm	5	0.1 mm	0.045 mm	No
Nov. 6	0.49 mm	0.32 mm	6 (?)	0.55 mm	6 (?)	0.57 mm	6 (?)		0.055 mm	No
Nov. 13	0.50 mm	0.38 mm	6–7	0.68 mm	6–7	0.68 mm	6–7	0.11 mm	0.055 mm	No*
Nov. 22	0.83 mm	0.73 mm	9–10	1.00 mm	9–11	1.10 mm	9–10	0.17 mm	0.07 mm	In some
Nov. 27	0.93 mm	0.80 mm	11–12	1.20 mm	14–15	1.20 mm	14–15	0.21 mm	0.075 mm	Yes
Dec. 4	1.16 mm	0.85 mm	14–16	1.55 mm	25 (?)	1.60 mm	?	0.30 mm	0.075 mm	Yes

*(except in one specimen)

rial, may furnish too much competition for the delicate nymphs, many of which perish. The four specimens mentioned above must have been exceptionally sturdy, for several times the water almost disappeared from their bowls. There were many protozoa in the containers, and during most of the time very little light reached the insects.

Table 3 gives the time required from oviposition to hatching for many of the nymphs which were hatched in the laboratory.

The figures in table 3 indicate that the fall and winter broods hatch much more rapidly than do those of the spring. No eggs were hatched during the summer; the time required for hatching in this season would probably be between that of the spring and fall (5–11 days). Then again the figures may be of no significance, for all specimens were hatched indoors where the fluctuation of temperature was slight as compared to that outdoors. The time necessary for hatching is among the shortest of North American species of *Caenis* for which we have been able to obtain data. Listed below are hatching times for a number of other species of mayflies hatched under laboratory conditions:

Caenis diminuta—5–11 days (Berner 1950)
Ephemera varia—15 days (Needham et al. 1935)
Hexagenia bilineata—9 days (Needham et al. 1935); 8–12 days (Fremling 1967)
Hexagenia limbata—11–26 days (Hunt 1953)
Leucrocuta hebe—12 days (Needham et al. 1935)
Litobrancha recurvata—15 days (Needham et al. 1935)
Neoephemera youngi—66–82 days (Jones 1977)
Stenacron interpunctatum—13–15 days (Needham et al. 1935)
Stenonema femoratum—11–23 days (Needham et al. 1935)
Stenonema modestum—25–28 days (Kondratieff and Voshell 1981)
Stenonema smithae—13 days (Berner 1950)

When the nymph of *C. diminuta* is ready to hatch, the chorion splits cleanly along the longitudinal axis. One nymph had freed its head when first observed; the antennae were still twisted but free. Two of the left legs had been released. By working the body from side to side, the other legs finally were pulled loose. With these, the nymph then seized the bottom litter, and clinging, even though its legs had not yet straightened, pulled the remainder of its body from the egg. The tails, however, adhered to the egg membranes so that the insect had to be detached mechanically. The entire process took about two minutes. When first hatched the antennae and tails of many nymphs are crinkled, the legs bowed, and the abdomen twisted to one side. This condition generally corrects itself within a few hours. At times the condition may persist for several days, possibly until the first molt.

The eggs are released by the female in a somewhat spherical mass that immediately breaks up when the female touches her abdomen to the water surface. The eggs then separate and sink. As they fall through the water, they release a tangle of threadlike, sticky fibers that cling to the first solid object with which they come in contact. Once an egg is attached, there is some difficulty in tearing it loose without injuring the filaments; if the egg is freed, the remaining threads may again become entangled. There is no swelling of the chorion nor any formation of a protective jellylike coat as in the eggs of many other species of mayflies.

Upon hatching, the nymphs begin to search for concealment and food. Although in many cases the spreading caudal filaments are evident, the young insects are rather transparent; so almost any background is sufficient for their concealment. Their swimming actions are very awkward. The young nymph lashes out with its caudal filaments and then bends them completely back over the abdomen and lashes out again, producing a series of jerky, somewhat undulatory movements. During this process, the legs are held widely spread and ready to grasp any support. Until the operculate gills are formed, the nymphs retain their whitish, opaque appearance. Shortly after the formation of these gills, brown pigment begins to color the immatures, which are further concealed by the detritus that adheres to the long hairs covering the body.

Emergence of adults occurs in late afternoon or at night. When ready to transform, the nymphs float at the surface in shallow water from a few inches to several feet deep and just inside the limits of attached vegetation. The subimago soon bursts from the nymphal skin but seems to experience some difficulty in taking flight. In many instances we observed that the subimago was unable to rise from the water; and, during its struggles the wings became wet, dooming the insect. Often the subimago will take off from the nymphal exuviae, but the flight results in only a short hop. After resting on the surface film, the insect makes another attempt to fly. Once free and safely in the air, the subimago flies to the nearest support and very shortly molts. In the instance of specimens reared in the laboratory, the molt occurred approximately five to six minutes after emergence from the nymphal stage.

This species is one of the shortest-lived of all mayflies in the adult stage. Laboratory-reared adults remained active for about four hours, although a slight reflex movement of the legs could still be observed 30 minutes later.

We have never been able to observe the mating of this species, and there appear to be no written accounts of the mating flight of any species of *Caenis*. A flight, which may have been the mating flight of *C. diminuta*, was observed on January 25 at about 3:00 P.M. At that time many subimagoes were rising from the surface of Orange Lake in Marion County. They flew to the nearest available support where they molted and, as imagoes, became very active. At 3:45 P.M. a single male was noted rising and falling in a typical mating-flight behavior about 300 yards from shore but still within the water-bonnet zone. Flying about five feet above the water, it rose and dropped vertically about two feet but seldom moved horizontally. This male was soon lost to sight, and no further flights were seen.

While he was collecting crayfish at Orange Lake a few days later, Dr. H. H. Hobbs observed the coupling of a pair of *C. diminuta* adults that were flying with little rise and fall about five feet above the water surface. After about 30 seconds the two individuals separated and soon disappeared.

BEHAVIOR. The food of the nymphs consists of plant debris, algae, and any other organic materials that chance may throw their way; even inorganic substances may happen to be seized by their raking feet. One nymph was observed feeding on a leg of a dead immature of the same species. When feeding, the nymph clings with the two posterior pairs of legs and one of the forelegs and at the same time extends the other foreleg; this leg, which is then drawn in toward the mouth, pulls along with it the debris lying within reach of the claw. When the food reaches the mouth, the maxillary and labial palpi begin an active movement, sorting and shoving the food into the mouth. As soon as one clawful of material is disposed of, the other leg may reach out, or the first may again be used if there is still material within reach; if not, the nymph moves slowly forward until it encounters more food. Pieces of the epidermal covering of plants are detached by the sharply pointed claws and pulled into the voracious jaws. The nymphs seem to feed continuously, and the anterior part of the alimentary tract is always well packed, as in all other mayfly nymphs.

The adults of *C. diminuta* are among the most pronouncedly phototactic of mayflies. A light set up near any body of water where the species is known to be present will attract males and females equally well. On some nights either males or females may dominate at the lighting sheet; on other occasions the two sexes may be attracted in approximately equal numbers.

When most mayflies alight, the wings are held vertically over the back. *Caenis*, however, alights with its wings spread wide, leaps up again, and repeats the performance several times, each time moving closer to the light source. Finally, flying stops and the adult begins to crawl toward the light—its wings spread in a horizontal plane, or even depressed until they almost touch the object on which the insect is walking. Once attracted to a light, the adult seems almost helpless and becomes easy prey for many insects, particularly ants.

Caenis hilaris (Say)

(MAP 24)

Berner 1950, pp. 185–187; 1958, p. 29; 1977,
  p. 34.
Cowell and Carew 1976, pp. 590, 592.
Jones 1977, p. 65.
Peters and Jones 1973, p. 247.
Schneider 1967, p. 203.

TAXONOMY. *Caenis hilaris*, one of the first recorded North American species of mayflies, is the smallest ephemerid found in Florida as well as one of the smallest known. The body and wing measurements are slightly over 2 mm. The species was described by Say in 1839 as *Ephemera hilaris*; later it was redescribed from Illinois material by Walsh (1862), after first having been placed in the genus *Caenis* by Francis Walker (1853). Hagen (1861) briefly described the adults; and Walsh, in his description, pointed out differences between Hagen's specimens and his own. Eaton (1871) was the next to redescribe *C. hilaris* and after an interval of nearly 50 years McDunnough (1931) revised the description of the species. Once again *hilaris* was described by Traver in 1935 in *The Biology of Mayflies*. Our specimens conform to descriptions by McDunnough and Traver fairly well; a few minor differences are probably individual variations.

GEOGRAPHIC DISTRIBUTION. In Florida, *C. hilaris* is confined to an area in the northwestern part of the state extending from the western boundaries to somewhat east of the Apalachicola River. The species is rather widely distributed over the eastern United States, but it is unknown west of Oklahoma and in Canada. It inhabits a wide variety of physiographic provinces, ranging from the Coastal Plain into the Appalachian Province.

In the Southeast, it has been recorded from Alabama, Florida, Georgia, Louisiana, Mississippi, North and South Carolina, and Tennessee (Berner 1977). Cowell and Carew (1976) reported finding nymphs of the species to be abundant from September to November in stream drift collections made in Hillsborough County. We believe that their specimens may have been misidentified and were, in reality, *diminuta.* Nymphs or adults have been collected from the following Florida counties (map 24): Bay, Calhoun, Escambia, Gadsden, Holmes, Jackson, Leon, Liberty, Okaloosa, Santa Rosa, Wakulla, Walton, and Washington. If Cowell and Carew's report is correct, Hillsborough County will also be included.

ECOLOGY. Nymphs have been collected only from gently flowing streams, predominantly of the sand-bottomed type, with debris accumulated near the shore. The habitats of the nymphs are identical with those of *Serratella deficiens* as described for Sweetwater Creek in Liberty County. In other streams, nymphs have been found in the vegetation near shore, among leaf drift, and on submerged logs and sticks. We have never taken specimens from the deeper, swifter parts of the streams, even where debris was present. In addition to the usual sand-bottomed streams where *hilaris* nymphs have been found, we have taken adults at Blue Springs Creek near Marianna but could find no nymphs. It is uncertain whether they inhabit the stream itself or the lake formed by the dam. This stream, which is decidedly basic, would be a rather exceptional habitat for the species, as it has a very soft bottom and an abundance of snails and had no vegetation at the time the collections were made.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The evidence at hand leads us to believe that, like *diminuta, C. hilaris* emerges throughout the year in Florida. Our collections include adults taken from April through November and last-instar nymphs recorded in November and December. Although our records have gaps, it seems logical from a study of younger specimens to assume that emergence must occur during the warm periods of other months.

In spite of the large amount of taxonomic literature concerning *C. hilaris,* its life history remains unknown.

BEHAVIOR. The nymphs are extremely minute and consequently difficult to see: some last-stage specimens are less than 2 mm in length. We have found that the most efficient method of taking nymphs is to put debris collected by means of a fine-screened coffee strainer into a white-enameled pan. When the pan is tilted and the water drains away from the

nymphs, a slight movement is discernible, as the insects attempt to follow in the wake of the liquid. As with *C. diminuta* nymphs, the movement is a slow crawl combined with a wriggling motion. The nymphs of this species do not tend to flick their tails over their backs; and both young *Tricorythodes* and damselfly nymphs may easily be confused with those of *hilaris* unless they are separated with a hand lens.

Strongly phototactic, *C. hilaris* adults are attracted to lights along with *C. diminuta* adults. At Blue Springs Creek a large electric plant, the lights of which are kept burning all night, faces the lake formed by the damming of the stream. The walls and windows of the illuminated porch were covered with spiderwebs, the spiders hiding in every crevice to catch the myriad insects that were attracted to the lights. We have examined the webs on several occasions and have been well rewarded for our efforts; the predominant insects present were midges, but *Caenis* adults were second in abundance, other insects occurring in much smaller numbers. Other adults have been collected in large numbers at lighting sheets just after dark at the Escambia River and at lighted store windows in Chattahoochee.

Brachycercus Curtis

Berner 1950, pp. 187–189; 1959, pp. 12–13; 1977, p. 33.
Burks 1953, pp. 48–49.
Jacob 1974, p. 96.
Jones 1977, p. 65.
Leonard and Leonard 1962, pp. 37–38.
Pescador and Peters 1974, p. 193.
Peters and Jones 1973, p. 247.
Soldán 1986, pp. 291–297.
Thew 1960, pp. 202–203.

The status of the name *Brachycercus* was reviewed in 1950 (Berner), and justification for use of the name was established. Subsequently, Jacob (1974) also reexamined the taxonomic tangles. Soldán (1986), in his recent review of the Caenidae with ocellar tubercles in the nymphal stage, recognized four genera, three of which he described as new. As now constituted by Soldán, the special group includes *Brachycercus,* which is Holarctic and Neotropical, and his new forms, *Cercobrachys, Insulibrachys,* and *Caenoculis. Cercobrachys* occurs in Florida.

In his comprehensive review of all species in the genus, Soldán separated *Brachycercus* from the other Caenidae mainly on the basis of nymphal characteristics. He pointed out that in the nymph, the antennal pedicel is at least one and a half to two times the length of the scape; the ocellar tubercles are well developed; the head has distinct posterolateral lobes; both maxillary and labial palpi are two-segmented; the fore coxae are widely separated; the claws lack teeth; and the posterolateral spines of abdominal segment 6 are not bent medially. Additional characteristics that distinguish Florida *Brachycercus* nymphs from the closely related *Cercobrachys* include the presence of long, anteriorly directed bristles on the anterior margins of the pro- and mesosternum of *Cercobrachys;* the lateral spines of abdominal segment 6 arise anterolaterally in *Cercobrachys* and posterolaterally in *Brachycercus;* and posterolateral spines on abdominal segments 7–9 are present in *Brachycercus* but absent in *Cercobrachys.*

Brachycercus nymphs are rather unusual in appearance, belonging to the large assemblage of mayflies that have operculate gill covers to act as protectors of the more delicate, highly tracheated, posterior gills. The nymphs are easily separated from those of *Caenis* by their depressed body form and the presence of ocellar tubercles. They differ from other nymphs with operculate gill covers, such as *Tricorythodes,* in having ocellar tubercles and rather square gill covers; from *Neoephemera* by lacking hind wing pads; and from many of the Ephemerellidae in that the operculate gills of *Brachycercus* are on the second abdominal segment rather than the third or fourth.

The genus is Holarctic and Neotropical and is distributed throughout most of North America. It has not yet been recorded from the extreme western part of the continent.

Brachycercus berneri Soldán

(PLATE 23. FIGS. 77, 163. MAP 25)

Berner 1950, pp. 191–193; 1958, p. 29; 1977, p. 33 (*Brachycercus* sp.), p. 34 (*Brachycercus* sp. A).
Pescador and Peters 1974, pp. 193, 195 (as *B. maculatus*).
Peters and Jones 1973, p. 193 (*Brachycercus* sp.).
Schneider 1967, p. 202 (*Brachycercus* sp. A).
Soldán 1986, pp. 298–301, 307–308 (*B. floridicola* n. sp.).

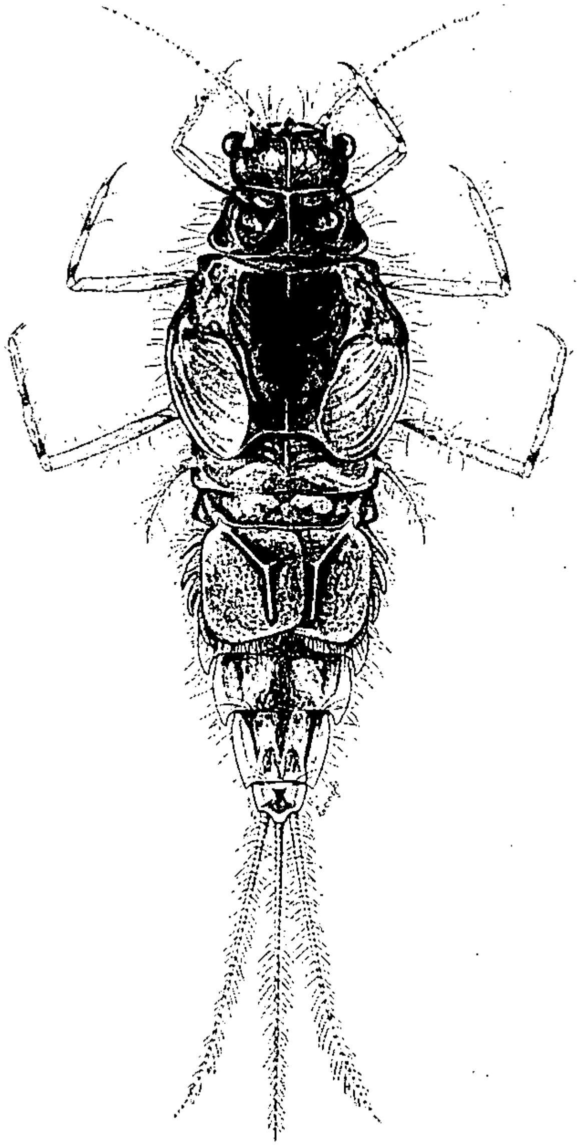


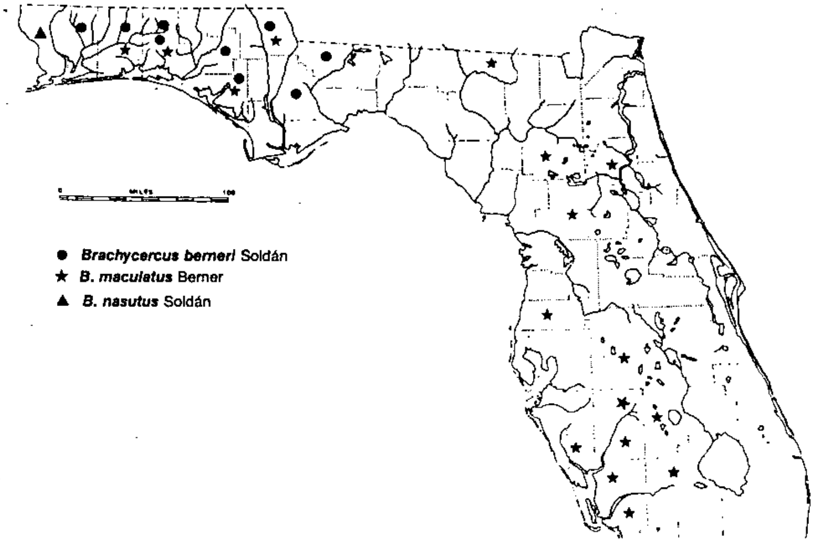
Plate 23. *Brachycercus berneri* Soldán, nymph

TAXONOMY. This species, formerly known as *Brachycercus* sp. A, was named and described by Dr. Soldán (1986) in his recent revision of the genus. *B. berneri* nymphs, the stage most readily identified, are differentiated from other Florida species by characteristics delineated in the key to nymphal forms; in particular, they are separated from *nasutus* by their much shorter ocellar tubercles and from *maculatus* by their apically oblique gill cover, presence of a pair of pronotal spines, the long spinous hairs on the lateral margins of segment 1 of the maxillary palpi, and the much longer and more attenuated tarsal claws. The adults are more difficult to separate, as they have no strikingly distinctive traits. Soldán differentiates the adults from other species by the following characteristics: the antennae are unicolorous; the pedicel is more than twice the length of the scape; the abdominal sterna are white, except that sterna 1–3 have dark stippling; and the penes are longer than wide, slightly produced posterolaterally, the posterior margin concave and with a sclerotized triangular structure in the middle and a pointed spine near the base.

Soldán (1986) has described a new species, *B. floridicola,* based on nymphal specimens from Florida. We have examined the nymphal holotype and paratypes of the species, as well as the type series of *B. berneri,* and have found that the two species are indistinguishable. In fact, the diagnoses of both species by Soldán are the same except for the pronotal spines which he claimed to be present in *B. berneri* and lacking in *B. floridicola.* We found that nymphs of *B. floridicola* also have pronotal spines. Although the adult stage of *B. floridicola* is unknown, its overwhelming nymphal similarities with *B. berneri* have convinced us the two are the same species.

Soldán describes *B. berneri* as having low and rounded posterolateral spines on abdominal segment 2. We are unable to locate these structures on the nymphs we have examined. There is a projection of the anterolateral corner of the operculate gill on segment 2 that appears to arise from the abdominal segment; it can be seen when the insect is examined in profile. This projection articulates with a socket on the abdominal tergite, and it may be the structure Dr. Soldán refers to as being the posterolateral spine on segment 2.

GEOGRAPHIC DISTRIBUTION. In addition to Florida, this species has been recorded from Alabama, Georgia, and South Carolina, inhabiting streams in the Coastal Plain, Piedmont, and Valley and Ridge physiographic provinces (Berner 1977; Soldán 1986). We have records of its occurrence in



Map 25. The distribution of *Brachycercus berneri, B. maculatus,* and *B. nasutus* in Florida.

the following Florida counties (map 25): Bay, Gadsden, Jackson, Liberty, Okaloosa, Santa Rosa, Walton, and Washington. We believe that the Wurtz and Roback record (1955) of *B. nitidus* from Escambia County is in actuality *B. berneri* and that Soldán's inclusion of the record as valid leads him to an erroneous interpretation of the geographic distribution of *B. nitidus.*

ECOLOGY. While one of us (Berner) was collecting mayfly nymphs in Sweetwater Creek, Liberty County, numerous individuals of *B. berneri* were found sprawling on the sand within a few inches of the water line. They normally chose sand with a small amount of silt mixed in it that was partially protected from the main force of the current by projecting vegetation. They could be taken most commonly beyond the area where silt had accumulated sufficiently for *Hexagenia* nymphs to be numerous. Frequently, when scraping the sand for *Brachycercus,* the strainer would also pick up small nymphs of *Hexagenia limbata* and the dragonfly *Progomphus obscurus.* The streams from which the nymphs were taken are typical of the sand-bottomed creeks with little vegetation that are described in the section on habitats.

SEASONAL DISTRIBUTION AND LIFE HISTORY. We have little concrete information regarding these subjects. As nymphs in all stages of development were collected in late April, we believe that the species emerges throughout the year but that the rate of emergence slows during the winter and stops completely during cold periods. We have adults collected in February, April, and June.

BEHAVIOR. Little is known of the habits of the nymphs of *B. berneri* other than that when the nymphs, which sprawl on the sand, are taken from the water, they can scarcely move—probably because of their long, spindly legs and attenuated claws. The slow wriggling motions of the nymphs, the flattened abdomen, and the broad thorax immediately identify *Brachycercus* nymphs to the naked eye.

Brachycercus maculatus Berner

(FIGS. 150, 162. MAP 25)

Berner 1946, pp. 76–77; 1950, pp. 189–191.
Soldán 1986, pp. 216–318, 326–327 (as *B. pini* n. sp.).

TAXONOMY. *Brachycercus maculatus* was described in 1946 from a small collection of adults and a single cast skin taken at the Santa Fe River in Alachua County. The species has not been encountered elsewhere with certainty other than those places listed by Berner in 1950 and below. The records of Lanquist (1953) and Berner (1977) from the Peace River in southwestern Florida may be Soldán's *Cercobrachys*. Jones's (1977) specimens from Bear Creek, Gadsden County, are *Cercobrachys;* those of Pescador and Peters (1974) are *B. berneri*. *Brachycercus maculatus* adults are easily distinguished from those of *berneri* by the dark brown stipplings on abdominal terga 1–6 and the posterolaterally rounded lobes of the penes. The nymphs are separated readily from *B. nasutus* by the short frontal ocellar tubercle, and from *B. berneri* by the apically rounded gill covers, lack of pronotal spines, and thicker, curved, and shorter tarsal claws.

In the revision of the Caenidae with ocellar tubercles in the nymphal stage, Soldán (1986) described a new species, *B. pini*, based on nymphs from Florida. The characters (length ratio between pedicel and scape, orientation of the lateral ocellar tubercles, and the spines of abdominal segment 6) in couplet 13 of the nymphal key that Soldán used to separate *B. pini* from *B. maculatus* are highly variable and unreliable.

Soldán (1986) stated that the figure of *Brachycercus* sp. A by Berner (1950) actually refers to *B. pini.* The figure shows no pronotal spines; it has symmetrical gill covers with rounded posterolateral margins; and the spines of abdominal segment 6 overlap segment 7. The drawing of *Brachycercus* sp. A (Berner 1950) was prepared by an artist, Esther Coogle, who failed to note the transparent posterolateral margin of the operculate gills. Our reexamination of the nymphal specimens on which the drawing of *Brachycercus* sp. A was based showed that the nymphs are indeed typical of *B. berneri,* and the original drawing has been modified to illustrate correctly the shape of the gills.

We have examined the type specimens of *B. pini* and the nymphs of *B. maculatus* and have found that they are indistinguishable. We cannot concur with Soldán that *B. pini* is a valid species, and we are not, therefore, treating it separately.

GEOGRAPHIC DISTRIBUTION. The species has been recorded from the following Florida counties (map 25): Alachua, Bay, Hamilton, Jackson, Marion, Okaloosa, Pasco, Putnam, Walton, and Washington. Cantrell, during his extensive studies of aquatic insects in southwestern Florida, found the species in Charlotte, DeSoto, Glades, Hardee, Highlands, and Sarasota counties.

ECOLOGY. Virtually nothing is known of the ecology of *B. maculatus.* The indications are that the nymphs may prefer basic streams as both the Santa Fe River and Silver Springs are somewhat alkaline, yet the finding of specimens in Orange Creek and the northern Withlacoochee River tends to contradict this, as both of these are brown-water streams. The nymphs collected from the Santa Fe River were found in shallow water, not more than three or four inches deep, where there was a bit of silt mixed with the sand on which the nymphs lived. Other Florida species have been taken from similar stream habitats.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Adults have been collected on February 28, April 6, and July 7; a last-instar nymphal skin was found May 7. These specimens indicate a late-winter through midsummer emergence. Our data are insufficient to speculate further about seasonal distribution.

Our adult males were collected before noon floating on the water surface of the Santa Fe River; their fine state of preservation makes it appear most likely that *B. maculatus* flies early in the morning. Adult life probably lasts for only a few hours in common with *Caenis.*

BEHAVIOR. We have no information on this subject.

Brachycercus nasutus Soldán

(FIGS. 149, 161. MAP 25)

Berner 1955, p. 11; 1977, p. 33 (in part).
Schneider 1967, p. 202.
Soldán 1986, pp. 321–322.

TAXONOMY. The striking nymph of *B. nasutus* is highly distinctive by virtue of its very much elongated frontal ocellar tubercle, which extends forward from the anterior margin of its head; the very prominent posterolateral abdominal spines; and the banded legs. The unmarked abdomen readily differentiates the adults from the other species of the genus in Florida.

When the nymph was first collected by one of us (Berner) in 1954, it was put aside as a distinct new species to be described at a later date and awaiting the taking of additional specimens. A few months afterwards, adults were collected, but it was not until Dr. Soldán reviewed the Caenidae with ocellar tubercles that the species was named and described. Dr. Soldán listed the distinguishing characteristics of the nymphs as follows: frontal tubercle twice as long as the lateral ones and three to four times longer than the width of the compound eye; the antennal pedicel is less than twice as long as the scape; the pronotum lacks spines or ridges; there are no sternal protuberances; the posterolateral spines of abdominal segment 2 are larger than those of segments 3–7; the labrum lacks lateral projections; and the operculate gills are nearly symmetrical and tapered apically. The species cannot be confused with any other Florida form in the genus *Brachycercus*.

GEOGRAPHIC DISTRIBUTION. We have collected specimens from the Escambia and Yellow rivers in extreme northwestern Florida. Soldán has also included a record from the Conecuh River, a tributary of the Escambia River, in southern Alabama. All Florida specimens are from Escambia County (map 25).

ECOLOGY. *Brachycercus nasutus* nymphs were collected from a sandbar, along with the nymphs of *Baetisca escambiensis*, in the Escambia River in shallow water varying from four to five inches up to about a foot in depth. Although the *Baetisca* nymphs were practically buried in the streambed, "I [Berner's field notes] did not determine whether the *Brachycercus* was also buried, although I assume that it was not but lay on top of the fine layer of silty mud which was over the sandy bottom. There was also an admixture of clay in the sand in the region where the specimens were collected. The current was relatively slow, and in some parts of the sandbar there was a growth of algae over the bottom. In almost every place the *Baetisca* nymphs occurred, and I assume the *Brachycercus* also, young *Hexagenia* nymphs were found."

The *Baetisca* nymphs were living on the sloping sides of the sandbar where the shelving was rather steep, the grade estimated to be about 20%. The relatively slow current was deflected laterally across this shallow zone. Where the algae were dense, no *Baetisca*, and presumably no *Brachycercus*, nymphs were found; but where the algae were sparse and the layer of silty mud overlaying the sand thin, the nymphs of *Baetisca* appeared to be common.

The Escambia River was clear and colorless at the time the collections were made in October. The water temperature was 65°F, and it was alkaline, as evidenced by the presence of large numbers of snails. The river has a very clean, white sand bottom with a swift flow in midstream.

SEASONAL DISTRIBUTION AND LIFE HISTORY. We have scant information on these subjects; however, we do have mature nymphs collected in April and August, and adults in August.

BEHAVIOR. We have no observations on the behavior of *B. nasutus*.

Cercobrachys Soldán

Berner 1977, p. 33 (DeSoto Co. record, as *Brachycercus*).
Jones 1977, p. 65 (as *Brachycercus*).
Lanquist 1953, pp. 21, 24–27, 62, 63 (as *Brachycercus*, probably *Cercobrachys*).
Soldán 1986, pp. 336–337.

In describing this genus, Soldán (1986) noted that nymphs of *Cercobrachys* differ from those of *Brachycercus* in many ways. He emphasized that the differences are much greater than those between nymphs of some of the other *Caenis*-like genera. Soldán further stated that the new genus was established in order to separate this distinct group with a "gill basket" and specialized legs.

Cercobrachys includes *C. etowah*, the single Florida species; *minutus*, a transpalaearctic species; *peruanicus*, from Peru; *petersorum*, from Thailand; and *serpentis*, from Idaho. The distribution is Holarctic, Neotropical, and Oriental.

Nymphs are most easily separated from those of *Brachycercus* by the following characteristics: the antennal pedicel is at most 1.1 to 1.3 times longer than the scape; the ocellar tubercles are small but apparent; the pro- and mesosternum have prominent, anteriorly directed, long setae at their anterior margins; the legs are long and slender with very long setae; the tarsal claws sometimes have minute teeth (present in the Florida species); the lateral abdominal spines of segment 6 arise anteriorly and are bent medially so that they are almost contiguous, to produce the so-called gill basket.

Adults are much less easily separated from related genera, as there are no venational characteristics nor segment ratios in the legs that are applicable. Soldán, in separating adults, indicates that the antennal pedicel is only slightly longer than the scape or equal in length, and abdominal spines on segment 6 are strongly bent dorsally. He gives some differences in the eggs as well.

Cercobrachys etowah Soldán

(MAP 24)

Berner 1977, p. 33 (in part).
Lanquist 1953, pp. 21, 24, 27, 62, 63 (as *Brachycercus maculatus*).
Soldán 1986, pp. 339–340.

TAXONOMY. While studying Florida specimens of *Brachycercus*, Dr. Soldán noted some Gadsden County nymphs in the Florida A & M collections that were quite distinct from the true *Brachycercus*. A detailed examination of the nymphs convinced him that he was dealing with a new genus and species, which he named *Cercobrachys etowah*. The name comes not from the Florida specimens but from nymphs collected at the Etowah River in north-central Georgia. Soldán separated *C. etowah* from other species of the genus on the basis of a number of traits, chiefly the following: small denticles are present on the tarsal claws; the tibiae of the forelegs are only two-thirds to three-fourths the length of the tarsi; and the posterolateral spines of abdominal segment 2 are very small. The species should not be confused with any others occurring in Florida. Lanquist (1953) identified his specimens from southwestern Florida (the Peace River) as *Brachycercus maculatus*. We now believe that his insects were probably *C. etowah*. Cantrell, however, thinks that Lanquist did find *B. maculatus* along with *C. etowah*. In his samples, Cantrell found *C. etowah* to be a minor component based on total numbers of nymphs collected.

GEOGRAPHIC DISTRIBUTION. The species is represented in our collections by nymphs or nymphs and adults from the western portion of peninsular Florida and the eastern part of the panhandle, as well as from southwestern and north-central Georgia. The record listed as *B. maculatus* from DeSoto County (Berner 1977) is, in reality, *C. etowah*. In Florida we have specimens from or the species has been recorded in DeSoto, Gadsden, Hardee, Highlands, and Polk counties (map 24), and the abutting county lines of Gilchrist, Dixie, and Levy counties (Suwannee River).

ECOLOGY. We have no observations of our own except for those relating to a collection made by one of us (Berner) at the Ichawaynotchaway Creek in Baker County, Georgia. A single specimen was collected from this fast-flowing stream, a tributary of the Flint River, which joins the Chattahoochee to form the Apalachicola River in Florida. The streambed was composed of coral rock and sand. The stream was deep, and mosses were attached to the rocks and cypress tree stumps. The river snail *Elimia* was common, indicating that the water was alkaline. When the specimen was examined microscopically soon after the collection was made, it was recognized as being very distinctive and was listed as *Brachycercus* sp. (Berner 1977).

Lanquist (1953), in his study of the Peace River, reported: "Of the mayflies *Brachycercus maculatus* [*C. etowah*?] was the dominant form being common wherever the sand bottom was covered by a thin film of organic silt. . . . Though most of the mayfly nymphs were present throughout the study, the velocities in the high water stages caused the disappearance of *Brachycercus* [*Cercobrachys*] in August and September 1951, and August 1952. The fact that it was present and common at Arcadia, where the current was slower, during August of 1952, is evidence that velocity may be a limiting factor in its distribution which must be considered. It may affect the available food or the animal directly." During his study, Lanquist found that *B. maculatus* (*C. etowah*?) was the deepest-penetrating mayfly, as he collected occasional specimens from water as deep as 22 feet, where they were apparently sprawling on the sandy bottom.

SEASONAL DISTRIBUTION AND LIFE HISTORY. We have virtually no information on these subjects except that adults were collected in May.

BEHAVIOR. No observations are available on the behavior of this species.

BAETISCIDAE

The unique mayflies of the family Baetiscidae are most striking in the appearance of the nymphal stage. The Baetiscidae were reviewed in detail by us in 1980 (Berner and Pescador) and in 1981 (Pescador and Berner) and the various stages described and illustrated for all known species. The genus *Baetisca,* the only one in the family, is endemic to North America with the species occurring over most of the eastern part of the continent into the Great Plains and northwestward to the Northwest Territories of Canada.

The unusual nymph has a stout, rotund body in which the mesonotum is greatly enlarged to form a mesonotal shield covering the dorsum of the mesothorax, metathorax, and abdominal tergites 1–5 and part of 6. The mesonotal shield also encloses the gills in a gill chamber. Various kinds of spiny ornamentation are found on the head and mesonotum. The adults have distinctive forewing venation, the body is short and stout, and the thorax is greatly enlarged.

Baetisca Walsh

Berner 1950, p. 147; 1955, pp. 1–2; 1959, pp. 8–9.
Berner and Pescador 1980, pp. 511–524.
Edmunds, Jensen, and Berner 1976, pp. 269–272.
Pescador and Berner 1981, pp. 163–228.
Unzicker and Carlson 1982, pp. 3.23–3.25.

The genus *Baetisca* is not a particularly large one, containing only 10 species. These insects are so distinctive that Ulmer (1933) placed them in a separate family (Baetiscidae), Spieth (1933) in a separate superfamily (Baetiscoidea), Traver (1935) in a separate subfamily (Baetiscinae), and Berner (1955) in Baetiscidae once more.

Baetisca nymphs are the most unusual-looking mayfly nymphs in North America. With their stout, spinous, humped-up bodies, they might well rival some of the most bizarre types of dinosaurs of the Mesozoic. In general, the adults of the genus are not as readily identified to species as are the nymphs. As Needham (1935, p. 235) observed, "In such genera (*Baetisca* and *Ephemerella*) differential characters are often better developed in the nymphs than in the adult. In general we believe that species are best described in the state that is most differentiated, and therefore, most easily recognized." Frequently, nymphs of one group of a genus may be readily identified, whereas in another group of the same genus, there are no really good separating characteristics.

We established two subgenera (Pescador and Berner 1981) to show that there are two clearly distinguishable clusters. The subgenus *Fascioculus* contains a single species, *B. escambiensis,* with a nymph that is so different from all others in the genus because of its striped eyes and body spination that it cannot be confused with any other species. The adult of this subgenus (*Fascioculus*) likewise has striped eyes and distinctively shaped penes. The other subgenus (*Baetisca* s.s.) includes the remainder of the species.

The species can be grouped phylogenetically, based on various degrees of specialization. In our 1981 paper, we showed our interpretation of the various relationships resulting from our study of the adult and nymphal morphology and related it to the geographical distribution of the species. We concluded that "the boreal endemic genus *Baetisca* (Edmunds et al. 1976) was pushed southward during the Pleistocene glaciation. With the receding of the ice sheet, the streams of northwestern Florida provided ideal conditions for speciation resulting in the comparatively large number of *Baetisca* species in the area. The species known to occur in the Florida panhandle are *B. becki, B. escambiensis, B. gibbera, B. laurentina, B. obesa,* and *B. rogersi.*"

The genus *Baetisca* is Nearctic; the species are distributed widely over most of the eastern part of North America into the Great Plains and northwestward to the Northwest Territories of Canada. No species is known to occur in the southwestern part of the United States. Generally, the distribution is along the eastern slope of the Rocky Mountains eastward to the Atlantic coast.

Baetisca seems to be a distinct entity in the phylogenetic arrangement of mayflies with an ancestral stock that presumably separated early from the remainder of the Ephemeroptera. Although it is a highly specialized form, *Baetisca* exhibits such ancestral characters as a relatively primitive venation, a large hind wing, and a highly developed cubito-anal area in the forewing. Edmunds et al. (1976) represented *Baetisca* (Baetiscidae) and *Prosopistoma* (Prosopistomatidae) as derived from a common ancestor, related to the Neoephemeridae and the Caenidae.

Baetisca (*Baetisca*) *becki* Schneider and Berner

(PLATE 24 A and B. MAP 26)

Berner 1977, p. 35.
Berner and Pescador 1980, pp. 513, 516, 519–520.
Jones 1977, p. 65.
Pescador and Berner 1981, p. 172.
Peters and Jones 1973, p. 247.
Schneider 1967, p. 203.
Schneider and Berner 1963, pp. 183–186.

TAXONOMY. *Baetisca becki,* described from the nymphal stage in 1963, is most closely related to *B. rogersi* and falls into that complex including *B. carolina* and *B. berneri,* as well. The adults, reared and later described by Pescador and Peters (1971), also reflect the close similarities of this species with *B. rogersi.* In our 1981 paper, we reported that *B. becki* in the adult stage is distinguished from other species by having the basal one-seventh of the forewings and the basal one-fourth of the hind wings flushed faintly with orange-brown color; abdominal tergite 10 has a pair of small black spots; and the penes are lanceolate, apically blunt and gradually enlarged basally. The mature nymph has a well-developed frontal projection that is slightly bifid; the genae are widely flared, broad, and truncate; the mesonotal shield has long, laterally serrate, sharply pointed spines; the dorsal projections are prominent and spinous; and the thoracic and abdominal sterna have large, dark brown spots.

GEOGRAPHIC DISTRIBUTION. *Baetisca becki* is known to occur only in the southern portion of the Coastal Plain and has been recorded from southern Alabama and northwestern Florida. We have found the species in the following Florida counties (map 26): Escambia, Okaloosa, and Santa Rosa.

ECOLOGY. No detailed studies of the ecology of *B. becki* have yet been conducted. Nymphs have been taken from the same streams inhabited by *B. rogersi*; however, our observations indicated that *becki* nymphs generally appear to be more abundant in swifter and deeper water where there is more shifting sand. The first collections of *becki* nymphs came from sand-bottomed streams where the water was only 6 to 10 inches deep, swiftly flowing, clear, and shallow. The pH was almost constant at 5.4, and dissolved oxygen remained near the saturation level throughout the year.

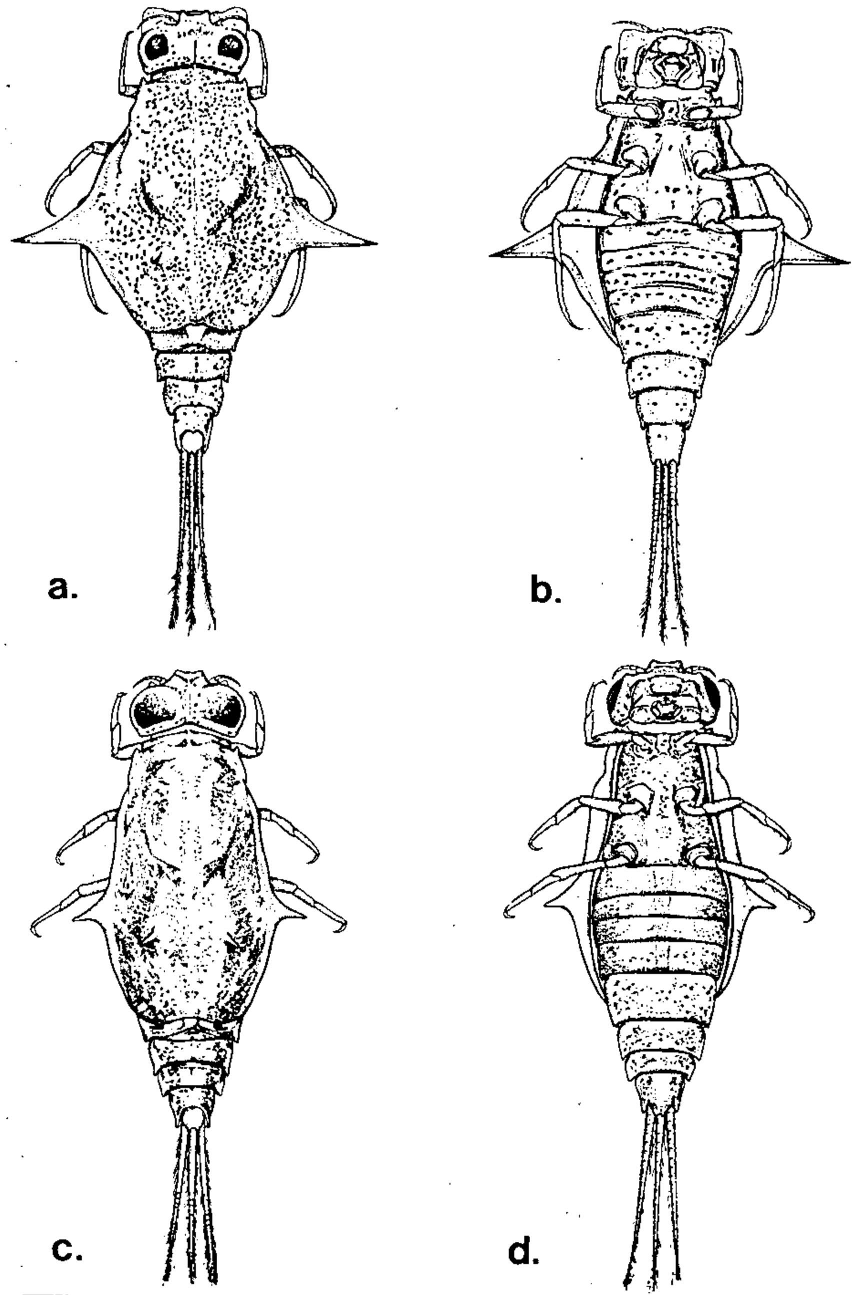
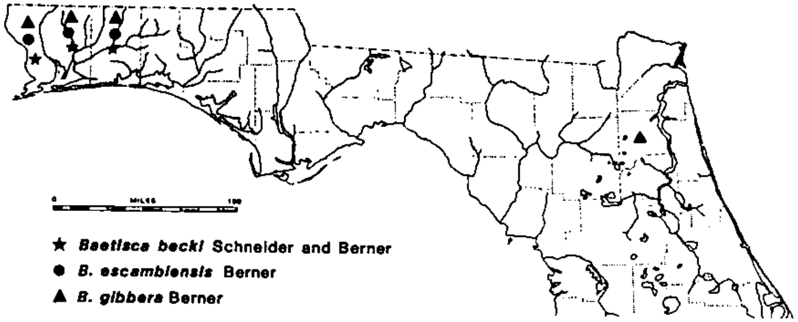


Plate 24. *Baetisca becki* Schneider and Berner, nymph, a and b. *Baetisca laurentina* McDunnough, nymph, c and d (from Pescador and Berner 1981)



Map 26. The distribution of *Baetisca becki*, *B. escambiensis*, and *B. gibbera* in northern Florida.

The holotype nymph was collected from a sandbar covered by a thin layer of organic detritus (Schneider and Berner 1963).

SEASONAL DISTRIBUTION AND LIFE HISTORY. There are few clues available to provide information on either of these subjects. Because of the ecological and morphological similarities of this species to *B. rogersi*, we speculate that *B. becki* is univoltine. Very small nymphs were collected in September; middle-instar specimens were taken by March; and those that were mature or nearly mature were found by middle April. Imagoes have been collected in early May.

BEHAVIOR. We have no data concerning behavior of *becki* as either nymphs or adults, but we assume that it would be similar to that of *B. rogersi*.

Baetisca (*Fascioculus*) *escambiensis* Berner

(PLATE 25. FIG. 87. MAP 26)

Berner 1955, pp. 2, 4–11; 1977, p. 36.
Berner and Pescador 1980, pp. 518–520.
Pescador and Berner 1981, pp. 220–222.
Peters and Jones 1973, p. 247.
Schneider 1967, p. 203.

TAXONOMY. This unique *Baetisca* is the sole species assigned to the subgenus. Nymphs are especially distinctive and cannot be confused with any other species. They lack frontal projections; the genal spines are strongly developed, long, flat, and slightly upcurved at the tip; the mesonotal

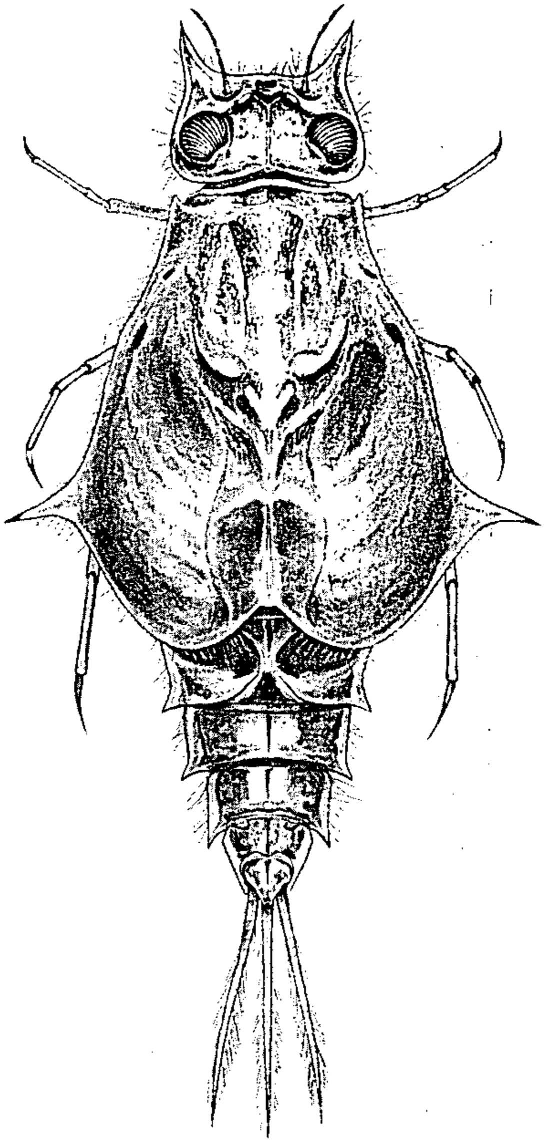


Plate 25. *Baetisca* (*Fascioculus*) *escambiensis* Berner, nymph

shield is compressed dorsoventrally but with a strongly carinated median line; the lateral, mesonotal spines are narrow and sharply pointed; and the lateral margins of the body are covered with long hairs. The eyes are banded with vertical stripes. The adult male (the adult female is unknown) has its wings flushed with a ruby tint; eyes are banded vertically; and the penes are sharply tapered distally.

GEOGRAPHIC DISTRIBUTION. *B. escambiensis* is known to occur only in extreme northwestern Florida and, from a single collection, in Mississippi. With additional collecting, the species should ultimately be found, provided suitable habitats are available, in southern Alabama and Georgia. The Florida counties where *B. escambiensis* has been taken are (map 26): Escambia, Okaloosa, and Santa Rosa.

ECOLOGY. Nymphs have been collected from sandbars in shallow water ranging in depth from four or five inches up to one foot. Here they lie partially buried in the sand where there is a fine layer of silt over the surface. Nymphs have been found most abundantly on sandbars where there is also some clay along with the sand. Other sandbars from which nymphs have been collected had a small amount of gravel mixed with the sand and silt, but we have found fewer nymphs in this kind of habitat. The current was rather slow where the nymphs occurred most abundantly.

One sandbar from which many nymphs were collected was about 15 feet long and 5 feet wide. The nymphs were concentrated on the sloping sides of the sandbar where the shelving was rather steep, and the water, flowing slowly, was deflected laterally across the shallow zone. Algae grew in some places and where the growth was heavy, no nymphs could be found; where algal growth was scanty and the layer of silty mud overlaying the sand thin, nymphs were common.

Young *Hexagenia* nymphs were collected along with *B. escambiensis* from the sandbars in the Escambia River. Apparently they were living in those parts where the accumulation of silt was somewhat deeper than that where the *Baetisca* nymphs occurred. *Brachycercus* nymphs were also found, but their presence was not unexpected, as they too rest on sand overlain with a thin layer of silt.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Contrary to seasonal patterns in other species of *Baetisca, B. escambiensis* adults emerge late in the year. All of our adults were reared or collected in October and November. It is likely that eggs are laid chiefly in late October, overwintering in that stage and hatching in late spring, with growth of the nymphs occurring during the summer and early fall months. We believe the species is univoltine.

Emergence has not been observed in the field. In the laboratory, the subimagoes emerge from midmorning to early afternoon. The subimaginal stage for the male lasts 40–44 hours in the laboratory and perhaps about the same in the field. Although we have had reasonable success in seeing males through the subimaginal molt, we have never been able to obtain female imagoes in spite of successful emergence of subimago females from the nymphal stage.

When the nymph has completed its development and is ready to transform, it crawls an inch or so above the water as do other species of the genus. After several minutes to as much as an hour, the subimago appears.

BEHAVIOR. The nymphs "lie partially covered in the soft, silty sand with only a small part of the mesonotum and a little of the abdomen protruding above the level of the sand. Most of them were so well concealed that they were not detectable until the sand was disturbed. Their coloration makes it possible for them to blend perfectly with their background" (Berner 1955, p. 10).

Nothing is known of the mating or flight behavior of this species.

Baetisca (Baetisca) gibbera Berner

(PLATE 26. MAP 26)

Berner 1953, p. 149; 1955, p. 192; 1958, p. 29.
Berner and Pescador 1980, pp. 513, 517, 519–520.
Pescador and Berner 1981, pp. 192–197.
Peters and Jones 1973, p. 247.
Schneider 1967, p. 203.

TAXONOMY. When *B. gibbera* was described in 1955 from Florida specimens, only the nymphal stage was known. As the nymphs of *Baetisca* are much more readily distinguished than the adults, it was felt that these specimens were adequate for specific differentiation. Subsequently, when the species was found by Dr. B. C. Kondratieff in Virginia, adults were reared and made available to us; we described them in 1981.

Adults are characterized by their hyaline wings; abdominal sternites are dark brown, with sternites 6–8 appearing to be annulate; the males have penes that are deltoid, apically pointed, and enlarged basally. The nymphs have a well-developed frontal projection; the genal shelf is broadly produced and flared outward; the mesonotal shield has short, blunt, lateral spines; and there are no dorsal projections.

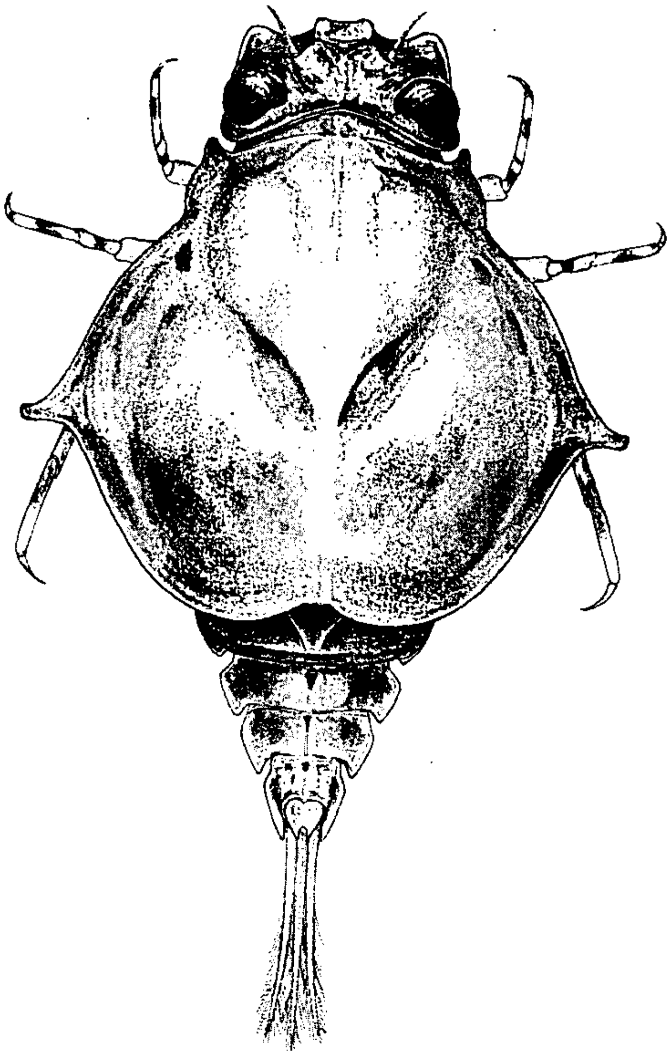


Plate 26. *Baetisca (Baetisca) gibbera* Berner, nymph

Phylogenetically, *B. gibbera* is related to *B. rogersi* and *B. becki*. "Massive broadening of the nymphal mesonotal shield (length subequal to width) coupled with the shortening of lateral spines (length subequal to width and mostly blunt) separate *B. gibbera* . . . from sister species *B. becki* and *B. rogersi* . . . which retained the ancestrally less massive mesonotal shield and longer lateral spines . . . , and a prominent pair of dorsal projections" (Pescador and Berner 1981, p. 224).

GEOGRAPHIC DISTRIBUTION. *B. gibbera* occurs in the southeastern Coastal Plain and in the mountain streams of Virginia and Tennessee. In Florida, there is a lone record from the northeastern part of the state; all other records are from extreme northwestern Florida. We have specimens from the following Florida counties (map 26): Clay, Escambia, Okaloosa, and Santa Rosa.

ECOLOGY. A single nymph of *B. gibbera* was first collected from Black Creek in Clay County, Florida. The stream, now much changed, was, at the time the collection was made, rather swiftly flowing, deep, and acidic. The specimen was found attached to a log that was firmly anchored in the streambed. Later, another nymph was found in the same stream where it was living in a pebbly riffle. In a southern Georgia stream, the Alapaha River, another nymph was discovered clinging to the underside of a log that was anchored at the bank. The Alapaha is a deep, dark-colored creek draining the Okefenokee Swamp. *B. obesa* nymphs were found near the place where the single *B. gibbera* was located. Another southern Georgia collection from the Ichawaynochaway Creek came from a pebbly riffle where the flow was swift and the water only three to five inches deep. Nymphs were also taken, along with those of *B. escambiensis*, from the Escambia River in northwestern Florida where they were living on a sloping bank covered with a thin layer of pebbles in about 3–12 inches of water.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The seasonal distribution of *B. gibbera* appears to be like that of other species of the genus—diapause in the egg stage during the hot summer months, hatching of the nymphs as the water cools in late summer, growth during the fall and early winter, and emergence in late winter and during the spring. Data are insufficient to draw firm conclusions about seasonal distribution in Florida, but the collection of nymphs in northern Florida and southern Georgia indicates the above to be true. Collections of nymphs have been made in these regions in February, April, September, October, and November.

Adults have been reared in Virginia in March, April, and late May. We believe the species is univoltine.

BEHAVIOR. We have no information about the behavior of either nymphs or adults.

Baetisca (Baetisca) laurentina McDunnough

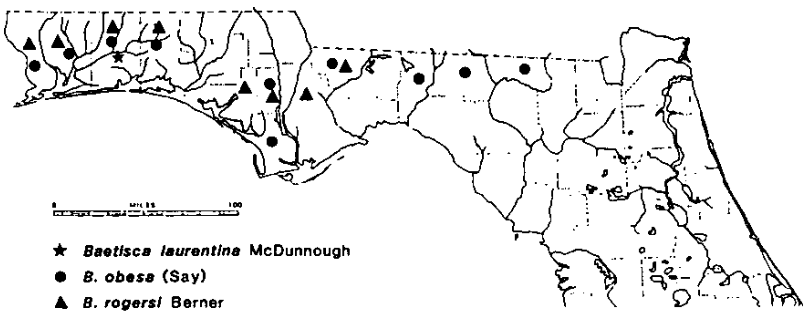
(PLATE 24 C and D. MAP 27)

Berner and Pescador 1980, pp. 513, 515, 519, 521.
Burks 1953, p. 76.
Edmunds and Allen 1957, p. 323.
Edmunds, Jensen, and Berner 1976, p. 272.
Hilsenhoff 1975, p. 9.
Leonard and Leonard 1962, p. 66.
Louton 1975, pp. 62–65.
Pescador and Berner 1981, pp. 202–208.
Pescador and Peters 1971, p. 332.

TAXONOMY. This species, reported only once from Florida, is represented in the Florida collections only in the nymphal stage. We reported (Pescador and Berner 1981) that imagoes generally have hyaline wings, their abdominal terga lack distinct markings, and the penes of males are deltoid, apically pointed, and gradually enlarged basally. Nymphs are much more easily differentiated from those of other species by observing the prominent, bifid, frontal projections; strongly flared and angulate genal shelf; mesonotal shield with relatively short spines as long as wide at the base; dorsal projections of mesonotum high; and ventral margin of mesonotal shield clearly outlined by a wide dark brown line.

The closest relative, based on nymphal characteristics, is *B. obesa.* The two are distinguished most easily by differences in the frontal projection of *obesa*, which is much more prominent than that of *laurentina.* The line forming a margin on the ventral side of the mesonotal shield is present only in *laurentina.*

GEOGRAPHIC DISTRIBUTION. This species is known to occur widely from central Canada southward through the middle section of the United States, generally following the Mississippi River drainage, to Louisiana, Mississippi, and to northwestern Florida. Its range extends eastward into Massachusetts. There is a single Florida record from the Blackwater River in Okaloosa County (map 27).



Map 27. The distribution of *Baetisca laurentina, B. obesa,* and *B. rogersi* in northwestern Florida.

ECOLOGY. We have no information about the ecological relationships of *B. laurentina* in the Blackwater River, but we believe that its habitat would be similar to that of *B. obesa.* Louton (1975, p. 65) stated that "[n]ymphs of this form were collected in clear rapid streams in west-central Louisiana. The nymphs were most often found among bunches of thin-bladed aquatic vegetation." In Michigan, Leonard and Leonard (1962) observed that nymphs seem to prefer medium-sized to large rivers, where they lie partially concealed in the flocculent surface layer of silt in quiet areas near the bank. Hilsenhoff (1975) found nymphs in Wisconsin inhabiting similar sites.

SEASONAL DISTRIBUTION AND LIFE HISTORY. Nothing is known of the Florida representatives of this species regarding seasonal distribution and life history except that a single mature nymph was captured on March 11. Louton (1975) collected nymphs in December, February, and March and reared adults in late March in Louisiana. Records from other parts of the United States indicate that adults emerge from March to August.

BEHAVIOR. We have no information about the behavior of the southeastern *B. laurentina.*

Baetisca (*Baetisca*) *obesa* (Say)

(PLATE 27. FIG. 86. MAP 27)

Berner 1953, p. 149; 1955, p. 14; 1958, p. 29; 1977, p. 36.
Berner and Pescador 1980, pp. 512, 514–515, 519–520.
Carlson 1980, p. 82.
Jones 1977, p. 65.
Pescador and Berner 1981, pp. 208–212.
Peters and Jones 1973, p. 247.
Schneider 1967, p. 203.

TAXONOMY. *Baetisca obesa* was described in 1839 by Thomas Say, who named it appropriately because of its short, robust body. In 1862, Walsh recognized that *obesa* was a member of his new genus after he obtained male adults. The male adults are separated from other species by their hyaline wings that lack color, except that C, Sc, and R_1 of the forewings are brownish basally; the abdominal terga are mottled with brown or purplish brown; and the penes are lanceolate, apically blunt, and gradually enlarged basally. The nymphal stage is characterized by the long frontal projections extending well beyond the anterior edge of the head; a small, broadly rounded genal shelf; well-developed dorsal spines on the mesonotal shield; broad, lateral, longitudinal bands on abdominal tergites 6–9; and prominent dark brown spots near the lateral margins of sternites 2–6.

Of the various species of its genus, *Baetisca obesa* appears to be most closely related to *laurentina*. Adults are similar and not easily separated except in size, where *obesa* is generally smaller than *laurentina*. Nymphs can be easily separated from *laurentina* by the significantly longer frontal projections of *obesa* and by the presence in *laurentina* of a solid brown line outlining the ventral margin of the mesonotal shield.

GEOGRAPHIC DISTRIBUTION. *B. obesa* is widely distributed in the central plains and the southeastern region of the United States. In Florida, the species has been recorded only from the northern tier of counties, including (map 27): Calhoun, Escambia, Gadsden, Gulf, Hamilton, Jefferson, Madison, Okaloosa, Santa Rosa, and Walton.

ECOLOGY. Although *B. obesa* has been known for nearly 150 years, no in-depth studies of the nymphal ecology have yet been conducted. We have

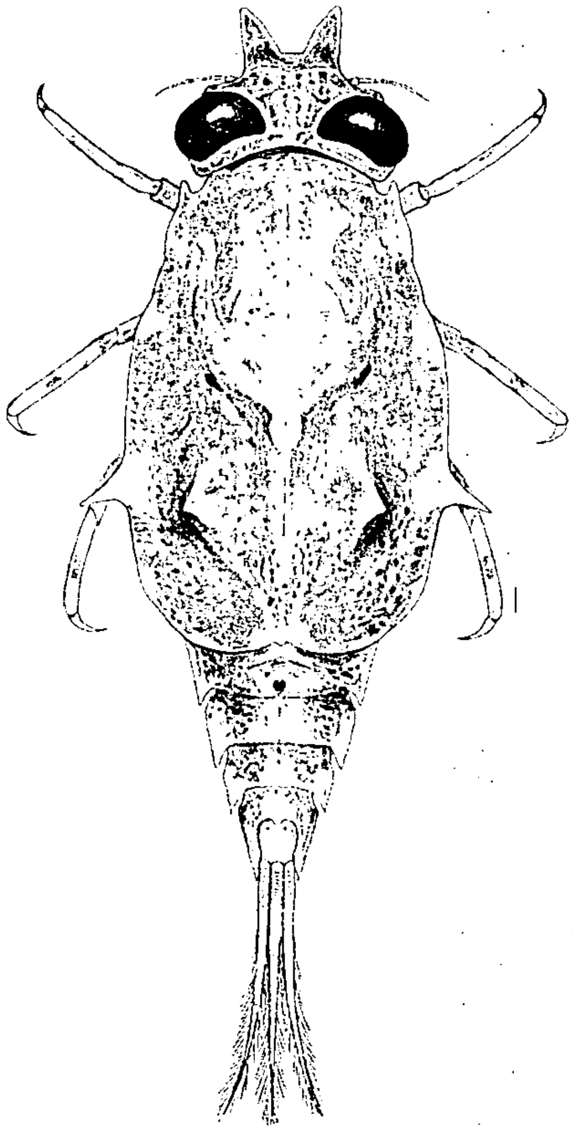


Plate 27. *Baetisca* (*Baetisca*) *obesa* (Say), nymph

collected specimens over much of northern Florida and have discovered nymphs in a variety of stream habitats. Our first encounter with the nymphs was in the Withlacoochee River, which arises in southern Georgia and flows southward to join the Suwannee River in northern Florida. Here, we found them to be common in very slowly flowing water where they lived in moss attached to submerged trunks of cypress, willow, and ash trees or in other vegetation. All streams from which nymphs have been taken are brown-water acidic, and deep. In March 1979 the Chipola River overflowed its banks, and as it receded, pools of water remained along its banks. Large numbers of *Baetisca obesa* nymphs were stranded, and we were able to collect them with ease. Most were fully mature and ready, or nearly ready, to emerge. We have also found nymphs on the underside of submerged rocks and logs and among packed leaves in rapidly flowing streams.

The habitat of *B. obesa* in Florida differs from others of the genus as *obesa* has not been found in or on sand but lives deep within vegetation mats and in rather slowly flowing water. Walsh (1864) referred briefly to the habitat where nymphs were collected from the Mississippi Rapids near Rock Island, Illinois, as being clear, rapidly flowing rivers. In them, the nymphs attach to the undersurface of submerged stones. Burks (1953) examined that part of the Mississippi from which Walsh's specimens came and he discovered that the river had been changed significantly by extensive dredging, channel straightening, and damming so that the rate of flow was much reduced. Burks did not collect *obesa* at Rock Island, and he stated of its habitat only that *obesa* "[d]evelops in cool, fairly rapid streams."

SEASONAL DISTRIBUTION AND LIFE HISTORY. No detailed studies of the seasonal distribution or of the life history of *B. obesa* have yet been conducted. Our Florida collection records include adults that have emerged as early as February to as late as May 4, with the greatest number of adults having been reared or collected in mid to late April. Nymphs have been collected from January through early May and from late October through December. It appears reasonable to assume that, as with other Florida *Baetisca*, this species is also univoltine. Adults emerge during the cooler spring months, mate and oviposit, and the eggs then presumably undergo diapause. Hatching likely occurs in September, thus accounting for nymphal collections in late October. Emergence of the subimago differs from that of other species as the nymphs do not necessarily climb out of the water (Berner 1955). That the nymphs do leave the water prior to emergence was reported in the above cited paper and by Walsh (1864).

BEHAVIOR. No studies of the behavior of this species have been made. Walsh (1864) did record a few observations about the swimming activities of the nymphs, and we have noted that they are very much like those of other *Baetisca* species.

Baetisca (Baetisca) rogersi Berner

(PLATE 28. FIGS. 22, 39, 85, 174. MAP 27)

Berner 1950, pp. 148–152; 1955, pp. 16–17; 1958, p. 29; 1959, p. 8; 1977, p. 36.
Berner and Pescador 1980, pp. 513, 516, 519–520.
Burks 1953, p. 77.
Carlson 1980, p. 82.
Jones 1977, p. 65.
Pescador and Berner 1981, pp. 212–216.
Peters and Jones 1973, p. 247.
Schneider 1967, p. 203.
Unzicker and Carlson 1982, pp. 3.14, 3.23–3.25.

TAXONOMY. The outstanding characteristics of mature nymphs of *Baetisca rogersi* are the presence of four prominent lateral mesothoracic projections; serrate margins of the mesonotum; small dorsal thoracic prominences; and conspicuous elevations on abdominal segments 7 through 9. The characteristic spines and tubercles are relatively more conspicuous in younger nymphs; in the last instar they may become somewhat obscured by the formation of the underlying adult structures. The adults may be distinguished chiefly by the reddish brown coloration in the basal third of the forewings and the basal three-fourths of the hind wings. They are short, bulky mayflies with a robust thorax, short abdomen, long forewings, and large hind wings.

Of the various species of *Baetisca, B. rogersi* appears to be most closely related to *B. becki*; however, the intensity and extent of wing pigmentation is greater than in *becki*, and abdominal tergite 10 lacks the dark brown spots of that species.

GEOGRAPHIC DISTRIBUTION. *B. rogersi* is known to occur in northwestern Florida from the Apalachicola River drainage westward into southern Alabama and northward into Georgia and South Carolina. In Florida, the species has been taken in the following counties (map 27): Bay, Calhoun, Escambia, Gadsden, Liberty, Okaloosa, Santa Rosa, and Walton.

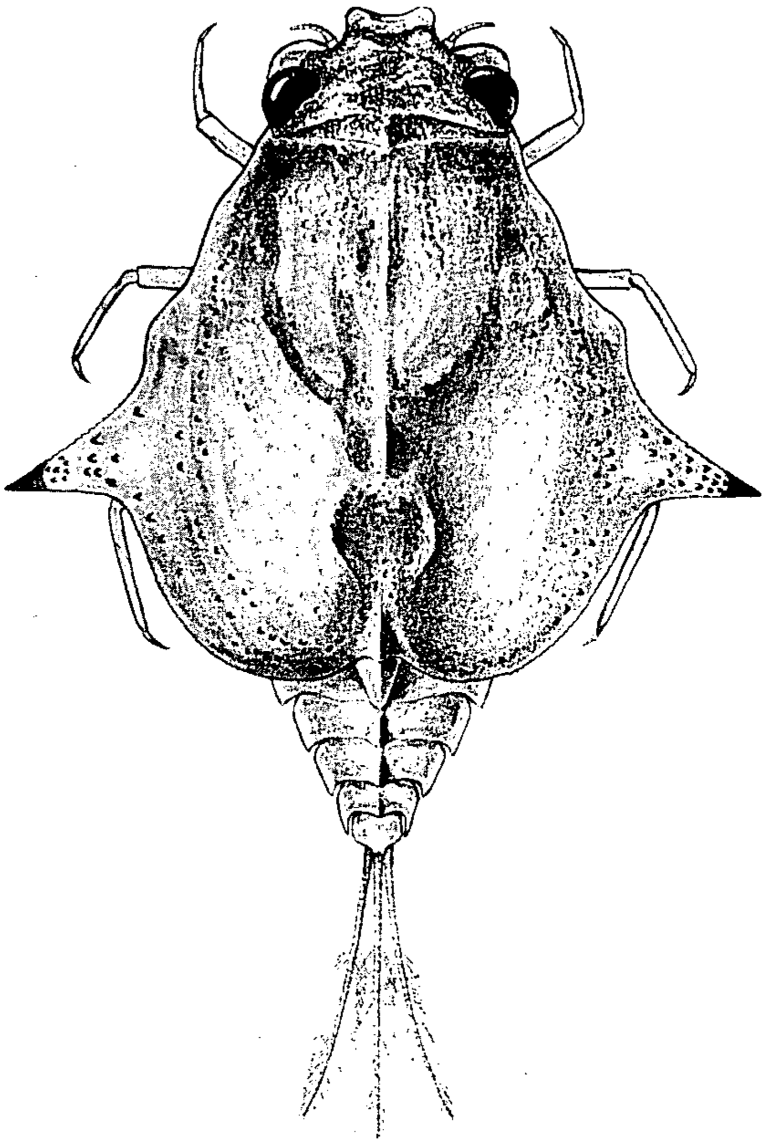


Plate 28. *Baetisca rogersi* Berner, nymph

ECOLOGY. The streams inhabited by *B. rogersi* nymphs are sand-bottomed, slightly acid or circumneutral, and clear. Because most of these streams drain upland regions where there is little swampland, the water picks up only small amounts of humic acids and is lightly colored. Of course, there are exceptions, and the coloration may vary depending on rainfall and other factors that influence the dissolving of the acids.

The sand-bottomed streams of Florida often have pebbly riffles in shallow water, and it is here that the nymphs are most frequently encountered. One of us (Pescador and Peters 1974) has made an in-depth study of the life history and ecology of this species and found the mature nymphs to be typical members of the riffle association. Sampling various habitats in these sand-bottomed streams led to the discovery that younger nymphs from the fourth through the seventh instars lived only in those parts where there was a dense growth of filamentous algae (*Spirogyra* sp.) and water moss (*Leptodictyum riparium*). As time approached for emergence, nymphs moved to quiet, shallow sections of the streams, apparently in search of places that provide egress from the water as emergence takes place above the water surface.

Larger nymphs may also be found on the underside of submerged logs or partially buried in sand in shallow water near the stream's edge. Laboratory studies of instars 8–12 showed that these larger nymphs preferred a pebbly substrate. If there was no such habitat available, they then sought sand as a substitute.

Other laboratory studies to determine the effects of light on the positioning of nymphs revealed that it has an important influence, with most nymphs moving to the well-lighted substrate.

The nymphs are adapted structurally to living in flowing water. The heavily sclerotized, curved, and sharply pointed tarsal claws are ideally suited for holding to objects in the streambed. The shape of the mesonotal shield apparently helps decrease resistance to water flow. The development of the conspicuous, lateral mesonotal spines appears to be correlated with the ability of the nymphs to maintain their short, rotund bodies in a stable position in pebbly riffles of moderately to swiftly flowing water where they rest partially covered by sand, head in an upstream direction.

To test the validity of the theory that the spines serve as stabilizers (Berner 1940), Pescador and Peters (1974, p. 190) removed the spines from mature nymphs. "Without them the nymphs could not balance themselves, or could barely maintain a normal position for a short time before turning over. Furthermore, the nymphs could not maintain direction."

Examination of food contents of the alimentary tract showed that the immatures are herbivorous or detritivorous. Dominant gut contents were found to be detritus, diatoms, mineral particles, and a few fragments of filamentous algae. The diatoms included *Navicula* sp., *Surirella* sp., *Nitzschia* sp., *Meridion* sp., *Pinnularia* sp., *Fragilaria* sp., and *Gomphonema* sp. A desmid, *Micrasterias* sp., was also found. Among the recognizable elements of algae were *Spirogyra* sp., *Cladophora* sp., and *Oedogonium* sp. No significant differences were found in the feeding activities of small or large nymphs collected throughout the growing season. During February, March, and April an increase in abundance of diatoms covering the rocks in one stream was reflected by an increased intake of them by the nymphs.

Phoresy has been reported occasionally between mayfly nymphs and chironomid or simuliid larvae or pupae. Pescador and Peters reported that on two occasions pupae of *Simulium* sp. were found attached to the medioposterior margin of the mesonotal shield of *B. rogersi.* No larvae were found. This is the only known instance of a phoretic association in this family of mayflies.

The imagoes, like most other mayflies, are normally confined to the mesophytic hammocks lining the stream margins. Here the humidity is fairly high and the adults experience little difficulty in undergoing their imaginal molt. The subimagoes rest on the lower branches of the trees and bushes fringing the streams and await their final molt.

SEASONAL DISTRIBUTION AND LIFE HISTORY. The emergence of *B. rogersi* in Florida corresponds with that of northern relatives in that it is strictly seasonal, with adult emergence beginning early in March and ceasing in early July. Peak emergence occurs in April, and there is a single generation each year.

The life history of *B. rogersi* has been studied in detail (Pescador and Peters 1974). Fertilized eggs hatched in the laboratory in about 21 days when the water was kept at a temperature in the range of 23°C. A few unfertilized eggs also developed and the nymphs hatched in from 20 to 31 days. Fertilized eggs did not hatch simultaneously; the hatching period extended from 7 to 17 days. In all, 12 instars are required for nymphal development. Pescador and Peters provided full descriptions and illustrations of each instar to show changes taking place as the nymphs develop.

Instars 1–3 were obtained from laboratory hatched eggs. The remaining instars were determined from collecting fourth-instar nymphs in the field and rearing them individually in the laboratory. A careful study of development demonstrated that approximately four months are required under laboratory conditions.

Pescador and Peters located young nymphs, probably in their fourth instar, on September 20, their earliest find of this stage. However, nymphs in the sixth or seventh instar were collected by one of us (Berner) in Santa Rosa County on August 12. As a result of their study, Pescador and Peters suggest that eggs generally hatch in early September as the water cools. They postulated that the higher temperatures of the summer months induce diapause, thus delaying hatching of eggs laid as early as March. They suggested further that any nymphs that hatched in April were probably killed by high temperatures and lower oxygen content of the water. They found that newly hatched nymphs under laboratory conditions where temperatures ranged from 22.2°C to 23.9°C died after one molt. At lower temperatures nymphs survived.

Growth is rapid at first, but as temperatures fall, it slows considerably. In December and January when water temperatures dropped to 5°C, nymphal feeding was slowed, reducing growth rate.

Subimagoes of *B. rogersi* have been observed emerging from 8:30 A.M. to 2:30 P.M. Most emerged before noon with peak emergence being between 8:30 A.M. and 10:30 A.M. To emerge, the nymphs crawl completely out of the water a distance of 1½ to 4 inches above the surface. Emergence requires 4 to 10 minutes. After eclosion, the subimago remains motionless for a short time, then crawls up the supporting surface. The subimaginal stage in the laboratory lasted from 12 to 30 hours, with an average of 21½ hours. Higher temperatures apparently shorten the subimaginal stage. To molt to the adult stage the insects required 8–11 minutes in the laboratory.

Adults, under laboratory conditions, lived from 8½ to 28½ hours. No significant difference in life span was found to exist between males and females.

Parthenogenetic reproduction has been reported more and more frequently among various mayfly species. It is now known to occur in *B. rogersi* as well. Although it does not appear to be a common method of reproduction, Pescador and Peters found that from a total of 9648 eggs taken from unmated females, 69, or 0.7%, hatched. They also found that eggs from subimagoes were mature as some of them hatched. Since the ratio of males to females is virtually equal, it appears that parthenogenetic reproduction must be exceedingly rare or may be only a laboratory phenomenon. Edmunds has informed us that it is common among insects for a very small percentage of eggs to be diploid and that these develop and hatch. This phenomenon may explain Pescador and Peters's results.

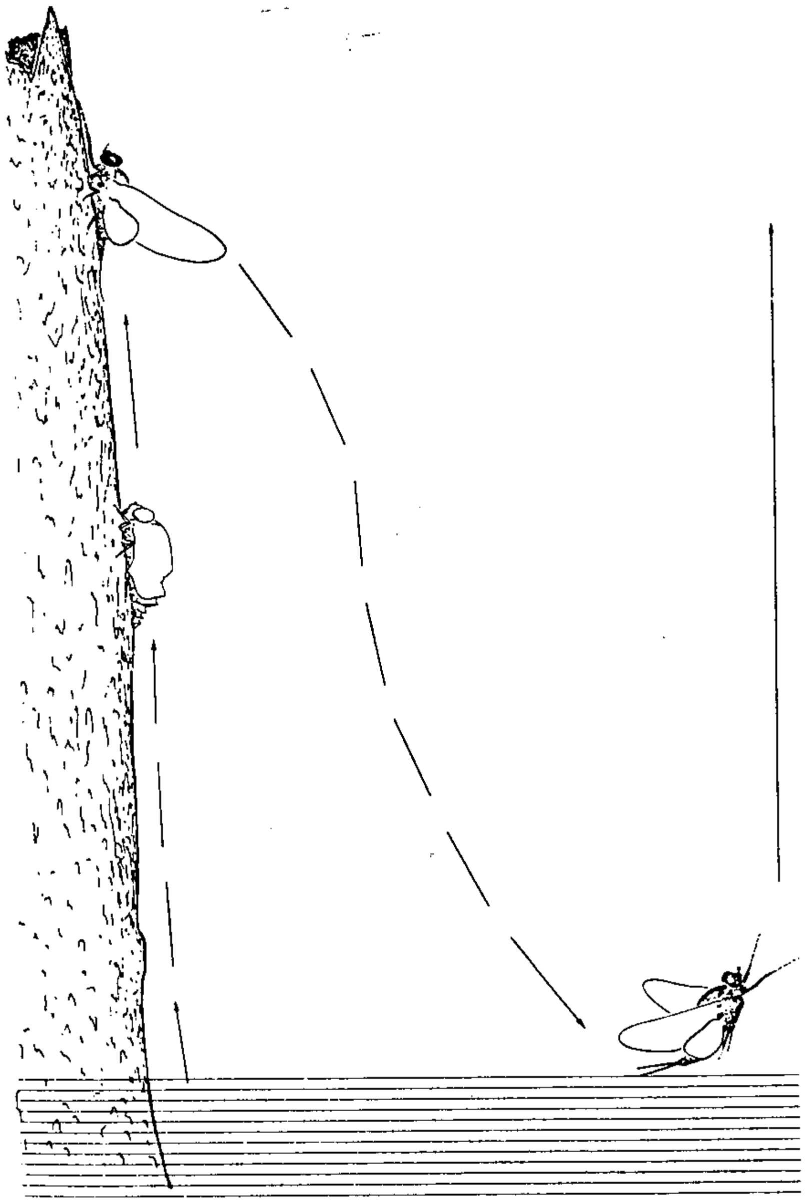


Fig. 174. Flight pattern of *Baetisca rogersi* subimago (from Pescador and Peters 1974)

BEHAVIOR. Nymphs are inactive during daylight hours, when they remain hidden or partially buried in sand. Resting nymphs bend the last three abdominal segments dorsally, elevating the caudal filaments over the body. Pescador and Peters reported a strongly positive phototactic response of nymphs in the laboratory, and they postulated that the light enables the nymphs to maintain their primary dorsoventral orientation. Nymphs swim by pulling their legs under their bodies, drawing together and depressing their tails, and rapidly vibrating the posterior portion of their bodies. They swim in short spurts, come to rest, then spread their legs and seize some supporting object. Legs are not used in swimming; the movement of the abdominal segments and the tails accounts for the forward movement.

Nymphs feed at night. In the laboratory, Pescador and Peters observed them browsing on the surfaces of rocks and crawling over the substrate apparently feeding. They were seen biting pieces of water moss and raking the substrate toward their mouths using their prothoracic legs.

The abdominal gills are enclosed under the thoracic notal shield, which is raised and lowered rhythmically to allow water to circulate inside the gill chamber. Inflow of water occurs when the notal shield is raised: as the water passes over the highly tracheated gills, it exits through a tube formed by the greatly modified sixth pair. The pair forming the tube fits into a space between a posterior elevation of the notal shield and the concave dorsal surface of the sixth tergite.

A study of gill function in *B. rogersi* nymphs was conducted in 1980 by Mary K. Notestine, a student at the University of Utah. Her findings (unpublished) are at variance with those of Pescador and Peters regarding inflow of water. She concluded that the abdomen of the nymph moves away from the notal shield and that it is kept lowered unless some disturbance occurs. The movement of the gills themselves causes the flow of water through the gill chamber. Notestine noted further that the sparsely distributed hairs on the posterior edge of the notal shield likely have a sensory function detecting potentially damaging substances, such as particulate matter, in the water.

In their detailed study of *B. rogersi*, Pescador and Peters noted that the subimagoes have a unique flight pattern (fig. 174). After emerging they first dive to the water surface, then fly vertically upward. They are strong fliers and disappear quickly into the fringing vegetation where they are probably protected from predators by the strongly mottled pattern of the wings.

Mating swarms of adults have not yet been observed, nor have ovipositing behaviors been reported.

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(The principal reference for each genus and species is listed in boldface type.)

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