

CONTRIBUTIONS TO THE AUTOECOLOGY AND ECOSYSTEMATICS
OF IMMATURE CERATOPOGONIDAE (DIPTERA),
WITH EMPHASIS ON THE TRIBES HETEROMYIINI AND SPHAEROMIINI
IN THE MIDDLE ATLANTIC UNITED STATES

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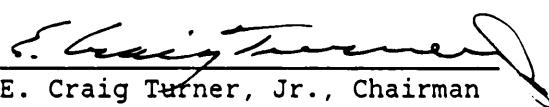
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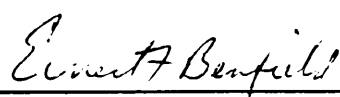
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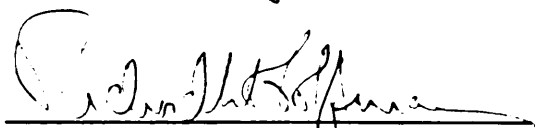
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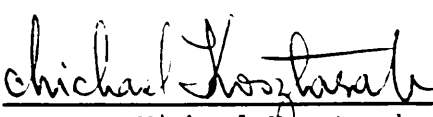
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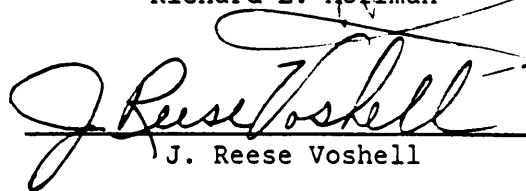
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*Contributions to the Autecology and Ecosystematics
of Immature Ceratopogonidae (Diptera),
with emphasis on the Tribes Heteromyiini and Sphaeromiini
in the Middle Atlantic United States*

by

Walter Ingolf Knausenberger

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Entomology

(ABSTRACT)

Biological and systematic study of the immature stages of the biting midges (Diptera: Ceratopogonidae) has been infrequent, although the family is one of the largest in the order, with over 4,000 species worldwide, and is ubiquitous among aquatic/semiaquatic environments. An ecosystematic analysis is presented here of the Ceratopogonidae in Virginia and contiguous states based mainly on a diversified biological field survey, with particular attention to associating immature stages with adults, and acquisition of ecological data. I emphasized (a) extraction of larvae and pupae; (b) two methods of rearing, developed for this study: individual rearing(IR) with an agar-nematode technique, and collective rearing from the habitat substrate in rearing cartons(RC); and (c) field trapping of adults at the habitats.

In Section I, a faunistic assessment -- the first of its sort -- is provided of the total Virginia-region ceratopogonid fauna, in all developmental stages, with a focus on *Culicoides*, including a comparative

evaluation of the relative abundance of the ceratopogonid genera with respect to methods of collecting and extracting.

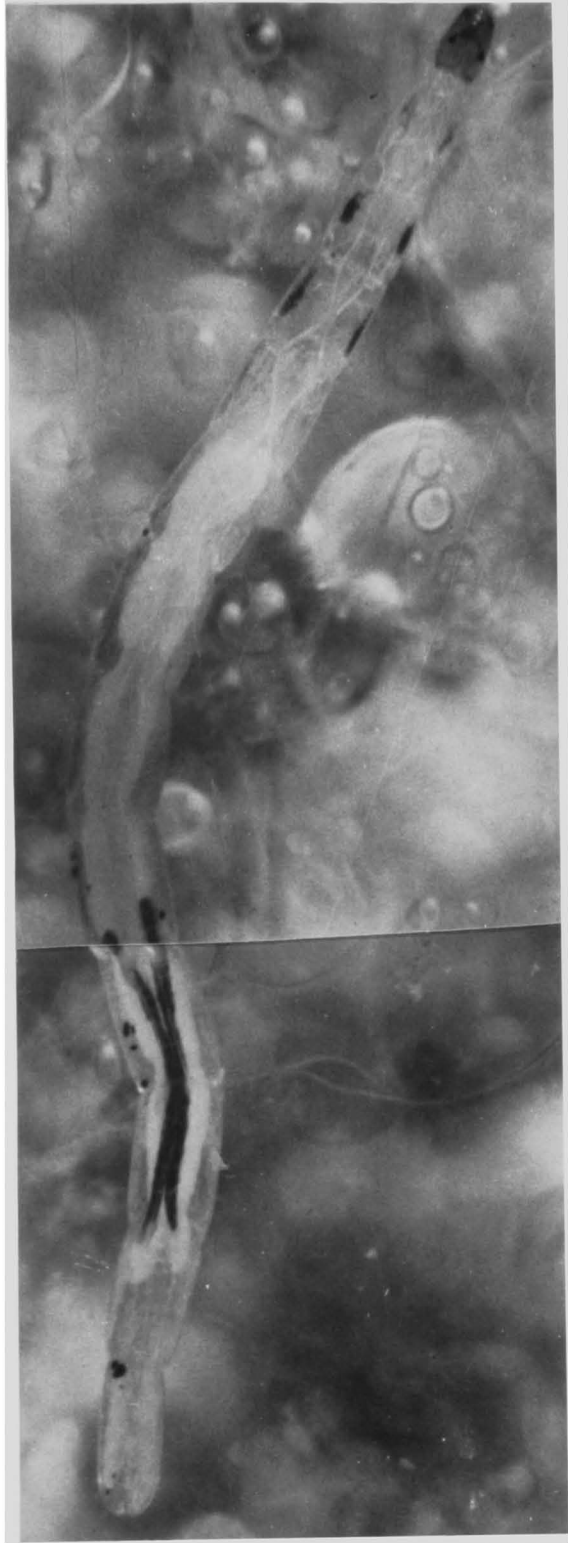
High taxonomic richness of the ceratopogonid fauna in the Middle Atlantic states is reflected in the 150 described and 42 undescribed (new) species recovered. A detailed geographic checklist for the 222 species of Virginia and the five contiguous states is presented and interpreted.

At least 54 *Culicoides* species are present in the Middle Atlantic U.S. About half of the larval species can be determined in Virginia. With the results of this study, 93% of breeding sites for the genus are known in Virginia, more than for any other state.

Section II assembles and synopsis data on the autecology, life history, habitat, morphology, systematics, as well as geographic and seasonal occurrence of 28 species (3 new) and 10 genera in two related tribes of predaceous biting midges, Heteromyiini and Sphaeromyiini (subfamily Ceratopogoninae). Shorelines are the "archetypical arena" in which these larvae thrive, typically above and below the water line. Their habitats and substrates are characterized in detail. The greatest diversity of larvae in these tribes consistently occurs in and along mid-reach streams (Order: 3 to 5).

Mechanisms of ecological partitioning by sympatric species, and the differential adaptive significance of larval, pupal and adult morphological characters are evaluated. Taxonomic and ecological diversity in these groups are clearly related.

Frontispiece. Live larva, on ice, of Culicoides bickleyi Wirth and Hubert (Diptera: Ceratopogonidae). Actual length: 4.5 mm. In this study, many larvae destined for individual rearing were first photographed on ice in this fashion, with no apparent detriment to larval viability.



Frontispiece

DEDICATION

This dissertation I dedicate
to my loving, capable
wife and soul-mate
Janice Gayle,
and to our sons
Erich, Cephas,
Ari and Anson

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I extend my sincere thanks to the current members of my advisory committee, Dr. Ernest F. Benfield, Dr. Richard L. Hoffman (Radford University), Dr. Michael Kosztarab, and Dr. J. Reese Voshell for their guidance and understanding despite unusual circumstances. In particular, for his wisdom, equanimity, and provision of the means to undertake this research, I gratefully acknowledge the debt I owe to my supervisory professor and friend, my "Doktorvater" Dr. E. Craig Turner, Jr. I wish also to express my thanks and respect to former members of my committee, who for one reason or another could not continue to serve: Drs. John L. Eaton, Donald Garling, Richard Lackey, and William H Robinson.

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PREFACE

Objectives and Rationale

This dissertation is divided into two major sections, together comprising seven chapters, plus the literature cited. An extensive nine-part appendix forms the final one-third of this work. The format and scope of Section II are outlined and explained in the Introduction to that section (parts II.4 and II.5).

My overall objective has been to advance the understanding of the faunistics, ecology and systematics of the immature biting midges (Diptera: Ceratopogonidae), with emphasis on the subfamily Ceratopogoninae in Virginia and surrounding states. I was guided by the principles of ecosystematics described below (see Chapter 1, Section 1.1.3), which emphasize association of ecological data with specimens, thus adding to the utility of taxonomy. From the outset, I adopted a multipurpose approach which I expected to provide data useful both to taxonomic and ecological interpretations.

I made the following assumptions at the outset of this study:

1. The lack of information on the life history and taxonomy of the immature stages of the biting midges is a major impediment to progress in basic and applied studies involving the group.
2. Significant amounts of identified and/or reared and associated larval, pupal and adult material would be available in existing collections in North America.

3. Intensive sampling of a wide variety of habitats with an array of collection and extraction strategies would obtain a taxonomically diverse body of material of high quality.
4. An emphasis on rearing and the immature stages would provide associated developmental stages most appropriate for meaningful taxonomic and ecological study.
5. No recent and comprehensive review of the ceratopogonid fauna exists for any state or region in the Nearctic.
6. The species richness of Ceratopogonidae in aquatic systems is significantly higher than recognized in the benthological literature.

Section I, consisting of a single extended chapter, deals with the biological survey in general. It reviews the present state of knowledge about Ceratopogonidae species numbers and occurrence in the Middle Atlantic states; summarizes the methods and procedures developed to acquire and study the specimens and associated data in this study; and provides an overall compilation and discussion of the results of the study with respect to the methods, and the Ceratopogonidae collected by these methods.

In this section, the specific aims are to:

1. Review the current state of knowledge of the ceratopogonid adult and immature fauna in the Virginia region and the larger geographic and biological context.
2. Briefly document the assembly, by diversified field collecting, recruitment and loan, of an extensive body of appropriate immature, reared and other specimens, especially larvae and pupae associated with imagoes, sufficient to permit comparative morphological study, emphasizing the "vermiform" larval groups (subfamily Ceratopogoninae).
3. Describe the development and application of effective procedures for collecting and extracting live larval, pupal and adult biting midges from diverse aquatic and semiaquatic substrates over a wide geographic area, as well as procedures for rearing and associating the various developmental stages, especially by laboratory propagation, including development and use of a universal larval diet.

4. Provide current and accurate checklists, and a faunistic assessment, of the entire ceratopogonid fauna of Virginia and the surrounding states, including results of the present survey, with a synopsis of the fauna of the Nearctic and the region east of the 100th meridian.
5. Present a comparative evaluation of the relative abundance and dominance of the various ceratopogonid genera and significant species in the Virginia region, with respect to the methods of collecting and extracting, and the nature of the habitat.
6. Summarize the present study's results as to *Culicoides* spp. collected, their geographic occurrence in the eastern Nearctic, and the status of larval, pupal and breeding habitat description for all species, including a comparative interpretation of adult feeding habits vis-a-vis the description status referred to immediately above.

In Section II, the focus is on the immature stages of the species of two relatively small tribes of predaceous biting midges, the Heteromyiini and Sphaeromyiini, based on a portion of the material obtained in the field collections. This focus permitted analysis of the life history, ecology, morphology, taxonomy and faunistics of individual species, with generic and tribal synopses. I then attempted to arrive at appropriate generalizations or hypotheses, especially as to habitat characterization and the adaptive significance of morphological structures, and behavior, of larvae, pupae, and ovipositing adults.

I chose these two tribes because the taxonomy of the adults is relatively stable and recently treated; they form comparatively small and presumably fairly synapotypic groups of species, but with considerable diversity of form; and the available information on their biology and immature stages is scattered and very limited in extent.

The specific aims of Section II fall into three categories:

1. Taxonomy, morphology and faunistics. Review the present state of knowledge on the description, taxonomy, faunistics and geographic occurrence of the members of the tribes Heteromyiini and Sphaeromyiini

in the middle Atlantic states region, and the zoogeographic context. Synopsise the available relevant details on the habitus (external aspect and morphology) of the eggs, larvae, pupae and adults.

2. Life history and autecology (bionomics). Provide a comprehensive synopsis from the present study's results and literature worldwide, of the individual species' life history and autecology, especially as related to habitat, with syntheses at the generic and tribal level, and an overall biological summary.
3. Ecosystematics. Assess the adaptive significance of known phenotypic, behavioral and life history attributes of the developmental stages, with respect to habitat partitioning and ecological segregation strategies. Evaluate species co-occurrence (synecological associations) and habitat classification schemes.

In the Appendices, supportive compilations are assembled on the collecting sites, and species collected. Also included are tables too lengthy for the body of the text(e.g., Tables 41 and 45). This is intended to facilitate access to data for further study, especially for the many taxa -- ceratopogonids and other aquatic organisms -- which were not reported on herein, but which have been preserved and can be related to the data by the standardized collection numbers. These appendices are presented in keeping with the ecosystematic concepts mentioned above in the preface and detailed in Chapter 1, Section 1.1.3.

SECTION I

FAUNAL SURVEY OF THE CERATOPOGONIDAE IN
THE VIRGINIA REGION, WITH EMPHASIS ON REARING

Erst unterscheiden, dann verbinden.
(First distinguish, then combine.)

J. W. v. Goethe
Faust I

CHAPTER ONE

1.1 Introduction and Literature Review

1.1.1. Background and Significance

Biting midges (Ceratopogonidae) constitute one of the largest dipteran families in the world, with over 4,000 species (Wirth et al. 1980). Immature Ceratopogonidae characteristically are found in an extraordinary variety of aquatic and semi-aquatic environments, of which they are often prominent members. They are arguably even more ubiquitous than the closely-related and ecologically very significant Chironomidae, though the chironomids are usually more abundant in freshwater environments (e.g., Thienemann 1954). Much is being written about Ceratopogonidae, yet about 75% typically concerns medical and veterinary aspects mainly relating to adult *Culicoides* biting midges. Most of the attention Ceratopogonidae receive is related to the habits of the adult female, such as bloodsucking (on humans and other mammals, birds and amphibians), predaceous behavior (on other insects, e.g., Downes 1978) and pollination (especially cacao, e.g., Bystrak and Wirth 1978).

Documentation of their significance as vectors of human and animal disease has advanced considerably in the past 20 years. They are now associated with numerous animal parasites, including 12 Protozoa, 18 filarioid nematodes, and several viruses (Linley 1985, Kettle 1984). The proven association of *Culicoides* species with transmission of filarial

parasites and viruses to humans has elevated the medical significance of biting midges to a new level (Linley et al. 1983). Yet, except for several of the medically and economically important bloodsucking species, details on the ecology and life cycles of Ceratopogonidae are poorly known.

This is particularly true for the immature stages. Fortunately, research on medically significant taxa gives much impetus to knowledge of relevance to the entire family. On the other hand, this work has brought into clearer focus the need for fundamental study of the biology and life history of the midges, especially the larval stage (Linley 1979, 1985).

Ecologic and faunistic studies on aquatic macroinvertebrates have almost universally ignored Ceratopogonidae, or treat them superficially. Benthological literature on the fauna of specific bodies of water seldom lists more than one or two species of Ceratopogonidae, if it goes beyond the family level at all. Yet, they are nearly universally listed as present in the fauna, and not infrequently they are among the more common of the taxa, especially if littoral samples are involved.

In fact, it is not commonly recognized that the taxonomic richness of Ceratopogonidae in a given body of water may be among the highest recorded for a single family or even order of aquatic insects. The potential diversity of aquatic Ceratopogonidae in lotic waters, for example, is demonstrated by the results of European investigators, who have historically placed more emphasis upon rearing than North American aquatic biologists have (Gertz, 1971; Guembel 1976; Havelka 1976a, 1976b; Havelka

and Caspers 1981; Krivosheina 1957a,b; Rieb and Kremer 1980, 1981; Thienemann 1954). For example, four spring-fed streams in central West Germany (near Schlitz) yielded 94 species collected as adult flies in emergence houses, which span the width of the streams (Havelka, *op. cit.*). About one-quarter of these species would be considered semi-aquatic only.

Similar work by Masteller and students (e.g., Masteller & Wagner 1984) in two small streams near Lake Erie, Pennsylvania yielded over 50 ceratopogonid species in a single year (E. Masteller, J. Rightor, pers. comm. 1985). At least 43 species were reared from littoral substrates of four southwestern Virginia streams affected by pollution (Turner and Knausenberger 1974). Examples of other extensive ceratopogonid collections in North American stream investigations include Harris (1981) and Morse et al. (1983), both of which yielded over 30 species, based mainly upon determinations of larvae and pupae by the present writer.

Larval ceratopogonids are commonly encountered in benthic surveys of polluted watercourses (Alexander 1925:459; Weber 1973; Turner and Knausenberger 1974). Interpretation of the pollution sensitivity and indicator status of these larvae is enigmatic due to sampling insufficiencies and inability to distinguish species adequately. The general impression is that ceratopogonids tend to be relatively tolerant, or facultatively so, to most organic and inorganic wastes.

Benthos studies frequently are hampered by inadequate sampling procedures, natural history information and taxonomic literature. The precision of studies possible in aquatic ecology has been limited by

the lack of association between immatures and adults (Wiggins 1966, Resh and Unzicker 1975, Resh and Solem 1978 (in Merritt and Cummins 1978), Hynes 1984). With respect to all these factors, Ceratopogonidae can often be a significant source of difficulties. In addition, their small size, narrow cylindrical shape of the larvae, and highly irregular but euryoecious distribution throughout the transitional aquatic to semi-aquatic ecotone, make it more likely that they are overlooked in aquatic surveys, and superficially included in benthic ecological studies.

The dilemma commonly faced by aquatic biologist, of encountering primarily immature stages of insects, yet being unable to identify these specimens adequately, is particularly acute for the Ceratopogonidae because this family is one of the few remaining diverse aquatic groups for which the available taxonomic resources on larvae are very limited. From considerations in this study, I estimate that only 16% of the Nearctic Ceratopogonidae can be determined as larvae, and 34% of the pupae. For the subfamily Ceratopogoninae (excluding *Culicoides*), which are most likely to be encountered by benthologists, those figures are 9% and 29% respectively. Even for the *Culicoides*, by far the best known genus, only 28% of the Nearctic larvae and 49% of the pupae are determinable, and descriptions are widely scattered. For particular geographic regions, such as certain eastern U.S. states, these proportions are higher (see Section 1.3.5 below).

Sieve-mesh size selectivity is an important consideration to be taken into account (e.g. Weber 1973). Most benthic surveys for macroinvertebrates use screens such as the U.S. Standard Sieve No. 30,

with mesh openings of 500-600 μ . Ceratopogonid larvae are likely to pass through such relatively coarse screens in large numbers, thus giving rise to significant underestimates of abundance.

Because of the limited number of workers who have turned their attention to immature Ceratopogonidae, the attention, support and therefore progress have not been commensurate with the difficulties involved. For example, the lack of sophisticated colonization methodology has limited the amount of fundamental study possible on the larval stage (Linley 1985). This situation is analogous to that in the sister group Chironomidae, for which, however, comprehensive biological reviews and generic diagnoses and keys to larvae and pupae of Holarctic region have recently begun to appear (Coffman 1978, 1984 in Merritt and Cummins 1978, 1984), Pinder 1986, Wiederholm 1983, 1985). The recent availability of such resources for the Chironomidae is likely to do much to advance opportunities for research with that family.

Nevertheless, interest in the Ceratopogonidae is reasonably strong among benthologists despite the difficulty in identifying larvae: in a 1984 North American Benthological Society (NABS) membership survey, nearly as many respondents indicated an interest in biting midges as in mosquitoes. Of the 10 families of Diptera listed, greater interest was shown only for Chironomidae, Simuliidae and Tipulidae. When descriptions and keys of Nearctic Ceratopogonidae become available, it is virtually certain that work on this family will greatly increase.

In relation to environmental protection and water quality considerations, Havelka (1980, 1982) and Arnold and Kremer (1982, Mosq. News

42(4):515-6) have drawn specific attention to the Ceratopogonidae, because these widely distributed and diverse flies are heavily influenced by destruction of wetland and other aquatic habitats, and by pollution and mosquito control efforts. These authors have specifically noted how the latter significantly reduce biting midge populations. Havelka (1980) indicated that some 169 species of European Ceratopogonidae might be considered to fall in one of four categories of threatened status, with nearly 50 being "endangered species", of about 700 species recorded. Havelka (1978) considers the family to be the least known of all insect groups covered in the *Limmofauna Europaeae*. Rather than propose the development of a list of endangered species for this or any group of insects, however, it is more sensible to advocate the preservation of habitats and entire communities.

In summary, aquatic ceratopogonids are of considerable significance in medical/veterinary entomology and aquatic biology, and offer challenges for basic and applied studies which interface fields such as ecology, systematics, and behavior, or water resource management, for example. The immature stages are of major importance to progress in bionomic and phylogenetic research, and other areas. A strong incentive exists to improve the determinability of the developmental stages, and to augment understanding of their environmental requirements at the species level, for all life stages.

1.1.2. Present State of Knowledge

Biennial international symposia on Ceratopogonidae were initiated in 1973, and an international newsletter "Ceratopogonidae Information Exchange"(CIE) was launched in 1968. Both developments reflect greatly increasing worldwide interest in these insects. Likewise, the development of catalogues for all zoogeographic regions, and the first generic synopses and keys of worldwide scope (Wirth et al. 1974; Wirth, in litt.) have served to considerably advance the research on this family. Atchley et al. (1981) produced a very useful comprehensive bibliography of over 3500 primary and secondary references on biting midges published worldwide up to 1978.

1.1.2.1. Faunistics and Taxonomy of the Adults

Significant and vital advances continue in description and faunistic reviews of Ceratopogonidae the world over. In the 10 years since the appearance of the valuable keys to the 63 genera then known in the world (Wirth et al. 1974), at least 12 new genera have been described, of which 6 are from the Neotropics alone:

Culicoidini

Neoculicoides Boorman and Lane 1979 (Afrotropical)

Ceratopogonini

Baeodasymyia Clastrier and Raccurt 1979 (Haiti)

Bothahelea Grogan and Wirth 1983 (Afrotropical)

Nannohelea Grogan and Wirth 1980 (all regions except
Nearctic)

Notiohelea Grogan and Wirth 1978 (Neotropical)

Schizonyxhelea Clastrier 1984 (Neotropical)

Stilobezziini

Heterohelea Clastrier 1984 (Australasian)

Kolenhelea deMeillon and Wirth 1981 (Afrotropical)

Heteromyiini

Physohelea Grogan and Wirth 1979 (Neotropical)

Sphaeromiini

Niphanohelea Grogan and Wirth 1981 (Oriental)

Palpomyiini

Amerohelea Grogan and Wirth 1980 (Neotropical)

Clastrieromyia Spinelli and Wirth 1985 (Neotropical)

We are fortunate to have reasonably current catalogues to the Ceratopogonidae of all zoogeographic regions. These works also provide essential interpretation of, and entry into, the significant comprehensive literature in the respective regions:

Afrotropical	Wirth, deMeillon and Haeselbarth 1980
Australasian	Debenham 1979
Nearctic	Wirth 1965, Downes and Wirth 1981
Neotropical	Wirth 1974
Oriental	Wirth 1973
Palaearctic	Havelka 1978

In North America, the taxonomic status of the family has been placed on very sound footing due to the valuable and prolific work of Wirth and colleagues. It is extremely supportive of further work by other investigators to have current systematic arrangements, revisions and keys for identification available, such as those to the 34 North American genera distinguished by Wirth et al. (1977). Currently, at least 36 genera are counted in the Nearctic, including *Amerohelea* (Grogan and Wirth 1981) and *Phaenobezzia* (Wirth and Grogan 1982). Downes and Wirth (1981) provided excellent illustrated keys to the Nearctic genera, with brief synopses of classification, distribution, adult, egg, larva, pupa, biology and behavior.

The tribes Stilobezziini and Ceratopogonini have been undergoing considerable redefinition in an effort to provide a more natural and clear-cut separation, and this has resulted in the transferals of certain genera from the Ceratopogonini to the Stilobezziini and the reverse (Grogan in litt., deMeillon and Wirth 1980, Wirth in litt., Wirth and

Grogan 1981b). Worldwide revisions of *Brachypogon*, *Ceratopogon* and *Isohelea* (Grogan and Downes, in litt.) and *Serromyia* (Borkent, in litt.) are in progress.

Similarly, major changes are transpiring in the Palpomyiini, which now consists of six genera, three having been recently described or re-defined. One, *Amerohelea* Grogan and Wirth (1981) has only one species, *A. frontispina* (Dow and Turner 1976), in the Nearctic. *Clastrieromyia* Spinelli and Wirth (1985) is known from South America only. *Phaenobezzia* was elevated from subgeneric to generic status (Wirth and Grogan 1982 following Haeselbarth 1975), with three Nearctic species, two of which are recorded from the middle-Atlantic states.

However, the most sweeping advances in the Palpomyiini appear to be occurring in the *Bezzia*, where in a continuing series of revisions and additions, eight species groups and genera have thus far been studied in depth since Dow and Turner (1976) (including *Amerohelea* and *Phaenobezzia*):

- Bezzia* (*B.*) *bivittata* Group (Wirth and Grogan 1983)
- B.*(*B.*) *nobilis* Group (Wirth 1983c)
- B.*(*Homobezzia*) *annulipes* Group (Wirth, Palchick and Forster 1984)
- B.*(*H.*) *bicolor* Group (Wirth 1983a)
- B.*(*H.*) *cockerelli* Group (Wirth 1983b)
- B.*(*H.*) *dorsasetula* Group (Wirth 1983b)

Additions to this series are in preparation, covering the *B.*(*B.*) *expolita* and *pulverea* Groups. All told, these revisions may double the total number of *Bezzia* species from 39 (Dow and Turner 1976) to about 80 in the Nearctic.

The active state of ceratopogonid systematics in North America is exemplified by the steady growth in the number of species reported:

- 388 -- Wirth 1956b including Greenland and Bermuda (this figure repeated by Merritt and Cummins 1978, 1984)
- 488 -- Wirth, Ratanaworabhan and Messersmith 1977
- 498 -- Downes and Wirth 1981
- 510+-- Wilkening, Kline and Wirth 1985
- 572 -- this study, Section 1.3.1. (not including Bermuda and Greenland).

Ceratopogonidae Treated in Individual States. Few locally comprehensive treatments or lists of Ceratopogonidae faunae have been produced within the zoogeographical regions. In the Nearctic, only California (Wirth 1952, Wirth and Stone 1956), Connecticut (Lewis 1959), North Carolina (Brimley 1938, 1972 Bowen 1983a) and recently Florida (Wilkening et al. 1985) have had reasonably representative species lists developed. The on-going series of Plummer's Island studies in the lower Potomac River Valley should eventually provide a complete review of the ceratopogonid species in that area (portions of Maryland, VA, and D.C.) (Wirth et al 1977, Wirth and Grogan 1979a, 1981). In an account of the aquatic and semi-aquatic insects of the Great Dismal Swamp (VA/NC), Matta (1979) lists only 5 species of biting midges, whereas Knausenberger and Turner (unpubl. obs. 1977) encountered 20 species of *Culicoides* alone there.

Carlson (1981) lists ca. 45 species from South Carolina, and Webb and Brigham (1982) list 64 species (incorrectly stated as 74; 61 species names therein are valid) of aquatic ceratopogonids for North and South Carolina. However, both the latter works draw mainly on Blanton and Wirth (1979) for *Culicoides* records as indicated on distribution maps only.

The genus *Culicoides*. The number of *Culicoides* species recorded in the eastern United States has more than doubled in the past three decades. Whereas 33 species were reported by Foote and Pratt (1954) in the U.S. east of the continental divide (108° -115° W) and 50 valid species east of the Mississippi River (ca. 90° W) were listed by Battle and Turner (1971), presently at least 78 species are known to occur east of 100° W, a longitude which closely delineates the westward isohyet of 20 inches of rainfall (see Section 1.3.5. below). This isohyet represents a consistent boundary of discontinuity in distribution of biting midges (e.g., Grogan and Wirth 1979; unpubl. obs.) and other insects.

Despite increasing attention being directed by researchers from many fields upon *Culicoides* and the diseases they vector, disproportionately little information is available about their immature stages, a point made forcefully by Linley (1979, 1985). Likewise, a synoptic summary of the present knowledge of the numbers, geographic occurrence, and prevalence of *Culicoides* species in the eastern Nearctic region is not available, particularly with respect to larval habitat, descriptions of immatures, and feeding habits.

Comprehensive systematic reviews of the *Culicoides* species present in eastern North America are available for only three states -- Florida (Blanton and Wirth 1979), New York (Jamnback 1965), and Virginia (Battle and Turner 1971). In addition, for Maryland, an accounting of species and county records has been compiled by Gazeau and Messersmith (1970b). Immature stages were treated only in the Florida and New York studies.

1.1.2.2. Systematics of the Immature Stages

Study of immature aquatic Ceratopogonidae had a strong beginning as a result of a succession of thorough treatments in the first half of this century, mainly by the Europeans Thienemann (1910, 1928, 1954), Rieth (1915), Goetghebuer (1923), Saunders (1924, 1956), Lenz (1934), and especially Mayer (1934b, 1934c) and the Americans Johannsen (1905), Malloch (1915, 1917), Thomsen (1937), and Wirth (1952). Pioneering work by Carter, Ingram and Macfie (1920, et seq.) on African *Culicoides* and other genera, and by Saunders (1924) on *Forcipomyia* provided the necessary morphological standards with which subsequent authors could provide adequate descriptions of larval and pupal setation and armature (esp. Mayer 1934b, Lawson 1951, Jones 1961a). The earliest important studies on immature stages of biting midges beginning in the 1880's are listed by Thomsen (1937) and Wirth et al. (1977).

All published information on immature stages published by the mid-1940's was reviewed and synopsized by Hennig (1948, 1950), who listed 278 species as having either egg, larva or pupa (or several stages) described, a surprisingly large proportion of an estimated "over-500" total number of species in the world at that time. Yet, even then, there were probably more like 1000 species described in all.

Although many scattered descriptions of immatures have appeared since then, relatively little comprehensive work has been done apart from the early American and European work, including Indonesian and African material treated by Mayer (1934b and 1955a, resp.). Much of the early progress with the Ceratopogonidae was undoubtedly related to the close

taxonomic relationship with the Chironomidae, of which the biting midges were commonly treated as a subfamily until the mid-1950's. Recent investigation and description of immature stages of ceratopogonids has lagged seriously behind that of adults. Taxonomists historically have had far readier access to adult specimens than immature stages of the same species, but the situation has been aggravated by the tendency of fewer investigators in the latter half of this century to rely on rearing of specimens than had been the case earlier.

Immature stages of only a few major genera have received serious comprehensive work, namely: *Forcipomyia* (e.g. Saunders 1924, 1956; Chan and LeRoux 1965; Bystrak and Wirth 1978); *Atrichopogon* (Nielsen 1951, Ewen and Saunders 1958); and *Culicoides* (Lawson 1951; Kettle and Lawson 1952; Jamnback 1965; Jones 1961a; Dzhaferov 1964; Nevill 1969; Kettle and Elson 1975a,b, 1976, 1978, 1980; Blanton and Wirth 1979). Recent years have seen a much-to-be-welcomed trend to include immature stages in systematic treatments of ceratopogonid genera other than the above, e.g. *Dasyhelea* (Waugh and Wirth 1976); Ceratopogonini (Grogan and Bystrak 1976, Grogan and Messersmith 1976, Elson-Harris and Kettle 1985); Stilobezziini (Grogan and Wirth 1977b, Wirth and Grogan 1981); Heteromyiini and Sphaeromiini (Debenham 1974, Grogan and Wirth 1975, Wirth and Grogan 1979, Palchick 1981), and Palpomyiini (Grogan and Wirth 1979, Wirth 1983a,b,c; Wirth et al. 1984; Spinelli & Grogan 1985). On the whole, very few larvae have been treated in these works.

As a result, little progress has been made in the development of comprehensive keys to the genera of larval and pupal ceratopogonids.

Indeed, the larval keys of Mayer (1934c) and/or Thomsen (1937) have provided the basis of practically every generic key to larvae published since then in general aquatic reference works (Hennig 1950; Wirth 1952; Bertrand 1954; Wirth and Stone 1956; Pennak 1953, 1958; Edmonson 1959; Hilsenhoff 1975; Parrish 1975; Tarter 1976; Merritt and Cummins 1978, 1984; and Webb and Brigham 1982). It must be remembered that the original keys by Thomsen (1937), as good as they were, include only 23 species in 9 genera (13 species are Ceratopogoninae) as larvae, and 29 species as pupae, based mainly on material from the Ithaca, New York, area.

Classification of the Ceratopogoninae has been seriously hindered by lack of good characters in the immature stages (Wirth et al. 1977). The status of the *Palpomyia-Bezzia-Macropheza* group of species has been considerably clarified by attention to eggs and pupae, in particular, such that now four distinct tribes are recognized based on characters of both the adult and immature stages: Heteromyiini, Palpomyiini, Sphaeromiini and Stenoxenini (Mayer 1952, 1957; Wirth 1962b, Wirth and Ratanaworabhan 1972a,b).

Nevertheless, larvae in the so-called "*Palpomyia-Bezzia*" complex of authors have been practically indistinguishable have tended to be lumped for lack of any alternative. The first major recent advances in the development of new descriptions and keys for immature stages of genera and species of the wider subfamily Ceratopogoninae have been made by Gutsevich and Glukhova (1970), Glukhova (1971, 1977, 1979b), Kettle and Elson-Harris (1981), and Elson-Harris and Kettle (1985, 1986a, b).

A real breakthrough is represented by Glukhova's(1979b) comprehensive treatment of the biology and systematics of larval Ceratopogoninae. This work includes keys to larvae for 98 species in 16 genera. As a result, about 20 % of the non-*Culicoides* and at least 30% of *Culicoides* species in the European U.S.S.R. can now be identified by this work alone. This compares to about 9% and 28% respectively in the Nearctic(for which many sources are presently required).

While Glukhova(1979b) reviews the morphology and anatomy of both the larval and pupal stages, pupae are not described or keyed in her volume, though they are included in her recent descriptions of new species of *Isohelea*, *Palpomyia* & *Bezzia*(Glukhova 1979a). In general, European investigators have given more attention to larvae than to pupae.

Very useful and thorough descriptions have been recently published of *Alluaudomyia* (Elson-Harris and Kettle 1985), various Heteromyiini(Elson-Harris and Kettle 1986a, including two *Clinohelea* species and *Pellucidomyia leei*), and Sphaeromiini (Elson-Harris and Kettle 1986b, including two *Nilobezzia* spp. and a *Lanatomyia* sp.) larvae and pupae in southeast Australia. Several laboratories are currently developing an emphasis in larval morphology, such as M. Kremer in Strassbourg, France, and G. R. Mullens at Auburn University, Alabama.

As suggested long ago by Kettle and Lawson(1952), the distinction of larvae should not pose any special difficulties once material is in hand. The promising recent advances in this area lend credence to this point.

1.1.2.3 Biology of Immature Stages

The ecological multivalency of the Ceratopogonidae, and the dearth of apparent morphological adaptations in the larvae, particularly in the "vermiform" subfamily, offer a particular challenge to the investigator of aquatic and wetland habitats(e.g., Wiggins et al. 1980).

Ceratopogonidae are particularly successful in littoral ecotones, but have established themselves in all imaginable lentic and lotic biotopes. They are commonly encountered in saline and other chemically modified environments. A species of Micronesian *Forcipomyia* has been reported from a sulfur spring at a pH of 1.4(Tokunaga and Murachi 1959, Insects of Micronesia 12(3)). Thermal waters may exhibit large monospecific stands, such as *Dasyhelea tersa* Johannsen from hot springs at 51 C(122 F) in Indonesia(Thienemann 1954). Many species are apparently well adapted to temporary waters(Hinton 1953, Wiggins et al. 1980).

Yet, very little is understood of the habitat requirements of Ceratopogonidae. The relationship between taxonomic diversity, ecological strategies and evolutionary adaptations is little explored. Even the assignment to functional feeding groups and mode of existence categories is difficult due to the lack of natural history data. Immature stages are a source of data for the solution of phylogenetic and classificatory problems, as has been demonstrated frequently with this family(Ewen and Saunders 1956; Mayer 1952, 1957; Wirth et al 1974, 1977). Studies of systematically related co-existing species often reveals both obvious and subtle mechanisms of resource partitioning and ecological segregation (Resh and Solem 1978 in Merritt and Cummins 1978).

In recent years, increasing attention is being given in North America to the Ceratopogonidae, for example, in streams and rivers (Riesen 1976, Fox and White 1980, Benke et al. 1984, Simpson et al. 1986), ponds and lakes (Bowen 1983a, b; Cowell 1984; Hilsenhoff and Narf 1968; Thorp & Bergey 1981), and peatland and bogs (Erman and Erman 1975). However, because few investigators collect adults or are in a position to rear their specimens to the adult stage, species level determinations are rarely provided.

1.1.3. Ecosystematics and Autecology

1.1.3.1. Ecosystematics

As necessary as the taxonomic study of the immature stages of Ceratopogonidae is, clearly more than merely description and characterization of unknown developmental stages and new species are needed to serve the broader needs of biological science adequately. Systematics of the current era strives to "study all the kinds and diversity of organisms and any and all relationships among them" (Simpson 1961 in Allen 1975). This is a biological definition universally accepted but not always followed by practicing systematists. Some advocates of "functional taxonomy" (e.g. Bahr 1982) dispute the need for a phylogenetic species-based taxonomy because of its ever-incomplete status and supposedly limited relevance to ecological realities, but this stance has been effectively refuted (e.g. Wiggins 1966, Resh and Unzicker 1975, Hynes 1984).

Truly biosystematic studies are a rarity. Such studies would involve, for example, analyses of morphology, histology, cytology, taxonomy and

geographic variation of all life stages of a group of organisms, and their evolutionary relationships, superimposed on *ad hoc* field studies of the ecology and biology of these organisms. Among the very few studies in the Ceratopogonidae approaching this ideal is one conducted on *Culicoides* subgenus *Selfia* (Atchley 1970).

I approached the present study according to the concept of "ecosystematics", a term proposed by Allen (1975) to signify the union of certain aspects of ecology and systematics, but applied to studies not intended to be as broad as biosystematic studies. Ecosystematics emphasizes the acquisition and use of ecological data to add to the utility of taxonomy. The term is used to designate a multipurpose approach which is expected to yield practical dividends both to taxonomic and ecological services, such as those in support of environmental protection. The need for such an approach has been articulated in the literature for at least two decades (Wiggins 1966, Arnett 1969, Heywood 1973, Resh and Unzicker 1975, Eldridge 1978, Hynes 1984).

In ecosystematics, the goal is not only to name and classify species (and developmental stages), but to ascertain the role of the species in the environment, what environmental factors determine its distribution, and the effect of the environment on the expression of the phenotypic characters of the species. Two important questions which ecosystematics should help to shed light on are (1) to what extent is the diversity among organisms adaptive; and (2) do the biological phenomena observed in the context of the systematic framework have any bearing on phylogenetic relationships and evolutionary processes (Allen 1975, Hynes 1984).

An ecosystematics approach fundamentally should involve most or all of the following:

1. Carefully planned, consistent collection and extraction of original material, rather than exclusive or primary reliance on existing collections made by a diversity of collectors whose collecting and processing methods are often inadequately characterized or unknown (Arnett 1969, Southwood 1978).

2. Increased data content with collected specimens, utilizing a standardized form for field data, rearing data and laboratory observations. An exemplary note-keeping system containing principles which inspired the forms developed in this study is presented by Hogue (1966). Emphasis is placed on detailed locality and habitat data, and a unique collecting number. Allen (1975), Arnett (1969) and Blackwelder (1967, in Allen 1975) suggested comparable forms for various purposes.

3. The means of correctly associating and retrieving biological information with the taxa and collections.

4. Work with living organisms, particularly by rearing, accurately associate developmental stages and metamorphic phases (Arnett 1969). With such material, more refined and meaningful taxonomic, geographic and ecological studies are possible (Atchley 1970).

5. Attention to eggs, larvae, pupae and adults of as many species as possible in the group being studied.

6. Attention to storage and labeling methodology even for specimens not the primary focus of the study, making the specimens more useful to others.

7. Maintenance of a properly curated and organized collection at a public institution including at least voucher specimens.

8. Ideally, incorporation into a system of automatic data processing for information storage processing and retrieval (Arnett 1969, Kim and Knutson 1986).

Taxonomy and ecology tend to be closely related, for reasons such as outlined by Hynes (1984). Narrower, higher and presumably more recently aquatic taxa are less ecologically diverse than wider, lower and more anciently aquatic taxa. Ecological diversity seems to occur more between families than within them, but especially for the more ancient

primary groups, including nematoceros Diptera such as the Ceratopogonidae, there is a wide range of life-style and habitat within a single family, mostly observable in the larval stages. Classification of insects is based largely on adults, but the force of selection has been primarily on the larvae, and adults tend to be conservative (Wiggins 1966, Hynes 1984).

The current-day trend in studies involving biological inventory and survey increasingly is to incorporate ecosystematic principles, although they are not usually characterized as such. A scientifically appropriate survey cannot be planned separately from the perspectives of taxonomy or ecology alone (Danks 1986 in Kim and Knutson 1986). Biological survey can be seen as a critical issue for environmental protection, resource management, and systematic biology.

Resh and Unzicker (1975) point out that benthic macro- invertebrate collections made as part of environmental assessment reports are also valuable because the collections may include detailed data on substrate, geology, vegetation and water quality, which can benefit both the taxonomist and ecologist. As pointed out earlier, aquatic insect investigations are increasing in sophistication -- meaning greater attention to appropriate diversified and discriminating collecting, extraction, identification and storage and retrieval procedures. As a result, Ceratopogonidae are increasingly being reported as significant components of aquatic habitats.

1.1.3.2 Autecology

Autecology involves detailed study of the bionomics of individual species; in this study, the focus is on larvae and pupae. In a situation similar to that found in Chironomidae (Pinder 1986, Hilsenhoff and Narf 1968), most of what has been written about the biology of Ceratopogonidae has been synecological in character, which has limited the amount of detail that can be obtained regarding individual species. There is a notable lack of detailed autecological studies on Ceratopogonidae. The main exceptions are found with several economically important *Culicoides* (e.g., Bidlingmeyer 1957; Becker 1958, 1961; Davis et al. 1983; Linley 1966, 1968a,b; Linley and Adams 1972), and *Leptoconops* (e.g., Linley 1968b, 1969a); some Forcipomyiinae (e.g., Boesel and Snyder 1944, Nielsen 1951, Saunders 1924), a few *Dasyhelea* (e.g., Bishop 1974, Hinton 1953, Kitching 1971, 1972), and a few isolated species in other genera (e.g., Chan and LeRoux 1967, Williams 1953).

Such studies ideally would consider the influence of the environment on all stages in the life cycle, and combine both field and laboratory investigations (Pinder 1986). However, autecological studies are primarily descriptive studies of basic life history phenomena as encountered in the field, such as life cycles and distribution in various habitats, for specific species (e.g., Allan, Ch. 16 in Resh and Rosenberg 1984). Attempts at synthesis and predictive classifications of animal communities such as those arrived at by Wiggins et al. 1980 for temperate annual temporary pools, would be impossible without detailed life history and autecological data for constituent species of a community.

1.2 Methods and Materials Including Brief Discussion
of Pertinent Rationale and Results

1.2.1 Approach to Data Acquisition and Survey

1.2.1.1 Obtaining Specimens

My primary focus in specimen acquisition was on locating reared and associated ceratopogonid developmental stages. It became apparent early in this study that very little appropriate material was available in existing North American collections. Therefore, I mounted an intensive field collecting program in Virginia and surrounding states, giving major attention to associating larvae, pupae and adults through a diversified sampling, extracting and laboratory rearing strategy. I acquired the specimens and assembled the data on which this study is based from four main categories of sources (in order of decreasing significance):

1. Breeding site and adult collections which I made for this study between 1975 and 1978: WIK Coll. Nos. 1-551; adult field trapping (AFT) Coll. Nos. 1-69 (Appendix F.1 and E, resp.). The methods used in this work, emphasizing rearing records, are discussed below.
2. Results of an extensive survey of breeding sites undertaken by Frank V. Battle (FVB) in Virginia, North Carolina and West Virginia, as part of his doctoral research under E. Craig Turner, Jr. at V.P.I. & S.U. Battle made collections from 1968 to 1970, but the great majority were taken in 1969 (FVB Coll. Nos. 1-192, Appendix F.2). The latter sites are recorded in

Fig. 2.

Battle held all of his samples in rearing containers for adult emergence. An aliquot of nearly all his samples was processed for soil chemical analysis by the V.P.I. & S.U. Soils Testing Lab. For one series of sample (the "800 series" from North Carolina), no soil analyses were done.

Most of the ceratopogonid midges emerging from Battle's rearings were mounted on microscope slides in the laboratory of E. C. Turner. The *Culicoides* were sorted out and used by Battle for study of the *Culicoides* of Virginia (Battle 1970, Battle and Turner 1969, 1970a,b, 1971, 1972). I determined all the remaining material (and some *Culicoides*) and evaluated them with their collection data for present study.

3. Earlier stream-side breeding site and adult collections from an unpublished study undertaken between 1971 and 1973 to determine the pollution indicator value of biting and non-biting midges communities (Turner and Knausenberger 1974). The methods used in this earlier work were similar to (but less extensive than) those in the later work (# 1 above), and also gave attention to rearing in cartons similar to those shown in Fig. 3. Four stream study areas in southeast Virginia were involved (Appendix H):

- a) Cedar Run, Montgomery Co.: pretreated toxic metal waste and secondary domestic sewage (Fig. 22, Table 54).
- b) Green Hill, South Fork Roanoke R., Montgomery Co.: organic waste from meat packing facility (Fig. 23, Table 55).

- c) Glen Lyn, New River, Giles Co.: thermal discharge from a coal-fired power plant, and fly-ash pond effluent (Fig. 24, Table 56).
 - d) Wytheville, Reed Creek, Wythe Co.: non-pretreated toxic metal waste and primary-treated domestic sewage (Fig. 25, Table 57).
4. Specimens acquired from outside sources: Larval, pupal and adult Ceratopogonidae from the eastern Nearctic which I acquired from an extensive correspondence, personal recruitment effort, and loan from individuals and established collections. Also, I ran notices soliciting reared material in several professional journals (Bull. Ent. Amer.; Ent. News; Cerat. Inform. Exch. Newsl.; Newsl. North Amer. Benth. Soc.; and Taxon) at several national meetings and at the International Congress of Entomology of 1976. Many unassociated specimens were submitted by aquatic biologists seeking identifications. Very few of these were reliably identifiable.

1.2.1.2 Geographic Scope and Approach to the Survey

I undertook an extensive survey (sensu Southwood 1978) of a wide range of representative habitats in all major river basins, biotic regions and physiographic provinces in Virginia and near-border regions of surrounding states (Fig. 1; Table 46 in Appendix C). My primary geographical focus was on the entire state of Virginia, as well as northern North Carolina and eastern West Virginia. The larger geographic scope of the work is the "Middle Atlantic United States", which I define as

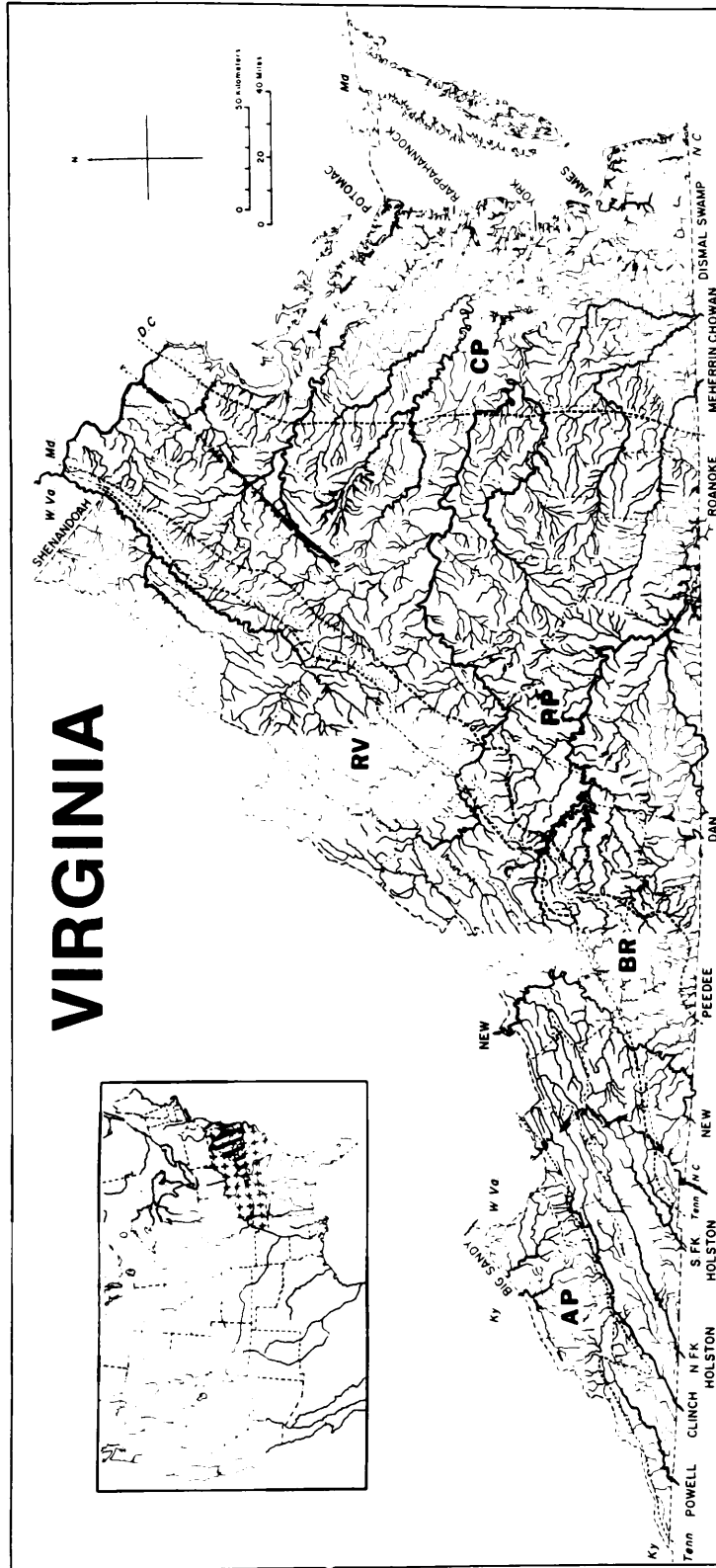


Figure 1. Physiographic provinces of Virginia, with inset showing the region covered in this study. Some relevant subdivisions of the provinces are indicated by shaded lines highlighting, respectively, the approximate boundaries of the (a) middle and southern sections of the Ridge and Valley province; (b) inner and outer Piedmont province; and (c) lower and upper Coastal Plain. The abbreviations are defined in the text and Glossary(Appendix I).

the six-state region including West Virginia, Maryland, Virginia, North Carolina, Kentucky, and Tennessee, plus the District of Columbia (inset, Fig. 1).

Thus, I paid particular attention to material deriving from these states, and to extracting appropriate literature records. Neither F. V. Battle nor I did much collecting in the District of Columbia, Kentucky, Maryland or Tennessee (Table 2), but by adopting this wider focus, I was able to develop a more comprehensive picture of the Ceratopogonidae fauna of the region than if I had concentrated solely on Virginia (e.g., see Table 45 in Appendix C). This is particularly relevant because no comprehensive reviews of the fauna of this family exist for any state in the eastern Nearctic, contrary to the case with other biting fly families, such as Culicidae, Simuliidae or Tabanidae or other aquatic insect orders (e.g., Merritt and Cummins 1984). Also, by taking the broader view, I was able to make prospective judgments as to the species expected but not yet found in the various states.

Figure 2 presents the collection localities (i.e., groups of sites) I visited for this study from 1975 to 1978, as well as F. V. Battle's 1969 localities. Also indicated are the stream pollution study sites (Tables 54-57) which yielded some valuable data (e.g., Table 38). The vast majority of primary habitat and rearing records in this study derive from these sources. Areas where too many samples were concentrated for effective depiction at this scale are indicated by fields of plus symbols. These areas are listed in Table 1, giving the number of sites sampled in each area.

Most of my collecting outside of Virginia's Montgomery Co. (which,

Figure 2. Collection localities in Virginia and contiguous states.

Symbols represent the primary collections processed for larval, pupal and adult Ceratopogonidae, on which the great majority of records for this study is based. Each arrowhead represents one to over 11 collections. Sites visited by the author (WIK) are distinguished from those of F. V. Battle (FVB). The collection sites, localities and habitat descriptions are presented in Appendix F. Outside the borders of Virginia the symbols are placed as accurately as possible, at the same scale (original map approx. 1:1,335,000) as the Virginia portion, to convey a visual impression of the number and distribution of the extralimital collections. The various symbols are scaled according to the number of collections accomplished at the localities marked. In regions where more collections were made than could be effectively depicted at this scale, blocks of plus symbols^{1/} were substituted. These areas are numbered and are identified in Table 1. Locations where adult-trapping collections were made in the field (AFT), by one or more of seven methods, are indicated by the six-pointed stars (Appendix E). Where these stars appear alone, the relevant adult-trapping effort was not made near a substrate collection site. Otherwise, they appear directly above the arrowhead or region number. Open five-pointed stars locate four stream pollution study sites sampled regularly over a two or three year period (Appendix H). The codes used for those sites on the map are: CR - Cedar Run; GL - Glen Lyn; RW - Reed Creek at Wytheville; SR - South Fork, Roanoke River.

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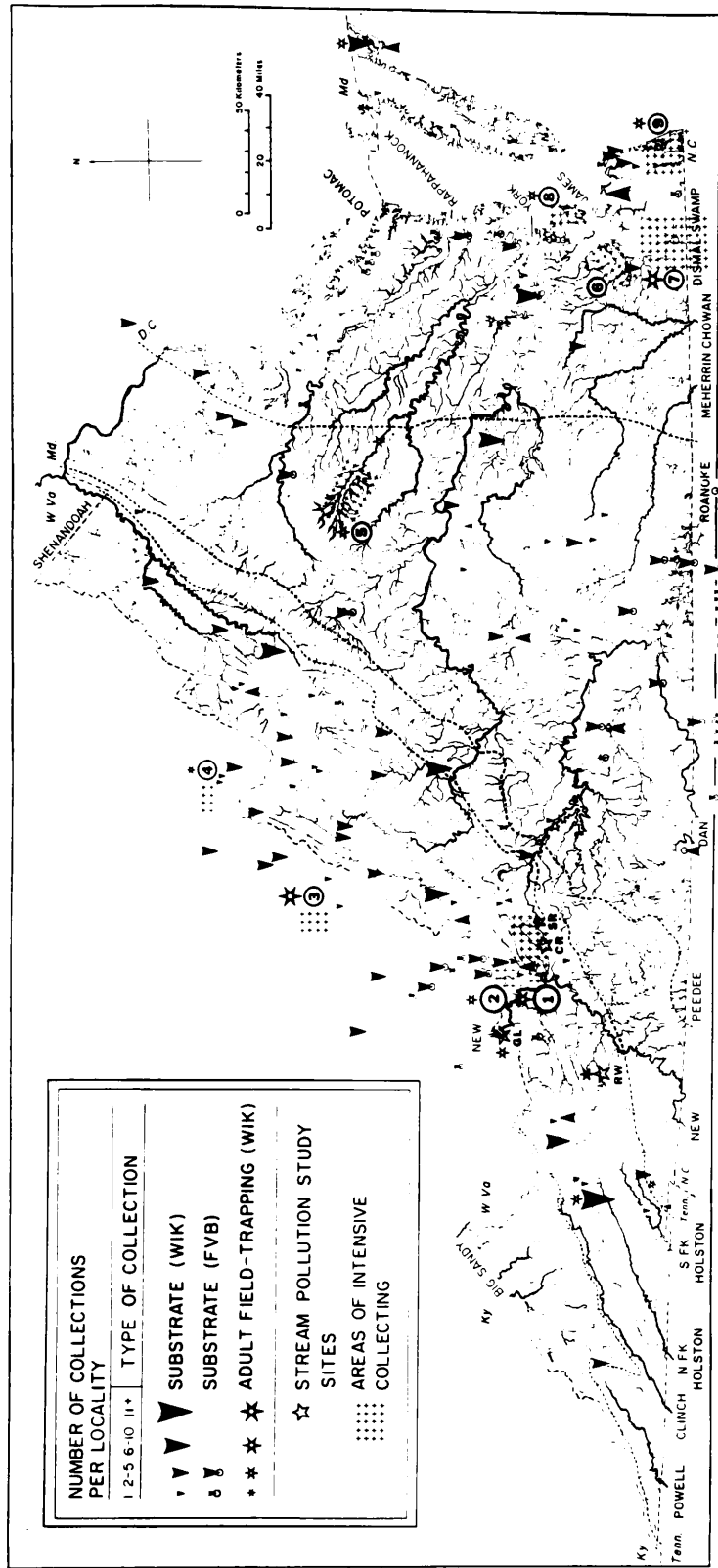


Figure 2. Collection localities in Virginia and near-border regions (scale ca. 1:3,608,000). See figure description on facing page.

Table 1. Key to the numbered regions highlighted with '+' symbol fields on the base map, which depicts collection sites (Fig. 2). The number of sites in the respective regions is listed.

No. on Map	Region	Number of Sites		
		WIK		FVB
		Substrate	AFT ^{1/}	
1	Salt Pond Mtn./Butt Mtn. Massif, Giles Co., VA (elev. 3000-4360 ft./914-1328 m)	24	2	6
2	- Northern Montgomery Co., VA, 1975-77	120	2	110
	- Stream pollution study sites, Cedar Run and S. Fk. Roanoke R., Montgomery Co., VA, 1971-73	395	10	n/a
3	Cranberry Glades, Pocahontas Co., WV (elev. 3355-3400 ft./1023-1036 m)	45	24	2
4	Spruce Knob/Sinks of Gandy region, Randolph Co., WV (elev. 3480-4860 ft./1061-1481 m)	23	1	-
5	Lake Anna Reservoir, Louisa Co., VA	19	5	-
6	Isle of Wight Co.; northern Suffolk, VA	17	10	-
7	Great Dismal Swamp, VA/NC	82	17	1
8	Hampton/Poquoson, VA	12	4	-
9	Back Bay and vicinity, VA/NC	15	2	1

^{1/} Adult field-trapping efforts. See Appendix, Table 50.

because of proximity and familiarity, yielded the greatest number of sites) occurred in a series of extended expeditions lasting 2-5 days. During the course of the study, I collected in every month except January. I obtained collecting permits in areas of particular biotic interests, notably the Cranberry Glades Botanical Area and Great Dismal Swamp (areas 3 and 7, resp., on Fig. 2). In choosing apt collection destinations, I found the Freshwater Fishing and Hunting Guide in Virginia and related guides by the Alexandria Drafting Co. (417 E. Clifford Ave., Alexandria, VA 22305) to be particularly useful. These guides provide detailed access data and maps for a large number of wetland and aquatic habitats in the region.

1.2.1.3 Habitat Data Collection

For data collection at sampling sites, I developed a standardized form, consistent with ecosystematic principles (e.g., Allen 1975, Hogue 1966), including descriptive site data, vegetation characteristics, and chemical/physical characteristics (Appendix D, Fig. 19).

Standard soil chemistry analyses were performed on most of the samples which were not purely vegetative material. Analyses performed by the Soil Testing Laboratory at the V.P.I. & S.U. Agronomy Department on all submitted samples included pH, organic matter content, soluble salts concentration, level of water, extractable nitrates, and available calcium, magnesium, phosphorus and potassium. The procedures used by the laboratory were detailed by Alley and Hawkins (1972). Occasionally, two or three replicate samples were submitted per collection site/sample. The same laboratory had processed Battle and Turner's (1972) samples.

The particle-size distribution of ca. 150 littoral substrate samples I determined by sieving after aqueous removal of silts and clays, for which I used the facilities of the Soil Physics Laboratory of the Department of Agronomy. However, the data are not treated in this work.

Aquatic chemistry measurements were limited in number and type. Only measurements of air, water and substrate temperatures were taken reasonably systematically, particularly where free water was present at the sample site. The other measurements of greatest interest to me were of electrical conductivity and of salinity (YSI S-C-T meter). In addition, I occasionally had an opportunity to measure water pH (determined electrometrically with a portable pH meter accurate to 0.1 pH), dissolved oxygen (iodometric microburette titration method, La Motte Chem. Co.) and total hardness (E.D.T.A. reagent system with automatic microburette titration system of La Motte Chem. Co.).

Condensed habitat data and locality descriptions for the primary sites in this study are presented in Appendices E, F, G, and H. This likewise is consistent with the desirability of increasing the amount of detailed data which can be associated with specimens in modern taxonomic studies (Arnett 1969, Heywood 1973, Allen 1975, Hynes 1984). In this way, the data are more readily available for use by others, especially for the many ceratopogonid species which I did not treat in detail herein. This also applies to the non-ceratopogonid taxa retained during the extensive survey and rearing efforts.

A breakdown of collection numbers by political and geographical units is given in Appendix C, Tables 48 and 49. Substrate and water chemistry information is presented in Appendix G, Tables 51, 52 and 53.

The original habitat and locality collection data are on file at the Department of Entomology, V.P.I. & S.U.

1.2.2. Field Sampling Procedures

1.2.2.1 Sampling for Immature Stages

As the basis for a systematic and extensive, but qualitative, survey for the immature stages of Ceratopogonidae and their habitats, I developed a diversified sampling strategy meant to adequately assess the fauna across the full spectrum of aquatic and semi-terrestrial habitats and substrates they occupy. I deliberately de-emphasized the more terrestrial niches, so that most *Forcipomyia* and many *Atrichopogon*, some *Dasyhelea*, and possibly a few species of other genera were not likely to be well collected by the methods used.

At promising collecting localities, I chose sampling sites on a

selective or stratified random basis, using past experience as a guide as to which substrates were likely to harbor specimens. To maximize the number and diversity of species and specimens obtained, I sampled in as many physiognomic habitat types (cf. p. 3 in Deonier 1979), in the aquatic and transitional zones, as possible. I particularly emphasized distinguishing microhabitats, and sampling them individually.

It was not practical, as a rule, to determine in the field the extent to which larvae and pupae were present. Yet, by making preliminary extractions (mainly by stirring and decanting, and close observation for pupal and larval activity), it was possible to get a good idea of which sites were promising. On collecting expeditions well removed from the laboratory, I would use such preliminary indications to spend several hours making collections at selected microhabitats, making behavioral observations, and the like. Also, I attempted to return to the more productive localities, preferably at different seasons. Appendix F.1.1 explains my method of assigning locality and collection numbers.

As to sampling tools, although I kept an array of different types available on each collection trip, the most universally adaptable was a variety of scoops (sturdy, flat-bottomed hand shovel, garden trowel, and/or large serving spoons). These scoops allowed sampling of substrate in many different situations, be it from crevices on wet cliff faces, bogs, mud at a pond, plant detritus in a cattail marsh, gravel and leaves among boulders at a stream, or wet stump holes.

Where habitat substrate could adequately be sampled by the scoop method (the majority of cases), I standardized by limiting the surface

area sampled to ca. 500 cm² and the volume to between 500 cm³ (pure sediment) and 1000 cm³ (including plant detritus). Habitat water was retained when present, later to be decanted through a sieve. In most cases, I did not attempt to routinely sample deeper than 2-3 cm.

For each collection, I attempted to obtain duplicate subsamples or aliquots from the same microhabitat, taken side by side. This was done in 470 of the 551 (87%) collections made. One of the duplicate samples I held for emergence of imagoes in 1/2 gal. rearing cartons (RC) discussed below (Fig. 2A, 3). The other sample destined for extraction of larvae and pupae I returned unpreserved to the laboratory as soon as possible. All samples were placed directly into plastic bags in the field.

Transport to the Laboratory. During all collecting expeditions, many extending more than one day, I placed the bags containing the samples into rearing cartons held in specially constructed racks in the back of a covered pick-up truck. In this way, imagoes emerging during the period between field sampling and return to the laboratory (typically 3 to 5 days) would be retained in good shape. Before placing the samples in their cartons, I would decant off any pupae floating at the top. These pupae were placed for emergence in cotton-stoppered vials in their own holding racks. To mitigate the possibly detrimental effects of excessive free water sloshing during travel, I decanted the water remaining in the sample through a sieve, retrieving any specimens.

During transport, temperatures inside the covered bed of the truck

did not normally exceed 2-3°C above ambient temperatures in the shade. Several factors contributed to the avoidance of excessive temperatures: the cover was of a highly reflective aluminum, the windows were kept wide open, and we routinely parked in the shade. Because the insects were transported within the natural substrate in vessels permitting free air exchange, rapid fluctuations in temperature were avoided. Mortality was reduced under these conditions because temperatures could equilibrate gradually and no stagnation would take place, as it might in sealed bags or vessels.

This approach to returning unpreserved samples back to the laboratory proved highly effective, permitting samples to arrive in a fresh condition even after several days' journey, while also allowing specimens to continue development or to emerge safely. The procedures allowed flexibility in timing, and avoided or minimized the problems normally encountered with unpreserved substrate samples containing invertebrates, e.g., decomposition, drowning, entrapment of specimens, need for equipment to keep specimens cool.

The problem of deterioration of unpreserved samples during transport has not received much attention in the literature. A particularly interesting approach that has come to my attention was worked out by Dzhafarov (1964) for *Culicoides* - containing samples in the southeastern USSR. He used colored cloth sacks to transfer and hold samples, soaking the sacks daily to prevent drying. He found that larvae and pupae survived for over a month. The problem is circumvented in the majority of routine sampling for aquatic macroinvertebrates, where standard procedure calls for preservation in the field (e.g., Weber

1973).

Other Sampling Tools. To assess the minority of other habitats not suited to the scoop method of sampling -- such as benthic sites, snags in streams, or floating plant beds -- or to evaluate promising alternative approaches, I also employed the following types of sampling tools, to a greater or lesser extent:

- aquatic dip nets
- artificial substrates (multi-plate, thermoplastic mesh)
- bulb syringes (large basting type) for small collections of water (e.g., pitcher plants)
- corers of various types, including fencepost hole digger
- drift nets
- grabs/dredges (Petersen, Ponar)
- unit-area samplers (Hess-type, Surber)

The more significant of these are briefly treated below in light of their success and usefulness in this study.

1. Artificial substrate samplers. These samplers collect organisms with a minimum of interfering sediment, are inexpensive, simple in design, easy to use, and they allow sampling in areas otherwise virtually impossible to sample (Beak et al. 1973). To a limited extent (ca. 25 samples), I utilized two designs of such samplers: a modified Hester-Dendy multi-plate sampler made of tempered hardboard (Fullner 1971), and black thermoplastic mesh (conservation webbing -- 3-M Corp.). Factors affecting the performance of such samplers are reviewed by Mason et al. (1973)

The 3-M webbing was used extensively by Voshell and Simmons (1977, 1984), emplaced in perforated plastic buckets along transects on the bottom of Lake Anna Reservoir, Virginia. Most of the samplers provided by them for evaluation in this study (no. 5 in Fig. 2, Table 1) were obtained on these artificial substrates. Apart from the latter group of samples (esp. WIK Coll. # 318, 333-342), this approach was not effective for my project requirements, because retrieval trips were required, vandalism was a problem, and because it was not an especially good source of specimens. I did not use multiplate samplers after the first year. Some of the results are discussed under *Mallochohelea atripes* and *Sphaeromias longipennis* in Chapters 4 and 6.

2. Drift net. I employed drift nets on several occasions (e.g., Coll. No. 397 et seq.) because, based on published observations and on material submitted to me by my colleagues who had used this approach, there was reason to believe that some interesting material could be obtained this way. Brundin (1956) and Thienemann (1954) were among the first to point out the value of drift netting for acquiring samples of floating midge exuviae. Coffman (1973) validated this in a remarkably diverse collection of chironomid pupal exuviae in a small creek in western Pennsylvania, where he obtained 143 species.

In 1975, in a visit to his laboratory at the University of Pittsburg, I examined some of the material from this work and discovered several ceratopogonid exuviae, particularly *Dasyhelea*

spp. Atchley (1970) reported success in locating *Culicoides* and other ceratopogonid pupal exuviae in natural accumulations created by the current in eddy pools or by the wind along the leeward margins of ponds, etc.

Larval *Bezzia* were reported in the downstream drift of a creek in Oklahoma (Riesen 1976), where the larvae adhered to the ecologically expected pattern of a nocturnal behavioral drift peak (Bournant and Thibault 1973, Waters 1972). I received larvae of *Probezzia* collected by Kennedy et al. (1981) with a 1 m² drift net in the New River, Virginia.

In this study, I assessed the presence of drifting ceratopogonid larvae with a Wildco brand drift net of No. 363 Nitex bolting cloth on a 30 x 45 cm frame, placed in narrowed sections of streams where the current was concentrated into a "chute" above a riffle. I kept the nets in place for 24 hours. The yield in the specimens per unit effort was not very high in the attempts I made. I collected only younger instar *Alluaudomyia*, *Bezzia*, *Culicoides* and *Mallochohelea* larvae, and those in small numbers, probably because I missed the seasonal emergence peaks. Inasmuch as my emphasis was on rearing from natural substrate, I did not pursue drift netting to any greater extent, although I consider the method promising for this family.

3. Grab Samplers. I used a modified lighter-weight Petersen grab (Entomological Supplies, Baltimore, MD), to obtain samples in deeper waters if the sediment was uniform. This modified grab

samples 40 in.² (258 cm²) per grab, ca. 25% of the area of the standard Petersen grab. Being lighter, the modified grab could be carried for some distance from the collecting vehicle, when necessary at out-of-the-way sites.

1.2.2.2 Field Collection of Adult Midges

To sample the adult ceratopogonid fauna alongside substrate collection sites, or in the immediate vicinity of larval habitats, I used seven different trapping methods, most of them non-selective. At any given site, I normally used only one method, although at certain larger, ecologically similar localities (e.g., Cranberry Glades or Dismal Swamp), several different traps were used. My intent was to:

1. qualitatively and numerically enrich the data on species present in a given locality, supplementing the rearing results;
2. allow comparisons of adult collections with rearing records;
and
3. provide useful supporting information to assist in determining immature stages by indirect association.

The 69 adult field trapping (AFT) events recorded as part of this study are summarized in Table 50 (Appendix E).

Listed briefly in order of prominence (extent to which used with success), the methods are:

1. BL --- Black Light Traps (short wave and long wave) mounted in timer-equipped New Jersey-type suction traps, powered by 12-volt batteries. Several samples were also taken with baffle-type passive interception traps

(i.e., BL-47, BL-53, and BL-58). Usually operated overnight in the immediate site area.

2. DV --- "D-Vac" backpack-mounted motorized suction trap with 30 cm diameter net. Each five minutes' operation alongside a larval site was considered a sample.
3. INC --- Incandescent Light (12-volt) mounted in New Jersey trap as above (BL).
4. TT --- Tent Trap; a Malaise-type (Health-ee-X[®]) interception trap placed over habitat area sampled; kept up about 1 day each.
5. ASP --- Aspiration of biting flies as they landed on collectors' arm. Collection was not standardized except at Cranberry Glades (WV) where flies were aspirated off a single arm for 15 minutes.
6. SW --- Sweep Net (fine mesh) sample, consisting of a one-minute sweep (ca. 50 swings) in immediate vicinity of larval habitat.
7. ET --- Emergence Trap, consisting of a large galvanized metal cone, having 1 m² coverage, with a glass recovery jar at the apex, and placed over suitable wetland substrate.

1.2.3 Sample Processing Strategy

Because of the major emphasis on dealing with living specimens in this study, I will provide herein the necessary details and rationale as to my strategy for isolating live larvae and pupae from the samples, rearing and associating developmental stages, and the essentials of specimen preparation and identification. These methods constitute an adaptation and considerable expansion of the rearing and processing methods of Battle (1972), Battle and Turner (1970-72), Hair and Turner (1966), Turner and Knausenberger (1974), and Williams and Turner (1976).

1.2.3.1 Extraction and Recovery of Live Larvae and Pupae

To isolate live, healthy Ceratopogonidae larvae and pupae from the unpreserved substrate samples, I required a versatile extraction and recovery strategy suitable for a wide variety of substrate types, many of which included considerable amounts of vegetative material and organic detritus, in addition to sediments of many textures. As expressed by Dzhafarov (1964), the extraction of larvae and pupae from sample residues for rearing requires time, patience and accuracy which can only be achieved in the laboratory.

The tedious and time-consuming task of removing organisms from the substrate is an enduring problem in aquatic ecological studies. A large body of literature dealing with the many specialized attributes of the sampling and extracting problem has been generated (e.g., see compilations in Hulings and Gray 1971, Merritt and Cummins 1984, Rosenberg 1978, Southwood 1978 and Weber 1973).

Nearly all the extraction work with the Ceratopogonidae has been done on *Culicoides* and *Leptoconops*, but the methodologies are quite applicable to the other aquatic ceratopogonids as well. These methods fall into two main categories, as do all extraction methods: mechanical and behavioral/dynamic (Southwood 1978).

Mechanical methods are not dependent upon the condition of the substrate nor the activity of the organisms. These include:

1. Direct hand-picking of the original substrate (e.g., Carter et al. 1920, Part I; Saunders 1924; Nielsen 1951; Kitching 1971).
2. Wet sieving and refloating (Williams 1955, Dzhafarov 1964).

3. Stirring and decanting (Jamnback and Wall 1958, Dzhafarov 1964, Atchley 1970), usually directly in the field.
4. Sieve-flotation -- wet sieving, followed by suspension in a solution of high specific gravity -- either of calcium chloride, magnesium sulfate, or sodium chloride (Kettle and Lawson 1952 [Ladell apparatus], Gutsevich and Glukhova 1970, Kline et al. 1975, and Glukhova 1979). Kline et al. (1975) found sieve-flotation to be the least time-consuming of the four larval extraction methods compared. The others were direct flotation, sand flotation and Tullgren funnels.
5. Direct salt flotation and decantation, using the same solutions as above (Davies and Linley 1966, Linley and Adams 1972, Mullens and Rodriguez 1984).

Behavioral-dynamic methods take advantage of the tendency of larvae to respond to a physical or chemical stimulus, such as changes in oxygen tension, heat, light or moisture. Procedures developed for retrieval of meiofauna (such as nematodes and microturbellaria) from sediments are particularly dependent on this sort of approach and thus provide a rich fund of experience (e.g., Hulings and Gray 1971, Schwank 1981a) which could be drawn upon for macroinvertebrates. The main overall advantage of this behavioral extraction approach is that once the apparatus is set up, series of samples can be run simultaneously and be left unattended. A basic disadvantage is that all methods are inevitably at least somewhat selective.

Behavioral methods used in ceratopogonid (i.e., *Culicoides*) extraction work are:

1. Wet-sieving, refloating, and larval self-concentration through phototaxis (Dzhafarov 1964 after Hill 1947).
2. Adult emergence from substrate in rearing vessels (Kremer 1966, Haig et al. 1966, Battle and Turner 1969-1972, Rieb and Kremer 1981).
3. Sand-layer flotation (Bidlingmeyer 1957; Williams 1960a,b; Kline et al. 1975; Boreham 1981).
4. Agar extraction (Kline et al. 1981, Greiner and Kline 1985) using 2% agar over the sample.
5. Inverted funnel-hypersaline process (Boreham 1981, Vaughan 1985).
6. Heat extraction via Tullgren funnel (Jamnback 1965, Kline et al. 1975, and Teskey 1962 for tabanids), in which washed or unwashed samples are used, the former being much faster.

A significant behavioral method, apparently little used for larval ceratopogonids, but widely applied to nematode retrieval, is a wet extraction procedure of the Baermann funnel or Whitehead tray type (Southwood 1978), which relies on organisms moving from moist substrate through cloth or a filter down into water to be collected. Dzhafarov (1964) found an application of this principle to be effective in extracting nearly all *Culicoides* larvae from samples within 20 minutes (after prior removal of pupae).

I experimented with a variation of the "Whitehead tray" approach, in which I placed samples on 10 to 18 mesh/in. U. S. Standard sieves supported on spacers in photographic trays. After flooding the trays with water to the level of the underside of the samples, I allowed them

to sit for 12-24 hours. While the results were promising, the numbers of larvae retrieved seemed erratic and raised doubts as to the efficiency of extraction among the different genera. For lack of time, I did not validate this procedure and, thus, did not use it further.

Likewise, although I occasionally used the sand-layer flotation method (albeit with sucrose) advocated by Williams (1960a,b), for freshwater bog and other substrates, and recommended for evaluation by Southwood (1978), I did not have confidence in the reliability of the results for the spectrum of general and substrate types I had to deal with. Comparable reservations have been expressed by Boreham (1981). Kline et al. (1975) demonstrated markedly differential results among three *Culicoides* species in the same salt marsh habitat. *C. furens* was extracted effectively, but *C. hollensis* and *C. melleus* very poorly. The biological basis for this is enigmatic at this time. Kline et al. (1981) cogently described the sand-flotation method as "messy" and likely to yield damaged specimens unfit for rearing. The only substrate to which I applied the sand-flotation method consistently, and then only as back-up, was with sphagnum-rich substrates. Non-*Culicoides* were not effectively extracted, however.

For flotation solutions, ceratopogonid researchers seem to have all used one of the inorganic salts CaCl, MgSO₄ or NaCl (mol. wts. 75, 120, 58, resp.). In my experience, however, for extracting living animals, there are significant advantages to using sucrose (m.w. 342) as a flotation solution. This technique was modified for aquatic macroinvertebrates by Anderson (1959), and widely adopted by benthologists (e.g., Pask and Costa 1972, Weber 1973).

As pointed out by Anderson (1959) and Southwood (1978), organisms shrink by fluid loss in any hypertonic solution and, therefore, increase in specific gravity. This leads to shorter flotation times and, in living animals, earlier dehydration and death, with inorganic salts as opposed to sucrose. I found early on that larvae extracted with salt solutions fared more poorly in individual rearing, as compared to those isolated by sucrose. The toxic effects of saturated NaCl and $MgSO_4$ solutions were evaluated on *Culicoides variipennis* by Mullens and Rodriguez (1984). They found that the average time to death for first instar larvae was only 0.6 min. and for third and fourth instars, 31 and 41 min. resp. While the time to death in $MgSO_4$ is significantly longer (averaging 89 and 193 minutes for instars 3 and 4 resp.), $MgSO_4$ nevertheless could have significantly detrimental effects on the viability of larvae if kept in solution too long.

Recently, a promising new class of synthetic heavy organic solutes, such as Ficoll[®] and Percoll[®] have been applied to biological extraction procedures (e.g., Viglierchio and Yamashita, 1983, J. Nematol. 15(3): 444-449). These compounds can be dissolved in water to increase density but are osmotically much less active than other solutions used. These authors state that nematodes immersed in solutions of these substances exosmose very little, and more of the animals remain spontaneously active. These new substances would seem to have considerable potential in aquatic ecology.

Extraction Procedures Used. A flowchart of the principal sampling, extraction and processing procedures employed in this study is pre-

sented in Figure 2A.

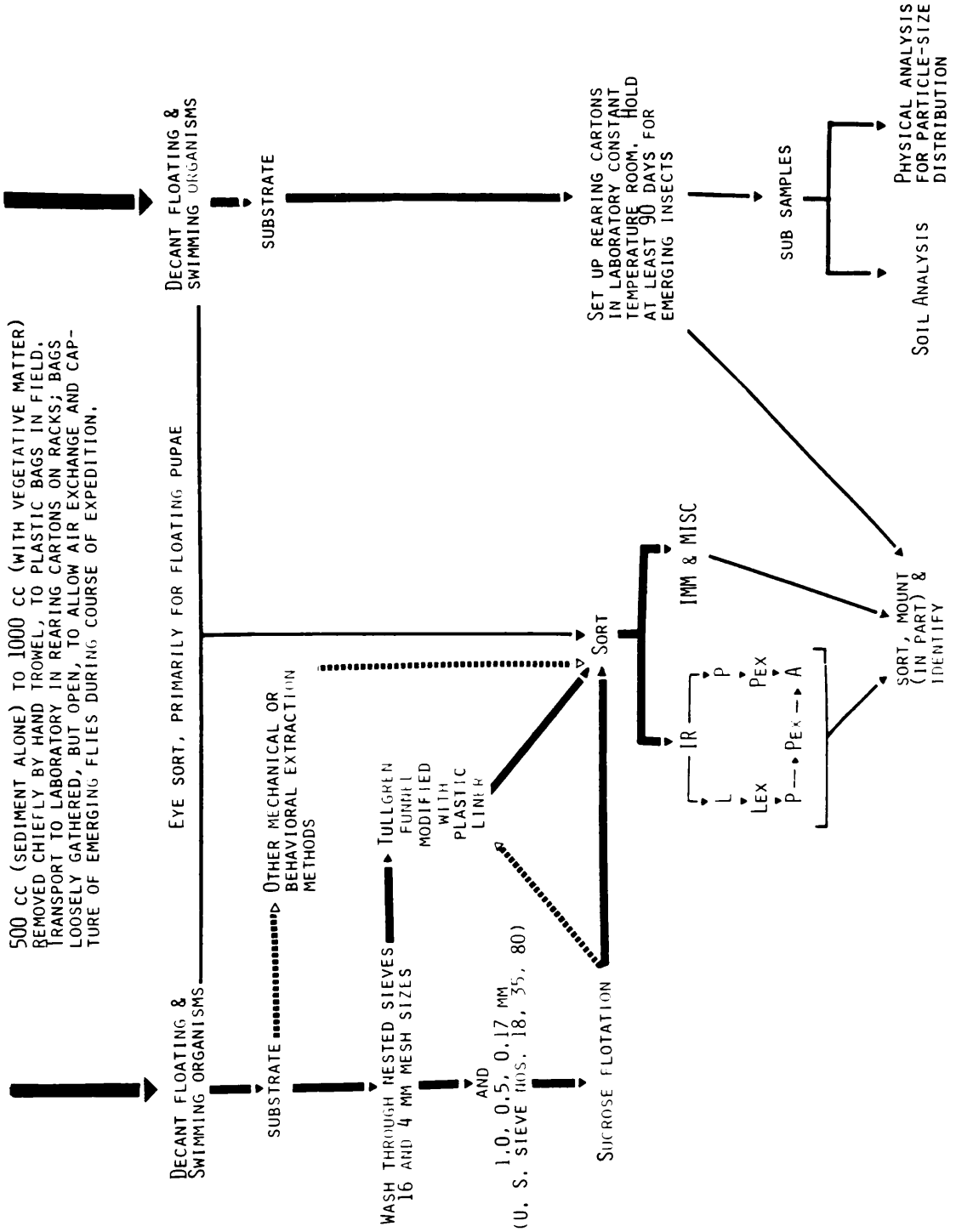
The extraction steps were as follows:

1. Decanting. Swirl sample gently, decant supernatant water (added previously, upon return to laboratory, if necessary) through an 80-mesh/in. sieve, to retrieve free-swimming/floating larvae and pupae. This spares them from the possible risk of injury during sieving. Place organisms in tap water in finger bowl (Stender dish) to await addition of specimens from flotation.
2. Sieve-washing. The substrate is carefully washed with a spray nozzle through a nested series of (U. S. Standard) sieves. The residue retained on the larger mesh sieves (2, 10, and/or 18 meshes/in.--16, 4 and 1 mm mesh size) is saved for possible placement in the modified Tullgren funnels (see below). The residue on the 30- and 80- mesh sieves is gently backwashed into a tray for flotation. The number of coarser sieves was adjusted as necessary to reduce the total bulk on the finest mesh sieves, and to rinse all surfaces adequately with a minimum of agitation.

The 80-mesh sieve with mesh openings of ca. 0.172 mm was chosen as a compromise between a need to avoid disproportionate loss of smaller larvae due to sieve mesh size selectivity (e.g. Mason et al. 1975), and the need to relatively minimize the time required to free sample of the salt and clay fraction through a finer mesh screen. The 80-mesh screen would retain the majority of 3rd and 4th instar larvae, the head capsules

Figure 2A. Flowchart of principal sample collection, extraction and processing methods used in this study to obtain Ceratopogonidae and associated fauna. Abbreviations: A = adult; IMM = immature stages preserved; IR = individual rearing, see Fig. 3A; L, Lex = Larva, larval exuvium; MISC = miscellaneous non-ceratopogonid fauna preserved; P, Pex = pupa, pupal exuvium; RC = rearing collectively in rearing carton (see Fig. 3).

DUPLICATE SAMPLES IN SAME MICROHABITAT



of which range from ca. 0.150 to 0.500 mm, and these instars are precisely the ones of greatest use in rearing.

3. Sucrose flotation. This procedure, as adapted from Anderson (1959), utilized a sucrose solution between 1.12 and 1.13 in specific gravity (the exact density is not critical), prepared by adding 350 g/l of granulated commercial sugar to water. Between 2 and 3 liters of the solution, enough to thoroughly suspend the washed residue, was added to 12 x 18" dissection or photographic trays. Flotation was most successful if the amount of residue did not exceed 250-300 ml. Sorting was done for at least 15 minutes per sample under an illuminator magnifier.

The sample was stirred several times, and organisms removed, with a fine mesh wire scoop, fine forceps or wide-orifice dropper, into plain tap water in a 250 ml Stender dish (biological specimen bowl). A deliberate attempt was made to retain representatives of all faunal groups retrieved, in addition to the Ceratopogonidae. The dishes were held at room temperature and shielded from light until the specimens could be sorted and processed for individual rearing or preservation. I found it useful to add an ice cube to the water in the specimen dishes, with the idea that by slowing down the energetically swimming larvae, they would deplete fewer energy reserves. Also, addition of strips of paper toweling or a loose ball of cotton to the water helped reduce active swimming.

After the first 15-min. extraction, the sugar solution was poured off through an 80-mesh sieve into a bucket for recycling, and water was added back into the tray containing the sample residue. While the first sample soaked in water, another sample could be floated out. The first sample was then refloated if the remaining activity justified it. Alternatively, the washed residue could be added to the modified Tullgren funnels, as a secondary extraction process.

Before reusing the sucrose solution, I poured it into a large separatory funnel to allow the particulate matter to settle out (several hours). This occasionally also yielded negligible numbers of small larvae and other organisms which had passed through the sieve. When the residue was drawn off, I added enough sugar to bring the solution up to the required density, using a hydrometer. The sucrose solution was stored in the refrigerator in sealed vessels, and in this way could be re-used indefinitely.

4. Tullgren funnel extraction. I used this method mainly as a back-up for vegetation and/or coarse detritus-rich samples; normally I used the material retained on coarse sieves after sieve-washing. On occasion, I would add the water-rinsed residue of a sucrose-floated sample if it was unusually intractable (e.g., high proportion of detritus which would not sink) or rich in specimens when time for sorting was limited.

The Tullgren funnels available were of the standard agricultural type, which I modified to reduce both the temperature of the

surface the larvae would contact, and the distance they would have to travel to reach the collection vessel (containing water). Thus, I added 4-mil plastic liners or plastic laboratory funnels inside the metal funnels, and placed the samples lower in the funnel than usual by forming the retention screens somewhat in the shape of a funnel itself. Up to 12 funnels were in use at a time. The heat source, a 60-watt light bulb, was kept on for 24 to 60 hours, depending on the bulk of the sample.

Contrary to Kline et al.'s (1975) findings, the results with this modified approach was sufficiently consistent to justify use of Tullgren funnels throughout the study, though numbers retrieved per sample were low (averaging 3-4 larvae). Indeed, at times, the only specimens retrieved from a sample were obtained by this method.

5. Other Behavioral Extraction Methods. As described above, I experimented with two other approaches to larval self-extraction, a modified Baermann-type flooded sample method, and the sand-flotation method. Neither were used routinely, for reasons given.

1.2.3.2 Rearing and Associating Developmental Stages

Techniques of associating, or correlating, adult and immature stages of aquatic insect species fall into two categories, direct and indirect. These methods can be adapted to both field and laboratory situations. However, because they are time-consuming and require experimentation and innovation to develop appropriately for given taxa, they are not routinely employed (Merritt et al. 1978, Provonsha and McCafferty 1975):

1. Direct methods, which provide the most unequivocal associations, include: (a) obtaining eggs from gravid females, then rearing out the newly hatched larvae (e.g., Linley 1965b); (b) individually-rearing single specimens of field-collected larvae or pupae in separate containers; (c) group rearings of presumed single-species assemblages, especially if they are readily distinguished macroscopically (to be done with caution); (d) determination of unemerged but pharate adults in mature pupae (e.g., mostly males of many Nematocera) or of larval skins attached to pupae (e.g., Trichoptera [Milne 1934] or *Forcipomyia* [Ceratopogonidae]).
2. Indirect methods include: (a) Methods of trapping adults over, or in the immediate vicinity, of the larval habitat. Non-selective methods, such as sweeping, tent traps, or emergence traps introduce the least amount of "interference" from irrelevant taxa. (b) Rearing unsorted specimens collectively en masse, from natural substrate, maintaining many individuals of one or more taxa until they emerge, such as in aquaria or

artificial streams. The immature stages may be retrieved before, during or after the rearing episode. (c) Collecting pupal exuviae by net, or from accumulations created in streams by drift, or in ponds and lakes by the wind. (d) In special habitats, it may be possible to obtain larvae known by various means to be the only larvae of a given genus or family present (e.g., certain *Culicoides* or Ephydriidae).

As outlined in Figures 2A and 3A, in this study I adapted and developed two main approaches to reliably associating ceratopogonid adult stages of the same species, thereby to be able to accurately assign names to the latter stages (Knausenberger and Turner 1978). Both approaches are based on rearing, and are indirect and direct methods respectively:

1. rearing collectively (mass rearing) in cartons containing natural habitat substrate (acronym: RC).
2. individually rearing larvae and pupae in small petri dishes or vials, respectively (acronym: IR). Both methods were developed to be suitable for a large number of samples and specimens from a wide variety of habitats.

Rearing Collectively (RC). In this approach, I achieved numerous useful indirect associations by placing one of two subsamples of substrate from a given macrohabitat directly into simple rearing cartons (Fig. 3) to capture emerging adults. The other subsample was subjected to extraction procedures to obtain immature stages (mostly larvae and pupae). Some

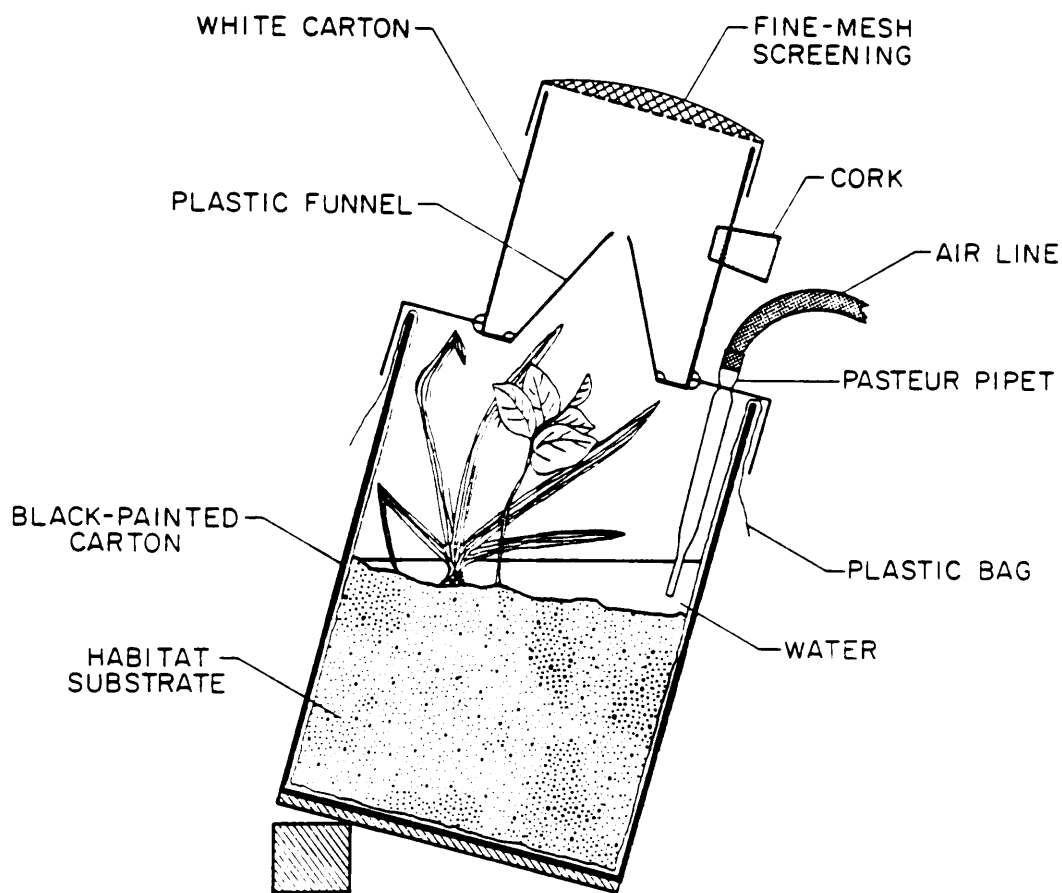


Figure 3. Rearing Carton(RC) design and use for trapping emerging adults from habitat substrate material brought into the laboratory.

of these immature specimens were preserved, others individually reared. Because the two subsamples were taken close together, I assumed them to have very similar, but not identical, faunal composition. Therefore, this procedure provided a means of obtaining relatively large amounts of reasonably closely associated developmental stages. The material was associated by virtue of a common collection number plus an appended acronym: e.g., 248-RC and 246-IMM represent, respectively, material reared collectively, and immature stages extracted, from the substrate of site 248 (see Appendix F.1.1 for further details on the major letter codes).

The rearing cartons are designed to allow "self-sorting" of the emerged adults from the sample but causing them to fly up towards the light through transparent funnels into an upper section where the specimens are retrieved. This assured well-preserved specimens.

To construct the rearing containers, I used heavy-duty paper "ice cream cartons", available inexpensively and in bulk (Neptune Containers, Neptune Paper Products, Inc., Jamaica, Long Island, NY 11418). The lower part of the unit, which receives the sample in a plastic bag, consisted of 1/2- or 1-gallon-size cartons painted black on the outside, to block out light. The top section was fashioned from unpainted (white) pint-size cartons. The top and bottom of the upper carton was replaced with fine mesh translucent plastic screening (32 meshes per inch), or organdy fabric. On the lower screen, I fitted a small clear plastic funnel (60 mm diameter at base) attached by glue to the screening, which was removed inside the funnel. This upper carton was then inserted into the lid of the lower carton and secured with

continuous beads of white glue or caulking compound. Specimens were readily removed with an angled aspirator tube through the hole sealed by a stopper.

To provide aeration for certain samples, I inserted Pasteur pipets attached to air hoses, and through gang valves, to one or more aquarium pumps. This was particularly useful to retard fouling in samples otherwise likely to foul quickly, such as of blanket algae, and to some extent was helpful for samples from rapid streams.

The entire unit was placed at a slant to provide for a "beach", or air-water-substrate intersectional line, critical to successful ceratopogonid emergence. The entire habitat sample with plant material was placed into the rearing cartons in the field to allow for emergence of any specimens which might otherwise be lost in transit. In the laboratory, these cartons were held in a controlled environment room at $70 \pm 5\%$ R.H. and 75 ± 5 °F. At any given time, 100 to over 200 of these rearing cartons would be in use. They were held at least 90 days from date of collection, and emerged specimens (chiefly Ceratopogonidae and Chironomidae) were aspirated daily into vials of 80% ethanol), although this interval could be extended to two or three days without much adverse impact, especially by the addition of a sugar meal (10% sucrose) on dental wicks placed on the top screen. All organisms which emerged were retained for identification.

Individual Rearing (IR) Processing and Association Procedures. An outline of the IR strategy as developed in this study is given in Figure 3A. Promptly after the immatures were isolated from the sub-

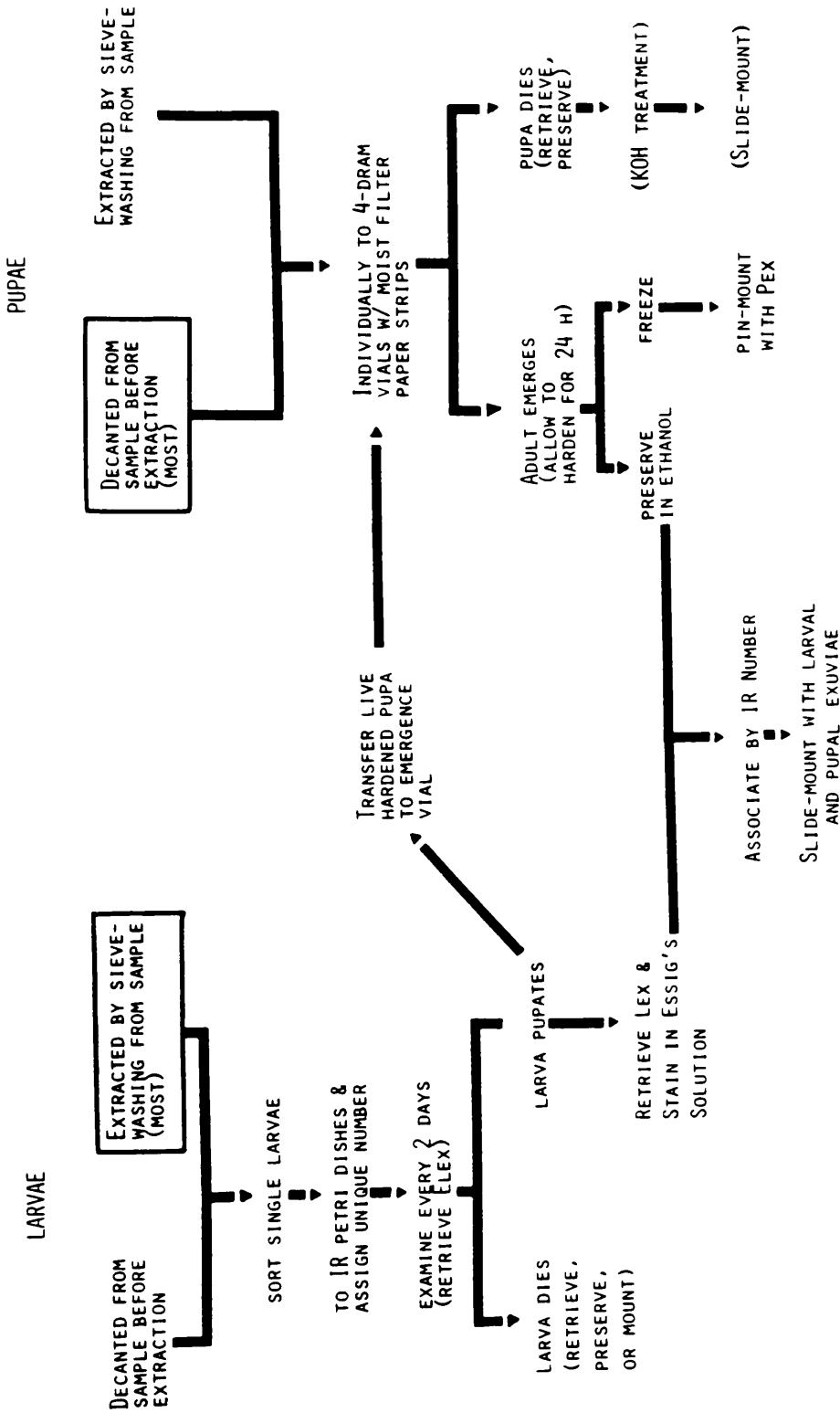


Figure 3A. Diagram of Individual Rearing (IR) and association procedures used in the laboratory for Ceratopogonidae larvae and pupae. Abbreviations: Elex = early larval exuvium from larval molts; Lex = larval exuvium cast after pupation; Pex = pupal exuvium. Compare Figure 2A.

strate into Stender dishes by the methods described, I transferred them singly to individual containers (see below). I sorted larvae by features such as swimming behavior; shape; size and color of head capsule; color and pattern of thoracic pigmentation. I selected only active and apparently healthy specimens for rearing, and preserved morbid specimens (NB: because of the behavioral differences among free-swimming ceratopogonid larvae, it is important to make the judgment as to "morbidity" with care. Members of some groups, such as *Culicoides brevitarsis* (Kettle et al. 1985), and many Stilobezziini (pers. obs.), are sluggish or unwilling swimmers. While I aimed to rear at least the largest representatives of all larval "types" present in a given sample, I also tried to preserve at least representatives of each in ethanol. Even the most rapidly swimming larvae would stop at least momentarily, permitting examination in the sorting dish, especially if narrow strips of paper toweling were placed in the water. I found that soft spring steel forceps and large-orifice droppers worked well in gently transferring specimens without injury (Fig. 7).

On a given long day after a collecting expedition, I could process 10 or more samples with an assistant, from original substrate samples to individually processed individual specimens. Typically, each sample would yield between 5 and 20 specimens for IR, but runs of 50 to 100 or more were not uncommon. To deal with this "flush" of material, I set up the IR process in production-line fashion, with arrays of rearing dishes and trays, vials and racks prepared and numbered in advance.

Several hundred dishes would be set up at a time during peak periods. On the average, however, I maintained 100-150 larvae in continuous

rotating production throughout about 30 months. Each dish needed to be examined at least every second day on alternating schedules, by tray.

Because the dishes are readily scanned, it usually was not difficult to locate pupae with the naked eye, but the larval exuvium had to be retrieved under a stereoscope at about 12-25x. In many cases, the exuvium is not directly beneath the pupa, contrary to the statement of Kettle et al. (1975). Thus, it is inadvisable to rely on proximity of larval exuvium and pupa to achieve direct associations in cases where several larvae are grouped in a single vessel. Likewise, I found it highly desirable to transfer the pupa, in a small amount surrounding agar, to a separate emergence vial as described, and to retrieve the exuvium immediately. This is because emerging adults often would not be in optimum condition in the petri dish due to inadequate flight room, and because the larval exuvium would deteriorate noticeably if it were not retrieved before adult emergence took place.

Each dish was in use an average of about 4 weeks, until the larvae either died or pupated. In exceptional cases, larvae lived up to a year (0.1% of cases). Food was replenished when needed, normally every 1 to 2 weeks. The larvae were transferred to fresh medium at intervals of about 3-4 weeks, when the old agar begins to liquefy and/or become clouded. Fouling by microorganisms -- bacteria and fungi, principally, -- was rare. Antibiotics were unnecessary, in contrast to the situation with larger tabanid larvae on agar media (Roberts 1966).

The only significant contaminant was an astigmatid mite, *Tyrophagus putrescentiae* (Schrank), which became established in most IR dishes kept at least several weeks. According to the determiner (Ian M. Smith

of the Biosystematics Research Inst., Agriculture, Canada), this mite is a common pest of laboratory cultures throughout the world. The mites, which probably originated from my nematode stock culture, did not seem to have any detrimental effects on the ceratopogonids. Indeed, the mites are saprophagous and themselves were consumed by at least some *Alluaudomyia* and *Culicoides*. Kettle et al. (1975) also observed larvae of *Culicoides* feeding on unidentified mites which had invaded their culture.

Each individually-reared specimen, whether larva or pupa, received a unique identification number (e.g., 385-4 IR or 288B-86 IR), based on the collection number and IR-sequence number. Wax pencils worked well in marking the bottoms of petri dishes, in that the marks held up even after months of handling the dishes. The vials were labelled with paper strips placed inside.

To monitor and record the development and status of each specimen, I used an ad hoc "IR-Record" form (Fig. 20). Here, I included concise information as to dates and stages of initiation, pupation and/or eclosion; size and appearance; behavioral observations; whether photographs were taken, etc. This form also facilitated the tracking of the various stages, which could become separated during rearing and processing. Additional notes and sketches could be put on the back of the form.

To record the color nuances of the living specimens adequately, I photographed many of the IR larvae while they were immobilized on ice, by the techniques described in Section 1.2.3.3.

IR Containers and Rearing Conditions. For the great majority of the ca. 1100 direct associations of ceratopogonid developmental stages achieved in this study, I used small, easily-scanned polystyrene petri dishes for the larvae, and 4-dram cotton-plugged vials for the pupae (Figs. 4 and 6). The petri dishes were either 35 x 10 or 60 x 15 mm in width and depth, and had loose or tight-fitting lids. I prefer the loose lids, for ease of removal and speed of handling. This was a significant factor because, at any given time, several hundred IR dishes could be in use. Instances of escaped larvae or other losses attributable to the loose lids were very rare. Figure 5 shows the production set-up for the IR dishes and holding trays. By placing the dishes in glass-covered trays, I could conveniently segregate them by date and collection number, and then stack the trays on shelves. In this way, I could accommodate several hundred larvae in a compact arrangement at any given moment. I kept the trays in subdued light by partially covering them, either by stacking, or with masonite boards. All rearing took place at room temperature .

To accommodate adult emergence in vials, I used two methods. In the first, I placed just enough water to float the pupae, then added a strip of filter paper or paper toweling which projected well out of the water. The pupae would either climb up the filter paper, up the glass wall, or remain floating in the water, depending on the requirements or preferences of the taxa involved. In the second method, and the one I found to be most satisfactory, I placed the pupae on moist filter paper or toweling circles, inserted at a slant over wet cotton or sponge (which prevented the paper from drying out). I cut (punched)

Figure 4. Top: Individual 60-mm diameter rearing dish (WIK#356-3 IR) with agar medium as substrate, and small amount of detritus and water from collection site. Note slant of agar, and added water, creating air-water-substrate interface. Bottom: Looped ceratopogonid larva (*Bezzia laciniastyla* Dow and Turner) readily visible beneath center of dish.

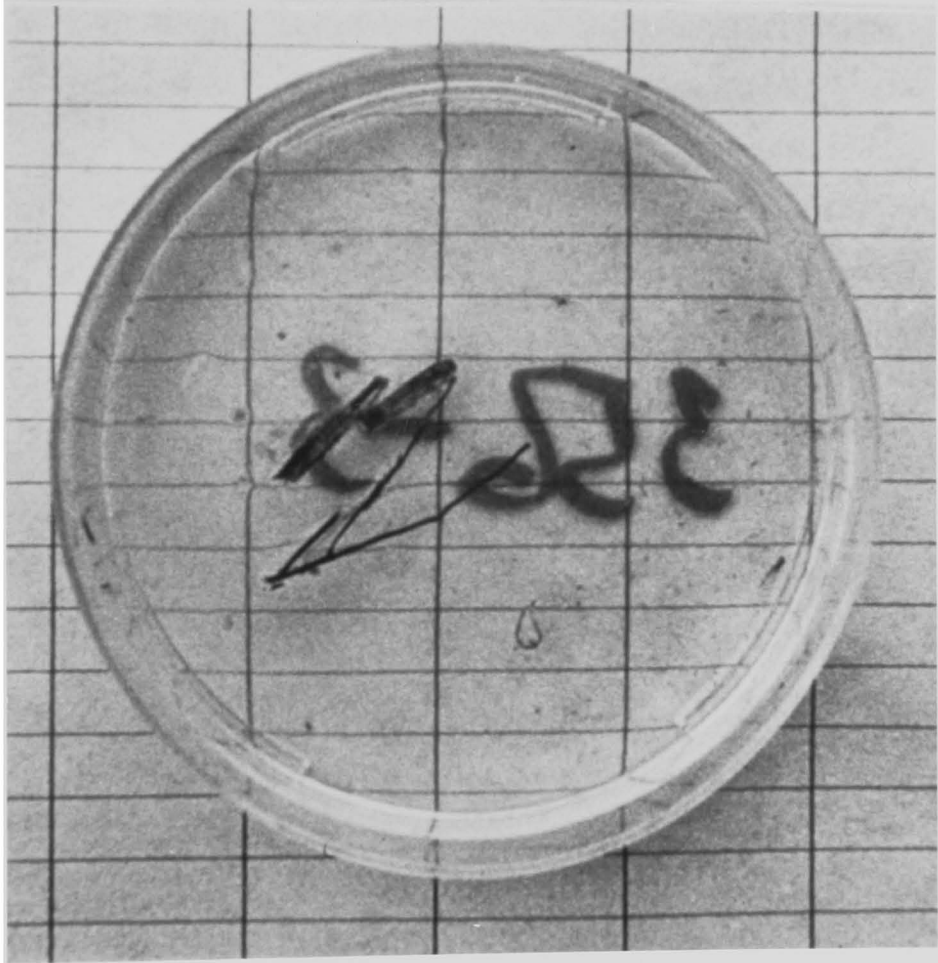
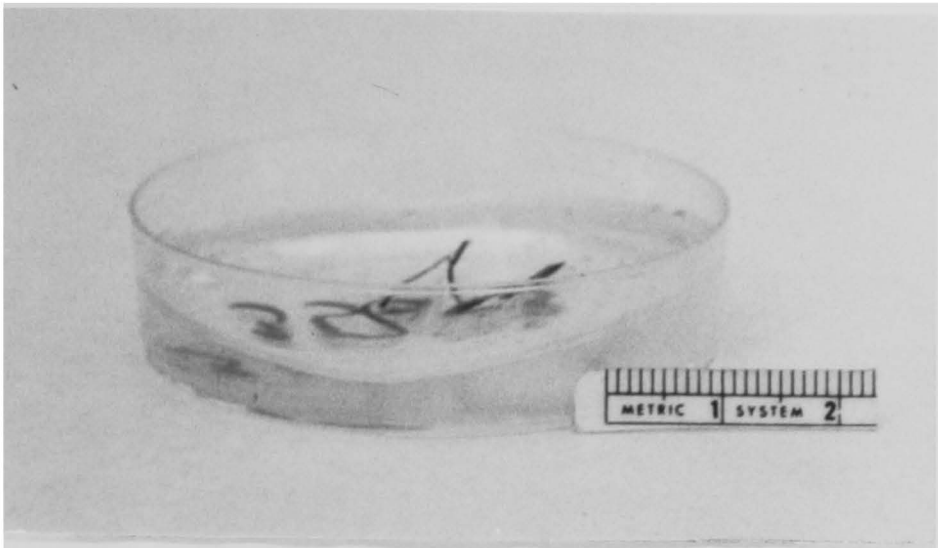


Figure 5. Arrangement of individual rearing dishes and covered holding trays in laboratory, allowing several larvae to be segregated by date and collection number, and compactly accommodated on shelves.



the paper circles out with cork borers, and placed the paper in the vials such that they formed a seal with the glass wall (Fig. 6). This prevented the pupae or emerging pharate adults from becoming entangled in the cotton. Entanglement was not much of a problem with sponge substrate.

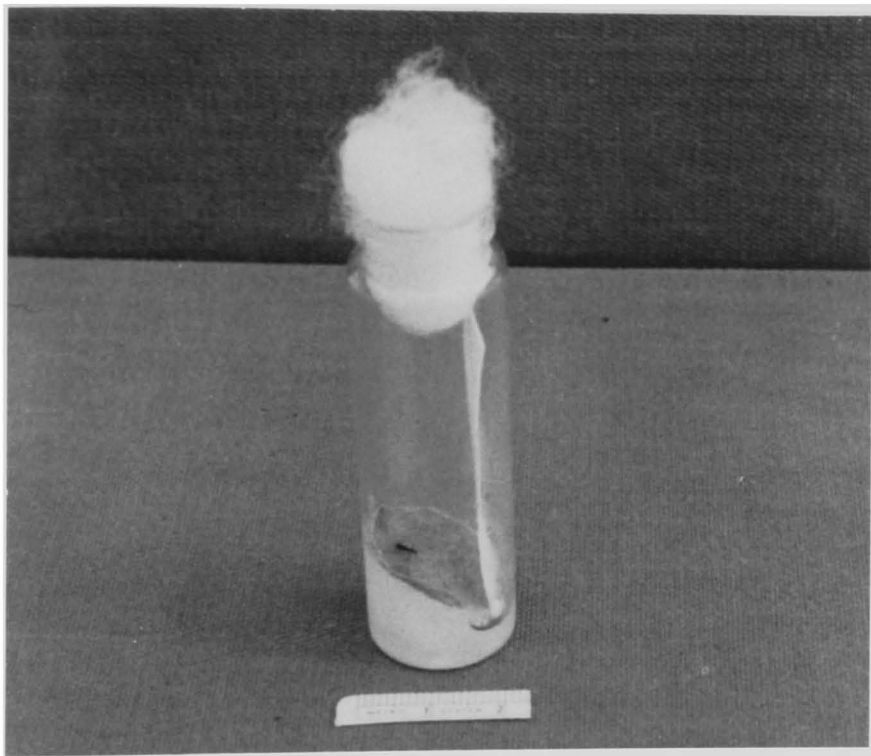
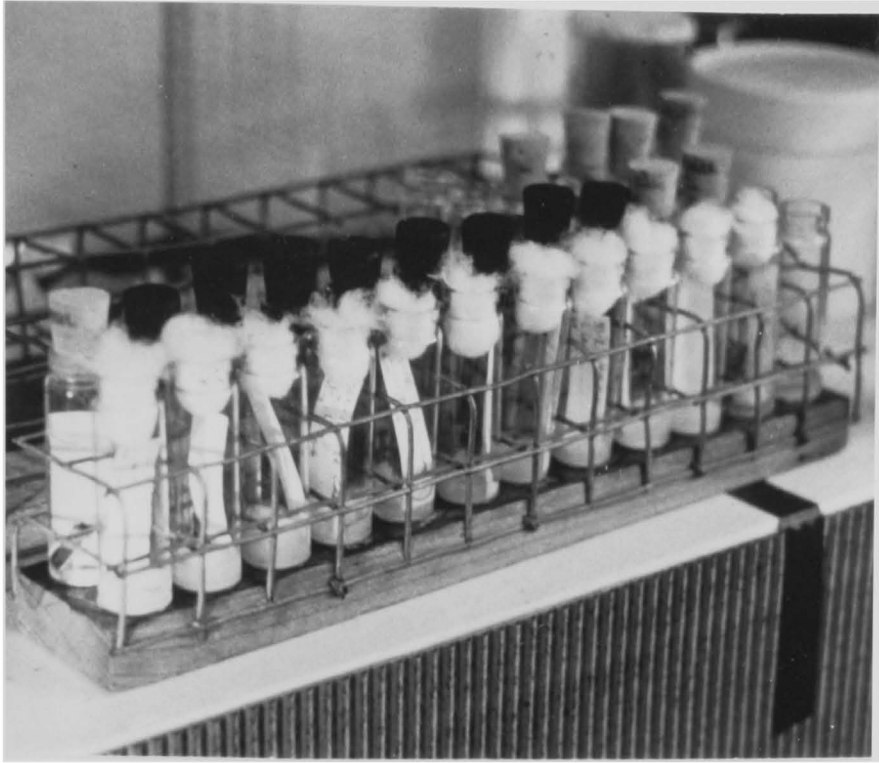
Moistened cotton alone, or water alone, are not conducive to problem-free adult emergence in the vials. Greatest success in obtaining adults in good condition occurs if:

1. The amount of free-standing water is minimized. The flies are then less likely to become entrapped in the water during the first few hours after emergence. The pupae are disrupted less during inevitable jostling of vials when they are handled. Also, there is less likelihood of fouling.
2. A moist paper strip is available, which mimics littoral conditions, and provides adequate footing during eclosion, and while hardening, darkening and wing expansion take place. Also, condensation on the inner walls of the vials, where the flies can get trapped as well, appears to be greatly reduced with the paper strips present.
3. The vials are monitored daily.

I held the isolated pupae for emergence, with their respective retrieved larval exuviae, in simple ad hoc vial racks which allowed viewing without removal of the vials (Fig. 6). To reduce the light to a level comparable to conditions in the microhabitats of many Ceratopogonidae, I covered the vial rack with a flap open at the ends.

In exceptional cases, such as when large numbers of larvae were

Figure 6. Top: Pupation vial holding rack, allowing both the monitoring of pupae and adult emergence without removal of the vials, and the juxtaposition, as appropriate, of vials containing retrieved larval exuviae with their respective pupae being held for emergence. Bottom: Method of isolating individual pupae for adult emergence on moist paper toweling in cotton-stoppered vials, with paper strips (labels) allowing the adult flies to climb and hang for wing expansion.

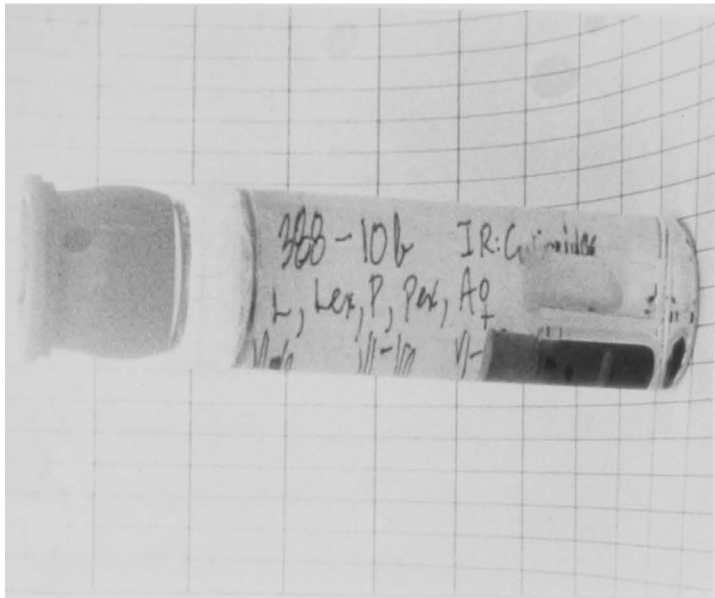


retrieved, and if they were readily grouped, then I would use larger vessels for group rearing, such as larger petri dishes, 1/2-pint jars or 15-, 20- or 50-dram vials. I also regularly attempted to rear selected series of specimens of other families, especially Chironomidae, Tipulidae and Tabanidae. Some of the alternative vessels are shown in Figure 7.

Larval Medium. Using the small culture dishes described, I initially evaluated several possible larval media and substrates. My objective was to develop an acceptable system for growth and development of individual larvae, which at the same time allowed easy monitoring of the larvae, and ready retrieval of the diaphanous cast larval exuviae. I began this work in May 1975, several months before the technique of Kettle, Wild and Elson (1975) for rearing individual *Culicoides* larvae was published. Briefly, the substrates I evaluated are:

1. small amount of cotton, polyester fiberfill, or glass wool (Jones et al. 1969, Boorman 1974) and water;
2. beach sand (e.g., Linley 1968a, 1968b), sieved in the size range of 0.125 - 1.0 mm, in 2-3 mm layers saturated with water;
3. strips of moistened filter paper or paper toweling, as used for immature Tabanidae (Philip 1928, Teskey 1969);
4. non-nutrient agar, as used successfully for smaller tabanid larvae (under 15-20 mm length) by Roberts (1966);
5. autoclaved and pulverized silt-loam (e.g., Williams and Turner

Figure 7. Left: Alternate rearing vessels with agar medium, for groups of larval ceratopogonids or larger Diptera; typical sorting and processing tools for individual rearing. Right: Method of preserving associated developmental stages, with stained larval exuvium maintained in separate microvial.



(1976), reconstituted with tap water, in a 1 to 2 mm thick layer;

6. small clumps of habitat source material from which the ceratopogonid fauna had been eliminated (Carter, Ingram and Macfie 1920, Kettle and Lawson 1952); and
7. small glass beads, 1-2 mm in diameter, in layers 3-5 mm deep, nearly covered with water. Roberts (1966) transferred larger (>20mm) tabanid larvae to substrates of 4-6 mm beads. I found ceratopogonid larvae and exuviae to be very difficult to locate without pouring the entire contents of the IR culture dish into another vessel of water.

With all the above media, I supplied the nematode and hay infusion cultures as food sources, described below.

The agar medium provided to be by far superior to all the others I tried. It allowed at least the maintenance of healthy larvae and perhaps most significantly, it was normally easy to locate larvae and exuviae (Fig. 4). Thus, I developed an agar-based rearing technique which I used for nearly all of my subsequent individual-rearing work. The technique I adapted from Roberts (1966) is very similar to the one developed independently by Kettle et al. (1975).

However, whereas Kettle and associates recommended an agar concentration of 1%, and Roberts used 0.8-1.0% plain agar, I had the greatest success with agar in the 0.5-0.8% range. This allowed me to accommodate the wide variety of species and sizes of larvae which I encountered. The softer agar allowed readier penetration and seemed definitely to favor acceptance of the medium, and growth and development, by the

larvae. The softer the agar, though, the sooner it ineeded to be replaced with fresh medium (2-3 weeks for 0.5%, 4-5 weeks for 0.8%).

Another helpful modification proved to be agar solidified in the petri dishes at a slant, producing an incline with agar from 0 to 6± 1 mm deep (Fig. 4). To this, I added water from the hay infusion culture, thus, simulating the littoral mud environment to some extent, and allowing larvae to seek their preferred moisture level.

Finally, in a significant difference from Kettle's technique, referred to above in the IR Processing section, I carefully removed the pupae from the IR dish, in a plug of agar, to a separate emergence vial. I did this to provide adequate footing and flight room for the newly emerged adults, thereby substantially improving the likelihood of obtaining properly hardened specimens.

These methods have proved satisfactory to maintain, and permit development of, mature larvae in all 15 of the ceratopogonid genera for which I was able to attempt it (Tables 6 and 38). Listed alphabetically, these are: *Alluaudomyia*, *Atrichopogon*, *Bezzia* (B.) and *B. (Homobezzia)*, *Clinohelea*, *Culicoides*, *Dasyhelea*, *Forcipomyia*, *Isohelea*, *Johannsenomyia*, *Mallochohelea*, *Palpomyia*, *Phaenobezzia*, *Probezzia*, *Sphaeromyias*, and *Stilobezzia*. This list encompasses all but one each of the Nearctic subfamilies and tribes in this family, the Leptoconopinae and Stenoxenini resp. (cf. Table 5).

Larval Food. Specific information on trophic relationships of larval Ceratopogonidae is scarce, but it is generally accepted that most members

of the subfamily Ceratopogoninae, at least, are chiefly predators, or "engulfers" (Mayer 1934d, Thomsen 1937, Weerekoon 1953, Kettle et al. 1975, Glukhova 1979b, Linley 1979, and Merritt and Cummins 1978:275). Most of the detailed observations on feeding habitats have been made with *Culicoides* larvae (Williams and Turner 1976, Linley 1979, 1981). From such observations, it is reasonable to assume that larvae in the subfamily are able to subsist on a variety of prey organisms, though some prey selectivity is likely (Linley 1981). Indeed, they are probably only facultatively predaceous in many instances, being able to function as collector-gatherers at least some of the time. This would apply particularly to the younger instars, during which most aquatic insects are thought to feed as selective omnivores (Cummins and Klug 1979; Hutchinson 1981). The larvae of the subfamilies Forcipomyiinae and Dasyheleinae tend to be herbivorous or saprophagous grazers and scrapers, or microphagous (Boesel and Snyder 1944, Ewen and Saunders 1958, Saunders 1924, 1956; Waugh and Wirth 1976, Glukhova 1981).

Because I expected to be rearing a wide diversity of larvae which I presumed to be primarily predaceous and selective, I provided a variety of food organisms. These were derived from two main sources, and provided a "cocktail" mainly of potential prey organisms:

1. "Vinegar eel" nematodes (*Panagrellus redivivus*) cultured on a slurry of oatmeal and water with a small amount of yeast added initially. I obtained my starter culture through Richard Sayer, U. S. Department of Agriculture, Agric. Res. Serv., Beltsville, Maryland. I added nematodes at about weekly intervals to the IR dishes. One drop from a Pasteur

pipette-dropper delivered about 50 nematodes from a healthily teeming stock culture. Because the stock culture becomes increasingly acidified as it ages, it is desirable to avoid adding the nematodes directly from the stock culture to the rearing dishes.

2. A xenic culture of microinvertebrates and microflora derived from a hay infusion with added Carolina[®] protozoa tablets, and irregular additions of natural habitat waters and substrate materials. The culture mainly consisted of a variety of bacteria, diatoms and other algae, protozoa and rotifiers, and occasionally microcrustacea, oligochaetes and/or platyhelminths.

As an apparently useful way to accommodate *Dasyhelea* and *Atrichopogon* larvae, and other semi-aquatic herbivorous grazers, e.g., *Stilobezzia* in part, I added a small plug of natural habitat material (e.g., strands of filamentous algae, small strips of plant detritus, etc.) to the agar medium. In this way, I attempted, with some success, to provide some of the "universal pabulum" which covers all surfaces in littoral freshwaters (Hutchinson 1981), as an inoculum. I segregated these dishes and provided them with more light than the others, to encourage autotroph production.

To larvae of other dipteran families which I attempted to rear, I also provided the above food sources, but for the large Tabanidae, Tipulidae and Dolichopodidae, I added young housefly maggots and mosquito larvae from laboratory cultures maintained at VPI & SU.

1.2.3.3. Specimen Preparation, Processing and Identification

Effective identification and morphological study of midges in all life stages requires discernment of microscopic characters, permitting precise comparisons of maximum systematic value. Fragile insects, such as midges, are difficult to preserve indefinitely in a condition offering the opportunity for successive examination of unaltered specimens. This is particularly a problem with type material. Pin-mounted adult midges readily lose parts, cannot be effectively examined for genitalic characters and do not lend themselves optimally to measurement and meristic evaluation. Thus, for example, the value of pin-mounted adult midges has been seriously called into question, as opposed to liquid-preserved and microslide-mounted specimens, as a basis for modern biosystematic study (Brundin 1956, Schlee 1966, Atchley and Jackson 1968, Atchley 1970, Saether 1977, and others). Schlee (1966) effectively rebutted criticisms levelled at alcohol preservation of midges. The virtues and methodology of permanently slide-mounting small insects have been discussed by several authors (e.g., Wilkey 1962, Schlee 1966, 1968; Wirth and Marston 1968, Saether 1977, Boesel 1978, Chaker 1982, Clastrier 1984). Important and useful general overviews on microtechnique which should be consulted include Peterson (1964) and Bradbury (1973).

Inasmuch as each method of preservation and study has its advantages and disadvantages, and because I needed flexibility in making associations and multiple comparisons over time, I chose to compromise by basing most of my collections in liquid, while permanently slide mounting extensive representative series as the work progressed, and

producing only small numbers of pin-mounted specimens as time and material permitted. Boesel (1977) and others have advocated such a parallel approach. The "multiple track" origin of material in this study, diagrammed in Figures 2A and 5A, lended itself naturally to parallel collection separated for processing and preservation in split series, some for alcohol preservation, some for slide mounting, and possible pin-mounting.

The methods used to characterize live and preserved immature and adult Ceratopogonidae specimens during this project are briefly discussed here in the context of particular experiences gained during the course of this work.

General. A Wild 5A dissecting microscope was used for the bulk of observations, while a Tiyoda compound microscope with bright and dark fields was applied to routine examination of slide-mounted specimens. A Zeiss phase-contrast microscope was used for work requiring the most discernment. All microscopes were equipped with ocular micrometers and grids. Camera lucida attachments on the Wild and Zeiss scopes were used to make drawings.

For a photographic record of macroscopic characters, mostly of larvae, I used the Wild M-5 with a trinocular beam-splitting phototube (75:25) and electronic flash in the reflector, at magnifications of 3 to 75x. Later work was simplified with a Wild MPS 55 photoautomat system. Every film and exposure was recorded individually as to the subject, IR number and conditions of photography (see Appendix F.1.1., footnote). To render pigmentation nuances adequately, I used primarily

color transparency film (Kodachrome 64 and Ektachrome 200). Of some 69 rolls and 1600 exposures, 90% were in color, the remainder on Tri-X Pan black and white film (see Frontispiece).

Notes on Color. Cuticular and subcuticular color characters can be of good diagnostic value, particularly in keys. Kettle and Lawson (1952), Jamnback (1965) and Glukhova (1977, 1979) are examples of ceratopogonid larval keys in which colors play a significant part. I made a particular effort to record colors of live or freshly killed specimens, especially if only a single individual was available. I used the MunnSELL Book of Color coding scheme to assign normative descriptive values to the colors in the live specimens, as well as from the color photographic record.

During the course of my diversified collecting and rearing work, I often found that coloration is subject to considerable individual differences within a species, especially if the likelihood of encountering teneral specimens is high. It is unavoidable that a certain significant proportion of specimens obtained during rearing will not be in prime condition. Also, colors will change or bleach in preservation, and can vary due to environmentally induced factors.

Chironomid systematists of the past few decades have de-emphasized color characters, because they previously have been accorded an exaggerated significance (Moeller 1966, Schlee 1966, 1968). Many ceratopogonid adult descriptions still place great weight upon pigmentation features. The prudent course would seem to be to record color attributes and their variability as carefully as possible on live and pre-

served specimens, so that the information may be available, but to use them sparingly in keys, in conjunction with meristic or structural characters.

Living Specimens. Because of the individual-rearing emphasis in this work, I spent considerable amounts of time observing living specimens, and making sketches and photographs of them, to facilitate further association and description, and to provide information on pigmentation and other characters which may be obscured in preservation or otherwise lost entirely if a specimen was not to be collected again. Changes occurring during the course of development have important bearing in appearance.

Nearly all specimens were alive when photographed, so to immobilize them temporarily, I placed them on ice cubes in watch glasses. Placed on backgrounds of various colors, the ice provided an interesting and effective background. The specimens, once photographed and replaced into their IR dishes, continued development seemingly unimpaired.

Liquid Preservation/Fixing. Practically without exception, all specimens were killed and preserved in 80% alcohol in 4-dram glass vials (Fig. 7). Within a few hours, or at most a few days, I would fix larvae and pupae by dipping racks of open vials into a boiling water bath for 15 sec, and then replenish the alcohol. This preserved the color well and kept the specimens in an optimum distended condition.

As pointed out, by Kettle and Lawson (1952), alcohol does not appear to cause significant color loss among most *Culicoides* larvae, even those kept preserved as long as 25 years. Likewise, I saw speci-

mens of *Bezzia nobilis*, *Palpomyia tibialis* and *Sphaeromyias longipennis* in the USNM which had been in alcohol for up to 50 years, with recognizable color features. On the other hand, specimens stored in vials with cork stoppers appear to deteriorate and turn a uniform dull yellowish, apparently due to tannins in the cork, as I have seen with specimens in the Johannsen collection at Cornell University.

To forestall or mitigate effects of uncommon yet inevitable drying out of vials, I added about 5 ml of glycerine to each. Methods applicable for the recovery of liquid-preserved adults or immatures which have dried out have been published by Peterson 1964, Schlee 1968 and Boesel 1977. I found the potassium hydroxide technique by Peterson to be the most practical and effective.

Associated developmental stages in liquid I generally preserved together, with separate microvials (individually labelled) for the larval exuvium, and the pupal exuvium with the adult (Fig. 7). The larval exuvium was optimally preserved, and stained for ease of retrieval and eventual microscopic examination, in Essig's aphid fluid containing lactic acid, phenol and acetic acid with 2% acid fuchsin stain (Wilkey 1962). The head capsule color was noted before staining.

Cast pupal exuviae often are encountered with a trapped air bubble, which cause them to float and either be easily lost or damaged when the vial is sealed and opened, or the bubble can be troublesome during slide mounting. I tried various ways to eliminate the bubble, including adding disperants to the liquid, alternative solvents, and heat. A method advocated by Boesel (1977) for removing air bubbles from dry mounts being converted into slide mounts was moderately successful but

too time-consuming. I finally resorted to two methods of dealing with the problem: (a) physically expelling the bubble by gently rolling an applicator stick or fine brush lengthwise from the tip of the abdomen towards the ecdysial split, pushing against the vessel's surface. Care should be taken not to lose the operculum, or to retrieve it if it detaches. The pupal exuvium is generally elastic enough to retain or regain its original shape; (b) trap the bubble-filled exuvium safely in a microvial by placing a small amount of glycerine into the vial, placing the exuvium inside, adding another layer of glycerine over this, filling with alcohol and quickly adding a cotton plug to the microvial while it is submerged in alcohol. Exuviae thus trapped can not rise quickly enough to cause a problem before the microvial is sealed.

Mounting and Dissecting. For the great majority of routine slide mounts of all developmental stages, I employed the phenol-balsam method of Wirth and Marston (1968), with appropriate modifications for larvae and pupae. For particularly critical specimens, especially those intended for species description, I utilized more than one coverslip (10 or 12 mm) per slide, to separately mount dissected parts of different thickness, and exuviae, after the manner of Schlee (1966). See also Clastrier (1984) for a similar technique.

Whole larvae are generally cleared adequately in phenol for examination of cephalic characters, but often the pigmentation of the thorax and abdomen is reduced or lost. I have found temporary mounts, especially on hollow slides, to be most useful for close examination,

allowing specimens' return to liquid. Glycerine¹, phenol, dilute phenol-balsam, or Hoyer's solution were useful for various applications. I normally examined only the 3rd and 4th instar larvae.

The larval exuvium is not ideally suited for permanent mounting because the body segments are more or less telescoped, and distorted, the head capsule is split, and often debris is attached to the exuvium. It is difficult to maintain the disassociated cephalic parts -- frontoclypeus, pharyngeal structures, mandibles, antennae, labium, lateral sclerites -- in predictable orientations in the slide medium. Nevertheless, the exuvium is an invaluable link in establishing the association between larvae, pupae and imago, and can indeed be mounted as all other stages. Once the exuvium is put on a slide, it cannot effectively be returned to a vial.

Pupae are best examined from shed pupal exuviae, because all characters are maintained in excellent condition. Whole pupae with pharate adults are also useful, but normally these have to be cleared in cold or hot 10% KOH. Before completely clearing however, it is very useful to examine the pharate adult for characters which may aid in identification. I have found tarsal claws and genitalic characters visible through the pupal integument to be particularly helpful. I mounted pupae face down, operculum removed and oriented convex side up, with cover glass slivers as spacers.

For particularly delicate dissections, at magnifications over about

¹ Comparable use of glycerine for temporary mounts of larval Chironomidae is described by Russell and Soptonis (1981), Entomol. News 92: 119-20.

25x, such as on larval head capsules, I used very fine dissecting needles which I made by sharpening tungsten wire electrolytically as described by Brady (1965); a very similar process is that of Galbreath and Galbreath (1977, Entomol. News 88: 143-4). These needles are very durable and strongly resist bending, a feature which tended also to minimize the chance of accidentally "catapulting" a specimen or part out of the dissection field or dish.

Determinations. Adult Ceratopogonidae in all genera I identified to species if possible, beginning with the generic keys of Wirth et al. (1974, 1977, in litt.) and continuing with dozens of species-level papers by Wirth, Grogan and colleagues. Drs. W. W. Wirth and W. L. Grogan determined many of the Forcipomyiinae and *Palpomyia*, respectively, and verified certain other species (for references, see Table 58).

Most determinations in this study were completed in 1979, but the nomenclature used herein is current through 1985 and consistent with generally accepted tribal classification. The Stilobezziini and Ceratopogonini apparently are in need of revision and the generic allocations need adjusting (e.g., Grogan and Wirth 1978, Pan-Pac. Entomol. 54: 283; Grogan 1982a; Wirth and Grogan 1981). In particular, this affects the assignment of the genus *Alluaudomyia*, now thought to belong to the tribe Stilobezziini. The matter is not yet formally settled, pending a revision of the Ceratopogonini. The change is reflected in some but not all of my species tables.

The fine keys and illustrations of Downes and Wirth (1981) to the Nearctic genera and subgenera of Ceratopogonidae provide the best cur-

rent entry into the relevant literature for identification of imagoes in the various genera. Since Downes and Wirth (1981), the most significant recent taxonomic literature for the Nearctic ceratopogonid fauna includes: Wirth 1983a,b,c; Wirth and Grogan 1979, 1981, 1982, 1983; and Wirth et al. 1984.

The foundation for examining and determining the immature stages was provided by the availability of identified reared adult midges taken from the same habitat. I did not make a concerted attempt to identify unassociated eggs, larvae or pupae to species independently of adult determinations. Most specific determinations which are reported are based on experience from individual rearing, supported by the few available descriptions whenever possible. The larval descriptions and keys of Glukhova represent a significant advance (see Introduction), but are of extremely limited value for species level determinations in the Nearctic.

A synoptic identification record form (Figure 21 in Appendix D) provided a convenient basis on which to compare the results by the four main processing/collection "tracks" -- individually-reared, immatures preserved, rearing carton-derived, or adults field-trapped. In the many cases for which I could not arrive at specific identifications, particularly of larvae and pupae, I assigned the specimens to the most appropriate genus, tribe or "complex" (Table 3, etc). After scanning the unassociated immatures preserved collectively in vials labelled by collection number, and ascertaining their taxonomic composition to the extent possible, I replaced the immatures back into their collection vials, pending future specific systematic attention to the various

genera. Faced with so many uncertainties in determinations, I did not hesitate to use qualifiers such as "prob." (but not the ambiguous '?', per Knutson et al. 1980).

1.3 Overview and Discussion of the General Survey Results

1.3.1. Summary of Collection Activity and Source Material

The field collection activity, which provided the great majority of the rearing and habitat data for this study, is summarized in Table 2. While seven states are represented in the nearly 2,300 collections, 86.5% of the collections were taken in Virginia, 8.8% in West Virginia, and 3.2% in North Carolina. All told, these collections represent 50 counties and 5 cities in Virginia, and 10 resp. 7 counties in North Carolina and West Virginia (Fig. 2, Table 48, 49). The remaining four states received only sporadic attention as opportunities presented themselves.

F. V. Battle's collections contributed about 16% of the total. Of his 11 collections from Alabama and New Jersey, only two (FVB 132, 133) yielded any specimens. This is probably related to the difficulty in transporting unpreserved samples over longer distances.

Among the 1610 habitat samples which I took in Virginia, about 31% were from the stream-side pollution study sites described in Appendix H. These were, on the whole, rather low-yielding in terms of specimens. The remaining samples, taken 1975-78, are fairly evenly divided among those which were placed in rearing cartons and those subjected to extraction procedures. The collection sites from which these samples were taken are described in Appendix F. The collection numbers are listed by state and county in Tables 48 and 49. Habitat substrates taken by F. V. Battle were held in rearing cartons for recovery of emerging adults; none of his samples were subjected to

Table 2. Numbers of field collections taken in Virginia and surrounding states, forming the bulk of the samples on which the present results are based. Includes only those collections taken by the author (1972-73; 1975-78) and those evaluated by the author but taken by F. V. Battle from 1968 to 1970.

Nature of Collections Taken	Number of Collections by State										Σ
	AL	KY	MD	NC	NJ	VA	WV				
Habitat Substrate ¹ By WIK	-	2	6	44	-	1610	164				1826
Habitat Substrate by FVB	9	-	-	24	2	363	14				362
Adult-Trapping Efforts (WIK)	-	-	-	5	-	51	24				80
Other Collections (Drift net, artificial substrate)	-	-	-	-	-	23	-				23
Total Collections	9	2	6	73	2	1983	202				2291

¹ Including ca. 20 collections where pupae and larvae were taken directly in the field without returning substrate to the laboratory for extraction.

² Including 11 Malaise trapping events at the stream pollution study sites (Appendix H).

washing/extraction procedures.

Of nearly 100 individuals and/or institutions contacted concerning availability of immature Ceratopogonidae from the eastern Nearctic, 32 respondents had specimens to offer. Many of them were aquatic biologists, actively involved in field projects requiring determination. Several of the submitters could also supply some habitat information, including material I sorted from existing institutional collections (notably Acad. Nat. Sci., Philadelphia; Cornell University; New York State Museum; Royal Ontario Museum; and U. S. Natural Museum). I received a combined total of nearly 11,200 specimens (Table 2A), representing the collections of over 65 people from 15 eastern states and Canadian provinces.

About 69% of these specimens were immatures, the remainder were adults largely unassociated with the immatures. Approximately 1000 adults were reared and associated with pupal exuviae, but fewer than 0.2% of the larvae were in any way reliably associated with adults. Practically none were explicitly associated with reared adults. The great majority of associations I found were either *Culicoides* or *Bezzia*. I processed and identified all of this material to the extent possible, and returned most of it, keeping only voucher specimens at V.P.I. & S.U. One major exception was a long series of slide-mounted larvae from reservoirs in South Carolina and South Dakota, provided by P. L. Hudson, who donated them. Because my main search was for larval material associated with other developmental stages, I did not take time to slide mount more than a few of the reared adults which had associated pupal exuviae.

Table 2A. Specimens of Ceratopogonidae processed and examined in connection with this study, according to origin and method of acquisition

Source of Material	Numbers of	
	Immatures	Adults
I. Present Study's Collections		
A. Rearing Carton - present writer	n/a	7,059 ^{1/}
B. Rearing Carton - F. V. Battle	n/a	6,633 ^{2/}
C. Adults Field Trapped	n/a	2,765
D. Individually reared ^{3/} ex larvae or pupae, and associated with other developmental stages	~3,000 ^{4/}	~1,100
E. Immatures extracted but not reared (Sub-totals)	<u>~5,950</u> (8,950)	<u>n/a</u> (17,557)
II. Other Institutions and Individuals		
A. Not reared or associated	7,030 ^{5/}	2,866
B. Reared and associated	<u>650^{6/}</u>	<u>650^{6/}</u>
Totals	16,630	21,073
Grand Total		37,703

^{1/} Including 5,535 collected specifically for this study (Table 6), 1975-78.

^{2/} Including about, 5670 *Culicoides*, of which 95% (all but *C. bergi* and *C. sphagnumensis*) were treated by Battle (1970).

^{3/} Estimates only; material not completely worked up. Excludes eggs.

^{4/} Including many aborted attempts and incomplete development cases.

^{5/} Including ca. 6,300 larvae; 130 larval exuviae; 635 pupae

^{6/} Largely pupal exuviae and associated adults, esp.

Bezzia (mostly a long series of *B. glabra* and *B. varicolor* (s.l.) reared from pond algae by Mark I. Dow), *Culicoides* and other genera reared by W. W. Wirth, H. A. Jamnback, or R. H. Jones).

The time and effort spent at such rather unrewarding activity was justified by the exposure it provided me to a broad range of fauna from widely dispersed areas and different habitats. Also, the habitat data made available for certain significant collections added to the value of the specimens.

The most valuable and numerically most abundant collections of immature stages I received were from : W. Ettinger (Ichthyological Associates, Pottstown, PA); S. C. Harris (North Dakota State Univ.) L. Hudson (U. S. Fish and Wildlife Serv., SC and SD); H. A. Jamnback (New York State Museum and Science Service); R. H. Jones and M. Lisitza (Colorado, and Univ. of Wisconsin, resp.); D. L. Kline (NC, SC); J. C. Morse (Clemson Univ., SC); L. L. Pechuman (Cornell University); S. S. Roback (Acad. Nat. Sci., Philadelphia, PA); E. C. Turner, Jr. and students (V.P.I. & S.U.); T. R. White (Clemson Univ., SC); G. B. Wiggins (Royal Ontario Museum, Toronto, Ontario); and W. W. Wirth (U. S. Nat. Museum). Other individuals who made collections available to me are acknowledged at the beginning of this document.

Because of the emphasis on diversified collection and processing methods, the breakdown in numbers of specimens obtained by origin and major method of acquisition shows several unusual features (Table 2A). On the order of 38,000 specimens from at least 17 states and several Canadian provinces formed the raw material examined during the course of this study. Of these, 44.1% were larvae, pupae or cast skins, and the remainder adults, in contrast to the predominance of either larvae or adults normally found. Fully 84% of the adult specimens taken in this study were reared from known habitats. An additional

ca. 1,000 adult specimens of the 3,516 made available by others, could be usefully associated with larval habitat information.

Of over 3,000 individual rearings I attempted, 1,100 resulted in successful association of adults and cast skins. Perhaps only 400 of these involve complete series of larval and pupal exuviae with the adult, although I did not have the opportunity to process all this material fully. Approximately 90 species are associated in all, about 50 of which involve the larval stage (Tables 2A, 6).

While my field trapping of adults yielded 15.7% of the applicable adult specimen sub-total, this represented only 3.5% of the unit sampling efforts. An average of 34 specimens was obtained per adult trapping event, as opposed to 6.7 specimens per substrate sample. However, the higher labor intensity and lower yield per effort of the habitat sampling versus field trapping are offset by the much greater precision of the latter data vis-a-vis habitat biology obtained for the species.

1.3.2. Checklists and Tabulations of Species Encountered

A checklist of 192 species of Ceratopogonidae encountered from all collections taken in seven states during this study is presented in Table 3. The species are consecutively numbered and alphabetically arranged within each subfamily, tribe, genus, subgenus or species group. Authors and dates of publication are given for each described species. Other taxa employed during the process of identifying the material, chiefly immature forms, are listed as appropriate. Asterisks highlight new records for Virginia (*), significant range extensions (**), and unnamed --- probably new --- species (***).

The classification of this checklist, and of the other comprehensive ceratopogonid tabulations presented herein (Tables 3, 5, 6, 7, 8, 38 and 45) largely follows that of Wirth et al. (1974, 1977) and Downes and Wirth (1981). The arrangement of certain tribes, in particular the Ceratopogonini, Stilobezziini and Palpomyiini, is adjusted to reflect, in part, recent advances in ceratopogonid taxonomy. In the Palpomyiini, the extensive revision and refinement of the classification of the genus *Bezzia* by Wirth and colleagues, described above in the Introduction, has been incorporated in most of the relevant tables. Contrary to Wirth, however, I prefer to treat the *B. pulvera* gr. as distinct from the *B. expolita* group.

The former two tribes have been undergoing some redefinition, also described earlier. The provisional transfer of the genus *Alluaudomyia* from the tribe Ceratopogonini to the tribe Stilobezziini, while not yet formally justified, is accepted here, but other proposed changes

are not adopted at this time. For example, *Echinohelea* is retained in the Stilobezziini and subgenera of *Stilobezzia* are employed, contrary to Wirth and Grogan (1981). *Brachypogon* and *Isohelea* are not combined, despite indications by Grogan (1982a, in litt.) that this may eventually be necessary.

A conspectus of all the collection sites at which each species in the checklist (Table 3) was obtained, is presented in Table 38 (Appendix A). The collection sites are listed by taxon, according to whether specimens were obtained by individually rearing, immature extraction, rearing carton or by trapping of adults in the field. Each collection site thus listed is described in Appendix E or F. A tabulation, by collection method, of species and numbers obtained at each site is not presented due to space considerations (it would require over 100 pages), but is on file at V.P.I. & S.U. and with the writer.

At least 42 ^{1/}new species, as yet undescribed, and 150 described species are included in the systematic checklist (Table 4). When the initial run of identifications was completed in 1979, the number of undescribed species stood at 52, but this has been reduced, thanks to the active state of current ceratopogonid systematics. Recent new descriptions, affecting this list, are in the genera *Alluaudomyia* (Glick and Mullen 1982), *Stilobezzia* (Wirth and Grogan 1981), *Macropoeza* (Knausenberger and Wirth 1980), *Bezzia* (Wirth 1983a,b,c; Wirth and

^{1/} Not including *Probezzia* sp. nr. *williamsi*, subsequently discovered; see Chapter 5.

Table 3. Checklist and systematic arrangement of all taxa of Ceratopogonidae encountered in this study. Species groups and other supraspecific taxonomic assignments, employed as needed, are included but not numbered. The asterisks indicate: (*) new record for Virginia, but occurrence in Virginia expected, based on previous known distribution; (**) new record for Virginia, represents significant range extension; (***) unnamed, probably new, species; 'FVB' indicates species collected only by F.V. Battle. All taxa were collected in Virginia, excepting the species indicated by the two-letter codes AL, NC or WV in brackets after the species names, representing the states in which the species were collected. See text and geographic checklist for further details.

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SUBFAMILY LEPTOCONOPINAE

Leptoconops Skuse

- * 1. (Holoconops) linleyi Wirth and Atchley, 1973

SUBFAMILY FORCIPOMYIINAE

Atrichopogon Kieffer

- ** 2. appendiculatus (Goetghebuer) [WV]
 * 3. fuscus (Coquillett), 1901
 * 4. fusinervis (Malloch), 1915
 * 5. geminus Boesel, 1973
 6. levis (Coquillett), 1901
 7. minutus (Meigen), 1830
 *** 8. spp. nr. peregrinus (Johannsen), 1908^{1/}
 * 9. cf. websteri (Coquillett), 1901
 - spp. undetermined

Forcipomyia Meigen

10. (Caloforcipomyia) glauca Macfie, 1934
 11. (Euprojoannisia) hirtipennis (Malloch), 1915 [WV]
 *12. (Forcipomyia) bipunctata (Linnaeus), 1767
 13. brevipennis (Macquart), 1826
 14. bystraki Grogan and Wirth, 1975
 15. fimbriata (Coquillett), 1901 [WV]
 16. pinicola Bystrak and Messersmith, 1980 [WV]
 17. solonensis Wirth, 1951 [WV]
 - sp. undetermined
 18. (Lasiohelea) fairfaxensis Wirth, 1951
 ***19. (subg. nr. Lepidohelea) n. sp. [WV]
 - Forcipomyia (no subg.) spp. undetermined

^{1/} At least two species

Table 3. (Cont'd)

=====

SUBFAMILY DASYHELEINAE

Dasyhelea Kieffer

- * 20. cf. atlantis Wirth and Williams, 1957
- ** 21. cf. brevicosta Waugh and Wirth, 1976 [AL,WV]
- 22. cincta (Coquillett), 1901
 - cincta gr.
- *** 23. sp. 8, nr. maculata Macfie, 1943 FVB
- 24. grisea (Coquillett), 1901
 - grisea gr.
- 25. leptobranhia Waugh and Wirth, 1976
 - leptobranhia gr.
- *** 26. sp. 9 [WV]
- 27. major (Malloch), 1915
- 28. messersmithi Waugh and Wirth, 1976
- 29. mutabilis (Coquillett), 1901
 - mutabilis gr. undetermined
- *** 30. sp. 1
- *** 31. sp. 2
- *** 32. sp. 3
- *** 33. sp. 4 [WV]
- *** 34. sp. 5
- *** 35. sp. 6 FVB
- *** 36. sp. 7 [AL] FVB
- ** 37. navaiiae Waugh and Wirth, 1976
- 38. oppressa Thomsen, 1935
- 39. pollinosa Wirth, 1952
- 40. pseudoincisurata Waugh and Wirth, 1976
- ** 41. cf. spiniforma Waugh and Wirth, 1976
- 42. stemlerae Waugh and Wirth, 1976
- *** 43. sp. nr. stemlerae Waugh and Wirth, 1976
- 44. traverae Thomsen, 1935
 - spp. undetermined

SUBFAMILY CERATOPOGONINAE

Tribe Culicoidini

Culicoides Latreille

- * 45. alexanderi Wirth and Hubert, 1962
- 46. arboricola Root and Hoffman, 1937
- 47. baueri Hoffman, 1925
- 48. bergi Cochrane, 1973
- * 49. bermudensis Williams, 1956
- 50. bickleyi Wirth and Hubert, 1962
- 51. biguttatus (Coquillett), 1901

Table 3. (Cont'd)

=====

Culicoides Cont'd

- 52. chiopterus (Meigen), 1830
- 53. crepuscularis Malloch, 1915
- 54. debilipalpis Lutz, 1913
- * 55. denticulatus Wirth and Hubert, 1962
- 56. footei Wirth and Jones, 1956
- 57. furens (Poey), 1851
- * 58. furensoides Williams, 1955
- 59. guttipennis (Coquillett), 1901
- 60. haematopotus Malloch, 1915
- 61. hinmani Khalaf, 1952
- 62. hollensis Melander and Brues, 1903
- ** 63. jamnbacki Wirth and Hubert, 1962
- * 64. juddi Cochrane, 1973
- 65. loisae Jamnback, 1965
- 66. melleus (Coquillett), 1901
- 67. mulrennani Beck, 1957
- 68. nanus Root and Hoffman, 1937
- 69. obsoletus (Meigen), 1818
- 70. paraensis (Goeldi), 1905
- 71. parapiliferus Wirth and Blanton, 1974
- 72. piliferus s.l., Root and Hoffman, 1937; s.s., Wirth and Hubert, 1962
- piliferus gr. undetermined
- 73. sanguisuga (Coquillett), 1901
- 74. scanloni Wirth and Hubert, 1962
- ** 75. sphagnumensis Williams, 1955
- 76. spinosus Root and Hoffman, 1937
- 77. stellifer (Coquillett), 1901
- 78. testudinalis Wirth and Hubert, 1962
- 79. travisi Vargas, 1937
- 80. variipennis s.l. (Coquillett), 1901
- 81. venustus Hoffman, 1925
- 82. villosipennis Root and Hoffman, 1956
- spp. undetermined

Tribe Ceratopogonini

Alluaudomyia Kieffer

- 83. bella (Coquillett), 1902
- *** 84. sp. nr. footei Wirth, 1952
- 85. megaparamera Williams, 1957
- 86. needhami Thomsen, 1935
- 87. paraspina Wirth, 1952
- 88. parva Wirth, 1952
- spp. undetermined

Table 3. (Cont'd)

=====

Brachypogon Kieffer

89. canadensis Downes, 1976 [NC,WV only]
 - spp. undetermined

Isohelea Kieffer

- *** 90. sp. 1 nr. serrata (Lewis), 1956
 *** 91. sp. 2 [WV] FVB
 *** 92. sp. 3
 *** 93. sp. 4 [WV]
 *** 94. sp. 5
 *** 95. sp. 6 [WV]
 - spp. undetermined

Tribe Stilobezziini

Echinohelea Macfie

96. lanei Wirth, 1951

Monohelea Kieffer

97. cf. bifurcata Wirth and Williams, 1964
 *** 98. sp. nr. floridensis Wirth and Williams, 1964
 - hieroglyphica gr.
 99. cf. macfieii Wirth, 1953 FVB
 **100. obscura Wirth and Williams, 1964
 101. stonei Wirth, 1953
 - spp. undetermined

Parabezzia Malloch

- *102. alexanderi Wirth, 1965
 103. cf. eupetiolata Grogan and Wirth, 1977 [NC] FVB
 104. (uncinata gr.) prob. huberti Grogan and Wirth, 1977
 - spp. undetermined

Serromyia Meigen

105. sp. undeterminable, prob. crassifemorata Mall., 1914

Stilobezzia Kieffer

106. (Neostilobezzia) lutea (Malloch), 1918
 107. stonei Wirth, 1953
 108. (Stilobezzia) antennalis (Coquillett), 1901
 ***109. sp. nr. antennalis (Coquillett), 1901
 **110. beckae Wirth, 1953
 111. bullae Thomsen, 1937
 112. coquilletti Kieffer, 1917
 113. diversa (Coquillett), 1901

Table 3. (Cont'd)

=====

Stilobezzia (S.) cont'd.

114. glauca Macfie, 1939
 115. pallidiventris (Malloch), 1915 [NC]
 116. sybleae Wirth, 1953
 - sp. gr. nr. sybleae
 * 117. sp. A nr. sybleae (= navaiae Wirth and Grogan, 1981)
 ***118. sp. B nr. sybleae
 119. viridis (Coquillett), 1901
 - Stilobezzia (no subg.) spp. undetermined

Tribe Heteromyiini

Clinohelea Kieffer

120. bimaculata (Loew), 1861
 121. curriei (Coquillett), 1905

Heteromyia Say

122. fasciata Say, 1825

Tribe Sphaeromiini

Jenkinshelea Macfie

123. albaria (Coquillett), 1895

Johannsenomyia Malloch

124. argentata (Loew), 1861

Macropeza Meigen

125. pamunkeiana Knausenberger and Wirth, 1980

Mallochohelea Wirth

126. albibasis (Malloch), 1915
 127. atripes Wirth, 1962
 ***128. sp. nr. caudellii (Coquillett), 1905
 129. smithi (Lewis), 1956
 - spp. undetermined

Probezzia Kieffer

130. albitibia Wirth, 1971
 ***131. sp. nr. albitibia Wirth, 1971
 132. pallida Malloch, 1914
 133. sabroskyi Wirth, 1951 [WV]
 134. smithii (Coquillett), 1901
 135. xanthogaster (Kieffer), 1917
 - spp. undetermined

Table 3 . (Cont'd)

=====

Sphaeromias Curtis

136. longipennis (Loew), 1861

Tribe Sphaeromiini, genus undetermined^{2/}

Tribe Palpomyiini

Bezzia Kieffer

(Bezzia) bivittata Group^{3/}

137. bivittata (Coquillett), 1905

138. gibbera (Coquillett), 1905

- spp. undetermined

(Bezzia) expolita Group

139. albidorsata Malloch, 1915

* 140. dentata Malloch, 1914

141. expolita (Coquillett), 1901

142. flavitaris Malloch, 1915

143. mallochi Wirth, 1951

144. perplexa Dow & Turner, 1976

*** 145. sp. 1 nr. mallochi

*** 146. sp. 2 nr. mallochi

*** 147. sp. 3 nr. media (Coquillett), 1901

FVB

*** 148. sp. 4 nr. flavitaris

FVB

*** 149. sp. 5 nr. flavitaris

*** 150. sp. 6 nr. flavitaris

*** 151. sp. 7 nr. mallochi

*** 152. sp. 8 nr. flavitaris

*** 153. sp. 9 nr. flavitaris

FVB

- spp. undetermined

(Bezzia) nobilis Group

154. nobilis (Winnertz), 1852

(synonym = setulosa (Loew), 1861)

(Bezzia) pulverea Group

* 155. laciniastyla Dow and Turner, 1976

156. pulverea (Coquillett), 1901

* 157. uncistyla Dow and Turner, 1976

*** 158. sp. 10 nr. pulverea

*** 159. sp. 11 nr. laciniastyla

*** 160. sp. 12 nr. laciniastyla

FVB

*** 161. sp. 13 nr. spicata Dow and Turner, 1976

FVB

*** 162. sp. 14 nr. uncistyla

*** 163. sp. 15 nr. laciniastyla

*** 164. sp. 16 nr. laciniastyla

*** 165. sp. 17 nr. pulverea

FVB

- spp. undetermined

^{2/} Applied only to immature forms, chiefly larvae

^{3/} Determined before Wirth and Grogan (1983) appeared

Table 3 . (Cont'd)

- =====
 (Homobezzia) annulipes Group
 * 166. fascispinosa Clastrier, 1962
 (syn. longiradia Dow and Turner, 1976)
 167. solstitialis (Winnertz), 1852
 168. varicolor (Coquillett), 1902
 - spp. undetermined
- (Homobezzia) bicolor Group
 169. glabra (Coquillett), 1902
- (Homobezzia) dorsasetula Group
 ** 170. dorsasetula Dow and Turner, 1976
 ** 171. obelisca Dow and Turner, 1976
 *** 172. sp. nr. dorsasetula
 - Bezzia [no subgenus, no species determined]

Palpomyia Meigen

173. basalis (Walker), 1848
 *174. canadensis Grogan and Wirth, 1979
 175. cressoni (Malloch), 1915
 - distincta gr.
 176. flaviceps (Johannsen), 1980
 - flavipes gr.
 177. hastata Grogan and Wirth, 1975
 178. lineata (Meigen), 1818
 - lineata gr.
 179. novitibialis Grogan and Wirth, 1975
 ***180. n. sp. nr. novitibialis
 181. plebeia (Loew), 1861
 182. plebeiella Grogan and Wirth, 1975
 183. rubiginosa Grogan and Wirth, 1975
 184. rufa (Loew), 1861
 185. scalpellifera Grogan and Wirth, 1975
 186. stonei Wirth, 1951
 187. subaspera (Coquillett), 1901
 188. tibialis (Meigen), 1818
 - tibialis gr.
 *189. walteri Grogan and Wirth, 1979
 190. weemsi Grogan and Wirth, 1979
 - spp. undetermined

FVB

"Palpomyia-Bezzia Complex"^{4/}

Phaenobezzia Haeselbarth

191. opaca (Loew), 1861
 192. sabroskyi Wirth and Grogan, 1982

^{4/} Applied to larvae which could not be, or were not, assigned to genus or tribe; includes chiefly Palpomyiini, but also Sphaeromiini, possibly some Heteromyiini. See text for further explanation.

Table 4. By-state summary of numbers of Ceratopogonidae species in the circum-Virginia region recorded in the literature (as of 1986), and in the present study from six states and District of Columbia.

	Numbers of Species															
	Published for Circum-Virginia Region						Recorded During This Study									
	DC	KY	MD	NC	TN	VA	WV	Σ	AL	KY	MD	NC	NJ	VA	WV	Σ
Described Species	19	13	158	74	61	150	44	207	3	1	9	42	0	137	83	150
New Records from This Study (Descr. Spp.)									0	0	1	20	0	28	56	13 ^{1/}
Total Number of Described Species	19	13	159	94	61	178	100	222								N/A
Unnamed Species Collected									1	0	0	6	0	32	12	42
Combined Total (Incl. Unnamed Spp.)	19	13	159	100	61	210	112	263 ^{2/}	4	1	9	48	0	169	95	192

^{1/} 13 species not previously recorded from any of the states included; 105 species in all were newly recorded from one or more of the states.

^{2/} An additional 33 described species are judged to be present in one or more states of this region, based on their known present distribution and prevalence in regions to the west, north and/or south (Table 45), but their presence awaits confirmation.

Grogan 1983; Wirth et al. 1984), *Palvomyia* (Grogan and Wirth, 1979) and *Phaenobezzia* (Wirth and Grogan, 1982). All new species descriptions and available records, through 1985, relevant to the middle Atlantic states are reflected in the Geographic Checklist in Appendix C, Table C.

The remaining 42 or so undescribed species, included in Table 3, are distributed among 11 genera, but 33 (78.6%) of the species are either *Dasyhelea* (9 spp.), *Isohelea* (6 spp.), or *Bezzia* (18 spp.). These three genera constitute, with the genera *Atrichopogon* and *Forcipomyia* (underrepresented in this study), the major ceratopogonid groups undergoing or still requiring contemporary systematic treatment. At least 30 undescribed Nearctic species of *Atrichopogon* are present in the U.S. National Museum alone (Wilkening et al. 1985). For the *Dasyhelea*, Waugh and Wirth's (1976) study covered mainly the fauna of the northeastern United States. According to Wilkening et al. (1985), collections of *Dasyhelea* from the southern United States contain numerous undescribed species.

The *Brachypogon*, *Ceratopogon* and *Isohelea* section of the tribe Ceratopogonini is receiving attention in a long-term project by Grogan (1982a) and Downes and Grogan (pers. comm., in litt.). Likewise, the *Bezzia expolita* and *pulvera* species are presently under revision by Wirth (Wilkening et al. 1985). The unnamed *Bezzia* species which I encountered are briefly characterized in Appendix B, Table 44.

Of the remaining six genera containing new species in the present study, two species each are in the genera *Stilobezzia* and *Probezzia*.

Thirty-two of the new species were found in Virginia, 12 in West Virginia, 7 in North Carolina and one in Alabama. Of the 20 new

species collected outside Virginia, 11 were obtained only outside of the state.

The current status in the numbers of biting midge species known in the region is summarized in Tables 4 and 5, in comparison with the results in species numbers obtained from the various states covered in this study. As was to be expected, by far the greatest numbers of species in the region have been recorded for Maryland (159) and Virginia (150). The species present in all six states and the District of Columbia are itemized in the Geographic Checklist (Table 45), based on an exhaustive search of literature records (Table 37), with the present results. Prior to this^{1/}, no recent comprehensive listing of ceratopogonids has existed for any particular state. Earlier lists were published for California (Wirth 1952a) and Connecticut (Lewis 1959).

New distribution records from this study are indicated in Table 45 by a delta symbol (Δ). Of the 42, 137 and 83 described species which I found in North Carolina, Virginia and West Virginia respectively, 20, 28 and 56 were new records for those states, thus, bringing the total of described species presently known there to 94, 178 and 100, in that order. The totals for Tennessee and Kentucky in particular, lag well behind, with 61 and 13, respectively. An index of how relatively unexplored North Carolina and West Virginia have been for Ceratopogonidae, compared to Virginia, is given in the ratio

^{1/} and the very recently issued annotated checklist of Florida Ceratopogonidae by Wilkening, Kline and Wirth (1985).

of new records to number of sites collected at (during this study in these states) namely, 0.91, 0.66 and 0.06, respectively for North Carolina, West Virginia and Virginia.

All told, at least 105 new records of described species were obtained for four states. Thirteen species were previously unrecorded from any of the Middle Atlantic states, including (double asterisks indicate significant range extensions):

- ** *Atrichopogon appendiculatus* Goetghebuer
- A. fusinervis* (Malloch)
- A. peregrinus* (Johannsen)
- Dasyhelea atlantis* Wirth and Williams
- ** *D. spiniforma* Waugh and Wirth
- ** *Culicoides jammaeki* Wirth and Hubert
- C. juddi* Cochrane
- ** *C. spagnumensis* Williams
- ** *Parabezzia eupetiolata* Grogan and Wirth
- ** *Probezzia sabroskyi* Wirth
- Bezzia dorsasetula* Dow and Turner
- ** *B. obeliscus* Dow and Turner
- B. unciostyla* Dow and Turner

Eight significant range extensions are recorded in this study, including the 7 double-asterisked species above, and D. brevicosta Waugh and Wirth, from Alabama, previously known only from Virginia and West Virginia north to New York. In addition, at least five other range extensions, reported in the recent literature, are confirmed: *D. navaiiae* Waugh and Wirth, herin recorded from VA and WV, reported by Bowen (1983) from NC, and previously known only from Michigan; *Monohelea obscura* Wirth and Williams, widespread from Michigan to Massachusetts, recorded here from VA and WV, recently reported also from MD (Wirth and Grogan 1981). I recorded *Stilobezzia beckae* Wirth, which is primarily neotropical (with records from Florida and Mississippi) from NC and VA, now also known from

Chapter 1. Survey Results and Discussion

MD (Wirth and Grogan 1981). *Bezzia dorsasetula*, which I found in VA and WV, and previously known only from New York, was recently reported from Florida (Wilkening et al. 1985). Finally, *B. fascispinosa* Clastrier, primarily a northern Holarctic species which I found in VA and WV, has recently also been reported in MD (Wirth et al. 1984 and Wilkening et al. 1985).

Of the 13 major range extensions referred to above, all but one represent significant southward extensions of species appearing to be primarily boreal, most of which having been previously known from the latitudes of Michigan to New York and north. The only notable northward extension of an austral species recorded here is that of *Stilobezzia beckae* (see above).

Representatives of 10 genera have been recorded for the first time from three states. Two genera are newly recorded for the Virginia fauna, *Leptoconops* and *Isohelea*, bringing the total of genera known from this state to 26. An additional three genera, *Ceratopogon*, *Nilobezzia* and *Stenoxenus*, are the unrecorded genera most likely to be eventually found there (Table 5), and in fact are presently known from one or more of the middle Atlantic states (including New Jersey). Three genera are recorded for the first time from North Carolina -- *Brachypogon*, *Isohelea* and *Stilobezzia*. In West Virginia, seven genera are apparently recorded for the first time: *Isohelea*, *Echinohelea*, *Monohelea*, *Clinohelea*, *Mallochohelea*, *Probezzia* and *Sphaeromias*.

Six of the 36 Nearctic genera^{1/} are not represented in collections from the region east of the 100th meridian, and of these, one rare monospecific genus, *Rhynchohelea*, is known only from Florida and California (Downes and Wirth 1981). Thus, 29 genera in all are known from the eastern Nearctic (Table 5).

With the results of this study and the published record, 222 described species are now known from Virginia and its five adjoining states and the District of Columbia (Tables 4 and 45). This comprises 38.8% of the 572 Nearctic ceratopogonid species I have been able to document (Table 5).

I expect that at least 234 described Ceratopogonidae are present in Virginia alone, and perhaps 250 species in the Middle Atlantic region as a whole. Together with the undescribed species encountered in this survey, the total number of species in the region would then be around 300 (Tables 4, 5 and 45).

The geographic checklist covering this region (Table 45) includes an additional 32 species not yet collected here, marked by ☆. These I judged more or less likely to be present, because either (a) they have been reported from adjacent states, (b) their published distribution includes states north and south of the region, or (c) the generalized nature of their present known geographic distribution and habitat suggests that their eventual discovery here can reasonably be expected. Eleven species are so far known only from one or more of the states in the Middle Atlantic region as defined in this study.

^{1/} This total would be 37, if one were to accept Wilkening et al.'s listing of *Schizohelea* Kieffer as a genus separate from *Monohelea* Kieffer.

Table 5. Number of species for all currently recognized genera of Ceratopogonidae in: (a) the entire Nearctic region, (b) east of the 100th meridian in the Nearctic, and (c) Virginia per se, together with the species totals resulting from the present study (status in 1986). Footnotes explained at end of table.

TAXA	Number of Described Species			Species Numbers With This Study's Results					Estimated Ranges In Projected Numbers Of Nearctic Species ^{4/}	
	Known to Occur In		Expected In Virginia ^{1/}	Collected During This Study ^{2/}	Unnamed Species Collected During Study	Total Species Number of Species Collected During Study	New Records For Virginia ^{3/}	Total Descr. Species In Virginia		Total Of All Species In Virginia
	Entire Nearctic Region	Nearctic East of 100th Meridian								
LEPTOCOPOINAE										
<u>Leptoconops</u>	23	4	0	1	1	0	1	1	1	21-30
FORCIPOMYIINAE										
<u>Atrichopogon</u>	28	17	4	10	8	2	7	9	11	51-75
<u>Forcipomyia</u>	108	60	17	33	9	1	2	17	17	151-200
DASYHELEINAE										
<u>Dasyhelea</u>	44	26	13	20	15	10	13	16	22	76-100
CERATOPOGONINAE										
CULICOIDINI										
<u>Culicoides</u>	142	78	36	49	38	0	7	43	43	151-200
<u>Paradasyhelea</u>	1	0	0	0	0	0	0	0	0	1-5
CERATOPOGONINI										
<u>Brachypogon</u>	2	2	1	1	1	0	0	1	1	1-5
<u>Ceratoculicoides</u>	3	3	3	3	0	0	0	3	3	6-10
<u>Ceratopogon</u>	4	4	0	1+	0	0	0	0	0	21-30
<u>Isohelea</u>	3	1	0	1	0	6	3	0	3	6-10
<u>Rhynchohelea</u>	1	1	0	0	0	0	0	0	0	1-5
STILOBEZZIINI										
<u>Alluaudomyia</u>	10	9	5	8	5	6	1	6	6	11-20
<u>Echinohelea</u>	1	1	1	1	1	0	0	1	1	1-5
<u>Monohelea</u>	19	14	5	10	4	1	1	6	6	21-30
<u>Parabazzia</u>	14	13	2	5	3	0	1	2	3	21-30
<u>Serromyia</u>	3	2	2	2	1	0	0	2	2	1-5
<u>Stilobezzia</u>	19	17	11	14	12	2	1	12	14	31-50
HETEROMYIINI										
<u>Clinhelea</u>	7	5	3	4	2	0	0	3	3	6-10
<u>Heteromyia</u>	2	2	2	2	1	0	0	2	2	1-5
<u>Neurobezzia</u>	1	0	0	0	0	0	0	0	0	1-5
<u>Neurohelea</u>	2	1	1	1	0	0	0	1	1	1-5
<u>Pellucidomyia</u>	1	0	0	0	0	0	0	0	0	1-5

Table 5. (cont'd)

TAXA	Number of Described Species			Species Numbers With This Study's Results					Estimated Ranges In Projected Numbers Of Nearctic Species ^{4/}
	Known to Occur In		Expected In Virginia ^{1/}	Collected During This Study ^{2/}	Unnamed Species Collected During Study	Total Number Of Species Collected During Study ^{3/}	Total Descr. Species In Virginia	Total Of All Species In Virginia	
	Entire Nearctic Region	Nearctic East of 100th Meridian							
SPHAEROMIINI									
<u>Jenkinshelea</u>	4	4	1	1	0	1	1	1	6-10
<u>Johannsenomyia</u>	2	2	1	1	0	1	1	1	6-10
<u>Macropeza</u>	2	2	1	1	0	1	1	1	1-5
<u>Mallochelea</u>	11	9	3	5	1	4	4	4	21-30
<u>Nilobezzia</u>	4	4	0	2	0	0	0	0	6-10
<u>Probezzia</u>	19	16	4	7	2	6	5	5	21-30
<u>Sphaeromias</u>	2	2	1	2	0	1	1	1	1-5
PALPOMYIINI									
<u>Amerohelea</u>	1	0	0	0	0	0	0	0	1-5
<u>Bezzia</u>	52	33	16	27	18	36	21	36	76-100
<u>Pachyhelea</u>	1	0	0	0	0	0	0	0	1-5
<u>Palpomyia</u>	31	22	16	18	1	18	2	19	31-50
<u>Phaenobezzia</u>	3	3	1	2	0	2	2	2	1-5
STENOXYENINI									
<u>Paraphoconus</u>	1	1	0	0	0	0	0	0	1-5
<u>Stenoxenus</u>	1	1	0	1	0	0	0	0	1-5
TOTAL	572	359	150	234	150	192	178	211	756-1115

^{1/} Based on published distribution records, including species found in surrounding states but not yet in Virginia.

^{2/} Including species from contiguous states.

^{3/} Including undescribed species which have been distinguished in this study.

^{4/} Nine range classes (1-5, 6-10, 11-20, 21-30, 31-50, 51-75, 76-100, 101-150 and 151-200). These ranges were derived by a subjective process based on the known and suspected diversity in the Nearctic and other zoogeographic faunae.

1.3.3. Comparison of Species Numbers and Taxonomic Richness

The actual numbers of individual specimens of the taxa encountered in the primary samples which I evaluated during this study are presented in Tables 6 and 7, representing my own and F .V. Battle's separate collections, respectively. These results are pooled for all sites sampled in Virginia and six other states (cf. Table 2), representing the sites listed by species in Table 38. The diversified methods of collection and processing resulted in high taxonomic species richness, with a more balanced cross-section of genera, species, and specimens per species, than is normally the case with most collections, which typically depend on light traps or other selective sampling methods.

The results presented here synoptically represent the total fauna obtained for all habitats sampled throughout the region covered. A breakdown and discussion of the results with respect to habitat or geographic distribution will not be presented here.

Data on the Ceratopogonidae of the Tennessee River Valley acquired by W. E. Snow and colleagues is assembled from six published sources and summarized in Table 8. Their survey of medically important insects of a river-reservoir system represents one of the very few systematic attempts in North America to determine and document all the aquatic ceratopogonid species encountered in aquatic sampling of an extensive region, in this case covering parts of six states. The results are of interest by way of comparison with my study for several reasons:

1. They represent collections made by a single group of investigators with a consistent purpose, using methods comparable to those I used.

2. A variety of collection methods was used in addition to light traps, notably rearing of adults from pupae taken in habitat water; 10 other methods were used to obtain specimens, mainly adults (Table 8, Footnote 3).
3. The geographic area covered overlaps somewhat the study area of the present study.

Apparently one of the few other studies in North America which has attempted to determine the ceratopogonid species composition representative of an entire state or larger region (other than California (Wirth 1952a)¹ is one undertaken by Lewis (1959) in Connecticut. In light traps run for 20 and 30 weeks during 1954 and 1955 at two ecologically and geographically distinct sites, Lewis obtained 80 presently valid species in 17 genera.

The data in Table 6 specifically represent the results of nearly 1050 collections made at 551 sites (most of which had separate samples for rearing and extraction), and 191 discrete localities (Fig. 2, Appendix F). About 19,900 individual specimens yielded some 180 species, 32 of which are undescribed species, in 24 genera. I obtained 21 genera by rearing (RC), and 19 genera each are represented by the immature and field-trapped material.

The 362 collections (Table 2) by Battle yielded 6,633 reared adult individuals comprising 82 species (67 described) among 14 genera (Table 7). Twelve species (10 of them undescribed) in his collections were not

¹ excluded here are the recent checklist for Florida (Wilkening et al. 1985) and the on-going regional faunal treatment in the Plummer's Island series for the lower Potomac Valley (Wirth et al. 1977, Wirth and Grogan 1979, 1981). See this chapter, Section 1.1.2.1. and 1.3.2. G. R. Mullen and students are presently investigating the ceratopogonid fauna of Alabama (Glick and Mullen 1982, 1983).

Table 6. Numbers of specimens of all ceratopogonid taxa obtained by the four main sampling or processing methods employed by Knausenberger in the present study, from 1975 to 1978. Results are pooled for all sites sampled in extensive field surveys in Virginia and four surrounding states. Acronyms are defined in the footnotes, and fully explained in the text. See Table 7 for the equivalent results from Battle's collections.

Ceratopogonidae taxa	Frequency of Collection (F _{coll.})	Number of Specimens Obtained By							
		IR ₃ /	IMM ₄ /	RC ₅ /	AFT ₆ /				
		AFT ₁ / Substr ₂ /		♂♂	♀♀	♂♂ + ♀♀			
Leptoconopinae									
<u>Leptoconops</u>	1	0	0	0	0	0	0	0	11
<u>linleyi</u>									
Forcipomyiinae									
<u>Atrichopogon</u>	2	0	0	0	0	0	0	0	2
<u>appendiculatus</u>									
(continued)									

- 1/ Number of adult field-trapping efforts which yielded the taxa indicated. See footnote 6.
- 2/ Number of substrate collection sites which yielded one or more specimens of the taxa indicated (collections for IR, IMM, and RC pooled).
- 3/ Specimens subjected to Individual Rearing attempts after extraction, not always resulting in development or emergence. Figures are best estimates (see text for explanation).
- 4/ Immature specimens extracted from habitat substrate but not subjected to rearing attempts. Figures represent best estimates.
- 5/ Specimens Reared Collectively from habitat substrate in rearing cartons, and not subjected to individual rearing attempts.
- 6/ Adults Field-Trapped by one or more of seven different methods (see Appendix E).

Table 6. Cont 'd.

Ceratopogonidae Taxa	F coll.		Number of Specimens Obtained By					
	AFT	Substr.	IR	IMM	RC			AFT
					♂♂	♀♀	♂♂ + ♀♀	
<u>Atrichopogon cont 'd.</u>								
<u>fuscus</u>	5	5	1	0	8	9	17	38
<u>fusinervis</u>	3	0	0	0	0	0	0	25
<u>geminus</u>	2	0	0	0	0	0	0	2
<u>levis</u>	6	0	0	0	0	0	0	29
<u>minutus</u>	1	1	0	0	0	1	1	1
<u>cf. peregrinus</u>	1	3	0	0	2	1	3	3
<u>cf. websteri</u>	3	1	0	0	1	3	4	11
<u>spp. undetermined</u>	17	20	4	21	20	22	42	139
<u>Forcipomyia</u>								
<u>(Calofoforcipomyia) glauca</u>	3	0	0	0	0	0	0	48
<u>(Euprojoannisia) hirtipennis</u>	0	1	0	1	2	5	7	0
<u>(Forcipomyia) bipunctata</u>	5	3	4	13	143	141	284	15
<u>brevipennis</u>	0	1	0	0	24	12	36	0
<u>bystraki</u>	0	1	0	0	0	1	1	0
<u>fimbriata</u>	0	1	0	0	1	4	5	0
<u>pinicola</u>	0	1	0	0	1	4	5	0
<u>solonensis</u>	1	0	0	0	0	0	0	1
<u>spp. undetermined</u>	2	6	6	10	26	38	64	4
<u>(Lasiohelea) fairfaxensis</u>	0	1	0	0	1	0	1	0
<u>(subg. nr. Lépidohlela) n. sp.</u>	1	0	0	0	0	0	0	1
<u>subgenus and species undetermined</u>	9	7	7	9	11	8	19	48
<u>Dasyheleinae</u>								
<u>Dasyhelea</u>								
<u>cf. atlantis</u>	1	1	2	0	5	5	10	2
<u>cf. brevicosta</u>	0	1	0	0	1	3	4	0
<u>cincta</u>	0	1	0	0	1	2	3	0

Table 6. Cont 'd.

Ceratopogonidae Taxa	F _{coll.}							Number of Specimens Obtained By		
	AFT Substr.		IR	IMM	RC		AFT	♂♂	♀♀	♂♂ + ♀♀
<u>Dasyhelea</u> cont 'd.										
<u>cincta</u> gr.	0	2	8	12	0	0	0	0	0	0
<u>grisea</u>	2	19	63	~60	109	138	247	10	10	10
<u>grisea</u> gr.	0	7	24	1	7	6	13	0	0	0
<u>leptobranchia</u>	0	3	5	2	0	1	1	0	0	0
<u>leptobranchia</u> gr.	0	3	6	7	0	0	0	0	0	0
<u>sp. 9 (leptobranchia gr.)</u>	0	1	1	3	0	1	1	1	1	1
<u>major</u>	2	6	9	44	1	5	6	4	4	4
<u>messersmithi</u>	0	6	8	2	8	6	14	0	0	0
<u>mutabilis</u>	1	22	6	17	20	39	59	2	2	2
<u>mutabilis</u> gr. undet.	1	4	10	2	3	7	10	4	4	4
<u>sp. 1</u>	0	4	1	0	41	58	99	0	0	0
<u>sp. 2</u>	0	2	0	0	5	7	12	0	0	0
<u>sp. 3</u>	3	0	0	0	0	0	0	182	0	0
<u>sp. 4</u>	1	1	0	0	0	1	1	2	2	2
<u>sp. 5</u>	0	1	0	0	0	1	1	0	0	0
<u>navaiaae</u>	0	1	0	0	0	1	1	0	0	0
<u>oppressa</u>	1	13	9	10	46	41	87	6	6	6
<u>pollinosa</u>	0	3	0	0	4	5	9	0	0	0
<u>pseudoincisurata</u>	0	5	9	3	16	22	38	0	0	0
<u>cf. spiniforma</u>	0	1	0	0	0	4	4	0	0	0
<u>stemlerae</u>	0	3	1	1	6	4	10	0	0	0
<u>sp. nr. stemlerae</u>	0	2	1	0	3	2	5	0	0	0
<u>traverae</u>	1	9	0	0	9	14	23	1	1	1
<u>spp. undetermined</u>	2	40	58	107	9	27	36	2	2	2
Ceratopogoninae										
Culicoidini										
<u>Culicoides</u>										
<u>alexanderi</u>	2	0	0	0	0	0	0	0	0	3

Table 6. Cont'd.

Ceratopogonidae Taxa	F coll.		Number of Specimens Obtained By					AFT
	AFT Substr.	IR	IMM	RC	RC			
					♂♂	♀♀	♂♂+♀♀	
<u>Culicoidini cont'd.</u>								
<u>Culicoides cont'd.</u>								
<u>arboricola</u>	6	3	2	0	7	8	15	12
<u>baueri</u>	1	18	6	0	21	25	46	1
<u>bergi</u>	0	6	0	0	19	12	31	0
<u>bermudensis</u>	1	3	51	19	3	5	8	2
<u>bickleiyi</u>	3	11	2	0	2	56	58	226
<u>biguttatus</u>	8	8	2	0	6	18	24	113
<u>chiopterus</u>	1	0	0	0	0	0	0	8
<u>crepuscularis</u>	1	70	37	58	136	188	324	5
<u>debilipalpis</u>	2	4	0	0	1	5	6	55
<u>denticulatus</u>	2	0	0	0	0	0	0	8♀
<u>footei</u>	1	0	0	0	0	0	0	2
<u>furens</u>	9	6	6	11	15	30	45	78
<u>furensoides</u>	3	2	1	0	3	3	6	39
<u>guttipennis</u>	3	17	12	35	18	25	43	7
<u>haematopotus</u>	7	96	98	85	140	152	292	13
<u>hinmani</u>	0	3	1	0	1	3	4	0
<u>hollensis</u>	2	2	4	8	6	5	11	8
<u>jambacki</u>	6	2	0	0	0	2	2	249
<u>juddi</u>	0	1	0	0	1	1	2	0
<u>loisae</u>	0	2	0	0	0	2	2	0
<u>melleus</u>	3	1	4	0	0	5	5	189
<u>mullrennani</u>	10	1	0	0	0	1	1	59
<u>nanus</u>	0	2	0	0	2	3	5	0
<u>obsoletus</u>	7	0	0	0	0	0	0	98
<u>paraensis</u>	4	1	5	0	0	0	0	140
<u>parapilliferus</u>	0	1	0	0	0	3	3	0

Table 6. Cont'd.

Ceratopogonidae Taxa	Fcoll.							Number of Specimens Obtained By		
	AFT	Substr.	IR	IMM	RC	AFT		AFT		
						♂♂	♀♀		♂♂ + ♀♀	
<u>Culicoidini cont'd.</u>										
<u>Culicoides cont'd.</u>										
<u>piliferus s.s.</u>	5	5	16	0	7	8	15			24
<u>piliferus gr.</u>	2	16	30	2	2	23	25			45
<u>sanguisuga</u>	7	4	0	0	11	7	18			340
<u>scanloni</u>	0	1	0	0	0	1	1			0
<u>sphagnumensis</u>	1	4	15	20	7	9	16			13
<u>spinosus</u>	0	13	13	0	27	22	49			0
<u>stellifer</u>	5	32	27	0	41	37	78			26
<u>testudinalis</u>	0	2	0	0	1	3	4			0
<u>travisi</u>	0	5	0	0	14	18	32			0
<u>variipennis s. l.</u>	1	29	82	~400	157	189	346			4
<u>venustus</u>	0	13	7	13	12	11	23			0
<u>villosipennis</u>	1	3	14	10	16	9	25			5
<u>spp. undetermined</u>	2	98	304	~2750	31	128	159			10
<u>Ceratopogonini</u>										
<u>Alluaudomyia</u>										
<u>bella</u>	2	44	78	18	28	40	68			27
<u>sp. nr. footei</u>	0	2	0	0	0	2	2			0
<u>megaparamera</u>	0	7	3	0	5	1	6			0
<u>needhami</u>	0	13	12	1	1	4	5			0
<u>paraspina</u>	0	6	8	0	3	4	7			0
<u>parva</u>	1	8	1	3	9	8	17			3
<u>spp. undetermined</u>	0	22	36	18	5	6	11			0
<u>Brachypogon</u>										
<u>canadensis</u>	1	1	0	0	1	1	2			1♀
<u>sp. undetermined</u>	0	1	0	0	1	0	1			0

Table 6. Cont'd.

Ceratopogonidae Taxa	F _{coll} ,							Number of Specimens Obtained By		
	AFT Substr.		IR	IMM	RC		AFT			
	♂♂	♀♀			♂♂ + ♀♀					
Ceratopogonini cont'd.										
<u>Isohelea</u>	1	10	8	2	19	16	35	4		
n. sp. 1 nr. <u>serrata</u>	1	3	0	0	4	1	5	2♂		
n. sp. 3	1	0	0	0	0	0	0	2		
n. sp. 4	0	1	0	0	1	0	1	0		
n. sp. 5	0	1	0	0	1	0	1	0		
n. sp. 6	0	1	0	0	1	0	1	0		
sp. undetermined	0	11	15	10	7	7	14	0		
<u>Stilobeziini</u>										
<u>Echinohelea</u>	1	1	0	0	1	2	3	2		
<u>lanei</u>										
<u>Monohelea</u>	3	0	0	0	0	0	0	5		
cf. <u>bifurcata</u>	0	1	0	0	1	0	1	0		
sp. nr. <u>floridensis</u>	0	1	0	0	1	2	3	0		
<u>hieroglyphica</u> gr.	1	0	0	0	0	0	0	1		
<u>obscura</u>	8	2	0	0	1	2	3	11		
<u>stonei</u>	0	1	0	0	0	1	1	0		
sp.										
<u>Parabezzia</u>	0	1	0	0	0	1	1	0		
<u>alexanderi</u>	0	1	0	0	0	1	1	0		
<u>uncinata</u> gr. prob. <u>huberti</u>	0	1	0	0	0	1	1	0		
sp.	0	1	0	0	1	-	1	0		
<u>Serromyia</u>	1	1	0	1	0	0	0	0		
sp. undeterminable										
<u>Stilobezzia</u>	2	11	8	1	3	4	7	6		
(<u>Neostilobezzia</u>) <u>lutea</u>										

Table 6. Cont'd.

Ceratopogonidae Taxa	F _{coll.}		Number of Specimens Obtained By				
	AFT	Substr.	IR	IMM	RC		AFT
					♂♂	♀♀	
<u>Stilobezzia (Neostilobezzia) cont'd.</u>							
<u>stonei</u>	3	1	0	0	1	1	2
<u>(Stilobezzia) antennalis</u>	3	59	154	57	119	129	248
<u>sp. nr. antennalis</u>	2	1	5	0	0	0	0
<u>beckae</u>	0	1	0	0	0	1	1
<u>bulla</u>	1	28	28	35	105	115	220
<u>coquilletti</u>	0	24	38	12	30	44	74
<u>diversa</u>	0	6	8	0	5	3	8
<u>glauca</u>	0	10	65	0	12	9	21
<u>pallidiventris</u>	0	2	0	0	5	8	13
<u>sybleae</u>	1	11	4	3	18	39	57
<u>sp. gr. nr. sybleae</u>	1	7	3	0	2	2	4
<u>navaiae</u>	0	6	0	0	2	11	13
<u>sp. B nr. sybleae</u>	0	7	3	0	0	0	0
<u>viridis</u>	0	10	9	5	4	10	14
<u>spp. undetermined</u>	0	25	28	63	0	2	2
Heteromyiini							
<u>Clinohhelea</u>							
<u>bimaculata</u>	3	12	2	0	7	25	32
<u>curriei</u>	0	1	0	0	0	1	1
<u>Heteromyia</u>							
<u>fasciata</u>	0	1	0	0	0	1	1
Sphaeromiini							
<u>Jenkinshhelea</u>							
<u>albaria</u>	1	0	0	0	0	0	0

Table 6. Cont'd.

Ceratopogonidae Taxa	Fcoll.		Number of Specimens Obtained By					
	AFT Substr.	IR	IMM	RC		AFT		
				♂♂	♀♀	♂♂ + ♀♀		
Sphaeromini cont'd.								
<u>Johannsenomyia</u>								
<u>argentata</u>	0	3	2	0	0	1	1	0
Macropeza								
<u>pamunkeiana</u>	2	0	0	0	0	0	0	7
Mallochohelea								
<u>albibasis</u>	0	1	0	0	1	1	2	0
<u>atripes</u>	2	6	9	25	1	2	3	>150
<u>sp. nr. caudellii</u>	0	2	1	0	1	0	1	0
<u>smithi</u>	0	1	3	0	0	0	0	0
<u>spp. undetermined</u>	0	4	2	20	2	1	3	0
Probezzia								
<u>albitibia</u>	0	1	1	0	0	0	0	0
<u>sp. nr. albitibia</u>	0	1	5	0	0	0	0	0
<u>pallida</u>	0	2	5	0	0	1	1	0
<u>sabroskyi</u>	1	0	0	0	0	0	0	1
<u>smithii</u>	2	1	1	0	0	0	0	2
<u>xanthogaster</u>	0	1	1	0	1	0	1	0
<u>spp. undetermined</u>	0	1	1	7	1	0	1	0
Sphaeromias								
<u>longipennis</u>	0	12	21	0	9	18	27	0
Sphaeromini (genus undetermined)	0	7	58	75	1	0	1	0
Palpomyiini								
<u>Bezzia</u>	0	11	60	150	2	5	7	0
<u>Bezzia</u> (no subgenus) sp.								

Table 6. Cont'd.

Ceratopogonidae Taxa	F coll.		Number of Specimens Obtained By					AFT
	AFT Substr.	IR	IMM	RC			AFT	
				♂♂	♀♀	♂♂ + ♀♀		
<u>Bezzia (Bezzia) cont'd.</u>								
<u>(Bezzia) bivittata Group</u>								
<u>bivittata</u>	0	1	1	0	0	0	0	0
<u>sp. nr. gibbera</u>	0	6	7	0	3	4	7	0
<u>(Bezzia) expolita Group</u>								
<u>albidorsata</u>	0	2	4	0	0	0	(1)	0
<u>cf. dentata</u>	0	1	2	0	1	3	4	0
<u>cf. expolita</u>	0	3	0	0	0	3	3	0
<u>flavitaris</u>	3	14	5	0	4	6	10	12
<u>cf. mallochi</u>	0	1	1	0	0	0	(1)	0
<u>perplexa</u>	0	8	3	0	4	4	8	0
<u>sp. 1</u>	0	5	0	0	3	4	7	0
<u>sp. 2</u>	0	1	0	0	0	1	1	0
<u>sp. 5</u>	0	1	3	0	1	0	1	0
<u>sp. 6</u>	0	1	1♂	2	0	0	0	0
<u>sp. 7</u>	0	1	1♂	1	0	0	0	0
<u>sp. 8</u>	0	0	0	0	0	0	0	0
<u>(Bezzia) nobilis Group</u>								
<u>nobilis</u>	6	127+	503	> 500	317	372	689	54
<u>(Bezzia) pulverea Group</u>								
<u>laciniastyla</u>	1	51	87	194	30	45	75	3
<u>pulverea</u>	0	4	6	0	2	4	6	0
<u>uncistyla</u>	0	9	19	0	4	5	9	0
<u>sp. 10</u>	0	3	0	0	3	4	7	0
<u>sp. 11</u>	0	1	0	0	0	1	1	0
<u>sp. 14</u>	0	1	1♂	0	0	0	0	0

Table 6. Cont'd.

Ceratopogonidae Taxa	F _{coll}		Number of Specimens Obtained By					
	AFT Substr.	IR	IMM	RC			AFT	
				♂♂	♀♀	♂♂ + ♀♀		
<u>Bezzia</u> (Bezzia) cont'd.								
sp. 15	0	1	0	0	1	0	1	0
sp. 16	0	1	0	0	1	0	1	0
spp. undetermined	0	7	36	100	1	1	2	0
(Homobezzia) <u>annulipes</u> Group								
<u>fascispinosa</u>	0	2	4	0	0	0	0	0
<u>solstitialis</u>	2	63	214+	145+	~170	~200	~370	13
<u>varicolor</u>								
spp. undetermined	0	8	26	30	-	-	-	-
(Homobezzia) <u>bicolor</u> Group								
<u>glabra</u>	2	34	95	125	42	80	122	3
(Homobezzia) <u>dorsasetula</u> Group								
cf. <u>dorsasetula</u>	2	7	17	0	8	8	16	2
cf. <u>obelisca</u>	1	16	30	0	35	34	69	1
sp. nr. <u>dorsasetula</u>	0	1	0	0	0	4	4	0
(Pseudobezzia) sensu Dow and Turner 1976								
spp. undetermined	0	17	48	250	0	0	0	0
Palpomyia								
<u>basalis</u>	0	1	3	0	2	0	2	0
<u>canadensis</u>	0	3	3	0	1	2	3	0
<u>cressoni</u>	0	3	8	0	2	0	2	0
<u>distincta</u> gr.	0	4	15	0	2	7	9	0
<u>flaviceps</u>	2	4	2	0	2	2	4	2
<u>flavipes</u> gr.	0	1	1	0	0	0	0	0

Table 6. Cont'd.

Ceratopogonidae Taxa	F coll.							Number of Specimens Obtained By			
	AFT Substr.		IR	IMM	RC		AFT				
	♂♂	♀♀			♂♂	♀♀		♂♂ + ♀♀			
<u>Palpomyia cont'd.</u>											
<u>hastata</u>	0	1	0	0	0	0	1	1	0	0	0
<u>lineata</u>	1	29	71	~110	7	7	7	14	2	2	2
<u>novitibialis</u>	0	31	95		2	12	12	14	0	0	0
<u>n. sp. nr. novitibialis</u>	0	3	1	0	2	0	0	2	0	0	0
<u>plebeia</u>	2	22	6	0	21	23	23	44	3	3	3
<u>plebeielia</u>	1	6	11	0	4	5	5	9	1	1	1
<u>rubiginosa</u>	0	5	0	0	9	8	8	17	0	0	0
<u>rufa</u>	2	8	7	0	6	5	5	11	2	2	2
<u>scalpellifera</u>	1	0	0	0	0	0	0	0	7	7	7
<u>stonei</u>	0	1	1	0	0	0	0	0	0	0	0
<u>subaspera</u>	0	11	46	0	10	9	9	19	0	0	0
<u>tibialis</u>	1	5	10	0	2	3	3	5	1	1	1
<u>tibialis gr.</u>	0	8	25	~220	0	0	0	0	0	0	0
<u>walteri</u>	0	8	3	0	11	15	15	26	0	0	0
<u>weemsi</u>	0	6	2	0	3	0	0	3	0	0	0
<u>spp. undetermined</u>	1	11	8	0	1	6	6	7	1	1	1
<u>Phaenobezzia</u>											
<u>opaca</u>	1	24	39	15	34	23	23	57	1	1	1
<u>sabroskyi</u>											
Palpomyia - <u>Bezzia</u> Complex	-	51	59	~375	0	0	0	0	0	0	0
Palpomyiini (genus undetermined)	0	24	22	15	0	0	0	0	0	0	0
TOTAL NUMBERS OF SPECIMENS	-	-	~3,103	~5,963	2,417	3,118	5,535	2,765			
TOTAL NUMBERS OF SITES	69	551	-	-	-	-	-	-	-	-	-

Table 7. Synopsis of numbers of Ceratopogonidae reared by F.V. Battle from substrate collections taken in Virginia (unless otherwise indicated). Includes the number of specimens for all species reared between 1968 and 1971. All Culicoides except C. bergi and C. sphagnumensis were determined by F.V. Battle, the remaining genera and species by the present writer.

Taxa	Number of			
	Sites	♂♂	♀♀	♂♂ + ♀♀
Forcipomyiinae				
<u>Atrichopogon</u> Kieffer				
1. spp. indet.	4	12	4	16
Dasyheleinae				
<u>Dasyhelea</u> Kieffer				
*2. <u>brevicosta</u>	1	2	1	3
3. (<u>cincta</u> gr.) sp. 8	2	6	2	8
4. <u>grisea</u> (Coq.)	4	4	8	12
5. <u>leptobranchia</u>	3	4	5	9
6. <u>major</u> (Mall.)	3	22	42	64
7. <u>messersmithi</u>	1	3	1	4
8. <u>mutabilis</u> (Coq.)	18	33	45	78
9. (<u>mutabilis</u> gr.) sp. 6	1	1	0	1
10. (<u>mutabilis</u> gr.) sp. 7	1	0	1	1
11. <u>navaiaae</u>	1	0	1	1
12. <u>stemlerae</u>	1	2	6	8
13. <u>traverae</u>	2	1	2	3
Ceratopogoninae				
<u>Culicoides</u> Latreille				
14. <u>baueri</u>	14	20	21	41
15. <u>bergi</u>	ca.30	50	50	100
16. <u>biguttatus</u>	10	60	43	103
17. <u>crepuscularis</u>	151	973	1019	1992
18. <u>furens</u>	3	69	22	91
19. <u>guttipennis</u>	1	1	0	1
20. <u>haematopotus</u>	156	826	892	1718
21. <u>hollensis</u>	2	15	21	36
22. <u>loisae</u>	4	5	6	11
23. <u>melleus</u>	1	1	0	1
- <u>piliferus</u> gr.	6	20	5	25
24. <u>piliferus</u> s.s.	11	23	10	33
**25. <u>sphagnumensis</u>	1	124	31	155

* Collected only in Talladega Co., Alabama (FVB No. 132)

** Collected only in Pocahontas Co., West Virginia (Cranberry Glades, 16-VII-1970)

Table 7. (Cont'd)

Taxa	Number of			
	Sites	♂♂	♀♀	♀♀+♀♀
<u>Culidoides cont'd.</u>				
26. <u>spinosus</u>	26	206	160	336
27. <u>stellifer</u>	51	128	111	239
28. <u>testudinalis</u>	4	0	7	7
29. <u>travisi</u>	11	16	27	43
30. <u>variipennis</u>	62	309	371	680
31. <u>venustus</u>	21	11	17	28
Ceratopogonini Newman				
<u>Alluaudomyia Kieffer</u>				
32. <u>bella</u>	5	3	5	8
33. <u>megaparamera</u>	1	1	0	1
<u>Brachypogon Kieffer</u>				
34. <u>sp.</u>	1	1	0	1
<u>Isohelea Kieffer</u>				
35. <u>n. sp. 2</u>	1	2	3	5
36. <u>n. sp. 3</u>	3	4	7	11
Stilobezziini Wirth				
<u>Monohelea Kieffer</u>				
37. <u>macfieii</u>	1	0	1	1
<u>Parabezzia Malloch</u>				
38. <u>alexanderi</u>	2	5	5	10
*39. <u>sp. cf. eupetiolata</u>	1	0	1	1
<u>Stilobezzia Kieffer</u>				
- <u>sp.</u>	2	0	2	2
40. <u>antennalis</u>	18	19	29	48
41. <u>n. sp. nr. antennalis</u>	5	15	8	23
42. <u>bulla</u>	21	62	69	131
43. <u>coquilletti</u>	16	30	35	65
44. <u>glauca</u>	2	1	1	2
45. <u>lutea</u>	1	0	1	1
46. <u>stonei</u>	1	2	1	3
- <u>sybleae</u> gr.	11	17	5	22
47. <u>sybleae</u>	6	10	11	21
48. <u>sp. A nr. sybleae (=navaiaae)</u>	1	0	1	1
49. <u>sp. B nr. sybleae</u>	8	5	13	18
Heteromyiini Wirth				
<u>Clinohelea Kieffer</u>				
*50. <u>bimaculata</u>	2	2	1	3

* Collected only in North Carolina

Table 7. (Cont'd)

Taxa	Number of			
	Sites	♂♂	♀♀	♂♂ + ♀♀
Sphaeromiini Newman				
<u>Mallochohelea</u> Wirth				
- sp.	3	3	4	7
51. <u>atripes</u>	2	1	1	2
<u>Probezzia</u> Kieffer				
52. cf. <u>albitibia</u>	1	1	0	1
<u>Sphaeromias</u> Curtis				
53. <u>longipennis</u>	7	6	1	7
Palpomyiini Enderlein				
<u>Bezzia</u> Kieffer				
54. (<u>Homobezzia</u>) <u>varicolor</u>	4	7	2	9
55. (<u>Bezzia</u>) <u>flavitaris</u>	16	18	22	40
56. (B.) <u>laciniastyla</u>	23	21	13	34
57. (B.) <u>mallochi</u>	2	2	0	2
58. (B.) <u>perplexa</u>	2	4	3	7
59. (B.) <u>pulverea</u>	5	4	4	8
60. (B.) <u>nobilis</u>	55	91	71	162
61. (B.) sp. 1	2	2	1	3
62. (B.) sp. 3	1	1	1	2
*63. (B.) sp. 4	1	1	0	1
64. (B.) sp. 7	1	1	4	5
65. (B.) sp. 9	1	2	0	2
66. (B.) sp. 10	2	1	2	3
67. (B.) sp. 12	1	0	1	1
68. (B.) sp. 13	1	1	0	1
69. (B.) sp. 17	1	0	2	2
<u>Palpomyia</u> Meigen				
- sp.	2	3	0	3
70. <u>cressoni</u>	3	0	3	3
71. <u>hastata</u>	3	2	1	3
72. <u>lineata</u>	1	1	2	3
73. <u>novitibialis</u>	13	10	13	23
74. n. sp. nr. <u>novitibialis</u>	4	4	0	4
75. <u>plebeia</u>	3	3	0	3
76. <u>plebeiella</u>	1	1	0	1
77. <u>rufa</u>	1	5	4	9
78. <u>stonei</u>	2	3	0	3
79. <u>subaspera</u>	11	22	3	25
80. <u>tibialis</u> gr.	1	1	0	1
81. <u>walteri</u>	1	1	0	1
82. <u>weemsi</u>	1	0	1	1

* Collected only in North Carolina

Table 8. Ceratopogonidae of the Tennessee River basin collected by W. E. Snow and others during field surveys of floodplain aquatic habitats, with a breakdown by method of collection.^{1/}

=====

Taxa	Number of occasions in which collected by			State
	Light Trap	Pupal Sample ^{2/}	Other Methods ^{3/}	
FORCIPOMYIINAE				
Atrichopogon				
1. <u>A. fuscus</u>	1			AL
2. <u>A. levis</u>	4	1	S(2) S(1)	AL, TN TN
3. <u>A. websteri</u>				
Forcipomyia				
4. <u>F. (Caloforcipomyia) glauca</u>	1			AL
5. <u>F. (Forcipomyia) bipunctata</u>	1	2	RT(1)	AL
6. <u>F. (F.) brevipennis</u>	4			AL, TN

^{1/} Records combined from Pickard and Snow (1955); Snow and Pickard (1953, 1954, 1958); Snow et al. (1957), and Wirth and Jones (1956). Species names updated where possible.

^{2/} Adults reared from pupae.

^{3/} Acronyms used to indicate methods or conditions of collection. BH - biting horse; BM - biting man; BMC - biting man in car; C - in car; JT - by jar trap over tree holes; L - larvae; RC - resting in chicken house; RF - resting on fence; RT - rotary trap; S - by sweep net in vegetation.

NOTE: Numbers indicate number of collections, not specimens.

Table 8. Cont'd.

Taxa	Number of occasions in which collected by				State
	Light Trap	Pupae Sample	Other Methods		
<u>Forcipomyia (cont'd.)</u>					
7. <u>F. (Microhelea) fuliginosa</u>	1		RT(1)		AL
8. <u>F. (F.) squamipes</u>	4				AL
9. <u>F. (F.) sp. 1 (cf. cinctipes)</u>		1			TN
10. <u>F. (F.) sp. 3 (n. sp. nr. pilosa)</u>	1				TN
11. <u>F. (F.) sp. 4 (cf. squamipes)</u>	1				AL
12. <u>F. sp. 2 cf. (Thyridomyia) monilicornis</u>		1			TN
<u>DASYHELEINAE</u>					
<u>Dasyhelea</u>					
14. <u>D. cincta</u>	1	2			AL, TN
15. <u>D. grisea</u>	6	6			AL, TN, VA
16. <u>D. major</u>			S(1)		TN
17. <u>D. mutabilis</u>	7	2	S(1)		AL, TN
18. <u>D. oppressa</u>		12	JT(3) L(4) S(1)		AL, MS, TN
19. <u>D. sp. 1 prob. traverae</u>	1	1			AL, TN
20. <u>D. tristyla (=jr. syn. fasciigera Kieff.)</u>	1				AL

Table 8. Cont'd.

Taxa	Number of occasions by which collected by			State
	Light Trap	Pupae Sample	Other Methods	
CERATOPOGONINAE				
<u>Culicoides</u> 1/				
21. <u>C. arboricola</u>	11	8	C(1) JT(3) RC(1)	AL, TN
22. <u>C. baueri</u>	7			AL, TN
23. <u>C. biguttatus</u>	9	11	BH(1) BM(9)	AL, TN
24. <u>C. crepuscularis</u>	14	11	BM(2) RC(2) S(1)	AL, NC, TN
25. <u>C. debilipalpis</u> gr.	1			TN
26. <u>C. footei</u> (as sp. 2)		1	JT(3)	TN
27. <u>C. guttipennis</u>	10	5	BM(10) C(1) JT(2) L(1)	AL, TN
28. <u>C. haematopotus</u>	11	6	BM(4)	AL, TN
29. <u>C. hinmani</u>		5	BM(6) C(1) JT(3)	AL, TN

1/ Light-trap collections for Culicoides represent locations primarily; traps were often operated up to 72 nights each.

Chapter 8. Cont'd.

Number of occasions by
which collected by

Taxa	Number of occasions by which collected by			State
	Light Trap	Pupae Sample	Other Methods	
<u>Culicoides (cont'd.)</u>				
30. <u>C. multipunctatus</u>	7			AL, TN
31. <u>C. nanus</u>		4		AL, TN
32. <u>C. obsoletus</u>	9		BM(10) C(1) RF(1) SF(1)	AL, TN, NC
33. <u>C. ousairani</u>	7			AL, TN
34. <u>C. paraensis</u>		3	BM(33) BMC(2) C(2) JT(3)	AL, MS, TN
35. <u>C. pilliferus</u> gr.	8	2		AL, TN
36. <u>C. snowi</u>	5	6	JT(1) BH(1)	TN
37. <u>C. spinosus</u>			BM(2)	AL, NC, TN
38. <u>C. stellifer</u>	9	3	RF(1)	AL, NC, TN
39. <u>C. travisi</u>	10	4	BM(2) RC(2)	AL, TN
40. <u>C. variipennis</u>	10	7	BM(1)	AL, TN, VA
41. <u>C. venustus</u>	11	1	S(1)	AL, GA,
42. <u>C. villosipennis</u>	9	1	JT(1)	NC, TN
43. <u>C. sp. 1 nr. spinosus</u>	4			AL, TN

Table 8. Cont'd.

Taxa	Number of occasions by which collected by			State
	Light Trap	Pupal Sample	Other Methods	
CERATOPOGONINI				
<u>Alluaudomyia</u>				
44. <u>All. bella</u>	2	1		AL, TN
45. <u>All. needhami</u>	3	1		AL, TN
46. <u>All. paraspina</u>	1	1		TN
47. <u>All. variegata</u>	1			AL
STILOBEZZIINI				
<u>Monhelea</u>				
48. <u>M. macfieii</u>		2		TN
49. <u>M. stonei</u>	1		RT(1)	AL, TN
<u>Stilobezzia</u>				
50. <u>S. (S.) bulla</u>		1		AL
51. <u>S. (S.) coquilletti</u>	2	3		AL, TN
52. <u>S. (S.) lutea</u>	1			TN
53. <u>S. (S.) sybleae</u>		2		AL, TN
54. <u>S. (S.) sp. cf. bulla</u>	1			TN
HETEROMYIINI				
55. <u>Clinohelea bimaculata</u>	2	1		NC, TN

Table 8. Cont'd.

Taxa	Number of occasions by which collected by			State
	Light Trap	Pupal Sample	Other Methods	
SPHAEROMIINI				
56. <u>Johannsenomyia argentata</u>	1			TN
57. <u>Mallochohelea albibasis</u>		1		AL, TN
58. <u>Probezzia pallida</u>		1		TN
59. <u>Sphaeromias longipennis</u>		1		TN
PALPOMYIINI				
<u>Bezzia</u>				
60. <u>B. (Homobezzia) glabra</u>		1		TN
61. <u>B. (B.) flavitarsis</u>		1		TN
62. <u>B. (B.) nobilis</u>	7	2		AL, TN
<u>Palpomyia</u>				
63. <u>subaspera</u>		2		AL, TN
<u>Phaenobezzia</u>				
64. <u>opaca</u>		2		AL, TN
Total number of species by method (s)	44	41	26	
Number of species <u>only</u> by given methods	19	12	3	

represented in mine (Table 3). Snow et al. obtained some 64 species (55 described at the time) among 15 genera (Table 8). Except for six species of *Forcipomyia*, and *Dasyhelea fasciigera* Kieffer (as *tristyla* Wirth), all of the Tennessee Valley species appeared in the present study.

Although a detailed analysis of the relative productivity and value of the various approaches to collecting Ceratopogonidae is not intended here, the comparative contribution of these approaches is exemplified well by comparing the data in my study with that of Battle, Snow and Lewis mentioned above. For example, my adult field trapping (AFT) results yielded 92 species, of which 21 were obtained only by this approach. The majority of the latter were Forcipomyiinae and *Culicoides*.

Habitat substrate samples yielded 159 species, 94 of which were limited to this direct source. The rearing cartons above yielded 154 species, 48 of which would not have been obtained by any other method. About 115 species were retrieved by the immatures extraction method (IMM + IR) and essentially all these species identifications were dependent upon associations made through rearing; 18 species and species groups were restricted to the individual rearing results alone.

Comparing the productivity of the 1015 collections yielding the results of Table 6, both the rearing carton (RC) and immatures extraction (IMM) methods yielded comparable results in terms of collections positive for Ceratopogonidae: 73% and 75% of the collections were positive by RC and IMM respectively (Tables 39 and 40). With both collections per site combined, the success of the collections increased to 85.5% of the 551 primary habitat sites. Battle's 362 collections, all evaluated by the

RC emergence method, were seemingly somewhat more successful on the whole, with 84.1% of his sites yielding one or more specimens. This is largely because 73% of all collections he took were repeated from 4-5 proven productive sites (94.7% positive) in Montgomery Co., VA (Sites A-E, Appendix F.2.2). By contrast, only 67.2% of his 119 collections taken elsewhere were productive, more typical of the stratified random approach in breeding habitat surveys (e.g., Jones 1961b, Williams 1964, Hair et al. 1966, Battle and Turner 1972, Lubega and Khamala 1976, Braverman 1978, Kremer et al. 1978, 1980).

These results compare quite well with those of other investigations of Diptera in comparable habitats studied over an extensive area. For example, Kremer et al. (1978) found 63.5% of 173 habitat collections to be positive for Ceratopogonidae in the floodplain of the Ried River, Alsace, western France. In a study of the *Culicoides* of the Camargue Swamp in southern France, Kremer et al. 1974 (*Ann. Parasit.* v.49(5):653-6) found only 37.5% successful emergence from 56 samples. It is likely that the long return trip to the laboratory reduced the emergence success. Braverman (1978) determined 71.7% of 138 sites in Rhodesia to be positive. Of 1475 samples taken by Lubega and Khamala (1976) in Kenya, 57% yielded *Culicoides*.

Larval tabanids are among the few groups living in habitats comparable to Ceratopogonidae for which significant amounts of collection statistics have been reported. From these reports it is apparent that the yield in specimens per unit sample is considerably lower than for ceratopogonids. For example, in 52.7% of 3241 soil samples which were

positive from six major semiaquatic and terrestrial habitat types in Mendocino Co., California, Lane (1976) discovered only 1437 larval and pupal tabanids (15 species), an average of 0.44 specimens per sample. Wilson (1969) found only 0.3 tabanid larvae per sample in 684 samples of alluvial vial wet bottomland in southern Louisiana. For his systematic study of immature Tabanidae of Arizona, based on extensive personal collecting, Burger (1977) obtained only 829 larvae and pupae. In the exemplary work on immature Tabanidae of eastern North America, Teskey (1969) drew on 4000 specimens collected over a 25-year period from 219 habitats, most sampled multiple times.

The value of the *en-masse* rearing/emergence method of obtaining Ceratopogonidae specimens from habitat samples placed into a container (RC) in the laboratory is amply demonstrated by the present results. While the approach has been widely used among the many investigators studying *Culicoides* habitats, the relative results are rarely compared with other methods. In this study, rearing and extraction yielded nearly identical results. The number of specimens extracted from the 545 substrate samples I evaluated averaged 11.0 per collection, very close to the average of 11.8 specimens which emerged from each of the 470 samples placed in the rearing containers. These figures are very similar on a per unit area of sample basis for the number of Ceratopogonidae retrieved by Kremer et al. (1978, 1980), who obtained 46.2 and 58.7 specimens per collection; each collection consisting of 500-600 cm². Thus, my samples and those of Kremer et al. yielded on the order of 10 specimens per 100 cm² sampled, averaged over all samples taken. This can be con-

sidered rather typical yield for an extensive survey of a broad spectrum of aquatic and semiaquatic habitats for Ceratopogonidae.

The contribution which rearing makes in area-wide collections is further exemplified by Snow et al.'s results (Table 8). There, pupal samples yielded 41 species, 12 of which were only obtained in that way, compared to 44 species by much more extensive light-trapping. In Trinidad, evaluating suspected *Culicoides* breeding habitats, Williams (1964) found that both emergence trapping in the field and incubating samples in the laboratory yielded 40% success rates.

1.3.4. Relative Abundance of Ceratopogonidae Genera

With respect to the relative generic and specific composition of ceratopogonid collections, it is generally considered axiomatic that *Culicoides* predominate, thanks to the sheer diversity of species in the genus (largest in the family--Table 5), and the large numbers in which some are known to be present. However, very few studies have systematically identified and enumerated the non-*Culicoides* occurring in surveys. While the results of this study and others I have evaluated here show that, on an area-wide basis, *Culicoides* do indeed collectively tend to rank first in abundance and species represented, I will show that *Culicoides* dominance is not so monolithic as it may seem. The picture depends very much on the method of collection and the nature of the sites collected at, as well as on the comparative weighting of density and frequency of collection.

Most surveys rely heavily on light-trapping, which inherently provides data skewed for those species which are attracted to light (e.g. Southwood 1978). Thus, *Culicoides*, *Atrichopogon*, *Dasyhelea* and *Forcipomyia* species make up the bulk of adult collections in this and most other studies. Some Stilobezziini can be moderately common at times.

But members of the tribes Sphaeromiini and Palpomyiini, in particular, are greatly under-represented in adult field trapping events as compared to their retrieval from habitat collections (e.g. Table 6). Also, in general, there is little correlation between abundance as collected by substrate and as collected by adult field trapping. In Table 6, *C. haematopotus* and *paraensis* provide typical cases in point: the former is much more common in rearings than in AFT, whereas with the latter the opposite is true.

The 14 most common genera in the Virginia region as recovered by the methods in this study are compared and ranked in Table 9. The 43 species encountered more than ten times by all methods in this study are listed in Table 10. These species account for some 80% of all records in the present work.

1.3.4.1 Abundance Index.

As a measure of the relative abundance of the genera and species reared from throughout the entire region collected, I calculated a single quantitative value incorporating the frequency and density of each species, which I termed the "Abundance Index":

$$A.I. = \sqrt{N_j} \times F_{coll}$$

where N_j is the total number of individuals (density) of each species observed, and F_{coll} is the frequency of collection, i.e., the number of sites at which the species was reared. In this case, all the values for each species in each genus were summed for all specimens reared from all relevant collections. This is the measure applied in Table 9 as well as in Tables 14 and 18 (Chapter 4) and Table 29 (Chapter 6).

The A.I. is related to the prominence value² used by Beals (1960) in the assessment of bird communities, and modified by others to apply to populations of benthic macroinvertebrates (Wilhm 1972). In determining the A.I., I considered frequency to be the most important figure, as an indicator of a taxon's relative breadth of distribution throughout the study area's sites, whereas the square root of the number of individuals serves to modify the frequency figure. In this way, species distributed over many sites will have relatively more weight than would a species reared in large numbers from a few sites. Thus, a species for which 100 specimens were taken from 25 sites would be six times as "abundant" as a species for which 100 specimens were found at four sites. Using standard prominence value calculations, the first species would be only 2.5 times as "prominent".

Whether one evaluates the species present on the basis of number of species per genus, number of individuals per species (summed by genus), percentage of total number of specimens, or A.I., the *Culicoides* always rank first, regardless of the collection or processing method (Table 9).

² Prominence Value = $N_j \times \sqrt{F_{coll}}$

However, the A.I. for the specimens reared shows the following order of abundance: *Culicoides*, *Bezzia*, *Stilobezzia*, *Dasyhelea*, and *Palpomyia*, followed by the considerably less abundant genera: *Alluaudomyia*, *Forcipomyia*, *Atrichopogon* and *Phaenobezzia*.

It is revealing to note that the *Bezzia* rank a strong second in abundance as determined by frequency of collection and number of specimens retrieved. In fact, by applying a measure of *biomass*, i.e., dry weight values, such as those obtained for related ceratopogonid species by Havelka and Caspers (1981), it may very well be that *Bezzia* species are a more significant element in some ecosystems in terms of secondary production than are *Culicoides* spp. I have assumed average weights of ca. 36-53 micrograms per individual *Culicoides* specimens, and 74-180 micrograms for individual *Palpomyia* species (which are comparable to *Bezzia* in size).

Simple ranking based on sheer numbers alone alters the order of abundance or prominence. Thus, comparing the ranks of the genera in my rearings by percentage of the total number of specimens retrieved, several genera switch positions: *Dasyhelea* now rank before *Stilobezzia*, and *Forcipomyia* and *Palpomyia* reverse ranks as 5th and 7th respectively. In the case of *Forcipomyia*, its position as 5th by simple numerical rank is largely due to the relatively large numbers, 284 specimens from only 3 sites, of a single species, *F.(F.) bipunctata*. The dominance of such species is reduced when the measure of abundance includes the distribution among sites, i.e. frequency of collection.

Table 9. Relative abundance of Ceratopogonidae genera in the Virginia region, as recovered by the methods used in this study. The genera are ranked in two ways: (a) simple rank, based on the percentage of the total number recovered by the collection or processing method involved; (b) abundance index values derived from the numerical abundance (number of specimens) and frequency of collection for the 40 most common species overall: $(\sqrt{N_T}) \cdot F_{coll}$. Abbreviations are explained in Table 6.

Genus	Simple Rank ^{1/}			Mean	Abundance Index ^{2/}		
	IR + IMM	FVB	RC		FVB	RC	WIK
n = 24 ^{3/}	n = 19	n = 14	n = 21	n = 24	n = 19	n = 19	n = 24
Culicoides	1	1	1	1.0	1	1	10,007
Bezzia	2	3	2	3.3	6	6	7,550
Dasyhelea	5	4	3	3.7	3	3	1,826
Stilobezzia	4	2	4	4.3	7	7	2,640
Palpomyia	3	5	6	6.0	10	10	1,039
Forcipomyia	10	-	5	6.3	4	4	246
Alluaudomyia	6	10	7	7.6	8	8	430
Atrichopogon	12	6	8	7.3	2	2	189
Mallochohelea	8	11	13	8.9	5	5	24
Isohelea	11	8	10	10.3	14	14	105
Sphaeromias	14.5	7	12	11.2	-	-	31
Phaenobezzia	9	-	9	11.3	16	16	180
Clinohhelea	18	12	11	12.0	9	9	69
Probezzia	14.5	9	15	12.8	-	-	14

^{1/} All genera which ranked in the top 10 in at least one of the categories are included.

^{2/} Sums of values for all species occurring among the 40 most common species. See text and Table 14.

^{3/} Number of genera applicable to column, of which those listed are the most common.

Table 10. Ceratopogonidae genera and species most commonly encountered in the present study (WIK and FVB records together). Numbers in parentheses give the actual total number of positive substrate collection sites and adult-field-trappings, combined.

Genus	Number of Sites at Which Species were Collected				
	≥10	≥15	≥20	≥50	≥100
Atrichopogon			[spp.]		
Forcipomyia		[spp.]			
Dasyhelea	oppressa (14)		grisea (24) mutabilis (42)		
Culicoides	bickleyi (11) mulrennani (11) sanguisuga (11)	furens (19) travisi (18)	baueri (29) bergi (36) biguttatus (26) guttipennis (20) palliferus (45) spinosus (40) venustus (35)	stellifer (89) variipennis (95)	crepuscularis (221) haematopotus (259)
Alluaudomyia	needhami (13)		[spp.]	bella (51)	
Isohelea			[spp.]		
Stilobezzia	lutea (12) viridis (11)	[sybleae Group]	coquilletti (45)	antennalis (75) bulla (51)	
Clinohelea	bimaculata (12)				
Sphaeromyias			longipennis (24)		
Bezzia	pulverea (11)	obellica (18)	flavitaris (32) glabra (35)	laciniastyla (75) solstitialis } 65L/ varicolor	nobilis (183)
Palpomyia	rufa (12)		lineata (32) novitibialis (45) plebeia (25) subaspera (22)		
Phaenobezzia			opaca sabroskyi } 25L/		

L/Species described or differentiated in literature after study completed.

The abundance of the genera is clearly a reflection of the α -diversity of the constituent species within a habitat, as well as of the γ -diversity, i.e., the richness in species of a range of habitats in a geographical area. The relative abundances can be considered to represent the basic pattern of niche utilization in the community (Southwood 1978). While generalizations about species diversity are not readily transferred to entire genera over a larger geographical area, the sort of switching in rank order referred to above, depending upon whether density alone or density and frequency are factored in, may well reflect real differences in resource-partitioning strategies among the genera. This assumes that species in a genus have a certain internal consistency from the ecological and evolutionary perspective.

In the case cited above, *Stilobezzia* and *Palpomyia* species appear to be more generally distributed among the habitats sampled than *Dasyhelea* and *Forcipomyia*, but the latter tend to occur in larger numbers per sample where they do occur. The latter two are more aggregated in semiaquatic niches (which are more generally distributed), while the former two tend to be less clumped, among more aquatic substrates (which are inherently more discrete). The relative abundance of *Bezzia*, *Stilobezzia* and *Dasyhelea* and *Palpomyia* species in the broad range of aquatic to semiaquatic habitats sampled in this study can be interpreted as an indicator of their generally wide distribution and eurytopic nature.

1.3.4.2 Analysis by Sampling Methods.

Comparing the influence of sampling methods on the spectrum of genera and species obtained, it is apparent that the rearing container (RC) approach yields consistent results, but that more selective approaches shift the species composition considerably. For example, in both Battle's and my rearing results, the five most common genera were *Culicoides*, *Bezzia*, *Stilobezzia*, *Dasyhelea* and *Palpomyia*, in that order.

The species composition can be compared between the various methods with a similarity coefficient (SC) such as Sorensen's:

$$SC = (2c/a+b) \times 100$$

where a = number of species taken by method A, b = number taken by method B, and c = number of species common to both methods (Southwood 1978, Wilhm 1972). To minimize the significance of rare species whose capture depends heavily on chance, the similarity coefficient was computed using only the 40 most abundant species found in this study.

By this measure, the RC results by Battle and myself (RC_{wik} : RC_{fvb}) were 70% similar. The similarity of the results obtained by RC and IR (RC_{wik} : IR) was 69%. However, the similarity between the species obtained by adult field trapping(AFT) and those by RC was only 33% and 43% for Battle's and my results respectively.

Therefore, overall, the AFT results did not complement the rearing results particularly well. However, a specific breakdown according to AFT method and locality of collection yields valuable supportive data on distribution and presence. Blacklight traps yielded the greatest number of species of the seven methods used to field-trap adult specimens, and

the D-Vac suction trap samples yielded the second-highest species total, but with a higher number of species per unit effort (Table 50). Also, the results by D-Vac were more directly associated with discrete macro- and microhabitats than were the light-trap results. The only specimens of *Leptoconops linleyi*, a new record for Virginia, were trapped by D-Vac in a discrete saltmarsh habitat (DV-14, Table 50). In general, D-Vac type samples have been shown to be less selective and to yield a greater number of species than other trapping methods (e.g., Tanner and Turner 1975).

For habitat-associated AFT species data, the potentially most valuable methods I used were emergence traps, tent traps, and sweeping, but the results were not sufficiently productive under the circumstances of my study to justify their extensive use. The results by sweeping, in particular, were quite unproductive; many attempts (not listed in Table 50) to sweep over suspected habitats yielded nothing. This is in contrast to the reliance ephydrid researchers place on sweeping by aerial net over "physiognomic habitat types" to ascertain habitat preferences of shore flies (e.g. Scheiring in Deonier 1979).

Estimates of the ceratopogonid species present along the aquatic shoreline and in aquatic/terrestrial ecotones are clearly best obtained by stratified random sampling of habitat substrate, but for species in hemiedaphic habitats which are more diffuse and widely distributed, AFT approaches provide more efficient indication of the area-wide presence and population of Ceratopogonidae.

Adult field trapping (AFT), combined, resulted in the following relative order of represented genera: *Culicoides*, *Atrichopogon*, *Dasyhelea*,

Forcipomyia, *Bezzia* and *Stilobezzia*, ranked by the abundance index. By specimen numbers (simple rank) alone, *Mallochohelea* occupies a surprising 5th position due solely to an unusually large number (>150) of *M. atripes* which appeared in a single highly productive light trap placed at a lakeside (BL-53). The fact that *Culicoides*, *Dasyhelea*, *Bezzia* and *Stilobezzia* occur among the six most abundant by both approaches -- rearing and trapping in flight -- reflects their ecological multivalency.

In the Tennessee River Valley, light trapping results yielded the following ranking of genera (by number of instances of collection): *Culicoides*, *Dasyhelea*, *Bezzia*, *Forcipomyia* and *Atrichopogon* (Table 8). However, the pupal samples taken in collections of open water, including treeholes, yielded species of the following genera predominately (decreasing order): *Culicoides*, *Dasyhelea*, *Stilobezzia*, *Bezzia*, *Forcipomyia*, and *Alluaudomyia*. For the latter samples, the most common single species was *Dasyhelea oppressa*, a tree-hole breeder.

Normally, in light trap samples, *Culicoides* species greatly outnumber ceratopogonid species of other genera. This applies throughout trapping seasons and over wide areas. Exceptions to this are apparently quite rare, and probably are limited to specific localities, and usually involve either *Atrichopogon* or *Forcipomyia* to displace *Culicoides* as the predominant taxa (e.g. BL-11, INC-61). Lewis (1959) found that *Atrichopogon* constitute 70.4% of the specimens and *Culicoides* 22.3%, at a single coastal salt marsh site in Connecticut sampled for 20 weeks. Yet at an inland site in the same study, *Culicoides* constituted 75.7% of the total, *Forcipomyia* 20.3%, and *Atrichopogon* only 1%. In an extensive study of

the aquatic Diptera of Upper Three Runs and other small streams in southeastern South Carolina, *Culicoides* were curiously nearly absent from light traps and substrate collections, as compared to other Ceratopogonidae (Knausenberger 1983, Morse et al. 1983).

With respect to rearing results, *Culicoides* also appear to predominate in most of the few studies which report other Ceratopogonidae, including those of Battle (Table 7), Snow et al. (Table 8), Kremer et al. (1978), Rieb and Kremer (1980), Dubrovskaya (1972), and Dzhafarov (1964). The prominence which *Culicoides* can attain even in reared samples is exemplified by Battle's data, where the genus constitutes 85.5% of all individuals, *Stilobezzia* 5.1%, *Bezzia* 4.3%, *Dasyhelea* 2.9% and *Palpomyia* 1.3%. Kremer et al. (1978) found that *Culicoides* occurred in 90% of all collections positive for Ceratopogonidae, and that 79% of some 8000 biting midges were *Culicoides*. Similarly, Rieb and Kremer (1980) found that 90.3% of 28,012 Ceratopogonidae which emerged were *Culicoides*. The other genera represented were *Dasyhelea*, *Stilobezzia*, *Monohelea*, *Mallochohelea*, *Probezzia*, *Palpomyia* and *Bezzia*.

Yet, studies such as the above tend to be restricted to sampling from alluvial, soft saturated to damp mineral sediments (hydro- and hygropel) or substrates high in organic matter, such as peaty muds. Typically, flood-plain habitats are involved. When one expands the range of substrates sampled to include materials such as moss-covered rocks, algal mats, film-covered plant detritus, lotic habitats including springs, plant beds, and benthic substrates, for example, then a wider taxonomic

diversity is encountered. While the *Culicoides* remain a significant component, they are no longer as dominant.

Thus, in my collections, which consisted of 58.4% lentic, 28.4% lotic, and 13.7% semi-terrestrial sites, *Culicoides* species only constituted 31.2% of the total number of reared specimens, whereas *Bezzia* comprised 25.8%, *Dasyhelea* 12.7%, *Stilobezzia* 12.3%, and *Palpomyia* 3.5% of the total. The genus *Bezzia* thus appears to be consistently comparable to *Culicoides* in abundance throughout the Virginia region in the wide variety of substrates collected, as has been clearly revealed here for the first time by the rearing approach.

In the relatively few ceratopogonid investigations which deal with the total biting midge fauna in a habitat, as in Krivosheina (1957a,b), a pattern of considerable diversity appears typical. For example, in a thorough analysis of the chironomid and ceratopogonid midge communities in semi-aquatic to damp terrestrial habitats sampled in northern and subalpine habitats in Germany, Strentzke (1951) encountered about 42 ceratopogonid and 43 chironomid species, mostly reared. Ten genera of biting midges were included in a revealingly diverse assemblage of species. *Atrichopogon*(5 spp.), *Forcipomyia*(7 spp.), *Dasyhelea*(5), *Culicoides*(5), *Isohelea*(1), *Monohelea*(2), *Stilobezzia*(1), *Serromyia*(2), *Palpomyia*(7), and *Bezzia*(6). The great majority of the species was associated with various subtypes of the "mesophilic hemiedaphon": consistently damp but not saturated substrates typically at lake margins and in wet meadows. The ceratopogonids were often characteristically associated with specific biocoenoses, i.e. midge communities representative of eco-

logical niches, or "centers of action", which are, as defined by Elton and Miller (1954), clearly recognizable structural units defining the place where a mixed population of species is engaged in the struggle for survival. *Culicoides* were prominent in only one of eight of the relevant biocoenoses.

Interestingly, these communities are apparently rather comparable to the ceratopogonid generic and specific composition (94 spp., 11 genera) encountered in emergence cages over four wooded spring brooks (order 1 and 2) in west-central West Germany (near Schlitz) by Havelka (1976a, b) and Havelka and Caspers (1981). Schwank (1981a, 1982b) thoroughly characterized some of the same stream systems' substrates and benthic microinvertebrates (with emphasis on the Oligochaeta and Turbellaria present) and found "many hundreds" of ceratopogonid larvae -- unfortunately, not many were retained (Schwank, pers. comm. 1984).

In the West German stream emergence studies, a divergent pattern in the species composition is revealed, when assessed by numbers of species and individuals as opposed to production biomass. While *Forcipomyia* and *Culicoides* species rank first and second in individual and species numbers, but when assessed by weight, *Palpomyia* and *Atrichopogon* rank on top, in both studies mentioned. By weight, *Forcipomyia* and *Culicoides* ranked between 3rd and 5th most prominent, which is also what *Atrichopogon* and *Palpomyia* ranked with respect to numbers of specimens (derived from data in Havelka 1976a and Havelka and Caspers 1981).

Emergence patterns of Ceratopogonidae from two first-order spring-fed streams that flow through climax forests near Lake Erie in western

Pennsylvania, have been determined by Rightor and Masteller (unpublished data, pers. comm. 1985), as part of series of studies on the emergence phenology of aquatic insects (e.g. Masteller and Wagner 1984) at these sites. The traps covered about 16m² of the stream and stream bank, and in general the study sites are comparable to those of the Schlitz emergence production studies in West Germany (e.g., Havelka 1976a). Over 50 species in 12 genera have been trapped from the two Lake Erie tributaries to date, and one-year's data shows a generic ranking, with respect to numbers of specimens, as follows: *Atrichopogon* (4 spp.), *Stilobezzia*(3 spp.), *Dasyhelea*(6), *Palpomyia*(9), *Forcipomyia*(7), *Culicoides*(10), and *Bezzia*(6), as the seven most abundant.

Results such as these reflect more accurately the true ceratopogonid species composition of such aquatic habitats than has been available from most existing sources concentrating on either single genera or other aquatic insects families and orders entirely. Likewise, diversified sampling, increasingly careful extraction procedures capable of retaining Ceratopogonidae, and attention to determination of the more intractable and smaller organisms has resulted in more complete lists of Ceratopogonidae, especially from lotic systems (e.g., Thienemann 1954, Roback 1976, Harris 1981, Knausenberger 1983, Simpson et al. 1986).

1.3.5. Synopsis of *Culicoides* Occurrence, Immature Stages, Breeding Sites and Biting Habits.

It is my intention in this section to incorporate the results of the present study into an overview with the following objectives: a) provide

a current synoptic assessment of the numbers, geographic distribution and prevalence of the *Culicoides* species of the Nearctic east of the 100th meridian, with emphasis on the species of the wider Virginia region; b) compile and tabulate the present state of knowledge about the species' larvae, pupae, and larval breeding habitats; c) summarize the adult feeding and host records vis-a-vis larval habitat knowledge for the species of the mid-Atlantic region. The published sources for the data are cited at the ends of Tables 41 and 42, and in Table 58.

1.3.5.1. Number of *Culicoides* Species and their Distribution.

Of at least 142 *Culicoides* species now known in the Nearctic (Table 5), 78 are recorded from eastern North America east of the 100th meridian (Table 41), including *C. jamaicensis* Edwards recently reported in Florida for the first time in North America (Wilkening et al. 1985)³. The most recent previous estimates of the number of Nearctic *Culicoides* were given by Wirth as 122 (Blanton and Wirth 1979:xi), and as 135 by Downes and Wirth (1981).

Arnaud and Wirth (1964) suggested an interesting rule of thumb concerning the relationship between the number of mosquito species (Culicidae) and the number of *Culicoides* biting midge species in a given geographic region: they pointed out that the ratio in numbers of mosquito and biting midge species may be close to 3:4, based on the example of the

³ Table 41 lists only 77 species because *C. jamaicensis* was reported after the table was completed. However, species number figures referred to in the context of FL and eastern Nearctic reflect this species.

British Isles, where prospecting for species in both groups is well advanced. There are now 33 species of British mosquitoes recorded (Service 1983, Vector Ecol. Newsl. 14(3):2), compared to 46 species of *Culicoides* (Boorman 1976), an exact 3:4 ratio. This ratio is not quite so close for France and Germany, where 45 species of mosquitoes are known (Service, *op. cit.*), as opposed to ca. 70 species of *Culicoides* (Havelka 1978).

This 3:4 ratio holds fairly well for states such as FL, MD, NY, or VA, where the *Culicoides* are adequately assessed. At least 167 species of mosquitoes are recorded in America north of Mexico (Darsie and Ward 1981), so there may eventually be *more* than 200 species of *Culicoides* found in the same region, in contrast to the estimate given in Table 5. Thus, the ratio of the species numbers figures of the two taxa, appears to be reasonably valid, at least for given regions in the Holarctic.

Distributional summaries and checklists of the status of larval habitat, as well as larval and pupal description information available, are summarized for 77 *Culicoides* species in Table 41, with records for the immediate Virginia region as determined by this study. Likewise, summary checklists for adult feeding habits and host records for the 54 *Culicoides* which are known or expected to occur in Virginia and adjacent states are provided in Table 42, in juxtaposition with the status of larval habitat knowledge, given for comparative purposes. In their geographic catalogue of species in the eastern United States north of Florida, Battle and Turner (1971) listed 50 valid species.

The totals of species now known for the most well-researched states are: 48 in Florida, 45 in New York, 44 in Virginia, and 40 in Maryland. Since Blanton and Wirth (1979) treated 47 species of Florida, one species was added by Wilkening et al. (1985).

For New York, Jamnback (1965) treated 36 species (not 37 as listed by him, because *C. dickei* Jones is a junior synonym of *C. furensoides* Williams). Since then, Cochrane (1973, 1974) added four new species (*bergi*, *franclemonti*, *juddi*, & *pechumani*). Guirgis (1984) encountered 37 species on Long Island, New York, of which 5 species (*footei*, *hinmani*, *mulrennani*, *nanus*, and *snowi*) were new records for the state; one sub-species, *C. variipennis australis*, was also newly recorded.

To the Maryland list, three species have been added since Gazeau and Messersmith (1970b) recorded 37 species. These three recoveries are: *C. husseyi*, by Wirth and Blanton (1971); *C. chewaclae* and *kirbyi* by Glick and Mullen (1982).

Since Battle and Turner (1971) recorded 35 species for Virginia, 4 others have been newly recorded in subsequent studies: *alexanderi* and *jamnbacki* (by Tanner and Turner 1975), *bergi* (by Cochrane 1973), and *husseyi* (by Zimmerman 1981 unpubl.). Of the 37 species I recorded in my study, 5 were new for Virginia: *bermudensis*, *denticulatus*, *furensoides*, *juddi*, and *sphagnumensis*. Thus, these 9 recent records (Table 11) bring the total known for Virginia to 44. All of these species, with the exception of *sphagnumensis* and possibly *furensoides*--both restricted to relictual bog habitats in VA and WV -- are additions which would have been expected because of their presence in neighboring states (Table 41).

An additional four species I believe most likely to be present because they have been collected both north and south of Virginia (Group 2 in Table 11). Another six *Culicoides* species I have judged potentially present, while perhaps uncommon in Virginia or immediately adjacent states (Group 3, Table 11). This latter group represents species with more or less wide distribution patterns either south or north of the Virginia region, and it is reasonable to expect species with either austral or boreal affinities to be encountered here, thanks to the favorable biogeographic position and topographic diversity of the middle Atlantic states. For the reasons given, one might expect Virginia to eventually show higher species totals for *Culicoides* than either FL or NY.

In North Carolina, 20 species are recorded (Brimley 1938, 1942; Wray 1967; Battle and Turner 1970b, 1971; Kline and Axtell 1976; Bowen 1983). The present survey added no new records of *Culicoides* in North Carolina. For South Carolina, Battle and Turner (1971) recorded 20 species, and Carlson(1981) lists 35 *Culicoides*, but nearly all of these are taken from distribution maps in Blanton and Wirth (1979) without substantiating data. In West Virginia, 18 species were recorded by Battle and Turner (1970a, 1971), but with 11 species added in this study, the total for that state is now 29. Kentucky has the fewest confirmed number of species recorded in the region, at only 11 (Table 41).

In an unpublished study of the *Culicoides* of Rockingham Co , in western Virginia, Jones (1974) collected 22 species by a combination of 3 collection methods (Table 43). I received many of the slides for ex-

Table 11. Culicoides species recorded in Virginia since 1971 (Battle and Turner, 1971) (Group 1), with an assessment of likely future collection of this genus in Virginia (as of 1985), in groups of decreasing likelihood. Asterisks represent first records. See also Table 41.

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Species

Published Distribution

Group 1. Recent records for Virginia obtained in this study.^{1/}

- *alexanderi Wirth and Hubert, 1962
- bergi Cochrane, 1973
- *bermudensis Williams, 1956
- *denticulatus Wirth and Hubert, 1962
- *furensoides Williams, 1955
- *husseyi Wirth and Blanton, 1971
- *jamnbacki Wirth and Hubert, 1962
- *juddi Cochrane, 1974
- *sphagnumensis Williams, 1955

- Mich., Que., Mass., Conn., Ky., Tenn.
N.Y. to Va.
- N.Y., N.C., Ga., La., Miss.
- Minn., east to Mass., S. to Md.
- Mich., N.Y., W.Va.^{2/}, Wisc.
- Ark., Fla., Md.
- Mich., Ontario, N.Y.
- Ala., Fla., La., Md., N.Y.
- Minn., Wisc., Mich., N.Y.

Group 2. Additional described species not yet recorded from Virginia, but whose presence there seems most likely.

- chewaclae Glick and Mullen, 1983
- kirbyi Glick and Mullen, 1983
- pechumani Cochrane, 1974
- tissoti Wirth and Blanton, 1966

- Ala., Md.
- Ala., Md.
- Fla., N.Y.
- Fla., Md., S.C.

(continued)

^{1/} All but husseyi from this study; husseyi from Zimmerman, 1981.

^{2/} as dickei Jones (1956), a junior synonym.

Table 11. (Cont'd)

Species	Published Distribution
Group 3. Other species not yet recorded from Virginia but whose eventual collection, while perhaps rare, reasonably can be expected.	
<u>alachua</u> Jamnback and Wirth, 1963	Ala., Fla., S.C.
<u>downesi</u> Wirth and Hubert, 1962	Maine, N.Y., Ontario, Mich.
<u>franclemonti</u> Cochrane, 1974	N.Y., Nova Scotia, Ontario
<u>multipunctatus</u> Malloch, 1915	Ala., Ill., Mo., Tenn. ^{2/}
<u>stilobezioides</u> Foote and Pratt, 1954	Minn., N.Y., Wisc.
<u>wisconsinensis</u> Jones, 1956	Iowa, Mich., N.Y., Wisc.
Group 4. Eastern Nearctic species least likely to be encountered in Virginia.	
<u>canadensis</u> Wirth and Blanton, 1969	Maine, Quebec, Wisc, Minn. ^{3/}
<u>utowana</u> Jamnback, 1965	N.Y. only
<u>West Indian</u> and <u>Gulf Coast</u> spp. (ca.10) ^{4/}	Peninsular Florida, etc.
<u>Southwestern</u> spp. (ca.10) ^{4/}	Oklahoma and west, south
Group 5. As yet undiscovered and/or undescribed species.	
<u>1/</u> and other central-southern states, to northern Mexico.	
<u>2/</u> and points north and west, to Alaska.	
<u>3/</u> see Table 45.	

amination, verification and identification. Included were two specimens of *C. juddi* Cochrane, the first record of the species in Virginia. My collections confirmed this record from another site in the Ridge and Valley province (WIK Coll. 159). In his Rockingham Co. work, Jones (1974) found 17 *Culicoides* in light trap collections, of which *C. sanguisuga*, *C. biguttatus* and *C. stellifer* constituted 82% of the specimens. Of seven species retrieved by emergence trap, 83% were *C. bickleyi* and *C. stellifer*. Collections of species biting man yielded five species, 93% of which were *C. sanguisuga* or *C. guttipennis*.

In a similar deciduous forest/open field situation at a camp only a few miles south of the above site, in Augusta Co., Murray (1957, *Mosq. News* 17 (2): 77-82) reported *C. obsoletus* as the strongly predominant (95%) species, among 15 species collected by light trap, whereas *C. sanguisuga* was not reported at all. On the other hand, Zimmerman and Turner (1983) reported *C. obsoletus* as the most common species at their Ridge and Valley light trap site, whereas Tanner and Turner (1975) recorded *C. sanguisuga* as the dominant (89%) species at a site a few miles west in the same physiographic province.

Among the 27 *Culicoides* in my light trap collections, *C. sanguisuga* and *C. obsoletus* ranked first and fifth respectively. Both species are very common in the deciduous forests of the Ridge and Valley, and the Appalachian Plateau Provinces (of Table 46). Their habitat requirements are similar, but apparently *C. sanguisuga* is more likely to be associated with higher elevation sites.

1.3.5.2. *Culicoides* Immature Stages and Habitats.

Jones (1961b) summarized larval habitat information for 29 species collected mainly in Texas and Wisconsin, but also from states in between. Jamnback (1965), in an extremely valuable contribution, summarized breeding habitat information for 32 species, including 29 species reared in his study. Battle reared 18 species (Table 7) in Virginia, and data for 16 of these (all but *C. bergi* and *C. sphagnumensis*) were incorporated by Battle and Turner (1971, 1972). In this study, I reared 33 species by RC, 20 by IR, while 27 species appeared in the AFT collections (Table 41).

For the Florida *Culicoides* fauna, Blanton and Wirth (197) described the habitat of 39 species, 83% of the total. The earlier literature on breeding sites is adequately summarized in the above references.

Among the 78 species now known in eastern North America, 32 (41.0%) are known as larvae (8 only incompletely, usually including only parts of the head capsule), 49 (62.8%) are known as pupae, and for 58 (74.4%) larval and pupal habitat data is at hand (Table 11A, 41).

Focussing on the greater Virginia Region, of the 48 species which are known, and 6 most possibly present there, 25 are at least partially described as larvae (46.3% of 54), 38 (70.4%) as pupae, and larval habitat known for 41 (2 incomplete) (75.9%).

Most of the species of *Culicoides* whose immature stages remain unknown are rare or localized in distribution. For example, in terms of absolute numbers of specimens of the 31 species collected in population studies by light and animal-baited trap at sites in three physiographic provinces of Virginia (Zimmerman 1981, Zimmerman and Turner 1983), the pupal stage

and larval habitat are known for over 99% of the adult *Culicoides*. As to the larval stage, 99.3, 94.6 and 86.3% respectively are known, in terms of *numbers* of adults collected in the Coastal Plain (CP), Piedmont (PP) and Ridge and Valley (RV) provinces. The only reasonably common species in Zimmerman and Turner's study whose larvae remain unknown is *C. spinosus* (2.8% of RV, 1.1% of RV population). Two incompletely known larvae are of the species *C. biguttatus* (7.4% PP, 4.5% CP) and *C. travisi* (8.7% RV, 1.2% PP). Other species whose larvae are yet undescribed will on occasion be prominent in adult collections, as *C. alexanderi* in a wooded section of Giles Co., in the Ridge and Valley of Virginia (Tanner and Turner 1975).

Similar considerations apply to reared specimens, although a higher proportion of the species tends to be rare. Of the 33 *Culicoides* spp. I reared, 18 (54.5%) are not known in the larval stage, but these represented only 16.3% of the total number of individuals reared. Battle reared 18 species (Table 7), 7 (38.8%) of which are unknown or incompletely known as larvae, representing only 12.2% of the total number of adults reared.

In the present study, combining all sites, the number of specimens of species unknown in the larval stage is proportionately higher in terms of total numbers recovered than in studies limited to a single habitat type or small geographic area. For example, Kremer et al. (1978) recovered 14 *Culicoides* spp. among 6300 specimens from floodplain mud habitats in eastern France, but merely 5 species comprised 98% of the specimens.

Despite the relatively high percentage of rare species reared in this study (an additional four species were recovered by adult trapping only),

the number of species for which significant new information can be added is limited because they constitute a small proportion of the total recovered. Thus, as to larval descriptions, for 6 species of *Culicoides* the present material may be sufficient to fill an existing gap in knowledge (Table 41): *baueri*, *bermudensis*, *paraensis*, *piliferus*, *spinosus*, and *villosipennis*. For pupae, the material from individual rearing in this study should allow first descriptions for three species: *hinmani*, *paraensis*, and *sphagnumensis*.

For an additional five species, new or significant supplemental information on breeding sites was obtained. No taxonomic descriptions will be presented here, but the larval habitats for the five *Culicoides* are characterized below. Habitat information for the other 28 *Culicoides* species recovered in this study to some extent adds useful new records or data, but largely it confirms what is already known.

Significant New Data on Larval Habitats.

1. *C. bergi*: Cochrane(1973) did not describe the habitat of this species although he did list several rearing records among the material studied: four were from creek or stream margins, one from a grassy puddle, another from a pond margin. He incorrectly listed specimens from F. V. Battle as light trap collections, rather than reared ones. Of ca. 20 sites which yielded *C. bergi* in Battle's rearings, all but two were in the Luster's Gate area in Montgomery Co., Virginia. The sites were about evenly divided among pond and stream margin sites, usually in livestock-enriched mud. Of the six sites yielding this species in my

studies, five were from loose sediment along stream and river margins, and one from thick gray-green to black muck (hygropel) along a farm pond, adjacent a fresh stand of *Alisma* water plantain.

The larval habitats of *C. baueri* and *C. bergi* are essentially indistinguishable, especially where their ranges overlap, such as in Virginia. Stream and spring margins are considered to be the favored habitat of *C. baueri* (Williams 1956b, Jones 1961, Blanton and Wirth 1979), which my collections verify, in that 14 of 16 records were from lotic margins. However, data from this study suggest that *C. bergi* is more likely than *baueri* also to be found breeding in pond-side mud substrates.

2. *C. debilipalpis*: In North America, the only existing habitat records are from wet tree- and stump-holes (Messersmith 1964; Smith 1965, 1966; Smith and Varnell (1967). In Trinidad, Williams (1964) reared specimens from decaying cocoa pods and bamboo stumps in dense shade. In Panama, the species was reared from a collection of very wet soil trapped on a split fallen tree trunk 10cm above ground level, and from a tree hole at 1.5m (Vitale et al. 1981).

Four productive sites in the present study yielded *C. debilipalpis* and only one of these sites was a tree hole -- a split black gum in the Great Dismal Swamp with decayed bits of damp wood and leaves near ground level (WIK Coll. 26). The other sites involved accumulations of wet seasoned leaves, either on the swamp forest floor (WIK Coll. 32, 313B) or in a marshy pasture (WIK Coll. 113A). Adults were collected in numbers

only in the Great Dismal Swamp by black light and sweep net, near sites 26 and 32.

Larval habitat preferences may be summarized as follows: Substrates normally comprise wet or damp decaying wood and seasoned leaf detritus, subject to flooding, but may contain an inorganic mud element. Tree-holes or -crevices and stump holes are typical habitats, though open forest sloughs with wet peaty substrates, including damp leaves and root material, may yield specimens, as have marshy substrates where leaves accumulate and age. Heavily shaded sites appear to be the rule: at least the immediate microhabitat was shielded from sun in all sites which have yielded this species. Production of this species in the southeastern U.S. may be analogous to that of swamp forest -inhabiting Tabanidae in that their breeding sites may not be stratified along a particular aquatic habitat, rather than distributed extensively throughout generally favorable wet wooded areas, with pockets of highly localized breeding in wet tree-hole habitats, especially those close to the ground.

The precise identity of this species is not fully settled. Wirth and Blanton (1971, Proc. Ent. Soc. Wash. 73(1):36) stated "there is a distinct possibility that [*C. debilipalpis* and *C. paraensis*] are wing pattern phenotypes of the same species, in which case *C. paraensis* has priority." Other species in the region which are very similar in appearance to *debilipalpis* are *C. furensoides* and *C. stellifer*. I have reared *C. paraensis* from only one site, a tree-hole in the Great Dismal Swamp (WIK Coll. 293A).

3. *C. furensoides*: Fresh sphagnum substrates in open sections of sphagnum bogs, often at the margin of water bodies, appear to be the preferred habitat of this little- collected species. It was recovered by Williams (1955, Proc. Ent. Soc. Wash. 57:269-74) in an emergence cage over sphagnum in a bog at the edge of a pond in Sheboygan Co., Michigan. In West Virginia, *C. furensoides* adults were taken at Cranberry Glades, as *C. dickei* Jones, which is considered a junior synonym (W. Wirth, pers. commun. 1977). Adult collections recorded in New York by Jamnback (1965) (as *dickei* and *furensoides*) suggest a pond- or lake-side marsh or bog association as well.

In four rearings during my study, three were at Cranberry Glades Botanical Area, Pocahontas Co., WV, in bog openings (glades) at 3350-3375 ft. elevation. All collections were from fresh sphagnum, sometimes including older basal growth and cattail or sedge stems. The pH of the water averaged 5.2. Sphagnum-free spots immediately adjacent to those from which *furensoides* were recovered yielded no specimens. These sites consisted of peaty slurry or peaty detritus with some emergent macrophytes.

An additional find represents a first record for Virginia, at the Beartown Mt. wilderness area, Tazewell Co., elev. ca. 4030 feet (WIK Coll. 400B). The collection was from a clump of sphagnum at the open margin of a pond. This site is a relictual representative of the Canadian Life Zone (Hoffman 1969) in the southern Ridge and Valley physiographic province (Table 46). The Virginia and West Virginia records represent a

significant south ward extension for *C. furensoides*, previously thought to exist only in Michigan and New York.

4. *Culicoides juddi*. Reared in a single collection of a rich brown mud substratum with cattail, sedge and rush detritus, taken from a marshy depression in a cattail stand surrounded by sloping pasture lightly stocked with cattle, in Roanoke Co, VA, Catawba Creek headwaters spring seepage (WIK Coll. 159, 22 Aug. 1975).

5. *C. mulrennani*: This species is abundant during June and July at Cranberry Glades, West Virginia, the only place I have collected it, with the exception of one biting record in Giles Co., VA (Table 38). It readily feeds on humans, at least in the eastern West Virginia and western Virginia region. This study yielded the first larval habitat record. A single female emerged from rich brown organic mud with plant detritus, sampled at a clump of emergent aquatic macrophytes in a mud flat adjacent Yew Creek, in a clearing of the bog forest at Cranberry Glades (WIK Coll. 277, 24 June 1976).

In Virginia, then, only 3 species (7%) of 44 *Culicoides* known at present remain to have their larval habitat discovered: *alexanderi* and *husseyi* (*piliferus* Group), and *beckae* (*guttipennis* Group). Members of the *piliferus* Group breed predominately in soft mud substrates in marshes, spring runs, etc. or in sphagnum bog situations. All known *guttipennis* group species are tree-hole breeders. Of the 54 species expected in the circum-Virginia region, an additional 6 species larval habitat remains unknown: *alachua*, *chewaclae*, *juddi*, *kirbyi*; and *pechumani* and *stilobezzioides* (*Segnis* Gr.). Together, these 9 species constitute 16.7%

Table 11A. Summary of the numbers of Culicoides species recorded in the eastern Nearctic, with numbers of adults, larvae, pupae and larval habitats known for each region and state listed. Figures in parentheses represent percentages of respective total numbers of adults.

State/Region	Numbers (%) Known in State Region			
	Adults	Larvae ^{1/}	Pupae	Larval Habitats
Eastern Nearctic [east of 100°W]	78	32 (41)	49 (63)	58 (74)
Mid-Atlantic U.S. [48 + 6] ^{2/}	54	25 (46)	38 (70)	41 (76)
Florida	48	19 (40)	35 (73)	39 (81)
Virginia	44	22 ^{3/} (50)	34 ^{4/} (77)	41 ^{5/} (93)
Maryland	40	20 (50)	32 (80)	33 (82)
New York	45	26 (58)	37 (82)	40 (89)

^{1/} Typically, 20% of larval descriptions are incomplete (e.g., based on head capsule alone).

^{2/} In Virginia and contiguous states, 48 species are known to be present, an additional 6 are possibly present (Table 11).

^{3/} Up to six more species could be added from material collected in this study.

^{4/} Up to three more species could be added from material collected in this study.

^{5/} Four species were added as a result of this study.

of the 54 species considered present in the region, but represent a very small proportion (perhaps 1%) of the *Culicoides* population numbers.

As a proportion of the total *Culicoides* population in the eastern Nearctic, the immatures known as larvae range from 41% for the region as a whole to 58% for the state of New York (Table 11A). Considerably more pupae have been described, so the proportions of pupae known for the various faunae range between 63 and 82%, for the same areas. With respect to the knowledge of the larval or pupal habitats, the figures range from 74% for the entire region, to 93% of the fauna recorded from Virginia to date.

It is pertinent to re-emphasize the point made in the beginning of this section (1.3.5.2.), that a higher proportion of immatures will be known with respect to the numbers of adults in the population collected by the most common adult-field trapping methods, than with respect to the number of species *per se*. Thus, numerically, between 85-99% of the Virginia *Culicoides* population collected by light trap and cattle-baited trap is likely to be comprised of species presently described in the larval stage.

Comparable figures were cited by Kettle and Elson (1978) for southeastern Queensland, Australia, another relatively well- prospected area. Great Britain's *Culicoides* population remains the best known proportionately, thanks largely to the work of Kettle and Lawson (1952, 1955). They were able to provide descriptions for 30 (88.2%) of the 34 species then known, to which some 12 species have been added since (Campbell and Pelham-Clinton 1960, Boorman 1976).

Despite the progress which has been made in description of larval and pupal stages of eastern Nearctic *Culicoides*, in particular, these descriptions remain scattered and uneven in completeness. The lack of revisionary syntheses and keys continues to be a major handicap in identifying the immature stages. Perhaps the present analysis and the larval and pupal *Culicoides* material reared and associated (ca. 20 spp.) in this study, but which was not further processed, will assist in the necessary next step, that of the eventual development of a monographic synthesis, including descriptions and keys which are more uniform and complete.

1.3.5.3. Host Feeding Records.

A disproportionately large percentage (39%) of the 18 species whose adult feeding habits are not definitely known (Table 42) also have no larval habitat records established. In contrast, of the 36 species whose feeding habits are known, only 4 (11.1%) have no larval habitat records. Similarly, fully 7 (78%) of the 9 species with unknown breeding sites also have no information on adult feeding. A significant proportion of these species are probably non-haematophagous.

As might be expected, the 12 most anthropophilic *Culicoides* in the mid-Atlantic region have more-or-less thoroughly characterized larval breeding places. In fact, with the discovery of *C. mulrennani*'s larval habitat in this study, *C. tissoti* remains the only species whose habitat remains undescribed of the 28 species recorded as biting man (Table 42). Five of the 31 species known or thought to feed on birds (columns 5 and 6, Table 42) do not have larval habitat records.

1.4. Summary and Conclusions -- Section I: Faunal Survey

1.4.1 Summarizing Discussion

Ceratopogonidae, despite being among the largest families of Diptera in the world, and ubiquitously distributed among aquatic and semi-aquatic habitats, have received only limited attention from aquatic biologists. Although studies on aquatic macroinvertebrates almost universally list biting midge larvae as present in the fauna, the family is treated superficially, if at all. Except for some of the economically important bloodsucking species of *Culicoides* and *Leptoconops*, details on the ecology and life history of biting midges are poorly known. Taxonomic resources on the immature stages are scanty and scattered.

Nevertheless, as I have discussed in this chapter, increasing numbers of studies, including the present one, are beginning to demonstrate the potential diversity of Ceratopogonidae in and along both lotic and lentic waters. Likewise, I have reviewed the major progress which has occurred in placing the adult systematics of this family on sound footing. The availability of excellent keys to genera, and to the species of many genera, has done much to advance opportunities for research with this family. By contrast, fundamental study on the biology and taxonomy of the immature stages, especially the larvae, has lagged seriously behind.

No evaluation had been done, before this study, on the actual status of larval, pupal and breeding site description, in terms of the proportion of species for which this information is available. Nor has a current

synopsis of the total ceratopogonid fauna of any particular state or region in the Nearctic been available.

The basic motivation for this study has been the lack of taxonomic literature to identify larvae and pupae adequately. The first step, then, was to assemble an appropriate body of specimens with which to proceed. This effort had two thrusts: acquisition of suitable material from existing collections, and field collection of original material. I chose to approach the latter guided by the principles of ecosystematics, which emphasize maximizing the amount of ecological, habitat and locality information associated with specimens, and the rearing of specimens.

In doing so, I had to address and deal with the very factors which have limited the attention given to this family in the past, and limited the precision of studies possible with immature Ceratopogonidae, for example:

1. Lack of association between immatures and adults, and limited attention to rearing in the past.
2. Inadequate sampling procedures, especially in the littoral zone.
3. Inefficient extraction procedures, particularly in light of the narrow cylindrical shape of the larvae, and a need for living, healthy specimens.
4. Small size of adults and immatures, with the corresponding hurdles related to specimen preparation.
5. Insufficient natural history information, especially to help focus the collection efforts in the most productive places and at the most appropriate time.

Specimens and Associated Data.

At the outset of this study, my expectation was that significant amounts of reared and associated or identified larval material would be available through loan, to supplement what I anticipated to be a relatively limited field collecting and survey effort. However, contacts with nearly 100 individuals and institutions turned up very little reliably identified and/or reared material, though over 7000 immatures were received(see Table 2A). Thus, one of my original premises at the outset of the study was not adequately realized.

As a result, it was necessary to place much greater emphasis than originally intended upon field collecting, and rearing by diversified means. While the original focus was on the genus *Culicoides*, I chose to process all Ceratopogonidae acquired, largely because the first season's individual-rearing results yielded only a handful of successfully associated *Culicoides*, but other genera were well represented. Also, earlier collections by students of E. C. Turner, esp. F. V. Battle, had resulted in considerable numbers of adults reared from habitat substrate placed in rearing cartons, from which only the *Culicoides* had been processed. I processed this valuable source of reared adults as part of this study.

Specimens and associated data were acquired from four main sources:

1. Breeding substrate collections and adult field trapping (AFT) by the present writer.
2. Previous collections of breeding substrate by F. V. Battle (1968-70).
3. Rearings from an earlier study on four Virginia streams concerning the impact of various effluents on littoral Ceratopogonidae and Chironomidae (1971-73).
4. Recruited from outside sources, other collectors.

Ultimately, Battle's collections constituted 16% of the 2291 collections I processed as a direct part of this study, which in total yielded nearly 9,000 larvae and pupae and about 17,600 adults. Some 14,800 of the adults were reared. Over 3,000 of the immatures were subjected to an ad hoc individual rearing (IR) process. Some 1,000-1,100 were directly linked with their respective larvae and pupae by IR. For approximately 90 species, adults have been associated with pupae, and I estimate that ca. 50 species have larvae individually linked with the adult and/or pupal stage as a result of this effort. I did not, however, attempt to review and sort the IR material fully. At least 40 species (in 11 genera) of larvae being reared in the IR dishes were photographed.

A considerable amount of time and effort went into the examination of the many unassociated immatures submitted by over 30 aquatic biologists from a dozen states. This activity, while relatively unrewarding in terms of definitive information received, did provide valuable exposure to a broad range of fauna from widely dispersed areas.

While the raw material of nearly 38,000 Ceratopogonidae specimens, all told, processed during this study is not particularly large compared to many benthological studies, involving, say, Chironomidae or Oligochaeta, it is appropriate to draw attention to the diversified nature of the collections (wide geographic scope, numerous habitat types, array of sampling tools and approaches for all developmental stages except eggs), which yielded an unusual balance between immatures and adults -- 44% and 56% respectively. Also, an unusually high proportion of the material is reared: fully 84% of the adult specimens are from known

substrates. Likewise, it should be remembered that individual rearing is highly labor intensive, as are the extracting, sorting, processing and identification activities for these particularly intractable organisms.

Any study emphasizing rearing and associating of developmental stages of insects by definition will be time-consuming and painstaking. To put the present study in perspective, for example, Mayer (1934c) relied chiefly on an extensive collection of reared and associated specimens assembled by A. Thienemann in 30 years' collecting. Mayer (1934c: 206) explicitly stated that his work of synthesis would not have been possible without "such a rich assemblage of material as contained in Thienemann's collection," together with Thienemann's rearing notes and literature collection. In addition, he obtained valuable collections of immatures and reared material from O. A. Johannsen, A. Remane, J. Zavrel, F. Lenz, F. W. Edwards and M. Goetghebuer, among others. Likewise, L. Thomsen (1937) had the benefit of decades of collecting by her supervisory professor O. A. Johannsen at Cornell University. Glukhova's (1979) monograph on larval Ceratopogonids was based on at least 20 years of painstaking sampling and rearing efforts (cf. Gutsevich & Glukhova 1970). Kettle and Lawson (1952) and Jamnback (1965) required over 5 years' intensive collecting to assemble the material for their *Culicoides* larval treatments.

While this study resulted in a rather extensive collection of Ceratopogonid larvae, pupae and adults from many sites throughout the Virginia region and the eastern Nearctic, I was not in a position at the time the study was underway in the field and laboratory to also process the specimens for full-scale taxonomic study. The need for such study

is urgent, so I trust that the necessary next step will be facilitated in part with the material assembled during this work.

Field Survey Methodology

A two-tiered approach to collecting and returning unpreserved samples back to the laboratory proved very effective, involving two subsamples per site, one subsample destined for extraction of live immatures, the other for rearing of adults from the original substrate in rearing cartons (RC), as summarized in Fig. 2A. Placing the unsealed sample bags in the cartons, and onto racks in the transporting vehicle, allowed specimens to continue development and even emerge successfully during transport. Most of the problems commonly associated with transporting unpreserved habitat substrates back to distant laboratory facilities were avoided, such as loss of developing and emerging specimens, drowning and physical damage of specimens through sloshing of water, a lack of air exchange, or heat build-up.

With the two types of samples, 85.5% of the collections, overall, were positive for Ceratopogonidae. Comparable values in the literature range between 37 and 72% positive. The use of a qualitative, but standardized, stratified random sampling strategy, and a variety of sampling tools for a diversity of habitat types, apparently contributed not only to productivity of the sampling efforts but also to high species richness, including many rare species, and over 40 new species(as yet undescribed). In addition to a selection of scoops, which were the mainstay in sampling, I consider artificial substrates (esp. the mesh-type), grab samplers and

drift nets to be promising as sources of ceratopogonid specimens which otherwise would be overlooked. Dip nets modified with finer mesh, underwater cone traps, creative designs of emergence traps (Bowen 1983, Pucat 1982, Rosenberg 1978) and floating traps (Boyle 1979) all would offer good possibilities for capture of the aquatic biting midges, especially in lakes and rivers.

The adult field trapping procedures were deployed as closely as possible to the sites of substrate collecting. The main aim was to provide more specimens to aid in diagnosing the species make-up of a habitat, on the assumption that a significant proportion of any immatures collected would not complete development into the imago. The most productive sources of specimens were: black light trap, D-Vac, and Malaise-type tent trap.

To make essential locality and habitat information associated with the specimens collected by myself and F. V. Battle more readily available to others, it is presented in condensed and collated form in the appendices. All specimens should be trackable based on the collection number and IR sequence number, as explained in Appendix F. Providing this information is consistent with the goals of ecosystematics (see Section 1.1.3).

Extraction and Recovery.

Of the several procedures used for extracting and recovering living larvae and pupae from the samples (Fig. 2A), the most suitable and efficient for a wide variety of substrates was sieve-washing followed by sucrose flotation. To increase the efficiency of retention of the cylindrical larvae, I employed screens of 325 or 172 μ mesh opening (U.S. Standard Sieve Nos. 60 and 80). My previous work and the literature indicated that sieves such as U.S. Standard Sieve No. 30 (595 μ), normally used to separate macroinvertebrates from the meiofauna, would not adequately retain ceratopogonid larvae, particularly since active escape was possible. Also, sucrose was used as a flotation solution, as opposed to $MgSO_4$, $CaCl$ or other salt solutions, because the latter are more likely to be toxic to the living specimens through dehydration. The sieve-flotation method of extraction yielded thousands of apparently fully viable specimens for individual rearing.

A behavioral-dynamic method of extraction, using modified Tullgren funnels, was also used fairly consistently, especially for bulky samples including plant materials, and routinely turned up specimens, though in small numbers. These specimens were not reared.

Recently developed or improved methods of extraction have considerable promise, such as the hypertonic solution/inverted funnel approach to larval self-extraction (Boreham 1981, Kline et al. 1985, Vaughan and Turner 1985). If used with the newly introduced density solutions of high molecular weight but low osmolality (see Section 1.2.3.1), the potential for dehydration toxicity would be minimized. Also, various elutriation

and Ladell-type extractors could be used successfully (e.g. Southwood 1978, Lawson and Merritt 1979), once they are validated for this family.

Rearing and Associating.

A direct (IR) and an indirect (RC) method of associating developmental stages formed the basis of all rearing efforts in this study. Individual-rearing (IR) was accomplished on soft 0.5 - 0.8% non-nutrient agar at a slant in 35 or 60 mm plastic culture dishes, with a "universal" food source provided from a hay infusion-based culture, and vinegar eel nematodes (*Panagrellus redivivus*). It was possible to simultaneously rear several hundred larvae at a time with this technique. Pupae were transferred in a plug of agar to emergence vials, and the larval exuviae retrieved from the clear agar (Figs. 3A - 6). The IR methods worked out in this study permitted development or prolonged survival of larvae in 15 ceratopogonid genera: *Alluaudomyia*, *Atrichopogon*, *Bezzia* (*Bezzia*) & *B.* (*Homobezzia*), *Clinohoelea*, *Culicoides*, *Dasyhoelea*, *Forcipomyia*, *Isohoelea*, *Johannsenomyia*, *Mallochohoelea*, *Palpomyia*, *Phaenobezzia*, *Sphaeromyias*, and *Stilobezzia*.

Thus, the IR procedure has proven most versatile for a wide variety of genera and species. It represents a major improvement in technique over those available for individual rearing of this group at the outset of this study. The main limitation of this technique applies to the provision of adequate nutrient sources, especially for the herbivores, and collector-gatherers, a problem which I did address to a limited extent (q.v.). Refinements of this individual rearing technique with an array

of appropriate modifications, taking the natural habitat characteristics into account, could make it an effective tool for rearing of wide variety of ceratopogonid and functionally similar organisms.

In the rearing cartons (RC), adults emerged from essentially the same substrate (subsample) as yielded the immatures (IMM), thus provided a comparatively reliable means of indirect association. Nearly 73% of RC samples and 75% of IMM samples were positive. The cartons were durable and portable, prevented the adults from returning to the substrate, and when set at an angle, provided an air-water-substrate intersectional line which permitted successful pupation.

Comparing the number of specimens obtained on the average from all samples, 11.0 individuals were extracted per IMM sample, and 11.8 adults emerged per RC sample. This suggests strongly that the RC results adequately reflect the true species composition of the samples. Up to 13 species were recovered from a single sample, but more typically, 3-6 species emerged per sample.

Species Numbers, Distribution and New Records.

At least 192 species of Ceratopogonidae, including 42 unnamed (new) species, were recorded during this survey, which included nearly 2300 collections in seven states. Most collections were in Virginia (86.5%), while 8.8% were in West Virginia, and 3.2% in North Carolina. Some 28 described species are newly recorded in VA, bringing the total known there now to at least 178, an increase of 18.7%. In WV, 56 new records were added, which more than doubled (127%) the number of species now known

there, to 100. For NC, only 20 new records were added, a 27% increase, to 94 species there. Among four states, there were 105 new records in all.

Two genera (*Isohelea* and *Leptoconops*) are recorded from Virginia for the first time, so that now 26 of the 36 Nearctic genera are known in Virginia (29 are found east of the 100th meridian). Three genera are newly recorded in NC (*Brachypogon*, *Isohelea*, and *Stilobezzia*), whereas 7 are new for WV.

The total number of 178 species in Virginia is the highest for any state other than Florida, where Wilkening et al. (1985) recently reported 212 species. Maryland's species list, at 159, is presently the third highest total recorded for the U.S. Most states, such as Tennessee, with 61 species, and in particular Kentucky, with merely 13 apparently recorded, lag well behind.

On the other hand, in a comprehensive geographic checklist (Table 45), I present an analysis of the fauna in the Middle Atlantic states, which reveals that at least 222 species are currently known from one or several states in that region, or 38.8% of the 572 Nearctic species total. Also, 32 additional species are listed, which I believe are most likely to be present, based on their known distributions, but which have not yet been collected. Thus, together with the undescribed species collected during the present survey, the total number of species in the multi-state region would approach 300.

Thirteen species have not been recorded previously from any of the Middle Atlantic states covered herein. I consider eight of the records

to be significant range extensions (Section 1.3.2), all of them of apparently boreal species southward.

New species are being described at an active pace. Thus, I have been able to document 572 species in the Nearctic, of which some 359 are found east of the 100° W., nearly as many as the 388 species confirmed only two decades ago for the entire Nearctic (Wirth 1965). I developed a conservative range for the true number of species in the Nearctic as 756-1115, based on rationale given in Table 5.

Of the 572 Nearctic species, I estimate that only ca. 16% are in any way described in the larval stage, while perhaps 34% of the pupae are identifiable, but it would take a specialist for many of these. For the *Culicoides*, by far the best known genus, 28% of Nearctic larvae and 49% of the pupae are theoretically determinable, but descriptions are widely scattered. My survey of the literature shows that as larvae, 21 Nearctic genera have descriptions of one or more species, and that 15 genera remain totally undescribed. For pupae, these figures are 26 and 10 genera, resp.

Members of the subfamily Ceratopogoninae, the vermiform larvae, are most likely to be encountered in aquatic studies, yet only 9% and 29% of the larvae and pupae, respectively, are determinable (excluding *Culicoides*). The "*Palpomyia-Bezzia* complex" referred to by many authors, could potentially include, at least superficially, nearly 150 species in nine genera and four tribes: Heteromyiini, Sphaeromiini, Palpomyiini, and even Stenoxenini. The great majority of these is likely to be aquatic, in the sense that they will be regularly found on emersed, submerged or saturated substrates.

The urgent need for up-to-date descriptions and keys is emphasized by the fact that every currently available generic key to larval Ceratopogoninae in North America is based on work that is 50 years old, and treats only perhaps 3% of the nearly 400 species in this subfamily. Important new descriptions and keys of ceratopogonine immatures in the European U.S.S.R. and Australia have appeared recently. They represent the beginning of a breakthrough, although their direct applicability to the Nearctic is limited, except at the tribal and generic level.

Species Richness.

The productivity of a multiple-approach collecting and extracting strategy, and emphasis on rearing, is demonstrated by the results of the present survey. This is reflected in: high species numbers; broad representation of genera; nearly even balance between male and female specimens; and balance between imagoes and immature stages represented in the collections. By not relying on a single method of collection, the potentials for bias were probably minimized. As is well known, for example, light traps typically yield a preponderance of females.

In my own collections, the rearing carton (RC) approach yielded 21 genera with at least 154 species, of which 48 were taken only by this method. Specimens extracted from substrate collections (IMM and IR combined) represented some 115 species (or more) among 19 genera; 18 of these species were taken only by this method. Since most of the identifications for this method depended upon the IR results and the immatures per se were

not all determined, it is most likely that even more species were obtained from the substrate collections.

The RC efforts of FVB yielded 82 spp (15 undescribed) in 15 genera. Twelve of these appeared only in his collections, 11 of those were undescribed.

The seven adult field trapping methods combined resulted in 92 species in 19 genera; 21 species were unique to this approach. The yield in specimens per unit sampling effort was considerably higher for AFT than for either RC or IMM/IR, but this is offset by the greater precision with respect to habitat information available through the latter.

The value of the RC collective rearing approach as a survey tool for Ceratopogonidae is further demonstrated by its productivity under two different conditions. Including only sites not previously visited, Battle's collections were 67.2% positive for ceratopogonids, whereas repeat visits to sites with known existing populations (e.g. sites A-D) averaged 90.3% positive per collection. The contribution which rearing can make is additionally exemplified by the results of Snow and others in the Tennessee River Valley (Table 8). There, pupal samples yielded 41 species, 12 of which were unique to that method, whereas much more extensive light-trapping yielded only 44 species.

Relative Abundance of Biting Midge Genera.

Very few studies have thoroughly identified and enumerated the non-*Culicoides* occurring in surveys. Alone the sheer diversity of the genus--with 142 species, the largest in the family -- gives the impression

that *Culicoides* would dominate the fauna. Yet, while the genus does indeed collectively tend to be among the very most prominent in biting midge collections of all sorts, both in terms of species and individuals, the situation is not so monolithic as it may appear.

The impression just described is largely the result of historical reliance on light trapping, which selectively attracts *Culicoides*, *Atrichopogon*, *Dasyhelea* and *Forcipomyia*, but greatly under-represents most Sphaeromiini and Palpomyiini, and less so, many Stilobezziini. The balance of species and genera, then, is affected by three main factors:

- o method of collection;
- o site/habitat of collection;
- o comparative weighting of density (# of specimens) and frequency of collection (# of sites);
- o an evaluation of relative biomass productivity.

For example, I "globally" evaluated the 14 most common genera and the 40 most common species, which accounted for 80% of all records in this study (Tables 9, 10). According to an "Abundance Index" (A.I.) which incorporates density and frequency, the ranking of genera is as follows:

- o RC/IMM/IR: *Culicoides*, *Bezzia*, *Stilobezzia*, *Dasyhelea*, *Palpomyia*,
Forcipomyia
- o AFT: *Culicoides*, *Atrichopogon*, *Dasyhelea*, *Forcipomyia*, *Bezzia*,
Stilobezzia

The A.I. gives greater emphasis to species distributed over many sites in modest numbers than to species present in large numbers but few sites.

The three most abundant species by far in this study, all records combined, were: *C. crepuscularis*, *C. haematopotus*, and *B. nobilis*. As a genus, *Bezzia* ranked a strong second overall. Most studies I reviewed showed the *Culicoides* constituting 60-90% of the fauna by numbers alone. In this study, *Culicoides* constituted only 31.2% of the total, while *Bezzia* comprised 25.8%. The fact that the abundance of members of the genus *Bezzia* may be comparable to *Culicoides* in area-wide collections has not been previously recognized.

It is likely that were one to take biomass (weight) into consideration, new light would be shed on the matter, based on indications from data on biting midge emergence production in streams (Havelka and Capers 1981). Many *Bezzia* spp. and other Palpomyiini, as well as Heteromyiini and Sphaeromiini, are considerably larger than other Ceratopogonidae. The evaluation of secondary production of Ceratopogonidae in terms of biomass, turnover, trophic relations, etc., would make very rewarding study.

The relative abundance of the genera is a reflection of the α -diversity of the constituent species within a habitat, as well as of the γ -diversity, that is, the richness in species in a range of habitats in a geographical area. Abundance can be seen to reflect the basic pattern of niche utilization in the community.

For example, *Stilobezzia* and *Palpomyia* species were more frequently encountered among the habitats sampled than *Dasyhelea* and *Forcipomyia*, but the latter occurred in larger numbers per sample where they did occur. These latter two tend to be more aggregated in semiaquatic niches (which

are generally distributed), while the former two tend to be less clumped among more aquatic substrates, which are more stratified and discrete.

While generalizations about species diversity are not readily transferred to entire genera over a larger geographical are, real differences are apparent in resource partitioning strategies among the genera. This assumes that species in a genus have a certain internal consistency from the ecological and evolutionary perspective. Here again, the data developed in this study should allow further evaluation of this sort in the future.

Culicoides Occurrence.

A synoptic compilation of all *Culicoides* species and their geographic distribution (Table 41) shows that there are now at least 78 species east of about 100°W, a band of discontinuity in distribution which can be recognized as approximately paralleling the isohyet of 20 inches of rainfall. Thus, slightly more than half of the 142 Nearctic *Culicoides* are east of this "boundary." In 1971, Battle and Turner recorded 50 species east of the Mississippi River. This compilation is presented in compact juxtaposition with notations as to:

- o which spp. were collected in this study by IR, RC or AFT;
- o whether the larvae and the pupae were described;
- o whether the breeding habitat is known.

The four states most thoroughly prospected for *Culicoides* in the region in question are FL - 48 species; NY - 45; MD - 40; VA - 44. At least 48 species are almost certainly present in Virginia, but not yet

recorded. I estimate that probably at least 54 *Culicoides* species are present in the Middle Atlantic states (Table 11). Because of the favorable biogeographic position and topographic diversity of Virginia in particular, the species total for Virginia eventually may well prove to exceed that of both Florida and New York.

This study yielded 37 *Culicoides* species in all. Battle and Turner (1971) treated 35 species from VA. Five *Culicoides* are newly recorded from Virginia: *bermudensis*, *denticulatus*, *furensoides*, *juddi*, and *sphagnumensis*.

The origin of recent records of distribution is summarized for the Middle Atlantic states and for Florida and New York.

I have confirmed the general validity for this region of an intriguing potential relationship between the numbers of species of Culicidae and *Culicoides* in a given geographic area. That is, the ratio between the species numbers apparently is fairly closely represented by the ratio 3 : 4 :: Culicidae : *Culicoides*. This was pointed out by Arnaud and Wirth (1964) for the British Isles. By this measure, one would expect around 208 *Culicoides* species to exist in North America, based on the fact that 167 mosquitoes have been reported.

Culicoides Immature Stages and Habitats.

To briefly summarize the deliberations presented on these points in Section 1.3.5.2 and Table 11A, among the 78 species now known in eastern North America, this is the status:

- o Larvae of 32 species (41%) described; at least 8 of these are incomplete. This contrasts with an estimated 28% of larvae described for the Nearctic as a whole.
- o Pupae of 49 species (62.8%) described (49% for Nearctic).
- o Some larval habitat data is apparently known for 58 species (74.4%).

For the 44 Virginia species, the following applies, with the results of this study:

- o Larvae: 22 species described (50%)
- o Pupae: 34 species described (77%)
- o Larval habitat: known for 41 species (93%)

The proportion of species' immatures and habitat which are known always increases as the geographic focus narrows. Thus, the species known as larvae range from 41% for the region as a whole, to 58% for the state of New York. Pupae are considerably better-known, so the proportions for the respective faunae of the same two areas are 63% and 82%. Habitats are at least basically identified for at least 74% of the species, up to 93% for the Virginia fauna, the highest for any state.

Four new larval habitat records resulted from this study: *C. bergi*, *furensoides*, *juddi* and *mulrennani*. Twenty-eight species in all were reared from habitat substrates. Also, based on collections and rearings resulting from this work, I estimate that adequate material exists therein to develop larval descriptions for perhaps six species for which none yet exist, and for the undescribed pupae of three species (cf. Tables 41, 42). Overall, I believe the material from this survey may contain usable larval specimens of possibly 20 species of *Culicoides*, and of as many as 30 species with pupae represented. However, these estimates are based on

my notes; I did not have an opportunity to fully sort and enumerate the immatures material. At most 50% of the above species' immatures have been successfully associated with adults.

Most species whose immature stages remain unknown are also rare as adults. As a result, a higher proportion of immatures will be known with respect to the absolute numbers of adults in the population collected by the most common field-trapping methods, than with respect to the number of species per se. Between 85 to 99% of Virginia's light-trapped *Culicoides* population numerically is likely to consist of species whose larvae presently are known, depending upon the location.

Similarly, a disproportionately large percentage of the species whose adult feeding habits are not definitely known also have no larval habitat records established. On the other hand, all but one of the 12 anthropophilic *Culicoides* species in the mid-Atlantic states have more-or-less thoroughly characterized larval breeding places (*C. tissoti* is the one exception). Clearly, the more commonly collected and the more economically important species have gotten the most attention. In this study, by contrast, a relatively higher (16%) percentage of species was rare, a reflection of the species richness due to the multiple-purpose methods.

1.4.2 Conclusions

A high taxonomic richness of the ceratopogonid fauna in the Middle Atlantic United States is reflected in the 150 described and 42 undescribed(new) species distinguished as a result of 2291 field collections made or processed during this survey. Collections represented seven states, but nearly 86% were in Virginia. There are now at least 178 species and 26 genera of Ceratopogonidae in Virginia, including new records for 28 species and two genera(*Isohelea*, *Leptoconops*), resulting from this study. The species total for West Virginia was raised by 56 to 100(127% increase), with seven genera newly recorded for there. In North Carolina, 94 species are now known, where 20 species and three genera were recorded for the first time.

At least 572 described species are present in the Nearctic, and I estimate that the true number of species ranges between 756 and 1,115. The present results, together with a close analysis of the literature for the ceratopogonid fauna of Virginia and the five contiguous states, produced a geographic checklist of 222 species in Mid-Atlantic region as a whole, plus another 32 described species likely to be found there eventually. With the 42 undescribed species from the present study, and others known to be present in existing collections, the total would exceed 300.

Only about 16% of the 572 Nearctic species are in any way described in the larval stage, while some 34% of the pupae are identifiable. For the *Culicoides*, by far the best known genus, 28% of Nearctic larvae and 49% of the pupae are theoretically determinable, but descriptions are widely

scattered. The vermiform larvae, that is, members of the subfamily Ceratopogoninae, are the most likely to be encountered in aquatic studies, yet only 9% and 29% of the larvae and pupae, respectively, are determinable (excluding *Culicoides*).

The productivity of the diversified collecting and extracting strategy employed in this study, with emphasis on two rearing methods, is reflected in high species richness; full representation of genera; large numbers of rare and new species; relatively balanced sex ratio(1.27 ♀♀ : ♂♂); and an unusually balanced representation of immatures and adults as proportions of the total(44 and 56%, resp.). Fully 84% of over 17,500 adults collected from known habitat substrates.

A multiple-purpose approach to sampling involving simultaneous subsamples, one for extraction of immatures and one to obtain emerging adults in rearing cartons, results in a high combined success rate for all samples. Extraction of immatures by sieve-flotation using sucrose density solution, was the technique most universally adaptable to a wide variety of substrates, and it yielded viable larvae for individual rearing.

The individual rearing(IR) procedures have proven most versatile for a wide variety of genera and species, and represented a major improvement in technique over those available for individual rearing of this group at the outset of this study. Refinements of the IR technique, particularly with respect to provision of appropriate food sources, could make it an effective tool for rearing a wide variety of ceratopogonid and functionally similar organisms. Also, this technique also provided 18 species not collected in any other way.

In the rearing carton (RC) approach, I found a productive source of specimens, and a comparatively reliable means of indirect association. This approach yielded 48 species which were taken only by this method. The cartons were durable and portable, prevented the adults from returning to the substrate, and when set at an angle, provided an air-water-substrate intersectional line which permitted successful pupation. In addition, the RC results appear to adequately reflect the true species composition of the substrates, i.e., there were no apparent biases due to the conditions in the rearing cartons.

The adult field trapping procedures, deployed as closely as possible to the sites of substrate collecting, provided specimens which overall were only 38% similar to the species obtained by rearing carton. Thus, the field-trapped specimens were of limited value in assisting in the determination of larvae not otherwise identifiable.

The relative abundance of the genera as determined by substrate-derived recovery differs significantly from the abundance resulting from adult collections. The ranking of genera for the reared and immature specimens was: *Culicoides*, *Bezzia*, *Stilobezzia*, *Dasyhelea*, *Palpomyia*, *Forcipomyia*. For the adult samples the ranking was: *Culicoides*, *Atrichopogon*, *Dasyhelea*, *Forcipomyia*, *Bezzia*, *Stilobezzia*.

The reason for the incongruence between the two is basically selectivity. Thus, for example, light trapping selectively attracts *Culicoides*, *Atrichopogon*, *Dasyhelea* and *Forcipomyia*, but greatly underrepresents most Sphaeromiini and Palpomyiini, and less so, many Stilobezziini.

The three most abundant species by far in this study, all records combined, were: *C. crepuscularis*, *C. haematopotus*, and *B. nobilis*. The abundance of members of the genus *Bezzia* may be comparable to *Culicoides* in area-wide collections, a fact which has not been previously recognized. As a genus, *Bezzia* ranked a strong second overall.

More than half(78) of the 142 Nearctic *Culicoides* are found east of the 100th meridian, which constitutes a "boundary of discontinuity" in distribution approximately paralleling the isohyet of 20 inches of rainfall. The four states most thoroughly prospected for *Culicoides* are Florida, with 48 species; New York, 45; Maryland, 40; and Virginia, with 44. Five of these were newly recorded from Virginia.

I estimate that probably at least 54 *Culicoides* species are present in the Middle Atlantic states (Table 11). Because of the favorable biogeographic position and topographic diversity of Virginia in particular, the species total for Virginia eventually may well prove to exceed that of both Florida and New York.

The proportion of species' immatures and habitat which are known increases as the geographic focus narrows. Up to 58% of the larvae can be identified for the state of New York, for example, and about half of the larval species can be determined in Virginia.

Habitats are much better assessed: at least 74%, and for Virginia, up to 93% of breeding sites are basically known. The latter is higher than for any other state.

Most species whose immature stages remain unknown are also rare as adults. As a result, between 85 to 99% of Virginia's light-trapped

Culicoides population numerically is likely to consist of species whose larvae presently are known, depending upon the location.

Similarly, a disproportionately large percentage of the species whose adult feeding habits are not definitely known also have no larval habitat records established. On the other hand, all but one of the 12 anthropophilic *Culicoides* species in the mid-Atlantic states have more-or-less thoroughly characterized larval breeding places

Considerable progress has been made in description of larval and pupal *Culicoides*, and their habitats, in the eastern Nearctic in particular. Nevertheless, the descriptions are widely scattered and uneven in quality and thoroughness. The lack of revisionary syntheses, descriptions and keys will continue to hamper efforts to identify immature Ceratopogonidae, and therefore the ability to proceed with the broad range of inquiries which such taxonomic resources would make possible.

Studies which resort to rearing or other means of obtaining adults from habitat substrates, as has the present study, typically turn up dozens of ceratopogonid species in a single stream or lake, and up to nearly 100 have been recorded. Application of precise and efficient collection procedures, together with improved larval keys, should result in wider recognition of the true taxonomic diversity of the family in and along lotic and lentic waters, and to increased involvement of the family in ecological investigations.

SECTION II
ECOSYSTEMATICS AND AUTECOLOGY OF THE
TRIBES HETEROMYIINI AND SPHAEROMIINI,
EMPHASIZING IMMATURE STAGES AND REARING RECORDS

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CHAPTER SEVEN

Summarizing Discussion and Conclusions

SECTION II -- INTRODUCTION:
ECOSYSTEMATICS AND AUTECOLOGY OF THE
HETEROMYIINI AND SPHAEROMIINI

II.1 Faunistic Overview

The two tribes, Heteromyiini and Sphaeromiini, form a biologically and morphologically closely-related group of species in the subfamily Ceratopogoninae. Larvae in the subfamily are vermiform, slender and generally rapid swimmers. Most are capable of a fully aquatic existence. These tribes constitute some 350 species in 29 genera worldwide, of which 57 species in 12 genera occur in the Nearctic.

The females of these medium to large midges are predaceous, normally on other Nematocera, Ephemeroptera, and often on their own mates. Striking secondary sexual characters, found in the female claws and fifth tarsomeres and abdomen, undoubtedly functionally related to the feeding and mating behavior, are used for primary taxonomic breakdown of tribes and genera in this section of the subfamily Ceratopogoninae, which includes the related Palpomyiini and Stenoxenini, plus three other tribes. Wirth et al. (1974) provide a most helpful worldwide synopsis of genera of the family, with taxonomic keys for separation of the genera, while Downes and Wirth (1981) present excellent keys and original illustrations to the 35 Nearctic genera recognized at the time.

The adult taxonomy of the Heteromyiini and Sphaeromiini is among the most thoroughly worked out in the family, and the fauna in the Nearctic is relatively well documented (Grogan and Wirth 1975, 1977a; Wirth 1962a,b, 1971; Wirth and Grogan 1977, 1979). This is particular-

ly true of the Middle Atlantic region of the United States. Very useful in this regard is the synoptic review of the taxonomy and biology of these tribes by Wirth and Grogan (1979) covering seventeen species in eight genera occurring in the lower Potomac River valley in the Maryland and Virginia counties, immediately adjacent to Plummer's Island and the District of Columbia. An important and welcome aspect of the latter work is the provision of pupal and larval descriptions for all the available material.

II.2 Status of Knowledge of Immature Fauna

Proportionately little attention has been devoted to the systematics of the immature stages of the Heteromyiini and Sphaeromyiini. Yet, for the genera which account for most of the species, at least representatives have been described. Of the 29 genera in the tribes worldwide, 5 have representative species which are known in the egg stage, 9 as larvae, and 13 as pupae (see Table 37, page). In the Nearctic and Palaearctic regions, of 12 genera, 5 are not known as larvae (*Heteromyia*, *Neurobezzia* and *Neurohelea*; *Johannsenomyia* and *Macropesa*; however, I have reservations about the *Jenkinshalea* larval descriptions -- see Chapter 3), whereas only two genera remain undescribed as pupae (*Neurobezzia*, *Neurohelea*). The known genera account for the great majority of species in the two tribes. On the other hand, the existing descriptions are usually rather sketchy, and the material is widely scattered among three or four zoogeographical regions. Also, the number of species described per genus is small, and, normally, the number of available associated specimens as such is very small. This situation

makes the development of valid keys difficult, because representative series are not available or readily acquired. While 10 of the 12 Nearctic genera have at least one representative pupal description from somewhere in the world, the number of species known as pupae in this region is relatively low. Pupae of at least 17 species (29.7% of the total fauna) are now described, of which fully 12 were treated by Wirth and Grogan (1979). The three species previously described include *Clinohoelea bimaculata*, *Jenkinshelea albaria* and *Sphaeromias longipennis* -- Chapters 2, 3 and 6). Unfortunately, all of the available pupal descriptions are less complete than is desirable to arrive at satisfactory distinctions. Only three Nearctic species have been treated as larvae, of which only one, *S. longipennis* (Loew), had been described prior to Wirth and Grogan's (1979) contribution of descriptions for *Jenkinshelea albaria*^{1/}, *Mallochohoelea atripes* and *S. longipennis* larvae. Although the proportion of described immature stages is low for the Nearctic as a whole, the situation is improved in the east Nearctic, where the majority of the descriptions have been made. Thus, while only 5.3% of Nearctic species are known as larvae, this proportion increases to 12% for the Virginia-region fauna. Similarly, nearly 50% of the pupae in the Virginia region are known in at least a preliminary way.

In Europe, the immature fauna, particularly larvae, of these groups is better known than in North America. This is partly because the fauna is less extensive (26 versus 55 spp. resp.), but importantly also,

^{1/} See generic discussion below, Chapter 3.

European aquatic biologists have tended to pay more attention to the immature stages of aquatic insects in general. The most significant work with respect to the European fauna in question is found in Rieth (1915), Goetghebuer (1923), Thienemann (1928), Lenz (1934), Mayer (1934c), and Glukhova (1971, 1977, 1979). Larvae of at least 11 species (42% of total), representing all but two (*Neurohelea* and *Macropesza*) of the eight European genera have been described and/or redescribed by Glukhova (1979), but no pupae are included in that work. Pupae have been briefly described for only about 7 species.

The only other zoogeographical region with a significant portion of the immature fauna described is the Australasian. Of some 65 species of Heteromyiini and Sphaeromyiini, about 15 species among 6 genera are known as pupae, but only 4 species in 4 genera as larvae (Debenham 1970, 1974; Kettle and Elson 1981). Only a handful of species is known in the Afrotropical (Ingram and Macfie 1921, 1922; de Meillon 1937; Mayer 1952, 1955a) and Neotropical (Mayer 1959) regions.

II.3 Biological Overview

Certain aspects of the adult biology have been reasonably well established for representative species. Thus, the insectivorous and mating behavior of the adult female has been noted by several authors, but most notably documented by A. Downes, who in 1978 published a monographic synthesis and summary of his own long-term observations, incorporating all previously published data. Downes devoted most of his attention to documenting prey capture, mating and related behavior,

but he also considered morphological attributes of the male and female, especially mouthparts, antennae and genitalia. He also speculated as to the possible functional significance of various structures.

Debenham (1974) contributed evidence that four species of Australian Heteromyiini and Sphaerommini, in the genera *Clinohoelea*, *Johannsenomyia* and *Nilobezzia*, prey on their males. She also described the presence, position and characteristics of the spermatophore in two species.

Oviposition behavior has been observed for several Sphaeromiini in Europe and America, but not yet for any Heteromyiini (Johannsen 1905, Wesenberg-Lund 1914, 1915, 1943; Rieth 1915; Hamm 1919; Munsterhjelm 1920; Lenz 1920; Thomsen 1937; Rieb 1981). This behavior is summarized below in the tribal discussion (Chapter 3, Section 3.1.2).

Biological information on the immature stages of these tribes is limited almost exclusively to rather brief qualitative observations relating to the habitat conditions under which larvae and pupae have been encountered.

I have drawn on all such observations available to me in discussing the autecology of the genera and species covered herein. Few studies have devoted specific attention to the biology and habitats of larvae and pupae. Eggs also have not been studied in any detail, except in connection with oviposition and notes as to hatching times (Johannsen 1905, Lenz 1934, Thomsen 1937, Williams 1955).

Much of the information which is available on immature stages of these groups deals with lake-inhabiting species. Muttkowski (1918) made detailed observations on the habitat distribution patterns of *Probezzia pallida* and *Sphaeromias longipennis*, as well as *Bezzia*

glabra and several other ceratopogonids he was unable to rear (and, therefore, identify), among the total fauna of the littoral zone of Lake Mendota, Wisconsin. At Loch Lomond Scotland, Weerekoorn (1953) observed the larval behavior of *Probezzia seminigra* (as *venusta*) and *Mallochohelea* sp. (poss. *nitida*), and provided strong evidence that the larvae leave the bottom substrate at night to seek pupation sites on the shoreline. He also made observations relevant to larval feeding preferences, suggesting that the larvae are predaceous. Williams (1955) added important observations on the pupation ecology of *Jenkinshelea albaria*, *Johannsenomyia ardentata* and several *Probezzia* spp. at the sandy margin of Douglas Lake, Michigan.

Benthic population structures and spatial distribution patterns of *Sphaeromias* sp. were assessed as part of the total midge population by Brundin (1949) in detailed limnological studies of several Swedish lakes. Glukhova (1979) also provided several observations on spatial distribution of *Sphaeromias* and other Sphaeromiini in various lakes of the European USSR, as well as data on the overwintering of *Sphaeromias* larvae and their developmental cycles, which, in most cases, appear to be univoltine. The secondary production of a composite of Sphaeromiini and Palpomyiini species from an oligo- to mesotrophic lake in North Carolina was estimated, using the size-frequency method, by Bowen (1983), one of very few quantitative studies of its sort done with any ceratopogonid.

Numerous ecological studies in lentic waters have involved unidentified Ceratopogonidae as part of the fauna. Many of the studies

include Sphaeromiini, judging from specimens received from collaborators and from specimens in existing collections. For example, larvae from colonization and distribution studies in a subtropical Florida lake (Cowell 1984, Cowell and Vodopich 1981) proved to include *Mallochohelea* prob. *atripes*. Other examples include Knausenberger 1983, Pearson et al. 1976, and White and Fox 1980. It appears that several of the early studies done by limnologists and aquatic biologists, which involved "*Palpomyia tibialis*" or "*Palpomyia* sp.", actually dealt with *Sphaeromyias* species. For example, in North America, Alexander (1925), Forbes and Richardson (1919), Lindemann (1942), and Surber (1951) reported considerable populations of *P. tibialis* in lakes and rivers, which I determined largely to be *S. longipennis*, from specimens at the Illinois Natural History Survey, U. S. National Museum, and VPI & SU Entomological Collection.

II.4 Systematic Order of Treatment

In the following systematic list (Table 12), 10 genera and 28 species (including the three probably new and as yet undescribed species) of the tribes Heteromyiini and Sphaeromiini likely to be encountered in the Middle Atlantic United States are presented in the order in which they will be treated in this section. The list includes 40 taxa, all of which are discussed in more-or-less comprehensive fashion according to the outline of subjects given below.

The numbers represent the species which were encountered in this investigation, in phylogenetic order, as they appear on the overall Ceratopogonidae checklist, in Chapter One (Table 3 on page 95). The

Table 12. Systematic List of the Heteromyiini and Sphaeromiini of the Middle Atlantic States, USA. Asterisks highlight:

* - Species not yet collected in Virginia or in immediately adjacent states, but whose recorded distribution indicates they should eventually be found in the region; ** - Species which are most commonly collected in this region. See also Tables 3 and 45.

=====	
Tribe Heteromyiini	Tribe Sphaeromiini (cont'd)
<i>Clinohelea</i>	** 127. <i>atripes</i>
** 120. <i>bimaculata</i>	128. n. sp. nr. <i>caudellii</i>
** 121. <i>curriei</i>	** 129. <i>smithi</i>
* - <i>nubifera</i>	<i>Nilobezzia</i>
- <i>pseudonubifera</i>	- <i>mallochi</i>
<i>Heteromyia</i>	* - <i>schwarzii</i>
** 122. <i>fasciata</i>	<i>Probezzia</i>
- <i>prattii</i>	** 130. <i>albitibia</i>
<i>Neurohelea</i>	131. n. sp. nr. <i>albitibia</i>
- <i>nigra</i>	- <i>jambacki</i>
Tribe Sphaeromiini	* - <i>nigra</i>
<i>Jenkinshelea</i>	** 132. <i>pallida</i>
** 123. <i>albaria</i>	133. <i>sabroskyi</i>
<i>Johannsenomyia</i>	** 134. <i>smithii</i>
** 124. <i>argentata</i>	- n. sp. nr. <i>williamsi</i>
<i>Macropenza</i>	135. <i>xanthogaster</i>
125. <i>pamunkeiana</i>	<i>Sphaeromias</i>
<i>Mallochohelea</i>	- <i>bifidus</i>
** 126. <i>albibasis</i>	** 136. <i>longipennis</i>
- <i>albihalter</i>	

geographic distribution of all of the described species treated in this section is presented in Appendix C (Table 45).

In all, 18 species, among 9 genera, have previously been recorded from Virginia specifically, and a careful review of the relevant literature has revealed that 25 described species in 10 genera may be expected in the region, including three (*Clinochelea nubifera*, *Nilobezzia schwarzi* and *Probezzia nigra*) which have not yet been recorded from any of the states contiguous to Virginia (see single asterisked entries in Table 12A below; an additional three species included in Table 45 but not here (*Jenkinshelea magnipennis*, *Nilobezzia minor* and *Probezzia albiventris*) are, in my judgment, considerably less likely to be encountered in the Virginia region than the former three (Bowen 1983 a,b; Grogan and Wirth 1977a; Knausenberger and Wirth 1980; Snow and Pickard 1953, 1958; Snow et al. 1957; Wirth 1951 a,b, 1962a,b, 1965 b, 1971; Wirth and Grogan 1977, 1979; Wray 1967).

For the present investigation, 19 species of these tribes were available from original collecting, including three new species and one recorded only from South Carolina (*Probezzia nigra*). Of the 19 species, 16 I managed to rear from habitat substrate samples.

Among the 16 described species found in the present study are 12 species which are clearly the most common in the region, marked with double asterisks in Table 12 . These 12 species comprise 91% of all specimens, and 86% of all collection sites for the 22 species, which have been collected in Virginia and surrounding states -- based on a compilation of literature records.

Five of the species recorded in the vicinity of the Potomac River

by Wirth and Grogan (1979) did not appear in the present study. All five can be considered uncommon or rare in the region: *Clinohelea pseudonubifera*, *Heteromyia prattii*, *Mallochohelea albihalter*, *Neurohelea nigra* and *Sphaeromyias bifidus*. On the other hand, four of the described species obtained in this study were not in the Potomac River valley fauna: *Macropesa pamunkeiana*, *Mall. smithi*, *Probezzia nigra* and *P. sabroskyi*. The former two are known from Virginia, while the last occurred in West Virginia only; *P. nigra* was collected near the Savannah River in South Carolina, and may well be found in North Carolina. An additional four species appear neither in this study nor in Wirth and Groan (1979): *C. nubifera* (recorded from New York to Florida), *Nilobezzia mallochi* (Maryland record), *N. schwarzi* (South Carolina record), and *P. jannbacki* (Maryland record). Therefore, two genera (*Macropesa* and *Nilobezzia*) and up to eight species may be added to the fauna represented in the study by Wirth and Grogan (1979).

II.5 Explanation of Format for Ecosystematic and Autecological Treatment

The following outline presents the organizational concept I followed in treating some 40 taxa (tribes, genera, species) consistently throughout the next five chapters, and briefly explains the scope and rationale of the coverage. The background to this species-oriented approach is given in the overall introduction, Chapter 1, Section 1.1.3.

This approach represents an eclectic assembly of ecological and systematic information and analyses about individual species analogous to the systematic descriptions found in classical taxonomic revisions.

It attempts to bring together and summarize all relevant data on the biology, ecology and systematics of each tribe, genus and species treated, while not presenting actual taxonomic descriptions (which had to be deferred). Discussions of the tribes and genera provide summaries based on all available published and original sources covered herein.

While the actual wording of section headings may vary according to the information available, the outline reflects the order of treatment adhered to in any case:

I. Synopsis of Systematics and Habitus

Reviews the current state of knowledge about the taxonomy and morphology of all life stages, but with emphasis on the immature stages -- especially the larvae and pupae -- from all relevant zoogeographical regions. Summarizes the key attributes of their habitus (external aspect and appearance), including sexual dimorphism, in the light of observations I made in doing determinations, and insights gained in using available descriptions. In the case of three probably new species and the larvae and pupae of several species, I provided some diagnostic details, but these are not by any means intended as species descriptions per se.

II. Habitat Characteristics: Results of Present Study

Presents the habitats and related biological information from collection and rearing records obtained in this study, and includes unpublished data which I gleaned from specimens submitted by collaborators, who, in many cases, sup-

plied habitat data when requested.

In making descriptive statements, in this and the next section, with respect to habitat, I sought to use consistent terminology based on normative sources dealing with aquatic habitat classifications, such as Cowardin et al. 1979; Elton and Miller 1954; Elton 1966; Illies 1961; Merritt and Cummins 1984; Pennak 1971; Southwood 1977, 1978; Vannote et al. 1980; and Wiggins et al. 1980). Sources dealing with classification of habitat distribution of fauna in littoral and wetland environments have also been helpful (e.g., Deonier 1965, 1979; Dubrovskaya 1972; Glukhova 1979b; Mayer 1934c, 1955a; Schwank 1981a,b, 1982a,b; Strentzke 1949; and Thienemann 1954). However, an effective synthesis of the habitat types at the aquatic/terrestrial interface is not available.

III. Autecological Discussion

Analyzes and interprets information on the ecology of individual species, focussing on the mode of existence of the immature stages (chiefly the larvae), with reference, as appropriate, to adult habits, in light of present results and a review of the literature. Presented under suitable subheadings, mainly:

A. Habitat Requirements/Preferences

Characterization of microhabitat and macrobiotope; physical and chemical attributes; factors governing larval/pupal distribution; substrate relationships, and

III. continued.

the like, as suggested by the observed distribution.

B. Larval and Pupal Habits and Behavior

Observations on larval movement, distribution, colonization pattern; prepupation and pupation behavior; morphological adaptations; phenotypic expressions, etc.

C. Trophic Relationships and Nutrition

Notes on feeding habits, based on personal observation during rearing and in the field, augmented by available literature records. I attempted to apply the terminology of Cummins (e.g., in Merritt and Cummins 1984).

D. Other Biological Observations

Includes rearing experiences, species associations or co-occurrence; natural enemies, overwintering pattern; other notable biotic interactions.

E. Adult Habits and Behavior

Comments on adult habits which have some bearing on distribution of immatures (i.e., eggs), such as oviposition, insectivory, mating, voltinism and seasonality.

IV. Geographic Distribution

Summarizes the known range of the taxa inside and outside the study area, with brief assessments of the biogeographic affinities and distribution among zoogeographic regions, physiographic provinces, etc.; an '*' denotes new county records.

V. Collection Records

Lists locality and collection data for all material

V. continued.

examined in this study in the autecological assessments, chiefly based on reared material. Generically identified larvae and pupae are occasionally listed if the data are referred to in the discussion. All collections are by the writer or F. V. Battle (indicated by collection number, with the initials WIK or FVB), unless otherwise stated.

Presented according to the following outline:

1. Individually reared (IR), or collectively in rearing cartons (RC).
2. Other sources of immatures (not reared).
3. Adults Field Trapped (AFT) (see Table 50).

VI. References

Annotated citations to literature, concentrating on works dealing with systematics of immatures and biology of the taxa involved. Includes appropriate references to taxa outside the Nearctic region, especially for genera. For taxonomic works dealing only with imagoes, mainly the most recent are cited, as these provide entry to the earlier taxonomic literature.

CHAPTER TWO

Ecosystematics and Autecology of the Tribe Heteromyiini

2.1 Tribe Heteromyiini Wirth 1962

2.1.1 Introduction

Of the 13 Nearctic species in 5 genera belonging in this tribe established by Wirth (1962a), 8 species in 3 genera are recorded from east of the 100th meridian. In Virginia, six species are now known (Figure 8 on page 212): 3 *Clinohelea*, 2 *Heteromyia* and 1 *Neurohelea* (see Table 5 on page 108 and Appendix C, Table 45 on page 578). Only three of the species were encountered in the present investigation.

The tribe is presently best represented in the Neotropical region, with 32 species among 6 genera (Wirth 1974, Grogan and Wirth 1979). In the Afrotropical region, 9 species are known from 4 genera, with many more species likely to be described (Wirth et al., 1980). Seven species in 3 genera are presently known from Australia and New Guinea (Debenham 1979). In Europe, only 2 species in 2 genera are present (Havelka 1978).

2.1.2 Systematics and Habitus Synopsis

Adult female Heteromyiini share the following main phenotypic characters (Wirth 1962a, Wirth et al. 1974, Wirth and Grogan 1979):

1. unarmed, often inflated fifth tarsomeres;

2. markedly bi-lobed or cordate, sometimes spine-tipped, fourth tarsomeres;
3. tarsal claws which are unequal, at least on the hind legs, or a single claw with a basal tooth;
4. abdomen lacking internal sclerotized gland rods (found in Palpomyiini and Stenoxenini, but not in Sphaeromiini);
5. lacking ventral pair of curved hair tufts near gonopore.

All of these characters apparently relate in some way to the insectivorous predaceous habit of the adult female, which has been documented, to some extent at least, for several genera in the tribe (cf. Downes 1978). However, the characters' specific adaptive value has not been determined. Phylogenetic relationships of the genera in the tribe were proposed by Grogan and Wirth (1979), who suggested that the Heteromyiini are monophyletic in origin.

Eggs of this tribe have not yet been described, to my knowledge.

Heteromyiini larvae are now known for three *Clinohelea* spp.: *unimaculata* Macq. in the Palearctic (Glukhova 1977, 1979), and two recently described *Clinohelea* species in Australia, also for the Australian *Pellucidomia leei* Wirth (Elson-Harris and Kettle 1986a). Until very recently, few valid generalizations at the tribal level could be derived from larval characters. Such a diagnosis has now been proposed by the latter authors based mainly on their detailed descriptions of the three heteromyiine species mentioned.

The larval head capsule of known Heteromyiini lacks the caudal triangular expansion apparently characteristic of Sphaeromiini. The combination of characters provided by Elson-Harris and Kettle (1986a)

should serve to also separate heteromyiine larvae from most (but possibly not all) instar IV Palpomyiini (for example, some *Palpomyia* have frontal sutures ending near sensillum "k", and share other common features in part). Particularly to be welcomed is their attention to description of pigmentation characters.

In her larval key, Glukhova (1979) distinguished Heteromyiini from both Sphaeromyiini and Palpomyiini more or less "by default", on the basis of the exceptionally long mandible of *Clinohelea unimaculata*, a character which applies to *Cl. bimaculata* in the Nearctic as well.^{1/}

Larval *Pellucidomyia leei* possess two unusual features which are in themselves distinctive: a clearly defined, curved transverse suture posteriorly on the head capsule dorsum, and the existence of distinct longitudinal grooves and pleats on the cuticle of the entire thorax and abdomen.

Pupae of four species in this tribe have been described from the New World: *Clinohelea bimaculata* (Loew) and *Heteromyia prattii* (Coq.) from the Nearctic, and the Neotropical *H. wokei* Wirth and Grogan and *H. clavata* Williston (references below). In Australia, the pupae of two *Clinohelea* species and *Pellucidomyia leei* have been described in detail (Elson-Harris and Kettle 1986a). An incomplete pupa of *P. leei* had also been described by Debenham (1970).

In all known heteromyiine pupae, the ventral glandular disks are absent. The tribal diagnosis provided by Elson-Harris and Kettle (1986a),

^{1/} In my collection there is larval material for *Clinohelea* prob. *bimaculata*, which remains to be described.

while excellent, does not account for features of *Heteromyia* pupae, which for example, possess very short am setae on the operculum. Known Heteromyiini pupae tend apparently to possess enlarged setal bases (abdominal or thoracic tubercles or both) and unusually developed setae or spines. On the other hand, the nature of spines and setal bases on the thorax and abdomen have not been characterized in existing descriptions of *Heteromyia*.

The pupae of the three known genera are strikingly different at the generic level, but at the tribal level, features they have in common remain to be homologized. Until Elton-Harris and Kettle's (1986a) contribution, existing heteromyiine pupal descriptions have been too incomplete, thus comparative analysis is difficult. In particular, necessary details of the abdominal armature (tubercles, setae, etc.) and cephalothorax as outlined by Mayer (1957) have generally been lacking. There is no doubt, however, that adequate characters exist in the pupae, and that they could contribute to a strong concordance between pupal and adult systematics.

2.1.3. Autecological Review

The heteromyiine species for which pertinent information is available appear quite consistent in their habitat characteristics: (a) moderate to dense shade under trees or among thick emergent wetland vegetation; (b) soft, water-saturated littoral emersed or submerged mud or sand with high organic matter content, largely coprogenous, usually including coarse particulate vegetative detritus (esp. *Clinohalea* spp.); or (c) a

phytophilic association, such as with mosses or floating/submerged vascular plants, often also in association with organic sediments (*Heteromyia*).

These heteromyiine sub-habitats are most often encountered in the forested, shrub, or emergent vegetation sections of palustrine wetlands. Less commonly, they may also be found along depositional and backwater stretches of lower perennial riverine systems.^{2/} Interestingly, however, all of the three recently described Australian heteromyiines were encountered in close association with streams. *Clinohelea tasmaniensis* Lee is the only species whose habitat appears to be somewhat inconsistent with the characteristics described above, in that it was collected from an unvegetated red clay margin of a stream.

The unusual species *Pellucidomyia leei* Wirth, has been consistently collected and/or reared from a variety of creek habitats in Australia (Wirth, 1960; Debenham, 1970, Elson-Harris and Kettle 1986a). Typically, pupae have apparently been found floating in partially-shaded temporary backwaters, along sandy stretches, at the sand-water interface where algae and leaf litter were present. Also, they were reared from a deep-sided timbered creek almost completely shaded. The pupae were floated out from an organic matrix at the creek margin. In the first habitat, several *Culicoides* species were also collected; in the second, no other Ceratopogonidae were taken. The only definitive recovery of larval *P. leei* was from moss attached to a rocky outcrop in the center of rapid water in a creek (Elson-Harris and Kettle 1986a). These authors

^{2/} in the sense of Cowardin et al. (1979): notably creeks, streams and small rivers.

speculate as to the possible significance of the differential development of the abdominal and thoracic tubercles and setae in light of distinguishable habitat features. This will be discussed in Chapter 7.

Known larvae swim with a moderately rapid, typical "anguilliform" or serpentine movement. Feed readily on nematodes (*C. bimaculata*, *C. tasmaniensis*) and are distinctly negatively photokinetic.

2.1.4. Annotated Taxonomic and Biological References

Debenham 1970:133-138 (pupa and habitat of *Pellucidomyia* in Australia).

Grogan and Wirth 1979a:51-59 (key to tribe, phylogeny; new Neotrop. genus, *Physohelea*)

Wirth and Grogan 1979:854 (keys, diagnoses, and biological notes for 6 spp. in northern Virginia region, incl. descr. of pupae of 2 spp., brief diagnosis of larva; references to earlier lit.)

Elson-Harris and Kettle 1986a:1-14 (larval habitat, keys and descriptions for larval and pupal *Clinohelea dryas* Debenham, *C. tasmaniensis* Lee and *Pellucidomyia leei* Wirth, Australia; notes on unusual larval and pupal characters in *Clinohelea* and *P. leei*)

See also the genera *Clinohelea* and *Heteromyia* below for additional references.

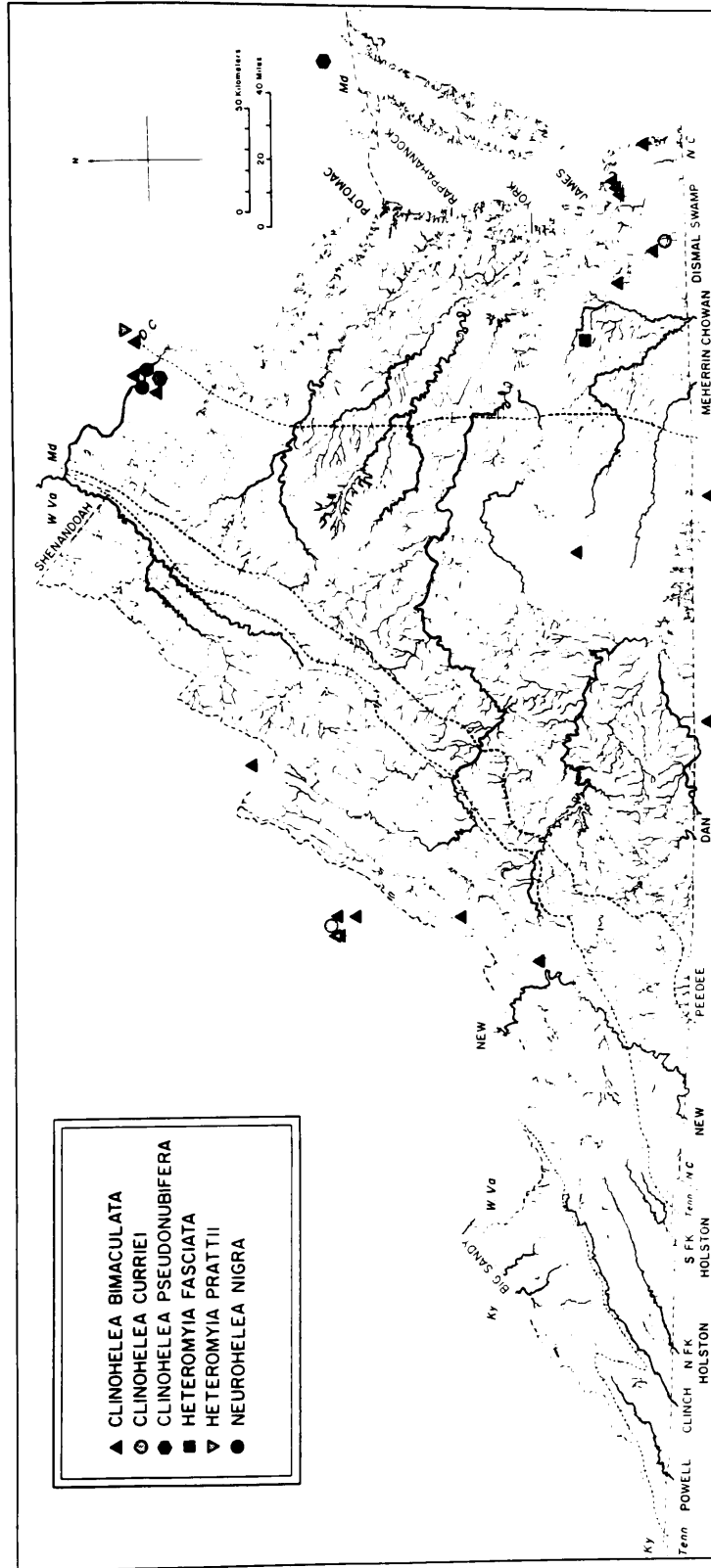


Figure 8. Geographic distribution of the six members of the tribe Heteromyiini in the Virginia region.

2.2 Genus *Clinohelea* Kieffer

2.2.1 Systematics and Habitus Synopsis

The only immature stage of the genus which has been described from North America is the pupa of *Cl. bimaculata*. The only larva described is that of the European *unimaculata* Macq., which has unusually long and slender mandibles about a third as long as the head³. Important new details on the sensillae and other structures of the "oral field" of larval *unimaculata* have been illustrated and described by Glukhova (1979:20-21) in the context of an overview of larval external morphology. Wirth and Grogan (1979) drew on Glukhova's (1977) figures to provide a diagnosis of the larva, including description of the setation. I identified several specimens of unassociated larvae as *Clinohelea* based in part on the similarity in pigmentation to the *Cl. bimaculata* reared⁴ in this study, but mainly on the basis of the presence of extremely long mandibles and other features I consider to be characteristic of the tribe (see above).

2.2.2 Autecological Review

The two Nearctic species (*bimaculata* and *curriei*) for which specific habitat information is available from rearings (see below), appear to prefer very wet substrates high in organic matter and which are rather heavily shaded, normally by deciduous hardwoods. The most common general habitat is a lentic swampy/marshy one, but margins of smaller watercourses regularly present suitable microhabitats.

³ Two Australian larvae have just been described (see Section 2.1.2).

⁴ To be described elsewhere.

A western Nearctic species, *Cl. usingeri* Wirth, occurring in the Mojave and Sonoran deserts (Grogan and Wirth, 1975), was judged by Wirth (1952) to be an inhabitant of algae in ponds and lake margins, on the basis of "repeated close association of adults with . . .this habitat".

In Europe, *Clinohelea unimaculata* is recorded from standing water habitats (Havelka 1978), and in the USSR, Glukhova (1977) describes the larval habitat as being heavily vegetated muddy substrates in riverine flood plain marshes where sedges and grasses abound.

A recently described African species from the Republic of Guinea, *Clinohelea hygropetrica* Clastrier 1983, was reared from a mixture of earth, roots and decomposing detrital organic matter in numerous small shallow rock pools draining from one to the other on a sandstone plateau bordering a river. The rockpools were subject to drying outside the rainy season. Another series of specimens was reared from a felt-like mass of roots at the base of a reservoir spillway and from hygropetric mosses moistened by splashing water from the overflow (Clastrier 1983). Another new species of *Clinohelea* was obtained by the same author from mud collected at the edge of a rice paddy.

Unpublished collection records for *Clinohelea* larvae, not determined to species (because unassociated with individually-reared adults), add useful information on the larval habitat characteristics of this genus in the eastern U.S.:

1. Two larvae, prob. *Clinohelea* sp. (deposited in Academy of Natural Sciences of Philadelphia, det. WIK), were collected by S. S. Roback from a littoral substrate, under water, in Wolf Creek, Pennsylvania,

during an acid mine survey (Sta. 6, 1-IX-1967). No further habitat data was obtained.

2. A set of three larvae, probably *Climohelea* sp., was one of 12 taxa among 40 larvae of ceratopogonids which I received for determination from Yellow Lake, a munitions plant effluent settling pond at Pine Bluff Arsenal, Arkansas (E. S. Bender, pers. commun. 1978).

The attributes of the latter collection area (Pearson, et al. 1976) are not only characteristic for the genus but are also instructive as to the apparent pollution tolerance of these larvae. Thus, Yellow Lake is a shallow, annually-flooded 80-ha pond in an isolated loop of an old meander in the Arkansas River. The *Climohelea* larvae were collected on 25-VII-1975, in 50-60 cm of water, from soft bottom mud which consisted of a 2-3 cm layer of rich, loose organic greasy clay (gyttja) over an anaerobic reducing layer. Analysis of the sediment showed an average of over 95% clay/silt, with 10-11% organic carbon, mostly of fine detritus and root fibers. Willow and other inundated trees shaded the sites, and floating vascular plants covered the surface, notably *Lemna*, *Azolla* (a fern) and *Potamogeton* spp. These latter habitat characteristics might be considered "archetypical" for *Climohelea*.

However, it is clear from the substrate chemistry and water quality data of Yellow Lake that this genus and possibly the other ceratopogonids collected there are at least facultatively tolerant of fairly severe pollution by elemental phosphorus and DDT-isomers, in waters with a pH averaging 8.6. The elemental phosphorus in the water ranged from under 1.0 to over 20.0 mg/l, in the sediments from about 0.1 to over 40 mg/kg

wet weight. Concentrations of phosphorus increased 10-fold after rains, and major bioaccumulation was detected in fish. DDT isomers were recorded at between 2.0 and 26.7 mg/kg in the substrates. Further details on the chemical/physical data of the Yellow Lake site are given in Pearson (et al 1976), together with data on biological collections.

2.2.3 Geographic Range

Five of the 7 species of *Climochelea* known to inhabit North America are found east of the 100th meridian: 3 in the *Unimaculata*-Group (*curriei*, *nubifera*, and *pseudonubifera*) and 2 in the *Bimaculata*- Group (*bimaculata*, and *longitheca*). Of these, only *Cl. nubifera* (NY, FL) and *longitheca* (FL) are *not* now known from the Virginia area, but it is only a matter of time until *Cl. nubifera* is reported from there, given its present known occurrence in New York and Florida. *Cl. bimaculata*, and to a somewhat lesser extent *Cl. curriei*, are fairly common and widely distributed species, but *Cl. pseudonubifera* is an apparently uncommon species.

2.2.4 Annotated Taxonomic and Biological References

- Wirth 1951a:321 (description and figures of pupa of *bimaculata*)
- Grogan and Wirth 1975:275 (revision of the seven Nearctic species, key, figs., distr. maps; pupa of *Cl. bimaculata*)
- Wirth and Grogan 1979:855-859 (descr. figs., and brief notes on habitat of 3 spp. in northern VA region; larval diagnosis)
- Glukhova 1977:437 (larva of *Cl. unimaculata* (Macquart) 1826, keyed, figured; habitat; Palaearctic)
- Glukhova 1979:21, 156-158 (larv. mouthparts and sensillae, larva of *Cl. unimaculata* descr. fig. biology, USSR)
- Clastrier 1983a:19-26. (habitat of 2 new Afrotropical species reared from pupae)

- Elson-Harris and Kettle 1986a:1-14 (larval habitats, descriptions and keys for pupae and instar IV larvae of two *Clinohelea* and one *Pellucidomyia* species in Australia)

2.3 # 120. *Clinohelea bimaculata* (Loew)

2.3.1 Systematics and Habitus Synopsis

Eggs and larvae of this species remain undescribed. From individual rearing observations in this study, the larva was noted to have rather strong subcuticular brown pigmentation broadly distributed on the dorsum of the thorax. The head capsule is a golden stramineous color, has small eyespots; the characteristic mandibles are long, narrow, and sickle-shaped. The one larva which successfully pupated, did so at 7 mm length and yielded a male adult.

The pupae of both sexes are stramineous to light brown, have a characteristic narrow operculum with a pair of rounded well-developed tubercles each bearing a long seta; the anal segment is about twice as long as broad, with sharp-pointed, heavily sclerotized tips directed straight caudad.

2.3.2 Habitat Characteristics in Present Study

All adults trapped in the field were taken at Cranberry Glades (ca. 3550 ft. (1020 m) elev.) on the open glade. A single male was reared from peaty ooze (tyrphopel or dy) in a small pool surrounded by sphagnum and sedges in an alder thicket between two glades. The other specimens taken from the Appalachian Plateau were reared from a seepage area along Spruce

Knob Lake (3871 ft. (1180 m) elev.) in a marshy loose muck among dense brush growth heavily infused with roots and culms of rushes.

Of the three Ridge and Valley sites, two were at margin of various richly vegetated ponds, in the emergent and floating vascular hydrophyte zones. One female emerged from sandy mud taken from a stream margin among willow roots.

Seven of the eight sites yielding *Cl. bimaculata* in the Piedmont and Coastal Plain were characterized by rich wet muck (hydropel) containing considerable leaf matter, coarse detritus, and/or root growth under the dense shade of riparian trees adjacent standing water in swampy situations. Another site, in the Back Bay National Wildlife Refuge, yielded a single male from a damp peaty substrate over sand in a depression adjacent to an open, wide ditch behind a coastal barrier dune. This is the only site from which this species was taken which had *no* significant shade. (WIK Coll. #192).

2.3.3 Autecological Review

2.3.3.1 Habitat Requirements

This is a consistently hydropelophilic species which occurs largely in moderately-to-densely shaded lentic-littoral sites, and in wetlands with a water-saturated loose silty mud or muck. The substrate appears always to have a high organic matter content, whether it be peat-like, leaf matter, coarse plant debris and finer detritus, emergent vegetation with reeds, sedges, rushes, or root mats. Wirth and Grogan (1979) aptly characterized this species as being a "common inhabitant of wooded, swampy

situations." Grogan collected "many males and females" by malaise trap in swamp at the Patuxent Wildlife Research Center, Maryland.

A less common habitat (2 of 14 in this study) is the lotic-depositional one, at the margins of lenitic segments along creeks and streams, such as in eddy backwater sediments. Again, rich, wet substrates with organic detritus, leaves or roots, in dense shade, appear to be preferred. Wirth (1951a) reared a large series of males and females from pupae taken at a stream margin in Fairfax Co., Virginia.

The preference for heavily-shaded habitats, especially with a riparian arboreal overstory of broad-leaved deciduous trees, seems quite characteristic. Only three of 14 sites were not under trees, and of these three only one was not shaded by thick emergent vegetation. Also, the larvae tended to be encountered in the thin, loose oxygenated layer of mud over anaerobic sulphurous black sediments.

2.3.3.2 Behavioral Observations - Larval/Pupal

The larvae are basically burrowers, but also are facultative "swimmers". They swim readily in a moderately rapid "anguilliform" (undulatory wave-form) fashion typical of the vermiform ceratopogonine larvae. Also, they are "climbers" in that they are capable of propelling themselves in snake-like fashion through the waterfilm on the surface of emerged vascular hydrophytes and detrital stems, mainly above the water surface. The larvae are strongly negatively photokinetic.

▪ Trophic Relationships

Larvae of this species are probably "engulfers": they appear to have accepted *Panagrellus* "vinegar eels" as food (though this was not directly observed), because two larvae pupated after 14 days, having grown from a

4-5 mm length, to a 6-7 mm. One pupa completed development, yielding a male within 48 hours of pupation. The unusually long larval mandibles, and the well-developed combs and teeth on the epipharynx support the supposition of a predaceous feeding habit.

2.3.3.3 Species Associations

Cl. bimaculata (30 females) dominated the D-Vac suction trap collections taken along the boardwalk at Cranberry Glades. Six other biting midge taxa were collected, including *Echinohelea lanei* (2 females), *Palpomyia plebeia* (3 females), three *Culicoides* spp., and about 10 *Forcipomyia* specimens. In the blacklight trap, nine *Culicoides* spp., *Dasyhelea grisea* (2 females, 4 males), *Alluaudomyia parva* (1 female, 2 males), *Stilobezzia stonei*, as well as some *Atrichopogon* and *Forcipomyia* sp., (8 females, 3 males) were associated with *Cl. bimaculata* (10 females).

Associations by rearing yielded 9 species of *Culicoides* distributed among 12 (86%) of the *Clinohalea* sites; 9 spp. of *Bezzia* at 11 (79%) of the sites; 3 *Stilobezzia* spp. and 3 *Palpomyia* spp. at 29 % and 36 % of the sites, respectively; 2 *Monohelea* spp. and 2 *Alluaudomyia*, both at 21% of the sites; and one each of *Parabezzia alexanderi* and *Probezzia nr. albitibia*. No *Dasyhelea* or Forcipomyiinae were reared together with *Cl. bimaculata*.

2.3.3.4 Adult habits.

Adults typically are to be found resting on vegetation bordering water in shaded habitats, such as the Cranberry Glades collections, where most the specimens were taken from low herbaceous growth in the older thickets immediately adjacent the open bog glades proper. Grogan has taken this

species from flowers and from a small grove of trees in Utah (Grogan and Wirth 1975).

The insectivorous habit of adult female *Cl. bimaculata* has been well documented by Downes (1978). At Black Lake, Ontario, he observed them entering all-male mating swarms of the tanypodine chironomid *Ablabesmyia monilis*, and capturing individual males. Female *Cl. bimaculata* also were seen eating conspecific males during mating. The females 5th tarsi and claws are armoured and modified for grappling.

2.3.4 Distribution

- Geographic Range

This species is known only from the Nearctic east of 100 degrees W longitude and south of 43 degrees N latitude: central Michigan to central Texas, and New Hampshire to Florida. The Virginia records established in this study are presented in Figure 8 on page 98.

- Biogeographic Distribution

Cl. bimaculata is a cosmopolitan species encountered in suitable microhabitats from about 1200 m in a relictual sphagnum bog on the Appalachian Plateau to sea level in a barrier dune pool on the Coastal Plain (Fig. 8). Over half of the present records, and the preponderance (54 of 70) of the literature records, place this species either in the Piedmont or Coastal Plain, however. Of the 16 which are not, 62% (10) were collected in the Mississippi River flood plain or near the Great Lakes. It appears to have distinctly austral affinities, in that 86% (60 of 70) records occur below the 40th parallel, and a full 44% are found in Florida alone.

2.3.5 Collection Locality Records

▪ Reared Material

North Carolina: Halifax Co.: 8 mi. W. of Roanoke Rapids on U.S. 158, 17-IV-1969, 1 male, 1 female (RC), FVB 810. Person Co.: 10 mi. W. of Roxboro on NC Rt. 57, 17-IV-1969, 1 male by RC (FVB 802); Virginia: Bath Co.: 7 mi. E of Warm Springs on VA Rt. 39, 25-VIII-1975, 1 male, 1 female (RC), WIK 166A; Craig Co.: 5 mi. SW of Paint Bank on VA Rt. 600, 15-X-1977, 1 female (RC), WIK 405; Isle of Wight Co.: Great Swamp, 20-VII-1975, 1 male (RC), WIK 119; Lunenburg Co.: Nottoway R. reservoir, 18-IX-1975, 2 males (RC), WIK 201C; Montgomery Co.: Tom's Cr., 0.5 mi. W of Kanodes Mill, 27-V-1975, 1 female (RC), WIK 253; Norfolk: Norfolk Botanical Garden, 28-VIII-1975, 1 female (RC), WIK 176; 1-VIII-1976, 1 female (RC), WIK 309 Suffolk: Dismal Swamp on Jericho Lane, 800 m E of escarpment, 29-VIII-1975, 1 male (RC), WIK 1979; Virginia Beach: Back Bay Nat'l. Wildlife Ref., 30-VIII-1975, 1 male (RC), WIK 192. West Virginia: Pocahontas Co.: Cranberry Glades Botanical Area, 21-VI-1975, 1 male (RC), WIK 53; Randolph Co., Spruce Mtn. L., 23-VI-1976, 1 female (RC), 1 male with Lex, Pex (IR), ca. 6 larvae, WIK 268-B.

▪ Adults Field-Trapped (AFT)

West Virginia: Pocahontas Co., Monongahela National Forest, Cranberry Glades Botanical Area, Round Glade boardwalk puncheon (cf. WIK 145 to 156) 30-VII-1975, 2 D-Vac samples, 5 min. each at dusk (DV-21, DV-24), 25 females, 5 females resp.; same, Flag Glade, middle, 31-VII to 1-VIII-1975, blacklight trap, 23:00 - 07.30h (BL-27), 10 females.

▪ Collection Records Summary

- IR (WIK 268B): started 6-8L; L-A: 1 male

- IMM (WIK 268B): poss. up to 6L
- RC (14 sites): 9 males , 26 females
- AFT (2 collections by DV, 1 by BLT): 4 females

Dates of substrate collection span from 17 April to 15 October.

2.3.6 Annotated Taxonomic and Biological References

- Wirth 1951a:321 (first descr., figs. of pupa)
- Grogan and Wirth 1975:282-3 (male, female, pupa redescr., fig.; map, distr., N. Amer.)
- Wirth and Grogan 1979:855-857 (diagnoses of male, female, pupa, habitat)

2.4 # 121. *Clinohelea curriei* (Coquillett)

2.4.1 Systematics and Habitus Synopsis

Closely related to the Palaearctic species *Cl. unimaculata* (Macq.).
Immature stages of *Cl. curriei* are unknown.

2.4.2 Habitat Characteristics in Present Study

Leaf matter at edge of a swamp highwater pool under dense canopy of blackgum, maple, water oak, pin and birch, 10 m from the edge of Lake Drummond in swamp forest; water pH 5.0. New York and bracken ferns among sparse understory in immediate vicinity of sample.

2.4.3 Autecological Review

The above rearing record, the first for this species, confirms the speculation by Wirth and Grogan (1979), based on adult records, that it inhabits wooded swampy sites. *Cl. curriei* apparently is often collected with *Cl. bimaculata* where their ranges overlap, though the latter species is generally more common.

This species was collected in association with *Culicoides variipennis* and *Bezzia* nr. *mallochi*, as well as about 20 helodid larvae (Coleoptera). In addition, over 60 chironomids and 5 tipulids (Diptera) emerged from the same sample, as did 14 Hydrophilidae and several other beetles.

2.4.4 Distribution

▪ Geographic Range and Affinities

Nearctic, continent-wide from Alaska and California to Newfoundland and Florida, but with a strong concentration of records in a belt from Wisconsin to New England. Uncommon below 40 degrees N (6 of 52 records), with only one in Florida (Grogan and Wirth 1979). Apparently is the ecological homologue of *Cl. bimaculata* in the appropriate habitats north of 40 degrees. Clearly more boreal in its affinities than *bimaculata*.

▪ Biogeographic Distribution in Study Area

Cosmopolitan from the Appalachian Plateau to the Coastal Plain. The present record is the southernmost for the species, apart from the single Florida record.

2.4.5 Collection Record

Virginia: Suffolk, Dismal Swamp at Washington Ditch landing adj. boardwalk. 21-VII-1975, 1 female (RC), WIK 122.

2.4.6 Annotated Taxonomic and Biological References

- Grogan and Wirth 1975:277 (male, female redescribed, figured; map and distr. rec. in N. Amer.; synonym *nebulosa*)
- Wirth and Grogan 1979:857 (diagnosis of males, female; habitat)

2.5 *Clinohelea pseudonubifera* Grogan and Wirth

2.5.1 Remarks

Nothing is known at present about the biology or immature stages of this comparatively uncommon species. Adults have been collected at four locations, ranging from southwestern North Carolina to Ottawa, Ontario. The other records are from northern Virginia and the eastern shore of Maryland. No specimens were found in this study (references below).

2.5.2 References

- Grogan and Wirth 1975:280-81 (male and female descr., locality records, distr. map, eastern N. Amer.)
- Wirth and Grogan 1979:859 (adult diagn., lower Potomac River valley records)

2.6 Genus *Heteromyia* Say

2.6.1 Systematics and Habitus Synopsis

A small, mostly Neotropical genus, with large species having fasciate wings, fore femur greatly swollen, with 20-30 stout spines, fore tibia arcuate, and hind leg of female with a single greatly elongated claw and short basal barb. (Wirth and Grogan 1977, 1979).

The pupa of *Heteromyia* possesses greatly elongated apicolateral processes on the abdomen, and has small tubercles with very short setae on the operculum. By contrast, in *Clinohelea bimaculata*, the pupa has normal apicolateral processes and large, greatly elevated tubercles with long setae on the operculum (Wirth and Grogan 1977). The pupa of the only other heteromyiine genus known, that of *Pellucidomyia leei* Wirth, is highly distinctive, having an exceptionally bulbous thorax, a short funnel-shaped respiratory horn, prominently bristled abdominal tubercles, and apicolateral processes short, stout proximally, finely pointed at the caudal tip (e.g., Debenham 1970:136).

The larva of *Heteromyia* is still unknown.

2.6.2 Geographic Range

This genus is restricted to the New World, with 11 species known in the Neotropics (Wirth 1974, Wirth and Grogan 1977) and 2 in the Nearctic region, *H. fasciata* Say and *prattii* (Coq.).

2.6.3 Annotated Taxonomic and Biological References

- Wirth and Grogan 1977:177 (revision of the 2 N. Amer. spp., (*fasciata*, *prattii*) redescr., illus.; keyed; first descr. pupa of 2 Neotropical spp. (*clavata* Williston, *wokei* W & G), map, locality rec.)
- Wirth and Grogan 1979:859 (male and female diagnoses, figs.; pupa of *prattii* illus., descr., habitat of *prattii*)

2.7 # 122. *Heteromyia fasciata* Say

2.7.1 Systematics and Habitus Synopsis

Immature stages not described⁵. Pupa of *H. prattii* described (see below).

2.7.2 Habitat Characteristics in Present Study

Occurred in a coastal plain swamp along the course of a blackwater river in a thick bed of floating aquatic vascular plant, esp. bladderwort (*Utricularia*), with loosely entrapped reddish mud in the root mass; in a stagnant pool with an accumulation of leaves (oak, cypress, sweetgum, loblolly pine). This site is exposed to flowing water only when water level is raised, such as during freshets. The site was shaded only during the early and late daylight hours.

⁵ One pupa is in present collection.

2.7.3 Autecological Review

2.7.3.1 Habitat Requirements.

Probably a phytophilic species, likely to be encountered in association with plants on aerobic mud substrates in emergent wetlands adjacent riverine environments. All three habitat records available for this species place it in direct or indirect association with flowing water. The available information for this and related species suggests a habitat in lower floodplains.

H. A. Jamnback reared one female of this species from "muddy" substrate at the margin of a stream forming the outlet of Big French Pond, North Sea, Long Island, NY (HAJ#11-IV-57-4) (unpublished record, specimen at New York State Museum).

Adult *H. fasciata* were collected by Mingo and Gibbs(1980) along the Narranguas River, in northeast Maine, on 16 July. With which of their collecting methods--sweeping, rearing, or emergence trapping -- they obtained their specimens is not clear. At the collection site ("Site 2"), the river is about Order 4, 9 m wide, with a substrate of small stones, coarse gravel, and sand. Aquatic vegetation was present along a narrow band adjacent to both shores. At this same site, "*Palpomyia*" larvae were also found. It is very possible that the *H. fasciata* emerged from the band of aquatic plants along the shore.

The other Nearctic species, *H. prattii*, was reared from pupae found in sphagnum moss in the floodplain of the Patuxent River, Prince George's Co., Maryland (Wirth and Grogan 1979). This habitat fits in a category which may be described as "hygrophilic mosses on marshy sediments"(cf.

Schwank 1981b, 1982a), and suggests a phytophilic character for the immatures of *H. prattii* as well.

In the Panama Canal Zone, *H. clavata* Williston was reared from a pupa taken among *Cabomba* sp. (fanwort) a floating vascular plant of the family Nymphaeaceae (Wirth and Grogan 1977).

2.7.3.2 Larval Behavior

Given their likely phytophilic occurrence, *H. fasciata* larvae undoubtedly negotiate the air-water-plant-mud intersections readily and have a mode of existence which combines a modified "sprawling" by serpiginous progression in the water film in plant surfaces, with burrowing in soft mud or tyrophel.

2.7.3.3 Species co-occurrence.

A rich assortment of ceratopogonids and other Diptera occurred at the site which yielded *fasciata*: three species of *Dasyhelea*, a group of herbivores and scrapers; the collector-gatherers *Stilobezzia viridis*, *S. bulla*, and predators were represented by *Alluaudomyia bella*, *A. paraspina*, *Bezzia laciniastyla*, and *Phaenobezzia opaca*. One other species was definitely unexpected, *Culicoides debilipalpis*, which normally is considered a tree-hole breeder. In this case, its presence was undoubtedly attributable to the leaf pack lining the pool, adjacent to and over which the bladderwort was growing. I have found *C. debilipalpis* in several other non-tree-hole sites, but all of the sites were very high in organic matter of a leafy or woody nature.

Among other fauna reared in some numbers at this diversely inhabited site were: the Diptera, Stratiomyidae and Dolichopodidae, and beetles in the families Hydrophilidae and Dytiscidae, all of which are predators.

Non-insects which I noted included large leeches (prob. *Helobdella* sp.), nematodes, cladocera, copepods, ostracods, and rotifers.

2.7.3.4 Adult Habits

Despite an obvious modification for a presumed predatory habit, in that the fore femora of the females are greatly expanded and armed with numerous spines, *H. fasciata* has apparently never been observed with prey or conspecific males. However, Downes (1978:25) has demonstrated that the salivary gland of this species does possess proteolytic enzymes.

2.7.4 Distribution

▪ Geographic Range

Maine to Florida. The record from Maine (Mingo and Gibbs 1980) extends the known distribution considerably northward from Massachusetts (Wirth and Grogan 1977). The two present records are consistent with the established distribution pattern.

▪ Biogeographic Distribution

Restricted to the Coastal Plain and outer Piedmont provinces, along the eastern seaboard of the U.S. The Virginia record is in a coastal plain swamp (Fig. 8). Apparently a thermophilous species.

2.7.5 Collection Records

New York: North Sea, Long Island, Big Fresh Pond outlet, "muddy edge of stream", 11-VI-1957, 1 female reared, with p.ex., Coll.: H. A. Jamnback.

Virginia: Sussex Co., Coppahaunk Swamp along tributary of Blackwater

River, between Waverly and Wakefield; 2-VIII-1976, 1 female by RC (WIK 313B).

2.7.6 Annotated Taxonomic and Biological References

- Wirth and Grogan 1977:179 (male, female diagnosis, distr. in N. Amer., figs.)
- Wirth and Grogan 1979:862 (brief diagnoses of male, female, figs.; pupa of *prattii*; distr. in northern Virginia region)
- Mingo and Gibbs 1980:34 (from river, Maine)

2.8 *Heteromyia prattii* (Coquillett)

2.8.1 Remarks

This species, very closely related to *H. fasciata*, is recorded from Illinois to Massachusetts and south to Florida. The only records between New England and Florida, however, occur in Maryland and Virginia, in the vicinity of the Potomac River valley (Wirth and Grogan (1977, 1979)). No specimens of this species were encountered in the present study.

Pupae of *H. prattii* were discovered by Shahin Navai on June 13, 1977, on sphagnum moss in a floodplain marsh along the Patuxent River, Prince Georges Co., Maryland. Wirth and Grogan (1979) described the female and male pupae, which possess the characteristically elongate, slender posterolateral processes which apparently typify the genus.

See above (2.7.3.1) for a discussion of the habitat.

2.8.2 References

- Wirth and Grogan 1977:179-82 (female, male diagn., locality rec., distr. map, eastern N. Amer.)
- Wirth and Grogan 1979:862-64 (adult diagn., pupa descr., figs., distr. in lower Potomac River valley and vicinity)

2.9 *Neurohelea nigra* Wirth

2.9.1 Remarks

This species has been twice recorded from northern Virginia in Fairfax Co. (Wirth and Grogan, 1979), but was not encountered during this study. Immatures have not yet been discovered for this species or any of the 5 species presently known in the Nearctic, Neotropical or Palaearctic regions. Little is known of the habitat other than that several females were captured beside two small streams in Virginia, once by sweep net in an *Osmunda* fern bog, and once by light trap.

This is one of two Nearctic species of the genus. The other, *N. macroneura* (Mall.), is recorded from Illinois and Kansas (Wirth 1965). *Neurohelea nigra* is now known from eight states and provinces: BC., CA, GA, NC, OR, TN, VA, WA (Wirth and Grogan 1979), although no specific locality records for the majority of the above have been published.

2.9.2 References

- Wirth 1952:208 (female, male descr., figs., CA)
- Grogan and Wirth 1979: 51 (descr. closely rel. genus *Physohelea* in resp. to *Neurohelea*)
- Wirth and Grogan 1979:866 (adult diagnosis, fig. antenna, wing, legs, fifth tarsom., claws, spermath., male genitalia; distribution, Potomac Valley, Virginia)

CHAPTER THREE

Ecosystematics and Autecology of Immature Sphaeromiini --

I: Tribal Overview and Genera *Jenkinshalea*, *Johannsenomyia* and *Macropeza*

3.1 Introduction and Overview of Sphaeromiini Systematics and Biology

Only seven of the 20 genera in this tribe are found in North America. Yet, these genera account for 75% of the 280 species worldwide, and include 44 species on this continent. East of the 100th meridian, 39 species are known. In Virginia, only 12 species in five genera have been reported (Wirth 1951a, 1971, Wirth and Grogan 1979), but at least 18, distributed among seven genera, are expected in the Middle Atlantic states. In this study, 16 species, including three new ones, are recorded for the region.

3.1.1 Synopses of Systematics and Habitus

Adult: Female characters, common to sphaeromiine genera, include (Wirth 1962a, Wirth et al. 1974, Wirth and Grogan 1979):

1. tarsal claws -- large and straight to gently curved, with blunt short basal tooth on external side (unique to this tribe), except *Sphaeromias*, which has slender, sharp teeth on the inner side of the claws.
2. fifth tarsomere -- armed ventrally with stout batonnets, not inflated.
3. fourth tarsomere -- cylindrical, not cordate or bilobed.

4. abdomen -- no internal sclerotized gland rods; venter of eight abdominal segment with ventral pair of curved hair tufts near gonopore, [except *Sphaeromias*] (see Figure 9). See below in this section for a discussion of oviposition.

No detailed phylogenetic analyses of this tribe or its genera have yet been published, thus, the relationships of the various character states and their derivatives are not clear. However, most of the adult key characters listed above are presumably secondary sexual characters, directly or indirectly related to the insectivorous habit of these predaceous midges, in that the armature apparently plays a role in grappling prey and in mating, as alluded to by Downes (1978), and possibly in oviposition (see below). For example, the extremely long basitarsus of *Macropeza* may be an adaptation for larger prey, such as Ephemeroptera (Downes 1978, Knausenberger and Wirth 1980). Elucidating the probable relationship between the behavioral biologies and differential phenotypic expression of leg armature, antennae, genitalic and mouthpart characters, for example, will likely remain a fascinating challenge for some time to come.

The genus *Sphaeromias* is anomalous in the tribe, being the only one of the North American genera lacking the ventral hair tufts near the gonopore, normally a conspicuous feature of female Sphaeromiini. This has important bearing on oviposition behaviour (see below). Likewise, it is the only genus lacking the blunt external teeth on the tarsal claws. The larva also diverges from the norm of the tribe, in the possession of a robust pharyngeal apparatus and a rather short,

ovoid-triangular head capsule, small relative to the body size.

Eggs: Known for all Nearctic genera except *Jenkinshalea* and *Nilobezzia*. With the exception of *Sphaeromias*, the eggs of all other known sphaeromiine genera are deposited in gelatinous helically-twisted ribbons 3 to 4 cm long, consisting of single overlapping rows of eggs displaced at particular angles with respect to the longitudinal axis of the ribbon. *Sphaeromias* lays its eggs in hemispherical gelatinous clusters up to 5 mm in diameter. Sphaeromiine eggs are all fundamentally similar, being elongate cigar-shaped to slightly S-shaped, creamish to grayish-brown in color, becoming darker as development progresses. In both *Johannsenomyia argentata* and *Macropeza pamunkeiana*, the eggs are about 0.4 mm long (Johannsen 1905, Knausenberger and Wirth 1980).

The structure and texture of the chorion and the micropyle (anterior pole) offer characters which have proven to be of great diagnostic value, allowing Mayer (1952) to point out the existence of the *Stenoxenus* group, which now constitutes a separate tribe. Johannsen (1905) and Thomsen (1937), Knausenberger and Wirth (1980) and others, have pointed out characters of eggs which may prove to be species-specific. Rieb (1981) characterizes *Mallochohelea* and *Probezzia* eggs as being surrounded by two envelopes, an internal one being the chorion, and an external one containing "adhesive spherules" which he termed the oophore. He maintains that the form of the oophore and the adhesive spherules are specific to the species he dealt with. Thus, clearly, eggs can contribute much to the eventual

concordance of developmental stage and imaginal systematic arrangements.

Larvae: Five of the seven Nearctic sphaeromiine genera are known in the larval stage (*Johannsenomyia* and *Macropeza* remain to be described; the status of *Jenkinshalea* is somewhat enigmatic -- see there). A characteristic set of larval features (mainly instar IV, sometimes III) apparently holds at the tribal level, which tends to support the grouping of the sphaeromiine genera as a natural one (based on personal observations, and confirming Glukhova [1977, 1979]):

1. The ventral margin of the postoccipital collar possesses a caudal expansion or process, which ranges from broadly triangular to scoop-like or nearly hemispherical in shape.
2. The head capsule is rather elongate (except *Sphaeromias*) and conical, often quite narrow anteriorly.
3. The frontal suture ends at midlength of the head, between setae 'q' and 's'.
4. Setae 'u' and 'v' nearly touch at the base.
5. The anal segment possesses relatively short setae, arranged on the dorsal and ventral lines as 2 posterior parts, and 2 pairs of setae in line in front of the latter pair.

The only other larval group which possesses a significant caudal expansion on the ventral side of the collar, is the *Palpomyia tibialis* group, in particular, *P. novitibialis*: in these, the expansion is broadly triangular. However, a ventral median suture, extending to about 1/3 the head length is present in the *P. tibialis*

group larvae, but not in the Sphaeromiini. The general habitus of *Sphaeromias* and *P. tibialis* group can be quite similar, but the pigmentation is distinctly different¹. In *Sphaeromias*, irregular groupings of blackish pigment spots are found on all thoracic segments, while in the *tibialis* group, the pigmentation is a rich brown in subdorsal patches on all thoracic segments, but often strongest on the prothorax (e.g., Fig. 17c). These pigmentation patterns remain readily visible in preservative (ethanol).

A reliable generic key to larvae of this tribe is still beyond reach. Specific characters are to be found in the head chaetotaxy pharyngeal details, in particular, the epipharyngeal comb; thoracic pigmentation; shape and color of ocelli and head; and anal setae. Future descriptions should include attention to details of the sensillae and setae in the oral field. Mayer (1934c), Lawson (1951) and Glukhova (1979: 51-53) have shown that significant structural differentiation occurs there. Chironomid larval description and keys often employ oral field characters in part (e.g., Wiederholm 1983).

Pupae: Although little systematic attention has been given to tribal classification of pupal Sphaeromiini, the work of Thomsen (1937), Mayer (1957, 1959), Wirth (1962b), Atchley (1969), Debenham (1974), Wirth and Grogan (1979), and Palchick (1981) gives ample evidence that satisfactory characters exist to separate genera and species, in general. However, arriving at a consistent set of

¹ I have encountered *S. longipennis* larvae identified incorrectly as *P. tibialis* in several collections made in the 1940's and 1950's (see Biological Overview in Introduction to Section II).

characters to delineate the tribe may prove to be more difficult, because of the great diversity found among the various genera. Mayer (1957) focussed on the abdominal tubercles and setae in attempting a concordance of adult and pupal systematics, and managed to develop seemingly natural groups, but these did not distinguish the Palpomyiini. Examination of the anal segment, respiratory horn, operculum, and the various pits, bristles and setae on the cephalothorax usually provides the necessary discriminators.

An interesting feature in the pupae of some species in five of the genera is the presence of ventral membranous patches, often referred to as adhesive glandular discs, on certain abdominal segments. The functional significance of these discs is discussed under the *Probezzia* generic discussion and in the general discussion (Chapter 7).

3.1.2 Oviposition Behavior

Two distinct egg-deposition behavior patterns occur:

1. oviposition by the female hovering over open water, near the shore, head pointing shorewards, in the evening;
2. oviposition from and on substrates at the water's surface, in full daylight.

The first type of behavior has been observed in detail for five sphaeromiine species among three genera. Johannsen (1905) provided the first published account of carefully observed oviposition behavior by a sphaeromiine, that of *Johannsenomyia argentata*, which was subsequently widely quoted (Rieb 1915, Munsterhjelm 1920, Lenz 1934, Thomsen 1937, Wirth and Grogan 1979). Other species for which the

behavior has been reported include: *Probezzia concinna* (Wesenberg-Lund 1914, 1915 [cited and confirmed by personal observation by Thienemann 1928], 1943 [reproduced in Thienemann 1954]; Rieth 1915, Munsterhjelm 1920, Lenz 1934, Mayer 1934c); *Probezzia seminigra* (Rieb 1981), *Mallochohelea nitida* (Hamm 1919); *M. remota*, *M. setigera* (both by Rieb 1981).

The second type of oviposition behavior has been observed in *Sphaeromias fasciatus*, recorded by Thienemann (1928), and in *S. longipennis*, by Malloch (1915), Muttkowski (1918), and by the present writer. This type of oviposition behavior, in which the female is alighted upon the surface where the eggs are deposited, is the norm among the Ceratopogonidae.

However, the hovering habit of oviposition appears to be unique to a closely related group of genera in the Sphaeromiini. It would appear that this behavior pattern is a derivative of the pleisiotypic alighted oviposition habit. All genera known to have the hovering ovipositional habit also possess well-developed long curved pairs of hair tufts near the gonopore on the venter of segment VIII (Fig. 9a). Significantly, *Sphaeromias* spp. lack these tufts. Of the 17 Sphaeromiini genera for which I could find suitable illustrations, 12 possess these hair tufts, developed to a greater or lesser degree.

Direct evidence that these hair tufts are significant to oviposition is provided by Rieb (1981), who states (translated from French): "The egg is deposited with its two envelopes; upon exiting the gonopore, it is directed caudad by gliding on the cerci, ... it

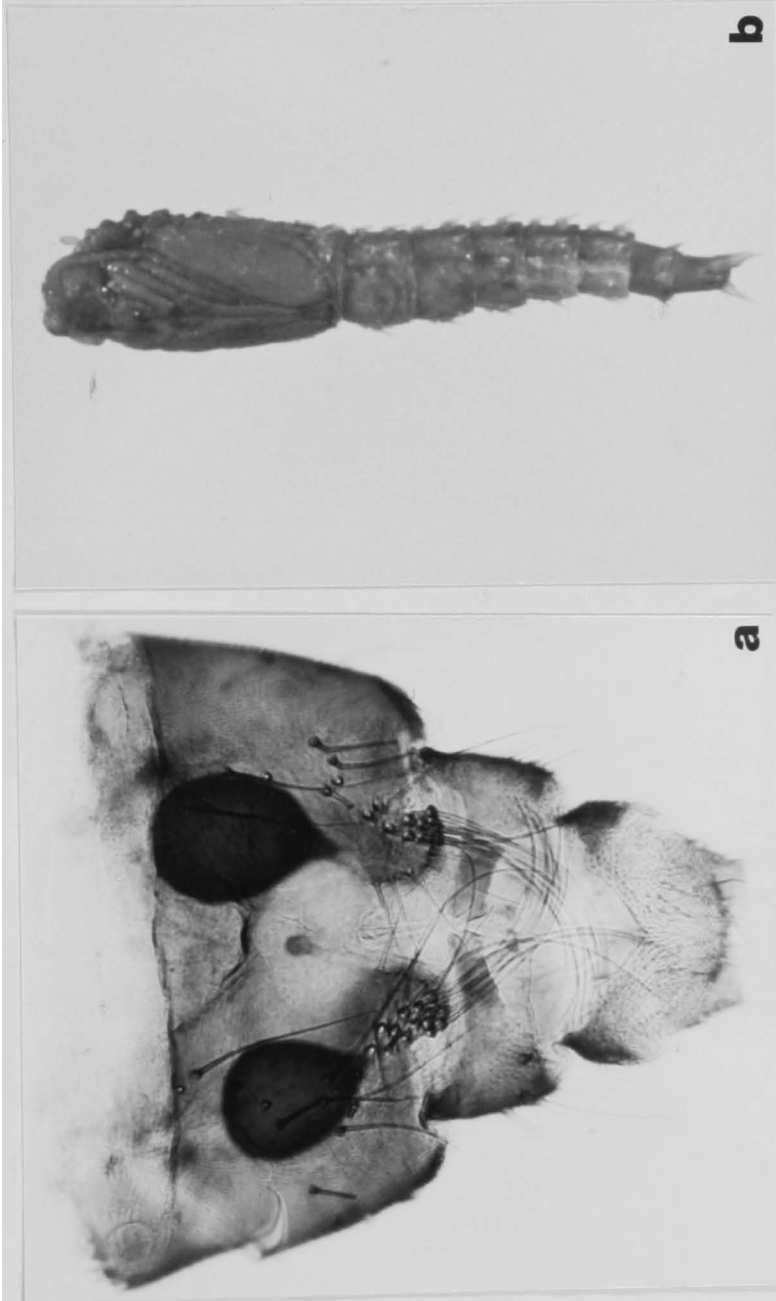


Figure 9. (a) *Macropeza pamunkeiana* female terminal abdominal segments, showing ventral hair tufts on segment VIII;
 (b) *Mallochohelea n. sp. nr. caudellii* pupa, in ventrolateral view, showing "blister-like protuberances" on dorsum of cephalothorax, large angulate dorsoposteromedian (dpm) tubercles on abdomen, and the comparatively indistinct ventral membranous patches.

is seized by the hind tarsi, then pushed forward and held between two fans of stiff setae situated on the 8th sternite and forming a 'prehensile basket.' The eggs are successively pushed into this basket, where the eggs join adhesively, to form the ribbon. The eggs are obliquely displaced and overlap, forming, with respect to the ribbon axis, an angle characteristic of each species: *M. setigera* = 45°, *M. remota* = 26°, *P. seminigra* = 25°. While no other observers have, to my knowledge, reported the use of the hair tufts in this way, the evidence seems sufficiently compelling to hypothesize that all genera and species, possessing well-developed hair tufts, as described, should eventually prove to be hovering ovipositors. In addition, the fact that the meso- and metathoracic legs play a role in guiding and paying out the egg string (Johannsen 1905, Wesenberg-Lund 1943, Rieb 1981), provides a clue as to the possible provenance of leg armature and tarsal characters.

The pelagio-littoral ovipositional habit is obviously of high relevance to the nature of the substrates which the larvae will occupy. Larvae of species which so oviposit are among the most fully aquatic of the ceratopogonids, apparently only leaving the water or bottom to pupate. The females normally will oviposit near shore in sheltered places of either lotic or lentic waters. Because of the morphological comparability of such habitats between lotic and lentic systems, it seems unlikely that a given female will determine an oviposition site based on discernment of substrate characteristics. Optimum habitat choice models (see "Microhabitat Distribution" under the *Probezzia*

generic discussion) suggest that, instead, the population or cohort from which the female developed will be the determinant, in that the same or similar place will be sought out as yielded the adults.

Useful insights into one likely method of ecological partitioning by related species in coincident habitats is provided by observations Rieb (1981) made along a river in eastern France: *Mallochohelea* species had their ovipositional flight when luminosity in the late afternoon ranged from 1200 to 30 Lux, whereas apparently *Probezzia* flew in the period during which luminosity decreased from 30 to 4 Lux. Temporal segregation of ovipositional flight at the same river margin site is evidently achieved by preference for different light intensities.

3.1.3 Larval Habitats

Larval Sphaeromiini are characteristically inhabitants of the littoral zone of lakes, ponds, rivers and streams. They do not occur to any significant extent in bogs, marshes lacking open water, or forested swamps. Extreme environments, such as temporary pools, intermittent streams, hot springs are not exploited as a rule, but *Nilobezzia* and *Sphaeromias* species may be abundant in alkaline resp. saline waters. Exotelmata are not utilized, in the temperate zones at least, though a few tropical species in wet forests have been found in phytotelmata, which often are the only available accumulations of water (see the *Mallochohelea* generic habitat discussion).

Discussions of larval autecology and habitat requirements are presented in generic overview and by species in Chapters 3-6, as well

as in summary form in Chapter 7.

3.1.4 Comments on Biogeography of Sphaeromiini

Of the 20 Sphaeromiini genera worldwide, 12 occur only in the Afro-tropical, Oriental and/or Australasian regions, as do 80% of the species in all genera combined. While it is not possible to state whether the tribe is polyphyletic or monophyletic, the center of origin of the ancestral species apparently was in the same general region, as is certainly the center of species diversification.

3.2 Genus *Jenkinshalea* Macfie

3.2.1 Systematics and Habitus Synopsis

This is a small genus of large, usually grayish pollinose biting midges distinguished as adults chiefly by a unique expansion in the anal angle of the wing, especially in the female¹. Males of Nearctic species are readily distinguished by their distinctive genitalia, but females are difficult to key beyond the species group level, especially where geographic ranges overlap (Grogan and Wirth 1977). A predaceous habit in

¹ This character distinguishes *Jenkinshalea* from all other genera in the Nearctic only. The Oriental and Australian genera *Crispomyia* Debenham and *Niphanohalea* Grogan and Wirth also possess the greatly expanded anal lobe of the wing (Grogan and Wirth 1981b, Debenham 1974).

the female may be presumed from the well-armed 5th tarsomeres bearing stout ventral batonnets (blunt-tipped spines). Downes (1978) noted female *J. magnipennis* Joh. eating the male during mating. Oviposition behavior has not been noted.

Eggs have not been described, and larvae were first tentatively described in 1979 (see under *J. albaria*). Rather remarkable larvae tentatively assigned to *Jenkinshalea* were described by Glukhova (1979). Their most prominent features include an apparently bifurcate caudal tip of the terminal abdominal segment, with six pairs of prominent setal brushes arranged along the dorsal and ventral lines of the segment. Also, the headcapsule appears to possess an unusually long extension of the labial area beyond the buccal opening. The mandible is unusually broad, nearly hemispherical in profile. The taxonomic status of the latter larvae is discussed under *J. albaria*.

A general pupal description was first given by Malloch (1914) (see below), but Mayer (1952) provided the first detailed pupal diagnosis of this genus, of *J. polyxenae* de Meillon, from South Africa. Ventral adhesive disks on abdominal segments 6 and 7, and short respiratory horns are common to all known *Jenkinshalea* species pupae. However, at this time, this genus can not be reliably distinguished from pupal *Mallochohelea*, which also possess these key characters in part.

3.2.2 Habitat: Present Study

Besides the reservoir-sited collection of *J. albaria* discussed below, two other unpublished records were obtained: a presumed *Jenkinshalea* sp. (det. WIK) represented by two pupae and a larva (in poor condition),

collected from Carnegie Lake, Princeton, NJ (ANSP); and one pupa of *J. magnipennis*, determined from a collection taken in shallow, quiet waters in the Mississippi River, Ontario, Canada (ROM). This specimen was taken with one larva and three pupae of *Sphaeromias longipennis* and a pupa of a *Mallochohelea* sp.

3.2.3 Autecological Review

3.2.3.1 Habitat Preferences.

In the Nearctic and Palaearctic, *Jenkinshalea* is clearly associated most often with lake and middle to lower river course habitats, particularly where sand and coarse silts form the margins. These margins are likely to be sparsely vegetated or bare. Wherever the composition of the habitat substrate is mentioned or inferable for a *Jenkinshalea* record, sand appears to be a common denominator (e.g., Williams, 1955, Wirth 1962, Wirth and Grogan 1979). Glukhova's (1979:92) "*Jenkinshalea* (?)" larvae were taken from the sandy edge of the Amu Darya River, the lower course of which flows through an extensive sandy desert on the river's way between the Uzbek and Turkmen Republics toward the Aral Sea in southcentral USSR.

Pond and creek habitats have also been recorded for *Jenkinshalea* in North America, though less commonly than have lakes and rivers. In temperate South Africa, *J. polyxenae* was obtained from a large pond (Mayer 1952).

Apparently, however, in Guinea, tropical West Africa, where definite wet-dry seasonality prevails, *Jenkinshalea* has adapted to temporary pool habitats. Thus, Clastrier (1983b) reared *J. djalonensis* Clastrier from

shallow interconnected rockpools pockmarking a sandstone ledge along a river in Guinea; these rockpools had a thin organic sediment and were filled with water only during the rainy season, when water trickled from one to the next. This interesting site was co-inhabited by *Clinohelea hygropetrica* and *Stenoxenus pastorianus* Clastrier.

3.2.3.2 Behavior.

Larvae are most likely to form part of the littoral benthos of lakes and rivers at less than 2 m depth. Mature fourth instar larvae head for shore and pupate in the typical sphaeromiine fashion. Pupae of this genus are known to be able to float at the water's surface. However, pupae are apparently able to leave the water directly by climbing up emersed objects such as rocks, plants, or even the side of a painted wood boat, as in the case of *J. magnipennis* (Wirth and Grogan 1979). The side of the boat in question was dry at the time the pupae were observed creeping up (Grogan, pers. comm. 1985). The pupae are able to scale smooth surfaces by laterally bending their abdomens, attached by the ventral membranous disks which apparently secrete an adhesive fluid which attaches them securely. The pupae are very active when disturbed (Williams 1955, Wirth 1962b, Grogan and Wirth 1977, Wirth and Grogan 1979).

Ventral adhesive disks appear to have a definite adaptive value for the emergence conditions to be encountered in the littoral zone. Pupae possessing them would have an improved opportunity to successfully pupate above the water's surface and to assume the most advantageous orientation (dorsum of thorax up and away from the substrate) from which to eclose.

3.2.4 Geographic Range

Sixteen species of *Jenkinshalea* are now known worldwide: four in the Nearctic (Grogan and Wirth 1977), six in the Afrotropical (Wirth et al 1980, Clastrier 1983), four in the Oriental (Wirth 1973; Grogan and Wirth 1981), and one each in the Palaearctic (Remm 1979) and Australasian (Debenham 1974) regions. In the past decade, the number of known species has doubled from eight. None are yet reported from the Neotropics.

The four North American species are all restricted to east of the 100th meridian, except for one extreme outlying record in British Columbia for *J. magnipennis* (Grogan and Wirth 1977).

3.2.5 Locality Records

- Other Sources

New Jersey: Princeton, Carnegie Lake. VII-11 and VII-14-1967, Sta. 1 and 3 resp., coll. Richardson (ANSP), 2 pupae, 1 larva of ?
Jenkinshalea. Ontario: Carleton Co., Mississippi R. VI-20-1966. Coll. P.D. Hebert (ROM), 1 pupa of *J. magnipennis*.

3.2.6 Annotated Taxonomic and Biological References

- Mayer 1952:585 (pupa of *J. polyxenae* deM.; S. Afr.)
- Williams 1955:94 (pupation, ecol. observ., Douglas L., Michigan)
- Debenham 1974:48 (brief diagnosis of pupa; New Guinea)
- Grogan and Wirth 1977a:126 (male, female descr. of 4 N. Amer. spp., incl. 2 new; pupal descr. of 2 spp.)
- Glukhova 1979:92 (larva of *Jenkinshalea* (?) sp., USSR)
- Clastrier 1983b:261-268 (male, female, habitat descr., 2 new spp.; Guinea, W. Afr.; spermatophore)

3.3 # 123. *Jenkinshalea albaria* (Coquillett)

3.3.1 Systematics and Habitus Synopsis

Two descriptions of the larvae of this genus were first published in 1979, by Wirth and Grogan (1979) for *J. albaria* and for a presumed *Jenkinshalea* sp. by Glukhova (1979).

Both larval descriptions must be considered tentative, in that neither was definitively associated with reared imagoes. The larva depicted as *J. albaria* by Wirth and Grogan is clearly a sphaeromiine, characterized especially by the strong expansion caudad of the post occipital collar along the mid-ventral line. However, it should be pointed out that the epicranial suture, depicted as running the entire length of the head capsule, is at variance with all other sphaeromiine larvae known to the present writer from his own collections and the literature. Normally this suture ends between seta 'q' and seta 'k'.

The larva was apparently among 3 larvae collected with at least 200 pupae of *J. albaria* taken along the sandy margin of the Potomac River at Scott Run by Wirth and Jones (Wirth 1962, 1971, Wirth and Grogan 1979). However, with these specimens were at least four other Sphaeromiini: *Probezzia albitibia* Wirth (at least 9 pupae yielded adults); *P. pallida* Malloch (3); *P. smithii* (Coq.) (8); and *Johannsenomyia argentata* (Loev) (22) (Wirth 1962, 1971b; Wirth and Grogan 1979). In the absence of more compelling direct evidence, it seems prudent to bear in mind the possibility that the putative *J. albaria* depicted by Grogan and Wirth (1979) may well be another species, possibly a *Probezzia*.

Glukhova's (1979) tentatively determined "*Jenkinshelea*(?) sp." was based on 6 unusual larvae obtained from the sandy margin of the Amu Darya river in southcentral USSR (see Autecological section under generic discussion of *Jenkinshelea* above). These larvae were assigned to *Jenkinshelea* based on a process of elimination in that larvae of only 2 sphaeromiine genera in the USSR were unknown -- this one and *Macropeza*. On the basis of the small size of the presumed fourth instar (ca. 6 mm), and the site of collection (river margin), Glukhova felt the larvae could be provisionally relegated to *Jenkinshelea*. However, not only are *Jenkinshelea* spp. adults physically quite large, but the known *Macropeza* species are associated with rivers as well, although the microhabitat characteristics for *Macropeza* are not yet known.

Lending support to Glukhova's supposition that the larvae in question are *Jenkinshelea*, is the fact that the only known Palaearctic species in the genus, *J. stenoptera* Remm (1979), was recently described from Serachs, Turkmen S.S.R., in southcentral USSR, the same geographical area from which the larvae were obtained. On the other hand, this species is among the largest of described *Jenkinshelea*, having a wing length of 3.65 mm. It is highly unlikely that 6 mm larvae will develop into adults the size of *J. stenoptera*. The larvae were collected in mid-June (1951), while the adult female was taken at a light in late August (1959). Quite possibly, therefore, the Amu Darya River larvae were not in the terminal instar. In any case, clearly the actual status of the putative *Jenkinshelea* larvae awaits confirmation by direct association of reared specimens.

Pupae of Nearctic species were described by Grogan and Wirth, for *J. albaria* and *J. magnipennis* (Joh). They did not refer to the brief pupal description by Malloch (1914), which illustrated the dorsal aspect of the thorax, third abdominal segment and anal segment in a general way.

3.3.2 Habitat in this Study

The light trap yielding a single female *J. albaria* was situated among a stand of emergent *Sparganium* and *Juncus* reeds at the margin of a calm lagoon. This site was a recently stabilized reservoir with a sandy-silty substrate. The trap was operated for only one hour before and after dark.

3.3.3 Autecological Review

3.3.3.1 Habitat Requirements

Most often associated with lakes, potomal sections of larger or slow-moving rivers, and to a lesser extent, with ponds. Pupal exuviae of this species were recovered by skim samples from the surface of Lake Norman, a large man-made reservoir in southwest North Carolina (T.W. Bowen, pers. comm. 1978). One male was reared from a pupa collected on the lake surface 17-VIII-1978 (Bowen 1983a).

A larval preference for sandy and silty looser substrates is clearly indicated. Emergent vegetation is apparently of secondary importance as an ecological factor in the biology of this species. Over 200 pupae and some larvae were recovered from an unvegetated sandy beach at the margin the Potomac River (Wirth 1962; Wirth and Grogan 1979). This species was also recovered by Williams (1955) from the sandy beach zone of Douglas Lake.

3.3.3.2 Larval and Pupal Behavior

Larvae are probably predaceous engulfers. When ready to pupate, apparently swim at the water's surface until they reach the beach or emersed objects, especially plants, where they either burrow in the substrate or climb up plants, as previously described.

Pupae are able to float and, using their ventral adhesive pads are able to scale smooth surfaces. Pupae apparently tend to occur within 15-30 cm from the water line, but may be found as much as 2 m horizontally from the water's edge (Wirth and Grogan 1979, Williams 1955).

3.3.4 Distribution

3.3.4.1 Geographic Range

Of the four known *Jenkinshalea* species in North America, only *albaria* is present in the Virginia area (Figure 10 on page) The species is widely but quite sparsely distributed east of the 100th meridian from Ontario south to Florida and west to Illinois, Arkansas and Texas. At the northern extent of its range, it overlaps with *magnipennis*. The latter does not occur south of 40 deg. N, and is more abundant in its range than is *albaria*. It is conceivable that *magnipennis* could eventually extend its range into the Virginia region, possibly through the Ohio-Kanawha-New River system or through the Cumberland or Tennessee River systems.

At the extreme southern extent of *J. albaria's* range, it overlaps with two recently described species, *J. stonei* Grogan and Wirth and *J. blantoni* Grogan and Wirth. These two species have only been found near the 30th parallel in Florida and Texas.

3.3.4.2 Biogeography

Associated largely with lower perennial riverine systems throughout its range. Apparently nearly absent from the entire Appalachian Mountain chain, records being concentrated in bands along the east coast and in the Mississippi River basin, at lakes and along larger watercourses.

3.3.5 Locality Records

Virginia: Louisa Co., North Anna Reservoir, Millpond Creek arm, Lagoon 2. 11-IX-1976, 19:30-21:30, by New Jersey blacklight trap; one female (BL-58).

3.3.6 Annotated Taxonomic and Biological References

- Malloch 1914:229 (pupa; as *Johannseniella*)
- Wirth 1962a:1-4 (separation of *albaria* and *magnipennis* as distinct spp., synonymies, distr.)
- Grogan and Wirth 1977a:126 (4 spp., 2 new; male, female, descr., illus.; pupae of *albaria*, *magnipennis*, biol. observations, distr., maps)
- Wirth and Grogan 1979:867-871 (diagn., figs., male, female, pupa, larva descr., figs.)
- Bowen 1983a:36 (rearing record from lake, NC)

3.4 Genus *Johannsenomyia* Malloch

3.4.1 Systematics and Habitus Synopsis

Two species are described for the Nearctic: *Joh. annulicornis* Mall. and *argentata* (Loew), of which only the latter occurs in the mid-Atlantic states. A previous record of *Joh. annulicornis* as occurring in northern Virginia has proven erroneous (Wirth and Grogan 1979). I consider it quite likely that the latter species will eventually be found in the immediate Virginia region (see Geographic Checklist, Table 45 on page 578).

Eggs and egg-laying by *argentata* were described by Johannsen (1905:107, as *Sphaeromyas*[sic]) and Thomsen (1937:73), and are summarized above under the tribe Sphaeromiini section. Egg hatch requires "4 or 5 days" (Johannsen 1905). Some of the eggs depicted by Thomsen (1937) as *Johannsenomyia* spp. are likely to be *Mallochohelea*.

Larvae of this genus remain undescribed apart from brief characterizations of the first instar hatchlings by Johannsen and Thomsen. These larvae have the typical slender cylindrical "vermiform" shape characteristic of the subfamily Ceratopogoninae, the head capsule being subconical, slightly more than twice as long as wide, and larger relative to the body than in mature larvae.

Pupae have been described for only two species, *albidorsata* of S. Africa (Mayer 1957) and *argentata* in the U.S. (Wirth & Grogan 1979). The *Johannsenomyia* pupal respiratory horn is 3 to 4 times as long as broad at the flared apical end; the abdominal tubercles are inconspicuous small and blunt, not conical or angulate; no glandular membranous patches

(disks) are present on the abdominal sterna. The anal points tend to be greatly divergent and bare, lacking denticulation.

Although the earliest pupal descriptions involve European species (see Hennig 1950), their taxonomy has not yet been brought up to date, so there remains some confusion about which species are in fact *Johannsenomyia*, and which *Mallochohelea* (Havelka 1978). In any case, these early descriptions generally lack necessary diagnostic detail.

3.4.2 Autecological Remarks

Members of this genus are most commonly encountered in the littoral zone of lakes and ponds, but are also regularly taken from the margins of larger rivers in all zoogeographic regions. See discussion of *J. argentata* habitat.

3.4.3 Distribution

Worldwide, 25 species have been assigned to *Johannsenomyia* (Wirth et al 1974) and no new species appear to have been described in the past decade. *Johannsenomyia* spp. are recorded from every zoogeographical region: two each from the Nearctic and Neotropics; three are Palearctic, five Afrotropical, and seven each from the Oriental and Australian subregions.

The two Nearctic species of this genus, *J. annulicornis* Malloch and *J. argentata* (Loew), are known only from east of the 100th meridian*.

* *Johannsenomyia annulicornis*, previously known only in the north from Illinois, Michigan to Ontario, was recently reported from two counties in Florida (Wilkening et al. 1985).

3.4.4 Annotated Taxonomic and Biological References

- Thomsen 1937:73, Pl.X, XI (eggs descr. illus., first instar larvae)
- Mayer 1957:30 (pupa & habitat of *J. albidorsata* (de Meillon), as *Dicrohelea*, S. Afr.)
- Wirth 1962b:276-277 (revision, synonymy, key, Nearctic spp.)
- Wirth and Grogan 1979:871-876 (diagnoses of male, female, pupa; biol. notes)

3.5 # 124. *Johannsenomyia argentata* (Loew)

3.5.1 Systematics and Habitus

Eggs are described by Johannsen (1905) and Thomsen (1937). An interesting and detailed account of oviposition behavior, summarized under the tribal discussion above, was provided by Johannsen (1905) for this species, and quoted extensively by Wirth and Grogan (1979:849) and Rieth (1915).

The larva and pupa are treated in the generic discussion above, which refers largely to this species. A larval exuvium of this species is among my individually-reared material(WIK 262-2 IR), as well as a few larvae from the same site.

3.5.2 Habitat Characteristics in this Study

Reared from three rather dissimilar sites: a small pond, a large lake and a small river. The pond was in an over-grown pasture which had not been used for at least a few years, and the sample, taken by a modified Petersen grab, consisted of soft brown mud 30 cm from the shore under 30 cm of water, with roots of 50 cm tall sedges in a sparse stand (WIK 262). It is significant that the pond was not frequented by cattle. *Bezzia* cf. *albidorsata* was reared here also, with numerous chironomids. The electrical conductivity of this water at this site was rather low, at 23 micromhos/cm.

On the buttress roots of a large cypress 100 m out in the water of Lake Drummond, 1.5 m deep at the time, a sample of moss and algae at the water line yielded this species and a female *Mallochohelea atripes*, to-

gether with numerous Chironomini (WIK 39). The bottom of this site is a mixture of tyrophel and sand among a complex bed of old stumps. The water is tea brown and acid (pH 4.5).

A sandy-silt among gravel along the water line of the South Fork of the Roanoke River (WIK GH-2), with interspersed roots of riparian trees and shrubs, produced *J. argentata* on one occasion.

All of these sites were unshaded.

3.5.3 Autecological Review

3.5.3.1 Habitat Preferences.

Of the 23 sites in which the habitat was known or could be reasonably inferred from the literature, 70% were associated with lotic environments (esp. rivers and larger streams) and 30% with lentic situations (ponds and lakes). Wirth and Jones reared 22 specimens from the sandy margin of the Potomac River at Scott's Run, referred to several times, and where four other Sphaeromiini were also collected (Wirth 1962). Pupae of this species were observed with larvae exuviae on cattail leaf shafts 6 to 12 inches above the water surface in the littoral zone of Douglas Lake, Michigan, and larvae were recovered at the water's edge (Williams 1955). Five other Sphaeromiini occurred with this species there.

A lakeside light trap on Lake Norman, NC, yielded 4 females, one male *argentata* between 1 June and 28 July (Bowen 1983a). Johannsen and Thomsen (op. cit.) also reported this species from several pond and lake sites in the Ithaca, NY area. Snow et al. (1957) captured *J. argentata* in a light trap at a reservoir near Athens, Tennessee in the Tennessee River basin. This capture occurred early in the season, on April 19th.

A pattern which suggests itself from the above and other records is that Sphaeromiini tend to occur in assemblages with other sphaeromiine species, and to a lesser extent with Palpomyiini and Heteromyiini.

Larvae of this species are members of the soft mud benthos, and are most likely to occur from up to 2 m horizontally beyond the water's edge to 4 m below the water line. The mature larvae follow the typical sphaeromiine pattern at pupation. The food habits of the larvae are not specifically known, but undoubtedly they are predaceous.

3.5.3.2 Adult Behavior

Adult Female

J. argentata are insectivorous, as are *J. annulicornis* Mall. observed by Downes (1978:12), and the males are eaten at mating. Some of the cues important to the female in oviposition are suggested by the observations recorded by Johannsen (1905): sunset, near-shore open water sheltered by vegetation. The fact that the female's head is directed toward the shore may mean that a visual cue, such as the contrast distinction at the shore-water line, is critical, similar to the situation with swarm markers.

In the case of the Lake Drummond site, it is possible that the ovipositing female deposited her egg string near the intersection of the cypress tree with the water line, which would presumably also provide the required visual cue. There is no reason to doubt that the larvae could have completed development far from the shore in the peaty and sandy substrate forming the bottom of the lake, which fluctuates between 0.5 to 2.0 m in depth normally. If the eggs had been deposited near the shore,

then the larvae would have had to move at least 100 m to reach the tree and pupate.

3.5.4 Distribution

- Geographic Range. Widely distributed in the Nearctic east of 100 deg. W, from North Dakota to Ontario and New York, south to Florida and Texas. Now known from at least 16 states: FL, IL, IN, IO, LA, MD, MI, NC, NJ, ND, NY, OH, PA, TN, TX, and VA. Distribution in Virginia is given in Figure on page . All records in this study constitute new distribution records for Virginia.

- Biogeography. Cosmopolitan in depositional habitats, usually in hypopelic sediments (often covered by water), and nearly always near the shore of non-montane lotic and lentic waters. Recorded from 2500 ft. (762 m) and 1500 ft (460 m) in the Ridge and Valley physiographic province (VA & TN resp.) to near sea level in the Coastal Plain. Definitely not associated with stream environments at higher elevations. There is a strong concentration of records in the Great Lakes and Mississippi River basins.

3.5.5 Collection Records

- Reared

Virginia: Chesapeake City, Lake Drummond, on cypress buttress root, 14-VI-1975, 1 male by RC (WIK 39); Highland Co., 2 mi E. on U.S. 250 from McDowell, Bullpasture Mtn., pond in old pasture, 22-VI-1976, larva (?), 1 p. ex., 1 female by IR (WIK 262-5). Montgomery Co., S. Fork Roanoke R, 20 m downstream from U.S. 11/460 northbound bridge at Roanoke Co. line, May 1972 by RC (WIK GH-2).

3.5.6 Annotated Taxonomic and Biological References

- Johannsen 1905:107-108 (oviposition behavior, egg, 1st instar larva descr.; as *Sphaeromyas*[sic]; NY)
- Malloch 1915:334 (habitat, *J. halteralis* (syn.), IL)
- Thomsen 1937:73 (eggs descr., photos; 1st instar larva descr, habitat; NY)
- Williams 1955:94,96 (pupation behavior; as *Dicrohelea argentata*² and *J. halteralis*; MI)
- Wirth & Grogan 1979:872 (female, male, pupal diagnoses, figs., biol. notes, synonymy, northern VA)
- Bowen 1983a,b (recorded from lake, North Carolina)

² Through a typographical oversight or some other circumstance, Wirth and Grogan (1979:852) mistakenly "updated" the nomenclature for this species as *Mallochohelea argentata*.

3.6 Genus *Macropeza* Meigen

3.6.1 Systematics and Habitus Synopsis

This genus is closely related to *Probezzia* Kieffer. *Macropeza* has long been known from Europe and Africa: the females of *M. blantoni* Wirth and Ratanaworabhan 1972 and *M. pamunkeiana* Knausenberger and Wirth 1980, from Florida and Virginia respectively. The males, larvae and pupae of these species remain to be described. Wirth and Ratanaworabhan (1972) provided brief and rather general characterization of the larva and pupa of this genus. These authors omit mention of the ventral abdominal "glandular disks" of the pupae, which are usually present in *Macropeza*, and are characteristic of many members of the tribe Sphaeromiini. Wirth (1962, 1971) has drawn attention to their diagnostic value. The existence of these "ventral membranous patches" on abdominal segments 6 and 7 was first pointed out by de Meillon (1937), who described and illustrated them for the pupae of *M. bayeri* and *M. natalensis*.

Wirth(ms. in litt., figs. 117p, q) illustrates the larval head capsule and general larval body habitus of *M. natalensis*. The head capsule is elongate, rather strongly tapering, and the sides appear somewhat convex, giving it a slightly "pear-shaped" appearance from the dorsal aspect. The eyespots are apparently very large with posterior extensions, similar to *Mallochohelea atripes*

3.6.2 Geographic Distribution

Of the 23 species now assigned to this genus worldwide, 17 occur in Sub-saharan Africa and Madagascar (Wirth et al 1980; DeMeillon and Wirth

1981), one each in Egypt and India (Wirth and Ratanaworabhan 1972), two in central and southern Europe (Havelka, 1978; Wirth Ratanaworabhan, 1972) and two in eastern North America. The preponderance of species in the African tropics, taken with the absence of the species in the Australian region, suggests that the genus has a Gondwanaian origin. This interpretation would be supported by the eventual collection of *Macropeza* representatives in the Neotropical Region, where the genus is presently unknown.

3.6.3 Adult Habits

One of the earliest reports on swarming and mating in the Ceratopogonidae was published by Loew (1864), who observed *Macropeza albitarsis* Mg. forming large mating swarms in the evening. He described the mating process in which the male hypopygium may be left tightly attached to the abdomen of the female after copulation. The insectivorous prey-capturing habits of female *Macropeza* are discussed in Downes (1978) and Knausenberger and Wirth (1980).

3.6.4 Annotated Taxonomic and Biological References

- de Meillon 1937:351, 355 (as *Macroptilum*; pupae of two species (*M. bayeri* de M. and *M. natalensis* deM.) reared, described and figured, with notes on habitat; Afrotropical);
- Mayer 1952: 585 (pupa of *M. aethiopica* I&M briefly described, habitat; Afrotropical);
- Mayer 1955:102 (habitat, Afrotropical);
- Wirth and Ratanaworabhan 1972:213 (generic diagnosis, including of larva and pupa; check list of world species; *M. blantoni* described, Florida);: Havelka 1978:443 (distribution in Europe; habitat).

- Wirth, de Meillon and Haeselbarth 1980:170 (list, Afrotrop. spp.)

3.7 # 125. *Macropeza pamunkeiana* Knausenberger and Wirth

3.7.1 Systematics & Habitus

The adult female of this species, with its greatly elongated hind basitarsus, exhibits to an extreme the "long-legged" character state which helps to distinguish the genus (*macro* -, large; - *peza*, foot), and the family in general. The eggs, cigar-shaped to slightly curved, are typical of the Ceratopogoninae.

3.7.2 Habitat Characteristics

Larval habitat unknown. Adults collected from two sites separated by 16 km along a fourth-order metarhithral stream in a narrow eastward-sloping valley, where no other significant bodies of water exist. No *M. pamunkeiana* were encountered in any of 10 reservoir-sited light traps operated between 1973 and 1976 along the L. Anna reservoir directly upstream from one of the streamside sites which yielded the species.

3.7.3 Autecological Comments

▪ Habitat Requirements

It seems reasonable to propose from the adult collection sites and from published collection records of other *Macropeza* species that *M. pamunkeiana* is a rhithral species, preferring small rivers and larger streams. *M. albitarsis* occurs in small rivers in Europe (Havelka 1978).

In Africa, *M. bayeri* de M. was reared from a pupa collected at the confluence of a tributary with the M'posa R. in Zululand, eastern South Africa (deMeillon 1937:351). Mayer 1952:584 described the pupa of *M. aethiopica* (I&M) (as *Macroptilum aethiopicum* I&M) taken from the margin of the Mselemi R., also in Zululand. Thus, all *Macropeza* spp. with known habitat data seem to prefer lotic situations.

▪ Adult Behavior

Female *M. pamunkeiana* produce at least 400-450 eggs, and apparently deposit them in ribbons, as is the case with other Sphaeromiini which have been observed (e.g., Johannsen 1905; Rieb, 1980).

3.7.4 Distribution

▪ Geographic Range

Known only from Virginia (Fig. 10).

▪ Biogeographic Distribution in Study Area

Collected in the outer Piedmont, in the York River basin, 16 to 32 km upstream from the Fall Line (and from the Coastal Plain physiographic province). This area can be assigned to the Floridian Biotic Region (Hoffman 1969), which generally coincides with the Coastal Plain, but the Floridian Biotic Region has major extensions westward along the larger river basins, such as the York. The fact that this species occurred only in July in two separate years, and at no other trap times, suggests a thermophilous predilection.

These considerations strongly point to Austral affinities for *M. pamunkeiana*. The only other species of *Macropeza* in the Western Hemisphere, *M. blantoni*, was collected in the uplands of the Florida

panhandle, in the Coastal Plain physiographic province. An informative discussion of the biogeographic attributes of the collection locality of this species is given by Blanton and Wirth (1979:28).

3.7.5 Collection Records

•Adult Field Trapping: 7 females in two UV light traps. *Virginia*: Louisa Co. - Spotsylvania Co. line on North Anna River, VA Rt. 601 at Smith's Mill Bridge, 400 m downstream from L. Anna impoundment dam, 28 VII 1977, coll. C.R. Parker: 4 females by light trap (BL-53). Hanover Co. - Caroline Co. line on North Anna River, VA Rt. 601 at Butler's Bridge, ca. 16 km downstream from L. Anna dam, 1-VII-1976, coll. J.R. Voshell, Jr.; 3 females by UV light trap (BL-47).

3.7.6 Reference

- Knausenberger and Wirth 1980:133 (male, female, oviposition, eggs described, biological notes; Virginia)

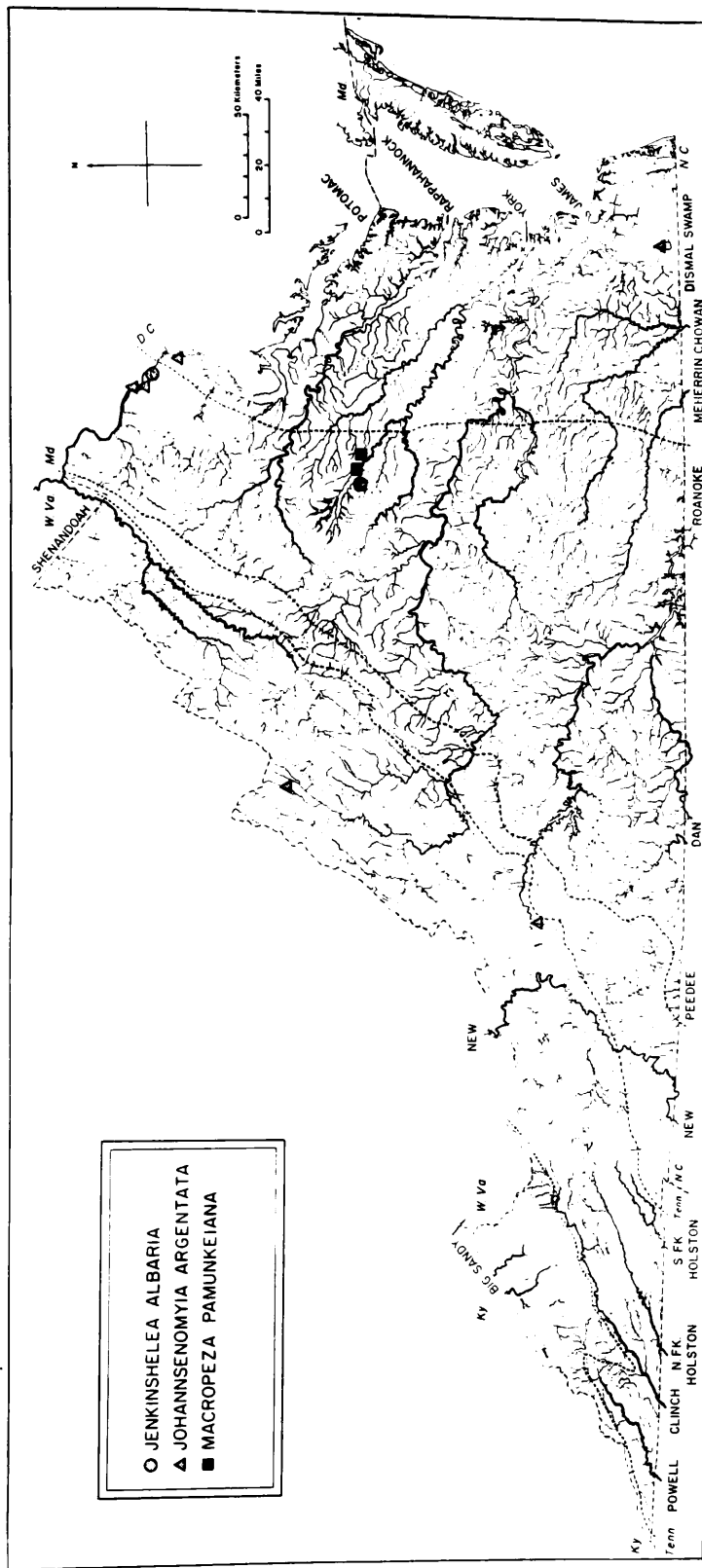


Figure 10. Geographic distribution of the Sphaeromiini *Jenkinshalea albaria*, *Johannsenomyia argentata*, and *Macropeza pamunkeiana*.

CHAPTER FOUR

Ecosystematics and Autecology of Immature Sphaeromiini -- II:

Mallochohelea and *Nilobezzia*

4.1 Genus *Mallochohelea*

4.1.1 Systematics and Habitus Synopsis

Adult: Females of *Mallochohelea* and *Nilobezzia* are similar, both having equal tarsal claws with an external basal tooth, wing with usually two radial cells (*N. schwarzii*), with a short costa reaching to no more than 0.8 of the wing length. However, *Mallochohelea* differs in that its thoracic integument is glabrous brownish to black, the femora and tibiae are usually unarmed (*M. aripes* femora are armed), no genital sclerotizations, and many other features detailed by Debenham (1974) and Wirth (1962b). Male *Mallochohelea* have a well-developed basimere and articulated telomere, whereas in *Nilobezzia* these structures are fused, the telomere being immovable and thumblike.

In practice, at least in the middle Atlantic region, there is far greater likelihood for unwary sorters of alcohol collections to confuse certain *Mallochohelea* and *Palpomyia* species, even though they belong to different tribes. This is because they can appear very

similar superficially (sometimes even close-up, particularly males), and because *Palpomyia* are far more common than *Nilobezzia*, especially in this region. Even so, they can be distinguished readily enough upon closer inspection, such as by the presence in *Mallochohelea* of well-developed ventral tufts of thick setae on the eighth abdominal segment, absence of genital sclerotizations and internal gland rods, and the presence of an external basal tooth on the tarsal claws (*Palpomyia* possess inconspicuous sharp internal basal teeth). With males, it is usually necessary to mount the specimens on microscope slides to arrive reasonably certain determinations, but in any case the presence of a short, stout external tooth on the claws serves to separate *Mallochohelea* from *Palpomyia*.

Sexual dimorphism in size between female and male is usually not as pronounced as in other genera in these tribes, notably *Probezzia*. Color differences, especially of the legs, tend to be the most useful key characters to distinguish species, and holds for both males and females, though in the males, the legs tend to be darker as a whole. However, variation can be considerable, such as in the hind tibia of *smithi*, which may be all infuscated to half of its length from the apex. Here again, incompletely hardened specimens can cause difficulties, requiring one to use meristic and structural details, which in *Mallochohelea* males are not readily available.

Two taxonomic "groups" of *Mallochohelea* can be proposed based on the expression of distinctive characters in three of the four developmental stages: larva, pupa and adult (Table 13). One group, which I shall provisionally term the "*albibasis* Group", based on the

Table 13. Separation of two possible *Mallochohelea* species groups on the basis of adult, pupal and larval characters.

Mallochohelea		
Character	albibus "Group"	atripes "Group"
ADULT		
Male claspettes	Entire	Divided
Fore femora	Unarmed	Armed
PUPA		
Pupal respiratory horn L/W ratio	Short, squat 1.5 - 2.5	More elongate, slender 2.9 - 3.5
Apical spiracles in horn	4 - 12	18 - 20
Large, blisterlike protuberances on dorsum of cephalothorax	8 - 12	Absent
Abdominal dpm ^{1/} tubercles	Prominent, elbowed backwards	Inconspicuous, angled backwards
Apicolateral processes	Relatively long, curved or straight, slightly to moderately divergent; 0.6-1.2x as long as base of segment.	Short, straight, greatly divergent, 0.4-0.5 as long as base of segment.
Ventral membranous patches	Present on sternites VI, VII	Indistinct or absent
LARVA		
Larval eye spot	Small, comma-shaped	Elongate, large, backswept

^{1/} dorso-posteromedian

genotype, includes all the species I have seen except *M. atripes*, which forms the basis of the possible "*atripes* - Group". Although I have not seen them, presumably the species *spinipes* and *texensis* would fall with *atripes* in one group, based on the armature of the femora and batonnets described by Wirth (1962b).

Eggs: In *Mallochohelea* spp., these are deposited in gelatinous ribbons 3-4 cm in length, containing 200-300 eggs (Rieth 1915, Wesenberg-Lund 1914, 1915, 1943 (in Thienemann 1928, 1954)). A fuller description of the oviposition is given under the tribal discussion.

Larva: *Mallochohelea* larvae are medium-sized, ranging in length as instar IV from 6 - 12 mm. The head capsule is moderately elongate and tapering, but not strongly conically produced, based on present specimens, and descriptions of 3 European *Mallochohelea* species (Glukhova 1971, 1977, 1979). Ventrally, a caudally directed protuberance on the "collar" is present, elongated to various degrees, and somewhat spoon-shaped. Similar expansions occur on the mid-ventral line of most or all sphaeromiine larvae known.

The larval head capsule color, eyespot size and shape and thoracic pigmentation offer some potentially useful sorting characters at the species group level (Figure 11 on page 272). The blackish thoracic pigmentation remains basically recognizable even in preserved specimens (Figure 12 on page 274). The head capsule in *atripes* tends to be darker, towards a light brown, whereas in other species it appears to be a lighter yellowish, usually with a darker postoccipital area.

The chaetotaxy and sensilla on the head capsule, with the shape and development of the combs on the epipharynx, appear to provide specific differences, but no consistent pattern in the chaetotaxy appears to hold at the generic level.

I have determined *Mallochohelea* larvae, which with the exception of *atripes* I have been unable to rear individually, on the basis of the following combination of characters, for instar IV larvae:

1. head capsule with caudal expansion on mid-ventral line of postocciput, not conically produced like some *Probezzia*, or slender and elongate like some *Palpomyia* and *Bezzia*, short and broad (several genera) *longipennis*), etc. or squat and triangular or ovoid (as in *P. tibialis* group, *Sphaeromias*);
2. head capsule shape and eyespots as in Fig. 11a,b or 12a-d
3. thoracic pigmentation similar to that in the figures above;
4. setae on anal segment in two linear rows.

This combination of larval characters regrettably does not permit definitive separation from all other Sphaeromiini, which are still very imperfectly known. In particular, earlier instar larvae have a more general appearance, and can be readily confused, mostly with some *Bezzia* and *Palpomyia*, and certain Sphaeromiini. However, with a knowledge of the fauna of a region by rearing or adult capture, awareness of the relative abundance of members of the various genera, and a grasp of the range in habitus of the larvae in the family, reasonably certain determinations are achievable.

Figure 11. *Mallochohelea albibasis* Group larvae and pupae:
(a) head and thorax of live *M. albibasis* (Malloch) larva, with nematode as food source (*Panagrellus redivivus*); (b) head and thorax of prob. *M. albibasis* Group (sp. unknown); (c) live *M. smithii* pupae, with "glandular disks" well-developed; (d) preserved *M. spp.* (prob. *williamsi* and *albibasis*) pupae from Ontario. Bars indicate 1 mm.

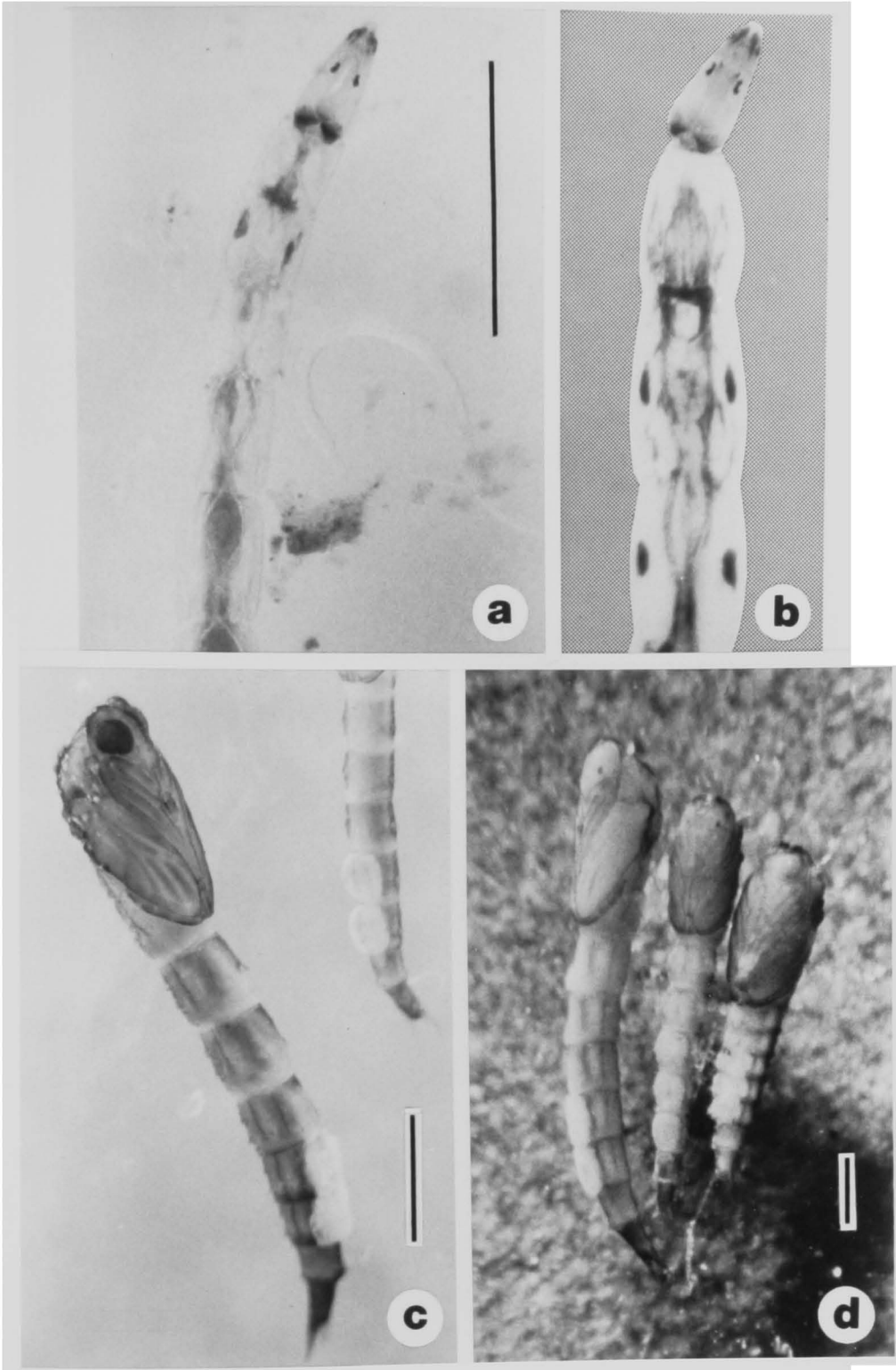
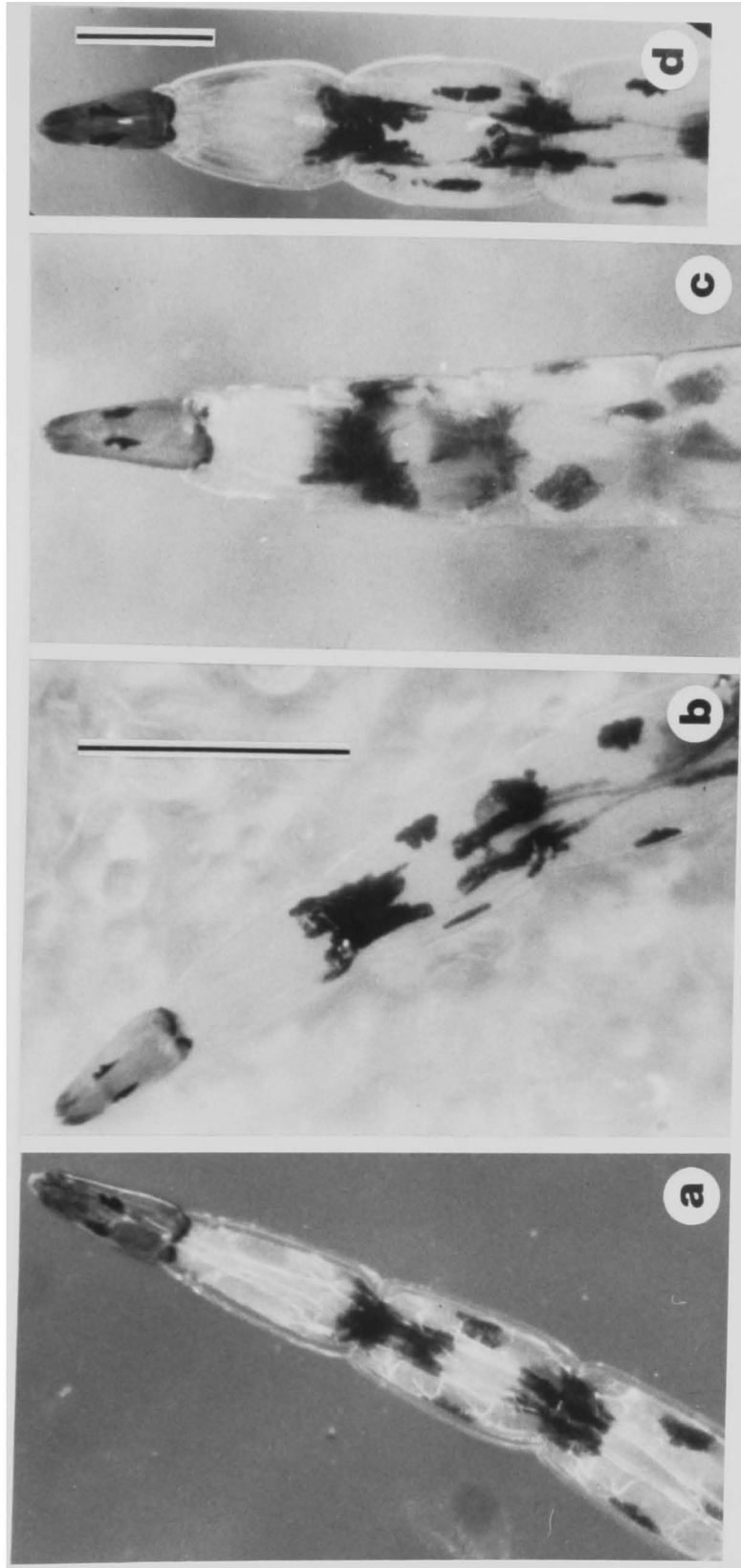


Figure 12.a-d *Mallochohelea atripes* larval head and thorax habitus: (a) live, third instar; (b) live, early fourth instar; (c) preserved in isopropanol; (d) live, early prepupal stage fourth instar. Bars indicate 1 mm (a-c same scale).



Pupa: Characteristically, the respiratory horn has a short, squat appearance, being 1.5-2.5 times as long as its widest point of usually at mid-length).

Because the horn's apparent shape may vary considerably depending on the aspect, L/W ratios of up to 3.5 can be obtained, especially with *M. atripes*. Other features typical of *Mallochohelea* pupae are given in Table 13 on page 269. The dichotomy of the pupal character state in particular bears mentioning: 8-14 prominent blisterlike tubercles occur on the dorsum of the cephalothorax of all "*albibasis* Group" pupae I have seen (*albibasis*, n. sp. nr. *caudellii*, and *smithi*); between 4 and 7 occur on either side of the ecdysial line (cf. Figure 9 on page 240 -- Fig.9b). These prominent tubercles have apparently never been described explicitly, although they are visible in photographs of the pupal exuvium of the Palaearctic *M. inermis* (Rieth 1915, Thienemann 1928). Apparently the tubercles, in this manifestation, are unique to the *Mallochohelea*, though there are possibly homologue setae, pits and inconspicuous tubercles present in other genera. Also, the presence of large angulate, backward projecting spinose tubercles on the dorsum of the abdomen (d.p.m. tubercles) is unique to this group of *Mallochohelea* (see also fig. 24 in Rieth 1915).

Ventral membranous patches are present on sternites six and seven in most species for which pupae are known. They are reduced or apparently absent in *M. atripes*, and three are present on sternites V-VII, in *M. inermis* of Europe. No specific mention of these structures is made by Wirth and Grogan (1979) in their pupal diagnoses of

three species, although the statement is made under the generic diagnosis that abdominal sterna six and seven possess membranous, glandular disks. The absence of attention to the membranous disks by the above authors is surprising in light of Wirth's (1962b) statement that discovery of *M. atripes* pupae "should serve greatly to clarify its relationships." Finally, in contrast to the statement that *Mallochohelea* apicolateral processes are relatively short and pointed (Wirth and Grogan 1979), in some species these can get prominent, e.g. *smithi*, being broad at the bases, curved, and as long as or longer than the base of the segment. In the one Australian pupae known, these processes are "long and straight, directed posteriorly" (Debenham 1974).

4.1.2 Habitat Characteristics: Present Study

Perhaps 50 larvae and 20 pupae of *Mallochohelea* not determined to species occurred among collections I examined from all sources. Among existing institutional collections which I examined, only the Royal Ontario Museum and Academy of Natural Sciences of Philadelphia contained significant numbers of specimens. Among collections I received directly from aquatic biologists, *M. sp. prob. atripes* appeared most commonly (treated in part under that species).

Stream and lake environments were nearly equally represented in the collections yielding *Mallochohelea*, but the specimens deriving from northern localities, e.g., Ontario or Quebec, were more likely to be from lakes, whereas streams dominated the sites of origin in the south.

From the Upper Three Runs Creek study by Morse et al (1980, 1983) at the Savannah River Plant, South Carolina, discussed in more detail under the *Probezzia* generic treatment, I determined up to 4 larval *Mallochohelea* types, of which the predominant one I considered to be *atripes*. Also in South Carolina, a study on recolonization of streams by insects, following channelization (White and Fox, 1980) yielded numerous Sphaeromiini, some which I considered to be *Mallochohelea*. These South Carolina sites primarily consisted of a sandy substrate. In the Alabama River, *Mallochohelea* appeared in a collection taken by C. J. Turner by Petersen grab from a sandy bottom under 9 ft. of water (River mile 63).

Among a series of larvae from two subtropical lakes in Florida (L. Brooker, L. Thonotosassa), reported by Cowell and Vodopich (1981) as "*Palpomyia* - *Bezzia* spp" and of which I subsequently saw representatives, were *Mallochohelea*, some probably *atripes*. The bottom in these lakes was predominantly sandy.

4.1.3 Autecological Review

4.1.3.1 Habitat Preferences

Of the twelve species of Nearctic *Mallochohelea*, only five have been reared from habitat substrate, and these species each have their respective Macrohabitat preferences, found either along running waters or in ponds or lake margins (Table 14). Their habitat is rather consistently shaded, and only *atripes* is significantly associated with aquatic plants. In this case, it is not emergent wetland plant stands, but beds of submersed hydrophytes that are involved. The habitats at which *M. atriipes* occurred were the least shaded of the species for

which I could assess that factor. Submersed mud is quite consistently a factor in the sites evaluated, even in the stream sites, where lenitic sites predominated. Nevertheless, it appears that *M. albibasis*, which could be termed a rheophilic species, is capable of moving about in significant current, at least in the boundary layer found at the substrate-water interface in running waters (Jaag & Ambuhl 1964). Only *Probezzia pallida* among the Sphaeromiini appears as likely to occur in running water habitats.

With the species occurrence data resulting from this study, and from published locality information, and by examining relevant maps (particularly with respect to estimating stream order), I attempted an assessment of *Mallochohelea* habitats on the basis of "habitat continua" (Vannote et al 1980, Merritt et al., 1984). The results, in Table 15, are suggestive of possible ecological segregation among and within species, though no direct geographical, seasonal or micro-habitat distinctions are possible from the data. Two species, *albibasis*, and *atripes*, for which the collections are most likely to be adequately representative of their populations, are clearly segregated from each other; *albibasis* is most often encountered at Order 3 streams, and *atripes* in the littoral zone of lakes.

Quite possibly, different cohorts from within geographically proximate populations of the same species will segregate into different habitats or subhabitats, according to optimal habitat choice theory (e.g., Powell and Taylor 1979). Another species, *smithi*, is apparently more likely to occur in larger streams than *albibasis*, as well as in lakes to a minor extent. No Nearctic *Mallochohelea* have

Table 14. Relative abundance of Mallochohelea species in lotic and lentic environments, with microhabitat summaries. Includes only those species for which rearing records are available (from this study or Wirth, 1962b; Wirth and Grogan, 1979)

Mallochohelea Species	Macrohabitat				Abundance Index	Microhabitat Summary
	Lotic		Lentic			
	No. Sites ¹	Abundance Index ²	No. Sites	Abundance Index		
albibasis (Mall.)	12	114.5	-	-	-	Smaller streams, hypopelophilic, along shaded banks.
atripes Wirth	5	17.3	29	218.9	-	Mostly along lake and pond margins, submerged soft mud or aquatic plant beds, usually with detritus present. Partially shaded sites.
sp. nr. caudellii (Coq.)	1	1.7	4	12.6	-	Mainly lake and pond margins, submerged mud substrates, apparently less associated with hydrophytes. In stream among riparian root mats and mud. Shaded sites.
smithi (Lewis)	6	24.7	1	4.0	-	Larger streams. Taken from algal mats and stream margin sediments. Habitat poorly known.
sybleae (Wirth) ³	1	3.9	-	-	-	Stream margin.

¹ Separate localities yielding specimens, combining literature and present study records.

² $(N_1)^3 \cdot F_{coll}$, where N_1 = no. indiv. (total), F_{coll} = frequency of collection (sep. localities).

³ Western U.S.

been taken from the profundal of lakes. One Palaearctic species has been found in small numbers at depths up to 14 m in lakes of the USSR (Glukhova 1979).

The number of records for the remaining 7 species is too small for the indications in Table 15 to be more than a synoptic overview of the habitat types known or suspected for these species. For two additional species, *pullata* and *variegata*, no judgments at all were possible as to habitat.

Comparable among-species habitat partitioning apparently also occurs with the five European *Mallochohelea* for which information is known: (a) *dentata* (Kieffer) is typically a lake inhabitant (Rieth 1915, Thienemann 1928; Lenz 1934, Mayer 1934c); (b) *inermis* (Kieffer)¹ is a member of the lake fauna, and also occurs in ponds, particularly in soft mud among dense emergent vegetation or floating beds of macrophytes (Rieth 1915; Thienemann 1928, 1954; Mayer 1934c, Glukhova 1971, 1977, 1979, Havelka 1978); (c) *munda* (Loew) has been taken from lakes in the USSR (Glukhova 1979). Two European species are known only from rivers: *remota*, observed ovipositing in a river in France (Rieb 1981); and *setigera* (Loew), observed by Rieb along with *remota*, ovipositing at a river margin; and taken consistently and at times in large numbers at several rivers in the USSR, at or below the waterline in soft silty substrate (Glukhova 1979).

In Australia, the single known reared species, *M. satelles*, was taken along the Nattai River, in New South Wales (Debenham 1974).

¹ in part as *nitida* (Macquart) (Goetghebuer 1923)

Table 15. Ecological partitioning of *Mallochohelea* along stream order and lentic habitat continua, based upon relative abundance index values: + = 1-10; ++ = 11-29; +++ = >30. The "?" indicates species for which no rearing records are available, but for which some locality data is suggestive of a habitat type.

Mallochohelea Species	Lentic System						Habitat			Continua		
	Stream Order						Pond			Lentic System		
	2	3	4	5	6	7	2	3	4	Littoral	Sublittoral	
albibasis (Mall.)	+	+++	++	++	+							
albihalter Wirth			?							?		
atripes Wirth	+	+				++			+++		+	
caudellii (Cog.)			?	?						?		
sp. nr. caudellii		+				+				+		
flavidula (Mall.)			+	+								
smithi (Lewis)			++	+						+		
spinipes Wirth								?				
sybleae (Wirth)	+	+										
texensis Wirth			?	?								
spp. undetermined	+	++	+	+	+	+	+	+	++	++	+	

1 $\sqrt{N_I} \times F_{Coll}$, where N_I = no. indiv. (total), F_{Coll} = frequency of collection (separate localities).

Finally, an unusual habitat for the genus is recorded from the tropics: in a rain forest in southeast Sumatra, *M. prominens* Joh. occurred in small collections of water in stems and trunks of unspecified plants (Mayer 1934b). Other genera of Ceratopogonidae, such as *Bezzia*, not normally occurring in phytotelmata, have also occasionally been reported from such habitats in tropical rain forests, where ground pools and ponds are rare relative to the great abundance of phytotelmata (Snow 1949, Mayer 1955, Lane 1958, Vitale et al 1981).

4.1.3.2 Larval and Pupal Habits

Mallochohelea larvae are highly active, vigorous swimmers, an impression created more by the very rapid oscillations of the body than the actual speed of propulsion, which is not markedly greater than that of most ceratopogonine larvae of comparable size. Mature larvae have a tendency to swim at the water's surface.

No specific observations on feeding habits of the larvae have been reported, nor did I see any direct evidence of food selection during individual rearing attempts. From the relatively delicate epipharyngeal combs, it seems likely that the larvae are primarily piercer-engulfers.

Pupae are relatively active and commonly are found attached to plants, particularly plants emersed directly in the water (pers. obs., Glukhova 1979, Williams 1955). They are capable of moving up and to a lesser extent down, by virtue of sharp side-to-side deflections of the abdomen. How significant the ventral membranous patches on the abdomen really are to plant attachment and scaling, is unclear, because

pupae can accomplish these acts at least to some extent without possessing the patches.

4.1.3.3 Adult habits

Oviposition behavior of three European *Mallochohelea* has been reported: for *nitida* by Hamm (1919) and for *remota* and *setigera* by Rieb (1919). In all cases the oviposition occurs in the waning light of the evening by females hovering in place on average about 50 cm above the water. In all observed cases this behavior occurs near the margin of open water bodies.

Adult predation records by Downes (1978) involve four species of *Mallochohelea*. All the prey but one (of about 12 observations) were chironomids, typically captured in the male swarms characteristic of many Nematocera. In England, *M. nitida* captured a male *Culicoides nubeculosus*, a large species of *Culicoides*, related to *C. variipennis* in North America. Most of the remaining observations were made by Downes in Ontario with *M. albibasis* (q.v.). An undescribed species and *M. albihalter* were the other species for which observations are given.

The seasonal flight activity of eastern Nearctic *Mallochohelea*, as judged from adult capture records (Table 16), shows that four of eight species are likely to be spring species, and two aestival (*atripes*, *smithi*), while for two others the available records are too few to judge. There are indications of distinct temporal segregation in adult emergence among species most likely to occur in the same area, for instance *albibasis* and *atripes*. Also, it appears likely that most *Mallochohelea* species are univoltine, with summer or early fall flight

Table 16. Synopsis of adult *Mallochohelea* spp. seasonal flight activity, by month, based on a composite of all available capture records of this study, and in the literature (mainly Wirth 1962b), for all locations. Only those species occurring in the eastern Nearctic are listed. Asterisks indicate those species occurring in the Virginia region.

Percentage of Total No. of Records/Month

Species	Mar	Apr	May	Jun	Jul	Aug	Sep	n ¹
*albibasis (Mall.)	0	16.3	36.7	30.6	16.3	0	0	49(7)
*albihalter Wirth	0	24.1	48.3	27.6	0	0	0	29(0)
*atripes Wirth	0	0	8.0	32.0	52.0	4.0	4.0	25(15)
*n.sp.nr. caudellii	12.5	37.5	50.0	0	0	0	0	8(8)
flavidula (Mall.)	0	27.3	54.5	18.2	0	0	0	11
*smithi (Lewis)	0	3.4	13.7	58.6	17.2	6.9	0	29(1)
spinipes Wirth	0	0	0	100.0	0	0	0	1
variegata Wirth	0	0	50.0	50.0	0	0	0	2

¹ Figures in parentheses are numbers of collections in this study.

activity occurs, and all the latest trapping records occur in the northernmost localities. Most the data taken in the study area tend to support this observation. Nevertheless, the data in the Table 16 should be taken only for what it is, an indication of emergence and activity trends which would need to be confirmed by specific detailed and regular trapping data in given areas.

4.1.3.4 Other Observations

Natural enemies. The only record of which I am aware which deals with any *Mallochohelea* is a case of phoresis or possible ectoparasitism by the hydracarine larvae of what was reported by Munchberg (1935) as *Hydrodroma despiciens* (in Thienemann 1954).

4.1.4 Distribution

Mallochohelea is distributed worldwide, with the number of species represented in the various zoogeographic regions as follows:

Afrotropical	(3):	Wirth et al. 1980, de Meillon and Wirth 1981
Australasian	(7):	Debenham 1974
Nearctic	(13) ² :	Wirth 1965, 1962b
Neotropical	(4):	Wirth 1974
Oriental	(3):	Wirth 1973
Palaeartic	(12):	Havelka 1978; Remm 1980, 1981

In North America, the greatest center of diversity appears to be in the Great Lakes region, as discussed in the species section (Figure 13 on page 333).

² Including at least two new species, one in this study and one in Downes 1978.

4.1.5 Annotated Taxonomic and Biological References

4.1.5.1 Nearctic

- Malloch 1914:230 (*M. flavidula* Mall. (as *Johannseniella*), pupal descr., figs. thorax, 3rd abd. segm., term. segm., Illinois)
- Wirth 1952a: (*M. sybleae* (Wirth) as *Johannsenomyia*, pupal descr., resp. horn, term. segm. fig., habitat, California, USA)
- Williams 1955
- Wirth 1962b:275-6, 278-283 (genus erected, 11 N. Amer. spp., 5 new, descr., keyed; diagn. pupal char.; distr. & rearing rec., N. Amer.; new comb. of 10 spp. from 5 other zoogeogr. regions)
- Downes 1978: several pp. (adult predation records, 4 spp., Holarctic)
- Wirth and Grogan 1979: (3 spp., male, female diagn., 3 pupae, 1 larva descr., biol. notes, Potomac Valley, USA)
- Pucat 1982:529 (*M. sp.* reared from lake, emerg. tr., Ontario)

4.1.5.2 Palaearctic

- Rieth 1915:403, 410, 418-9 (*M. dentata* (Kieffer), *M. inermis* (Kieffer) (as *Johannseniella*) pupae descr. briefly, figs. 19-24 pup. resp. horn, abd. tub., term. segm.)
- Hamm 1919 (oviposition behavior, *M. nitida*, as *Ceratopogon*, England)
- Goetghebuer 1923:184-5 (*M. nitida* (Macq.) (as *Johannsenomyia*, ponds, Belgium)
- Thienemann 1928:595-6, 601 (*M. dentata*, *inermis*, *nitida* , (as *Johannsenomyia*) photo p. ex. abd., brief descr.; habitat, summ. avail. descr. developm. stages, Germany)
- Lenz 1934:120, 122 (*M. dentata*, *inermis*, *nitida*, (as *Johannsenomyia*) brief descr., pupa, fig. resp. horn)
- Mayer 1934a:292 (*M. inermis* (as *Johannsenomyia*) habitat and spp. co-occurrence, lake, N. Germany)
- Mayer 1934c:244-5 (*M. dentata*, *inermis*, *nitida* (as *Johannsenomyia*), pupal descr., figs. resp. horn, operc., habitat notes, Germany)

- Mayer 1952(likens pupae of *M. dentata* (as *Jenkinshalea*) to African *Jenkinshalea polyxenae*)
- Munchberg 1935:737 (phoretic mite on *M. inermis* (as *Johannsenomyia*), N. Germany)
- Hennig 1950:221 (review and list of early pupal descr. of Europ. spp. *M. dentata*, *inermis*, and *nitida* (as *Johannsenomyia*))
- Bertrand 1954:245 (brief note on immature stages, Europe)
- Thienemann 1954:253, 524 (546) (*M. nitida* (as *Johannseniella*) female preying on male, per Staeger 1838; *M. inermis* (as *Johannsenomyia*) in Alsacian ponds with co-occurring midges, per Gowin 1936, 1937)
- Krivosheina 1957:69, 72 (habitat of *inermis*, USSR)
- Glukhova 1971:104 (larva, habitat of *inermis*, *munda* (Loew), USSR)
- Glukhova 1977:442 (key to larval *M. inermis*, *munda*, *setigera* (Loew), European USSR)
- Glukhova 1979:40, 58, 68, 104-108 (biol., behavior, distr., habitat of larvae, *inermis* & *munda* larv. redescr., *setigera* larv. descr.; USSR)
- Havelka 1978:447 (list, European spp., distr., note on synonymy of *nitida* (Macquart) with *inermis*(Kieff.).)
- Remm 1980:85 (*M. n. sp.*, Central Asia)
- Remm 1981:27 (synonymies, 3 spp., Centr. & East. Eur., U.S.S.R.)
- Rieb 1981:114-5 (oviposition of *M. remota* Kieffer, *M. setigera* (Loew), France)

4.1.5.3 Other Zoogeographic Regions

- Debenham 1974:82, 86; Figs. 215, 216, 228, 229(generic diagn., pupa; descr. *M. satelles*, figs. incl. gland. disks; reared, eastern Australia)
- de Meillon and Wirth 1981 (n. sp. descr., key to 7 Subsaharan spp.)

4.2 # 126. *Mallochohelea albibasis* (Malloch)

4.2.1 Synopsis of Systematics and Habitus

This is the genotypic species of *Mallochohelea*, a small midge with a shining back thorax, wings 2.0 mm long, clear at the base, darkened on the distal two-thirds; the legs are unarmed. Sexual dimorphism in size is not significant in this species.

Eggs and larvae have not been described yet. A basic pupal description is given by Wirth and Grogan (1979). The pupal respiratory horn is short, L/W ratio of 2.0-2.5, smooth-surfaced, with 7-12 spiracles. The dorsum of the cephalothorax is prominently studded with blister like protuberances, a feature characteristic of the group of *Mallochohelea*, as explained under the generic discussion. The abdominal tubercles are prominent, the dorsal ones being elbowed backwards at a 90 deg. angle; the apicolateral processes on the terminal segment are also prominent and long, tapering in a smooth curve from broad bases to sharp tips, somewhat in the shape of cow horns. Ventral membranous patches are present on abdominal segments 6 & 7 (see Figure 9).

I have collected or received numerous Sphaeromiine larvae, some of which I consider to be probable *Mallochohelea albibasis*, on the basis of indirect association and a process of elimination¹. The

¹ For example, at a Tom's Creek site (Montgomery Co., Virginia, WIK 245), adults were reared by rearing carton, and one pupa was reared by IR, but no larvae of the tribe developed to adulthood, though one pupated. Only one, possibly two, appropriate larvae were in the series of 30 immatures reared from that site; four species were deter-

larvae are about 7 mm long in the fourth instar (based on one which pupated (WIK 245-2)), with head capsules a stramineous color except for the darkened postoccipital region, small comma-shaped eyespots, with reddish markings in the prothorax and mesothorax (Figure 11).

4.2.2 Habitat Characteristics: Present Study

Seven widely-scattered sites in three states yielded 8 female and 4 male specimens of *M. albibasis*, with one associated male and pupal exuvium; a few of the larvae from some of these sites I suspect belong to this species, but no individual rearing attempts succeeded with larvae.

The habitat characteristics for all seven positive collections are remarkably consistent: all are taken from creeks to smaller rivers, in a substrate of soft mud which always contained sand and some gravel, always directly at the margin of, or in the running water. Finally, all sites were moderately to rather moderately to rather heavily shaded by riparian vegetation, or, as in two other cases, by large boulders (WIK 269C) and a bridge (FVB 811).

mined among the specimens, not including *M. albibasis*. No duplicate specimens of the suspected *M. albibasis* larvae were among the immatures extracted separately, and the reared specimens did not yield usable material. However, on the basis of laboratory notes at the outset of the rearings, I was able to provisionally relate similar larvae preserved intact from other collections to the putative *M. albibasis* larvae at Coll. 245. Similar experiences of indirect or near-association tend to support this; nevertheless, confirmation by direct association is needed.

Emergent aquatic macrophytes were not significant at any of the sites, but accumulations of organic detritus were often present, usually riparian tree leaves and grasses. In one case, a clump of the aquatic moss *Fontinalis* was prominent, attached to the boulders mentioned above, at the point at which Gandy Creek descends into a cave.

The habitat substrate pH averaged 7.1 (5.8-7.8, n=5) and the organic matter content was fairly low, averaging 2.4% (1.8-3.4%, n=4). One site on the S. Fork of the Roanoke R. (GH-1) directly within the influence of the effluent from a meat packing plant. This site was sampled monthly for one year and yielded a rich complement of Ceratopogonidae as well as Chironomidae, Tipulidae and Dolichopodidae.

4.2.3 Autecological Review

4.2.3.1 Habitat Requirements

A rheophilic, hydropelophilic species, tending to occur along shaded banks of epirhithral streams (Orders 2 to 3). Of the 12 explicit rearing records (all sources together), all are running water habitat associated.

Stream order could be estimated for 11 of these, and eight (70.3%) were either 2nd or 3rd order, none were first order, and three ranked as 4th to 6th order.

A first-order tributary of Fourmile Creek near Erie, Pennsylvania, yielded a few *M. albibasis*, captured by emergence trap tent placed over the creek (Rightor, J. & E. C. Masteller, pers. comm. 1985). In addition, another three adult capture records taken near rivers (Wirth

1962b) provide further evidence for a lotic habitat preference, if not requirement.

On the other hand, four adult capture records from lake-side sites emphasize the possibility that *M. albibasis* may well occur in lakes as well, at least to a limited extent. All of the possible lake records are from northern latitudes, esp. Michigan & Ontario (e.g. Downes 1978). This in itself suggests a certain cold adaptation, which would be satisfied in the cooler waters of streams at the more southerly latitudes.

4.2.3.2 Larval and Pupal Habits

The larvae which I consider *M. albibasis* are extremely active swimmers, fast enough to visually set them apart from other larvae in a given sample. While it is likely that they are engulfers/predators, I cannot state so definitively. As Fig. 11a shows, they were offered nematodes, but I did not observe feeding, nor did development appear to occur with the nemas present.

Pupae of *M. albibasis* are rather mobile in that they can move upwards, sideways and apparently to a lesser extent, downwards as well, on plant stems, in this case sedges. They moved upwards with sharp deflections of the abdomen, similar to the behavior reported for *Jenkinshoelea albaria* and *J. magnipennis* (Wirth 1962b, Grogan and Wirth 1977a, Wirth and Grogan 1979).

Both of these species also possess adhesive disks on segments 6 and 7. The dorsal angulate tubercles which *M. albibasis* and others in the genus possess may play a role in pupal positioning on a plant

substrate. The functional significance of the large rounded blister-like protuberances on the dorsum of the cephalothorax is not known.

4.2.3.3 Adult Habits

Seasonal Activity. Peak flight activity of *M. albibasis* appears to be from May into June throughout its range (Table Table 16 on page 173). Although there are insufficient data at any one locality to definitely determine this, emergence appears to be unimodal on the whole. However, it is quite possible that small cohorts of given populations may complete two generations in the period April-July. The earliest record is a collection by Battle on 17 April in Augusta Co., VA, and by Snow on 21 April in Florence, AL; the latest capture dates are between 10 to 18 July in Wisconsin, northern Ontario and at Aklavik, Northwest Territories 55 deg., and 68 deg.N resp.).

Prey Capture. Predation by female *M. albibasis* has been observed by Downes (1978) on about 10 occasions at various lakes in Ontario. At least five species of Chironomidae, notably *Ablabesmyia monilis* Tanypodinae), were preyed upon in their mating swarms. Male midges were the prey in all cases. Mating and oviposition behavior have not been reported for this species.

4.2.3.4 Species Associations

Twenty species of Ceratopogonidae in 6 genera co-occurred with *M. albibasis* at the seven sites from which rearing records were available (Table 17). The *Culicoides* were most commonly represented, with seven species, all of which characteristically occur at flowing freshwater

Table 17. List of Ceratopogonidae co-occurring with Mallochohelea albibasis, a species found only in lotic habitats, based on rearing records from seven sites.

```

=====
Culicoides
  bergi
  haematopodus
  loisae
  piliferus
  spinosus
  stellifer
  travisi

Bezzia
  aldidorsata
  flavitarsis
  laciniastyla
  n. sp. nr. mallochi
  nobilis
  varicolor

Dasyhelea
  grisea
  messersmithi

Mallochohelea
  n. sp. nr. caudellii

Palpomyia
  stonei

Stilobezzia
  antennalis
  lutea
=====

```

habitats, most also typical of shaded habitats (see Blanton and Wirth, 1979, for review); *C. haematopodus* occurred at 86% of the sites, *stellifer* at 43%, and *spinosus* at 29% (i.e., 2 of 7).

The *Bezzia* were well represented by six species, but only the cosmopolitan and euryoecious *B. nobilis* occurred at more than one of the *M. albibasis* sites, at 5(71%). Of the species listed in the table, *B. laciniastyla*, *B. nobilis*, *B. varicolor*, *D. grisea*, *M. sp. nr. caudellii* and *St. antennalis* are not primarily stream-dwellers or cool-adapted species, and most of these have a tendency to be rather ubiquitous.

Apart from the new species of *Mallochohelea* (at GH-1), only one other member of the genus, *M. sybleae* (Wirth), has been reared in association with *M. albibasis*. This was from Berry Creek near Corvallis, Oregon (Wirth 1962b).

Species richness at most of the *M. albibasis* sites was quite high, an average of 5 biting midges per site. Two sites, WIK 245 and GH-1, had 8 and 9 species each, in addition to dolichopodids and tabanids, but curiously no chironomids. At the organically enriched GH-1 site (meat packing plant effluent influence), four species of dolichopodids were reared, dominated by *Tachytrechus protervus*, and also the tabanid *Chrysops brunneus* Hine. At the same site, on different sampling dates, considerable numbers of *Alluaudomyia megaparamera* males and females were reared, in addition to hundreds of *Culicoides*, especially *haematopodus*.

At the Sinks of Gandy, West Virginia (WIK 269C) stream site, which was directly in the current, several adult Plecoptera² were reared with *M. albibasis* (the only dipterans present), and ephemereid mayfly nymphs were also present. In a small creek in Halifax Co., NC (FVB 811), Simuliidae emerged from the sample. These latter results emphasize the truly lotic nature of the *M. albibasis* habitat.

4.2.4 Distribution

4.2.4.1 Geographic Range

This is at present apparently the most widely distributed of the Nearctic *Mallochohelea*, although *M. atripes* was more abundant in the study area (i.e., middle Atlantic states). It is recorded from extreme northwestern Canada (Aklavik, NWT, 68 deg. 28'N) east to Great Whale River, Quebec (55 deg. N), south to northeastern California (42 deg. N, elev. between 2,000 to 5,000 ft.) and, in the east, south to Baton Rouge, Louisiana (30 deg. 28'N).

Now known from 14 states and provinces: CA, CN, IL, LA, MD, MI, *NC, NWT., OR, QU., TN, VA, WI, *WV. In the study area it is known from the following counties: MD: Montgomery; NC: *Halifax; VA: *Augusta, Fairfax, *Montgomery, *Stafford; WV: *Randolph (* = New distribution records)(Figure 13 on page 333).

4.2.4.2 Biogeographic Considerations

Mallochohelea albibasis perhaps is distributed widely enough over nearly 40 degree of latitude to be considered cosmopolitan, yet less

² *Leuctra (L.) ferruginea* (Walker), det. B.C. Kondratieff

than one-quarter of the nearly 50 records for this species are south of the 40th parallel. It is clearly a predominantly boreal, thermiphagic species as evidenced by its occurrence well north of the Arctic Circle and early spring emergence in the southern part of its range.

In the study area, its distribution is analogous to what it is in North America on the whole, ranging from over 1000 m in the Appalachian Plateau, WV, to near sea level in the Coastal Plain. The emergence dates are sequenced according to elevation, ranging from mid-April at the Coastal Plain sites to late - June at the WV site.

4.2.5 Collection Records

▪ Reared.

NORTH CAROLINA: • Halifax Co., small creek on U.S. 158, 8 mi. W. of Roanoke Rapids, 17-IV-1959, one male, one female by RC (FVB 811). VIRGINIA: • Augusta Co., Christian Creek, U.S. 340, 4 mi. W of Stuart's Draft, 18-IV-1969, one male by RC (FVB 42); • Montgomery Co., S. Fk. Roanoke River, right bank 20m downstream of second northbound bridge of U.S. 11/460, 1150m upstream of confluence with N. Fk. Roanoke R. 29-IV 1971, two females, one male by RC (GH-1) coll. E. C. Turner, Jr.; Montgomery Co., Poverty Cr., at outlet of Polyscientific Pond (sic), 18-V-1966, 1 male, 2 females by rearing carton, coll. J. Humphreys; Montgomery Co., Tom's Creek, 100 m downstream of Shadowlake Rd., 4-V-1976, one male with p. ex. by IR, one male by RC (WIK 245); • Stafford Co., Muddy Creek, Va. Rt. 3, 10 mi. W of King George, 18-IV-1969, two females by RC (FVB 37). WEST VIRGINIA: Randolph Co.,

Sinks of Gandy nr. Osceola, elev. ca. 1070m. Gandy Cr., 23-VI-1976,
1 male (WIK 269C).

- Summary of Collections

IR(1 site): 1 male w/p. ex.

RC(7 sites): 8 females, 4 males

4.2.6 Annotated Taxonomic and Biological References

- Snow et al 1957:33 (pupa reared (as *Johannsenomyia*), ex river bottom, Tennessee, USA)
- Wirth 1962a:280 (disting. char. female, male; male gen. fig.; presence of pupal glandular disks; distr. & rearing records, USA)
- Downes 1978: (female prey capture records, Ontario)
- Wirth and Grogan 1979:878-9 (female, male diagn., figs., pupa descr., fig. resp. horn, term. segm.; Potomac Valley, Maryland, Virginia, USA)

4.3 *Mallochohelea albihalter* Wirth

4.3.1 Discussion

This species was not collected during the present study. Wirth and Grogan (op. cit.) record it from the Potomac Valley, though it is quite uncommon, because it apparently has not been recollected in the region since 1914, despite relatively active collecting activity in the Potomac Valley area over the years.

Of the five³ *Mallochohelea* known from the mid-Atlantic area, *albihalter* is the only one with whitish halteres. This species is small, in a size class with *albibasis*.

The pupa is the only immature stage which has been described, albeit incompletely. The number of apical spiracles (5-6) in the respiratory horn serve to distinguish this species from all others which occur here, however.

Habitat of immature stages. No rearing records have been published for this species as yet. While describing the pupa, Wirth and Grogan (1979) made no reference to the habitat it was derived from. However, Wirth (1962b) lists the Rideau River in Ontario as the site of collection of 10 females. This site yielded 4 other species of Sphaeromiini (Wirth and Grogan 1979:900), including *M. smithi* (Lewis), many of them reared from pupae. I have seen the *M. albihalter* specimens reared from the site in the U.S. National Museum collection.

³ Including *M. n. sp. nr. caudellii*

In Illinois, Malloch (1914) obtained long series of *albihalter* adults (not reared) along the Big Muddy River and Matanzas Lake. I expect this species will prove to be primarily rheotopic.

Distribution. The center of distribution for this species is clearly in the upper Midwest. Nearly all of the records fall in the Mississippi Valley and Great Lakes region. Indeed, the Maryland records are the only ones which fall outside this range.: The published distribution encompasses eight states and provinces: IL, IN, LA, MD, MI, MN., QU., and WI (Figure 13 on page 333).

Adults Habits. From adult capture records, *M. albihalter* is apparently a thermiphagic early spring species, which completes a unimodal emergence flight, before the month of July even in the northernmost part of its range, about a month sooner than the other species in the genus with comparable ranges (Table 16 on page 285). The latest seasonal occurrence is on 18 and 24 June at 45 deg.N latitude in Wisconsin and Ontario, respectively, the earliest, at Baton Rouge, Louisiana (30 deg. 28'N) on April 5th.

Downes (1978) recorded one instance of preying by *M. albihalter* on a male chironomid *A. monilis*.

4.3.2 Annotated Taxonomic and Biological References

- Wirth 1962a:280-1 (male, female descr., figs., locality rec.; eastern U.S.)
- Downes 1978: (adult insect predation records, Ontario)
- Wirth & Grogan 1979 (male, female diagnosis short pupal descr., figs. female legs, male gen., pupal operc., resp. horn, term. segm.; Potomac Valley).

4.4 # 127. *Mallochohelea atripes* Wirth

4.4.1 Synopsis of Systematics and Habitus

Adult-- A moderately large species, with a wing length of 2.6 to 3.0mm, about same size as *M. smithii* and n. sp. nr. *caudellii*, but about 1.25 x the size of *M. albibasis* and *albihalter*. The stout and sharp ventral spines on the femora of *M. atripes* distinguish this species from any other *Mallochohelea* in the area, though *M. spinipes*, known to date only from Georgia, also possesses spines, but the latter species is otherwise readily distinguishable. The split claspettes of the male genitalia set *M. atripes* apart from the other species of the genus for which males are known.

Larva. --Mature larvae are 9-10 mm in length, with uniformly yellowish-brown subconical head capsules, which have distinctive, large back swept eyespots straddling the epicranial suture. The thorax is well marked with ash-black to dark brownish black epidermal pigment concentrations in the meso- and metathorax as well as subepidermal bands in the intersegmental areas (Figure 12 on page 274). Lighter brownish pigment streaks are present laterally in the abdomen, presumably associated with the fat body. The pigmentation pattern is basically retained in preserved specimens (Fig. 12c).

The exuviae lack the internal "flaps" at the intersegmental conjunctiva (see Table 27 on page 416 in the *Sphaeromias longipennis* section). Chaetotaxy of the head is described and illus-

trated in Wirth and Grogan (1979). This is the only Nearctic species in the genus for which larvae are reasonably well known.

Pupa. --Readily distinguishable from other *Mallochohelea* for which pupae are recognized by the longer respiratory horn, lack of prominent blisterlike tubercles on the cephalothorax, small, pointed abdominal tubercles and small straight and greatly divergent apicolateral points. Significantly, ventral membranous patches are very indistinct or absent on the abdomen of the pupae I have seen.

The color of the pupal pelt is a uniform dark brown, consistent with the typical reasonably open lake margin habitat.

4.4.2 Habitat Characteristics: Results of Present Study

Mallochohelea atripes occurred in lake or pond environments in 29 (85%) of the 34 substrates collections positive for this species, taken at 12 localities in Virginia and North Carolina. These collections yielded over 60 larvae and 3 pupae; 5 adults were successfully reared. Many additional adults were captured, mainly by light trap. About one-half of the number of collections and larvae derived from a significant series of ceratopogonids obtained in Lake Anna, Virginia. This was the result of a major post-impoundment colonization study undertaken by Reed, Simmons and Voshell (Reed and Simmons 1976, Voshell Simmons 1977, 1984) and which I describe more fully below in connection with the discussion on *Sphaeromias longipennis*.

All of the remaining five (15%) positive substrate collections yielded larvae taken from various streams in the Upper Three Runs Cr.

water water basin at the Savannah River Plant, South Carolina. Ten larvae⁴ were collected from three sites there. Because these larvae were not directly associated with adults, a possibility exists that they represent another species, such as the closely related *M. spinipes*, known only from Georgia, and of which no immatures or males are yet known. However, sixteen female *M. atripes* were captured in 5 light traps and one malaise trap situated near these streams, and the larvae appeared to be identical with other *M. atripes* larvae associated with adults from other collections. In Virginia, a long series of over 150 females was taken at a light trap in the narrow N. Anna river valley, 16km downstream from the Lake Anna reservoir, in a stretch where submerged aquatic macrophytes were abundant (Table 50 on page 618).

The habitat sediments in which *M. atripes* occurred are characterized by aerobic conditions and textural complexity related to the presence of plants and plant parts. Larvae were never encountered in sediment where a microzone had formed over anaerobic black mud. Coarse organic detritus, submerged macrophyte beds with periphyton and other aufwuchs, and deep soft aerated mud at the water's edge or submersed, often were found in a diverse combination.

Most of the substrates yielding *M. atripes* were completely submerged. Samples of mud above the water line never yielded any larvae of this species. Pupae occurred on emerged *Scirpus* sedges in one of the Pandapas Pond collections.

⁴ Identified as "*M. sp. prob. atripes*".

The larvae at the Savannah River Plant sites (Upper Three Runs Cr.) in South Carolina were all taken along snags and in depositional stretches where detritus accumulated.

Two unusual sites in the Dismal Swamp yielded *M. atripes*. Both sites were characterized by "textural complexity": a thick layer of moss and algae growing at the water's line on the buttress root of a cypress tree in the middle of Lake Drummond; and a mat of riparian tree roots and moss, on peaty soil, exposed to gentle wave action along the Feeder Ditch.

Shade over the substrates was never dense, nor were the habitats exposed to the full sun. Open sites supporting plant growth were the rule, but always in our environment which screened the sunlight at the microhabitat level.

The pH of the substrate sediments was slightly acid, averaging 5.9 (range 5.6 to 6.6, n=4). The bodies of water in which the larvae occurred were more circum-neutral, averaging 6.6 (range 6.0 to 7.4), and the conductivity was low, ranging from 58 to 318 micro-mhos/cm (based partially on data in Morse et al 1980, and Reed and Simmons 1976, for Upper Three Runs and Lake Anna, resp.).

Adults were collected at seven localities in South Carolina and Virginia, six of which were near to the habitats yielding immature stages of this species.

4.4.3 Autecological Review

4.4.3.1 Habitat Requirements

Lakes and Ponds. *Mallochohelea atripes* is predominantly an inhabitant of lake margins and ponds with well-developed beds of submersed and emergent hydrophytes and soft sediment deposits. Normally, at least sparse overhead shading is provided by riparian or emergent vegetation. Large populations have developed under suitable conditions, which seem to be optimally provided by aquatic plant beds with a well-developed epiphytic aufwuchs community.

In the only specific habitat record published for this species, Wirth and Grogan (1979) found it to be abundant in algae-covered purslane (sic) (*Didlipis* sp.?) in a richly vegetated marsh pond at the Patuxent Wildlife Research Center in Maryland. In a light trap operated at this site, J. E. Scanlon once collected 200 female *M. atripes*. Wirth collected over 270 adults at a lake margin site in New Brunswick, New Jersey, also by light trap (Wirth 1962b).

Less productive, but undoubtedly significant and characteristic of many lake habitats are the unconsolidated sediments in the littoral and sublittoral zone of lakes. I sampled several larvae from a soft-loose detritus-rich mud up to 30cm thick in water 1m deep near the edge of Otter Lake (WIK 316D) but 5 m from the nearest significant growth of aquatic plants.

In particular, the occurrence of *M. atripes* larvae in small but consistent numbers in Lake Anna provides evidence that lake-dwelling larvae can and do range away from the plant beds, and suggests also that they can thrive there year round. The data in Table 18 indicate

that the larvae apparently preferred the leaf pack substrates, and that they were more apt to occur at 2 m than at 4 m depth. Only in the winter months did they appear at 4 m. This pattern is similar to that of *S. longipennis* (Table 29 on page), but *M. atripes* seemed just likely to occur at 2 m, even during the winter months. The preference for leaf substrates is consistent with the observation earlier that organic detritus is often an important component of the *M. atripes* habitat. The leaves had been conditioned for at least 2 months by the time these larvae appeared, and undoubtedly supported a microflora and-fauna which the *atripes* larvae were able to exploit directly or indirectly.

These larvae are more likely to remain nearer to shore than are *S. longipennis* and lake-dwelling *Probezzia*. I have seen no larvae which I would consider *M. atripes* taken from profundal depths (>7 m) in any of the numerous lake collections I have examined (reviewed under *Probezzia* and *S. longipennis*, esp.). Other larvae of what may be *Mallochohelea* (species unknown) have appeared occasionally in those collections, and at least one European species, *M. inermis* is known to occur at profundal depths (see generic discussion).

Occurrence in streams. A lotic habitat is apparently the exception of *M. atripes*, and should be considered provisional until some direct association by rearing of adults from this habitat type has confirmed its validity. Because this is the only larva in the genus which is reasonably well known, it is prudent to be cautious about the identification of these specimens. Yet, this species appears to be the

Table 18. Occurrence of *Mallochohelea* cf. *atripes* larvae in Lake Anna, according to month, depth, and sampling method, during the year beginning December 1973.

Depth m	Sampling Method	Month												Abundance Index ¹		
		XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI			
0.5	Kick ²						4								4	2.0
2	Leaf	3	1			1	2	3				3			13	21.6
2	Web						1	3				1			5	6.7
4	Leaf														1	1.0
4	Web														4	4.0
4	Stone ³	1													2	2.8
	n=	4	1	1	5	1	3	10				4			29	

¹ (N_I)¹ x F_{Coll}

² 1974-75.

³ 1972-73 feasibility study.

most common in this genus, at least in the southeast U.S., and, as pointed out above, *atripes* adults were the only *Mallochohelea* collected in stream-sited light traps.

Further, on the principle that streams contain numerous subhabitats which are lentic in character, and the fact that snag/debris and aquatic plant bed habitats (consistent with *M. atriipes* habitat characteristics seen elsewhere) were thoroughly sampled in the Upper Three Runs Creek study, there is sufficient reason to accept the likelihood that it is indeed *M. atriipes* that is involved here. Also, the canopy above the stream was sufficiently open at the sites where the larvae occurred to permit the growth of aufwuchs.

Additional support for the supposition that *M. atriipes* breeding may well take place in significant amounts in riverine systems, is given by the collection of the 150+ females in the light trap situated on the North Anna R. far from any apparently suitable pond or lake (see Habitat Characteristics and Collection Records sections). At this site, the aquatic plant beds (esp. water willow) growing in the river could easily have provided suitable conditions for *M. atriipes*.

Microhabitat Summary Hydropelophilic and phytophilic, optimally in oxygenated substrates combining soft deep sediments with submersed beds of floating aquatic plants and an abundance of plant detritus, all surfaces supporting aufwuchs (either autotrophic and/or heterotrophic). Submersed substrates are the rule, and apparently neither full sun nor deep shade are preferred.

4.4.3.2 Larval and Pupal Habits

Larvae of *M. atripes* are active swimmers, but the specimens I observed were not nearly as rapid in their oscillations as *M. albibasis*. Wirth and Grogan characterized them as extremely active; swimming near the surface of the pond in which they were found. The larvae I collected at Otter Lake (Coll. 316C) in early August, among floating bur-reeds, pupated after three weeks. This almost certainly represented the second, perhaps the third, generation to develop that season.

Pupae of this species occurred on sedges in one collection, providing further support for the suggestion that the "adhesive disks", which *M. atripes* I have seen do not possess, are not essential for attachment by pupae to plant substrates.

4.4.3.3 Species Associations

The seven collections from which adults were reared yielded 13 species in seven genera of Ceratopogonidae (Table 19).

All of these species are ecologically closely associated with lake margin and pond environments. The *Bezzia* species found there, and *Palpomyia lineata*, are chiefly associated with floating filamentous algae (data in this study; Chan and LeRoux, 1965). The other *Palpomyia* are largely found on mud substrates at pond margins (data in this study; Grogan and Wirth 1979). *Dasyhelea mutabilis* occurred with *M. atripes* at more sites than any other species (43%). It seems unlikely that this species association is significant, because *D. mutabilis* was the 15th most common species in this study, and is a eurytopic species distributed throughout North America (Waugh and Wirth 1976). Yet, it

Table 19. List of Ceratopogonidae co-occurring with *Mallochohelea atripes*, mainly a lake-dwelling species, based on rearings from seven sites.

Genus	Species	Instances
Palpomyia	cressoni	1
	lineata	1
	subaspera	1
	tibialis	1
Bezzia	glabra	1
	laciniastyla	2
Dasyhelea	varicolor s. s.	1
	mutabilis s. s.	3
	traverae	1
Alluaudomyia	bella	2
Johannsenomyia	argentata	1
Sphaeromias	longipennis	1
Stilobezzia	bullata	1

is intriguing that the far more abundant *B. nobilis* was not present at any of the sites, which suggests a possible subtle ecological discrimination taking place here. This may be related to the feeding habits of *D. mutabilis*, a scraper and collector-gather, which I have found consistently associated with submerged or very wet detritus-rich sites (usually with a minimum of mud present) which also is characteristic for *M. atripes*, whereas *B. nobilis* is chiefly a hygropelophilic species (damp mud substrates).

4.4.3.4 Adult Habits

Seasonal Activity. *Mallochohelea atripes* appears to be predominantly an aestival species with an emergence peak in July, a month later than most other species in the genus (Table 16 on page 285). The latest light trap capture occurred on 9-10 September at Pandapas Pond, Montgomery Co., Virginia; the earliest seasonal record is a light trap capture at the Savannah River Plant site in South Carolina, 12-13 May 1980.

This species probably is bivoltine or even multivoltine at least in the southern part of its range, based on captures in South Carolina in mid-May and again late June and late July, and a combination of rearing observations and trapping records in MD, NC and VA. Mature larvae which are successfully reared were collected in May (Wirth and Grogan 1979), June and July (this study). Partially successful rearing attempts were made with larvae collected in August, most of which were not in the fourth instar.

This species is seemingly much more prone than most other species in the two tribes under discussion to be attracted to light traps, judging from the several instances in which hundreds of specimens appeared in a single light trap, and the consistency with which it was collected in South Carolina over an 18-month period compared to other Sphaeromiini.

Adult Feeding and Mating: This species has mandibles typical of the insectivorous biting ceratopogonine midges, but no direct observations of such activity have been made. Mating and oviposition behavior also have not been specifically noted for this species.

4.4.4 Distribution

4.4.4.1 Geographic Range

Occurs only in the eastern Nearctic from Michigan to Ontario, south in eastern seaboard states to Florida. Only 16% of the available adult collection records (25) occur north of Maryland, ca. 40°N .

Presently distributed in eight states and one province: FL, GA, MD, MI, *NC, NJ, ON., *SC, and VA. In Virginia, it is found in five counties and in the Dismal Swamp (City of Chesapeake): *Amherst, *Fairfax, *Hanover, *Louisa, and *Montgomery (Figure 13 on page 333).

4.4.4.2 Biogeography

Mallochohelea atripes is a relatively thermophilous species, as evidenced by its mid-summer emergence peak, lack of early spring flight records, and the preponderance of its distribution records being south of the 40th parallel. It has appeared in all physiographic provinces

except the Appalachian Plateau, and it seems unlikely that it will be found extensively inhabiting higher elevation or high latitude sites.

4.4.5 Collection Records

• Reared. NORTH CAROLINA: Caswell Co., U.S. 58, 5 mi. E of Yanceyville, marshy pond margin, 6-VI-1969, 1 male by RC (FVB-85). VIRGINIA: Amherst Co., Otter Lake on Blue Ridge Parkway, 2-VIII-1976, 3P, 2L by IR (WIK 316C, 316D); Chesapeake, Dismal Swamp, Lake Drummond, 14-VI-1975, 1 female by RC (WIK 39); Chesapeake, Dismal Swamp, Feeder Ditch, 300m W. of dam, 14-VI-1975, 1 male by RC (WIK); Louisa Co., Lake Anna Reservoir, Lagoon 3 leaf pack basket sample, 11 Sept. 1976, 5 L by IR (3L to 1MM), J. R. Voshell; Montgomery Co., Pandapas Pond, 14-VII-1976, 1 female by RC (WIK 281); same, 20-VII-1971, 1 female reared by R. E. Williams, coll.

• Adults Field Trapped.

SOUTH CAROLINA: Savannah River Plant, Upper Three Runs Creek and tributaries: 26-27-VI-1979, 2 females at light trap, SRP8/8&7; 2 females at light trap, SRP8-1 (Site "A"); 23-24-VII-1979, 2 females at light trap, SRP 8/8&8; 12-13-V-1980, 8 females at light-trap, SRP8/8&8; 16-17-VII-1980, 2 females by malaise trap, SRP E-2 (Site "C"). All collected by J. C. Morse & colleagues. VIRGINIA: North Anna R., Hanover - Caroline Co. line, Va. Rt. 601 at Butler Bridge, 1-VII-1976, 3 females by blacklight trap (BL-47) J. R. Voshell, coll.; North Anna River, Louisa-Spotsylvania Co. line, Va. Rt. 601 at Smiths Mill Bridge, 16 km downstream of dam, 28-VII-1976, over 150 females

by blacklight trap (BL-53) C. R. Parker, coll.; Montgomery Co., Pandapas Pond, 9 to 10-IX-1976, one female by blacklight trap (BL-50).

•Other Sources.

South Carolina: Upper Three Runs Cr. at SRP Route 1 (Site "A"), 14-XII-1976 to 17-V-1977, 7 larvae in 5 collections; Mill Creek 2.75 km upstream from SRP Route E-2 (Site "E"), 4-XII-1976, 2 larvae; Boggy Gut Creek (Site "D"), 3-V-1977, 1 larva. All taken by J. C. Morse and colleagues. VIRGINIA: Louisa Co., Lake Anna, 29 larvae prob. *M. atripes* (4 at 0.5 m, 18 at 2 m, 7 at 4 m), Dec. 1973-June 1975, coll. J. R. Voshell & G. M. Simmons, Jr.

• Collection Summary

Forty collections from 18 localities in three states yielded at least 219 *M. atripes* specimens, 165 of which were as adults captured in six light traps and one Malaise trap. The breakdown is as follows:

- IR: 4 L, 3 P (3 sites)
- IMM: 42 larvae (5 sites)
- RC: 5 females, 3 males (5 sites)
- AFT: >165 (6 sites)

4.4.6 Annotated Taxonomic and Biological References

- Wirth 1962b:962 (female and male descr., male gen. fig., loc. rec., eastern U.S.)
- Wirth and Grogan 1979:880-2 (female, male diagn., fig. many female parts, male gen., pupal resp. horn, operc., term. segm., larval head capsule, Potomac River Valley, USA)

4.5 # 128. *Mallochohelea* n. sp. nr. *caudellii* Wirth

4.5.1 Synopsis of Systematics and Habitus

This new species is similar to the western species *caudellii*, especially with respect to the tibiae, which are entirely dark, and other features, but it is smaller (female 2.7-2.8 mm, compared to 3.0 mm for *caudellii*), differs in the infuscation of the femora and tarsomeres (being darker overall, particularly in the male), and in the male genitalia.

Legs in female brown except for dark yellow fore femur (extreme apex blackish), hind and mid femora yellowish on basal 1/2 to 2/3, tarsomeres 1-2 yellowish apex brownish). In the male, the legs are a darker brownish-black, with basal 1/3 to 1/2 of fore and mid femora, and basal 1/4 to 1/3 of hind femur yellowish, and tarsomeres as in the female. Sexual dimorphism is marked, the male wing length about 2.2-2.3 mm, ca. 80% the size of the female.

In the male genitalia of the new species, the aedeagus is elongate as in *smithi*, but with less of an expanded tip, and the claspettes (parameres) are considerably more elongate and slender, than those of any other *Mallochohelea*, extending for 1/6 to 1/5 of its length beyond the aedeagus. The claspettes are split to 3/4 of their entire length, and their tips are not significantly expanded.

Pupa: Color of exuvium is a light grayish brown, and overall features correspond to those of the "albibasis-Group", except that the respiratory horn is longer than usual, L/W ratio 2.5-2.9; horn with 6-8 apical spiracles. Pupal length, female: 5.5-6.0 mm; male: 4.5 mm. Terminal segment of male elongate, narrow, 1.6x longer than broad, in female as long as broad; apicolateral processes long and prominent, as long as base of segment in both sexes. The large size and length of the apicolateral processes sets this species apart from *albibasis*, *albihalter*, and especially *atripes*, where the processes are ca. 0.65, 0.65 and 0.48 as long as the basal segment of the terminal segment.

4.5.2 Habitat Characteristics: Results of Present Study

Six collections in three states yielded 12 specimens, including six individually reared from pupae. Four of the five habitat collections were from lake margins or ponds. One site, at the margin of a fourth-order stream, consisted of silty-sand and clay among a mass of roots intruding from riparian trees in a small depositional pool.

All of the habitat collection sites were moderately to densely shaded, most commonly by alders, the substrates were under water where sampled, consisting of a clayey mud (except for a sandy substrate at Thompson Lake, WIK 359); three of the sites (60%) were significantly influenced by root mats from riparian alders, willows, and/or emergent cattails. One collection was of pupae among flottage at the surface of the Lake Norman reservoir in North Carolina.

At the Savannah River Plant, South Carolina, one female was taken by light trap sited adjacent Upper Three Runs Cr., in early May.

4.5.3 Autecological Remarks

Habitat

This species appears to be mainly an inhabitant of lake and pond margins, evidently preferring shallowly submerged mud to sandy substrates in well-shaded situations. Accordingly, there was no particular association with algae or aufwuchs in the environments where the larvae were encountered, (though an algal mat occurred beside one of the microhabitats sampled) nor were submersed floating aquatic hydrophytes present at any of the sites.

The appearance of this species in lotic systems shows, once again, that suitable microhabitats do occur in streams for species with a lentic water preference, albeit generally the habitats are more limited in extent. In this case, the common denominator appeared to be the presence of root mats and shade.

Seasonal Activity: *Mallochohelea* sp. nr. *caudellii* is seemingly an early spring species, in that no captures or rearing were in late March from a sample collected in early March at a Blue Ridge lake (WIK 359) (Table 16).

4.5.4 Distribution

Recorded from South Carolina, North Carolina and Virginia. In South Carolina, it has been collected only in the Southern Sandhills Aquabioc Province (Carlson 1981) at the edge of the lower (eastern) Piedmont; in North Carolina it was collected in the western Piedmont,

and in Virginia, only in the Blue Ridge and Ridge and Valley Physiographic Provinces.

4.5.5 Collection Records

- Reared.

North Carolina : Mecklenburg Co., Lake Norman, 1-VI-1978, 2 females with p. ex., coll. T. W. Bowen. South Carolina: Aiken Co., Savannah River Plant, Upper Three Runs Cr., 9-10-V-1979 (SRP 8/8&8), 1 female by light trap, coll. J. Morse. Virginia: Fauquier Co., Thompson Lake, Blue Ridge, submersed sandy substr. among cattails, 25-III-1977, 1 female by RC, emer. by 25-III-1977 (WIK 359 RC). Montgomery Co., Pandapas Pond area, swampy willow bottom, 27-V-1976, 1L, 1P(in IMM); 1 female by RC (WIK 255 RC); same, pond's edge, 27-V-1975, 4 males with p. ex. by IR (WIK 7 IR); same, S. Fork Roanoke R. at Greenhill-Elliot, coarse silt at stream margin (GH-1), 29-IV-1971, 1 male by RC, coll. E. C. Turner, Jr.

- Collection Summary

IR: 2 F, 4 M with p. ex.

IMM: 1 L, 1 P

RC: 2 F, 1 M

AFT: 1 F

4.6 # 129. *Mallochohelea smithi* (Lewis)

4.6.1 Synopsis of Systematics and Habitus

A moderate-sized species, about the size of *atripes* and n. sp. nr. *caudellii*, but with largely yellow legs. Sexual dimorphism is not marked, the males being only slightly smaller than the females. See references below for more complete diagnosis.

Pupal exuvium is a dark grayish brown, markedly darker than that of the other species seen. The pupa fits the general pattern of the "*albibasis* - Group"; the respiratory horn is short, L/W ratio 2.1 to 2.2 (female), with 4-6 spiracles at the apex (both sexes); in the male the horn is shorter, L/W ratio 1.9-2.1. The apicolateral points are very long, 1.15x as long as the base of the terminal segment, which is somewhat longer than that of *M. n. sp. nr. caudellii* (0.95-1.00) and longer than those of the other species seen.

4.6.2 Habitat Characteristics in this Study

Only one site yielded this species during this study, namely three pupae taken from an algal mat floating on a quiescent section of Deep Cr., Powhatan Co., VA. I examined a female with pupal exuvium taken from Crystal Brook, Washburn Co., Wisconsin on 23-VII-1954 by R. H. Jones (Jones No. 4576). This specimen, received from Jones, was not recorded in Wirth 1962b.

4.6.3 Autecological Review

Of 29⁵ collection records available, only seven⁶ offer some information as to habitat associations based on rearing. Six of the seven are from lotic systems, mostly streams of about third to fourth order. A record of adults taken at a stream margin near Mt. Solon, Virginia, by Wirth (1962b), can be taken to support the supposition that *M. smithii* is primarily a stream dweller.

The single exception is based on a series of 8 females and 8 males reared from a lake in Algonquin Park, Ontario (Wirth 1962b). The balanced sex ratio of the latter collection emphasizes the fact that rearing almost invariably will provide male material, as opposed to the great predominance of female specimens in light trap samples.

Specific habitat characteristics are poorly known, and that which is available is based on pupal collections. Thus, pupae have been recovered from blanket algae in a stream (this study, a sand bar in the Yellow River, Wisconsin (Jones), and from mud and sand at the margin of the Rideau River, Ontario (Wirth 1962b, Wirth and Grogan 1979). These are not necessarily indicative of actual larval habitats, because of the tendency of the larvae of this tribe to leave the bottom substrate or aquatic plant bed and migrate toward shore to pupate.

As to pupal movement, the pupae I collected from blanket algae lashed their abdomens back and forth actively, at a rate of about 1 - 2 /sec until placed in the rearing carton. Later, they had scaled up the plastic bags(containing the samples) several centimeters.

5 27 from Wirth (1962b).

6 five from Wirth (1962b).

4.6.3.1 Species Associations

The pupae yielding the present specimens were found floating alone among the algal strands and no other species were at that site at that time. A series of *M. smithii* was among an unusual congregation of seven Sphaeromiini reared by Wirth from mud and sand along a short stretch of the Rideau River, Ontario (Wirth and Grogan 1979:900), where species of *Bezzia* and *Stilobezzia* also occurred.

4.6.3.2 Seasonal Activity

The pupae taken in Powhatan Co. on 30 April emerged on May 5, which constitutes the earliest record for this species. In the Virginia region emergence begins in May and continues at least until late July, the latter likely representing a second emergence peak. By far the majority of the flight captures occurred in June (Table Table 16 on page 173), 90% of these in the Wisconsin to New York belt. The latest record, 24 August, is from central Michigan (Clinton Co.), and, probably also represents a second generation.

4.6.4 Distribution

4.6.4.1 Geographic Range

Presently *M. smithii* is known only from the northeastern U.S./southeastern Canada, approximately bounded by 50 deg. and 35 deg. N and in the northwest by 93 deg. W, from Wisconsin east to Connecticut and south to North Carolina and Tennessee. Records are available for at least 9 states and 2 provinces (Wirth 1962b). Distribution in Virginia area : MD: Montgomery Co., Prince Georges Co.,; NC: Macon

Co.; TN: Hamilton Co., VA: Alexandria, *Powhatan (Figure 13 on page 173).

4.6.4.2 Biogeography

Apparently the center of diversity for *M. smithii* is located in an east-west band spanning the Great Lakes: 75% of the records for this species are in Wisconsin to New York. Southward extension occurs along the Appalachian Mountain chain, and the southernmost records are at higher altitude, such as the Highland, NC record at 3800 ft. (1160m) elevation. This corresponds closely with the Alleghanian Biotic Region (Hoffman 1969).

4.6.5 Collection Record

Virginia: Powhatan Co., Deep Creek, bridge on U.S. 60, 30-IV-1977, 2 males, 1 female w/ p. ex. by IR, emer. 4-V-1977 (WIK 379 IR).

4.6.6 Annotated Systematic and Biological References

- Williams 1955:
- Lewis 1956:47 (male described (as *Johannsenomyia*, Connecticut)
- Wirth 1962b:282 (female and male diagnosis, figs. male gen.; mention of glandular disks on pupa; locality rec., N.E. U.S.)
- Wirth and Grogan 1979:900 (mention of co-occurrence with other Ceratopogonidae at river margin site, Ontario)

4.7 Genus *Nilobezzia* Kieffer

4.7.1 Generic Overview

With at least 60 species represented worldwide, *Nilobezzia* is the largest of the 29 genera in the tribes Heteromyiini (9 genera) and Sphaeromyiini (20). Only 7 species are known in the Americas, 4 in both the Neotropical and Nearctic regions, with one (*schwarzii*) common to parts of both. *Nilobezzia* are very sparsely represented in the Middle Atlantic U.S. None were encountered in this study, nor was the genus treated by Wirth and Grogan (1979) in their study of Potomac Valley biting midges. However, three species have been recorded east of 80 deg.W longitude (Wirth 1962b):

1. *N. mallochi* Wirth -- basically has a center of distribution in the Mississippi-Missouri River basin (Saskatchewan to Ontario south to Oklahoma), with an "outlying" record in Maryland (Dorchester Co.) on the Delmarva Peninsula near the Chesapeake Bay. No specific habitat information is available, but the adult capture records tend to suggest a lentic (esp. lake) habitat association.
2. *N. minor* (Wirth) -- basically a western species ranging from a 68 deg.N in the Northwest Territories to 29 deg.N at Big Bend, Texas, but with records in Michigan and as far east as 75 deg.W at Great Whale R. (55 deg.N), Quebec. The only rearing records are from the edge of the Rio Grande R., but other capture records suggest both riverine and lacustrine habitats.

3. *N. schwarzii* (Coquillett) -- essentially an austral species, ranging from Florida, Louisiana and Texas through the West Indies and Central America to Brazil. The northern most record is from Bluffton, South Carolina, which falls in the Southeastern Coastal Plain "Aquabiatic Province" of Carlson (1981). A single rearing record is from lake in Louisiana, but several other records point to riverine and lacustrine possibly estuarine, habitats as well. The remaining species, *N. brevicornis* (Wirth), is restricted to the southwestern U.S. west of 96° W. Of these, I would consider *N. mallochi* and *N. schwarzii* most likely to eventually be collected in Virginia.

4.7.2 Synopsis of Systematics and Habitus

Adult --Excellent generic diagnoses are available in Debenham 1974 and Wirth 1962b. Debenham provides very useful original differential diagnoses distinguishing females of the two related genera *Mallochohelea* and *Nilobezzia*. Wirth et al (1974, 1977) provide effective keys to distinguish the genera as well.

Male *Nilobezzia* are characterized by unique structural modifications: in the male genitalia, the basimere is entirely fused with the telomere, which persists as an unmovable apical thumblike lobe. Likewise, the antenna is modified, and the antennal plume is much reduced. As Downes (1978:51) states, "it seems evident that considerable structural transformations are taking place in *Nilobezzia*, doubtless accompanied by substantial changes in behavior."

Sexual dimorphism is marked in most species: males are often only 50% the size of females. This is not invariably the case, though; for example, *N. triquetrinotata* Debenham are about the same size, the male actually having a somewhat longer wing (Debenham 1974).

Larva: At least three, and possibly up to five, species are presently described (Table 20). The head capsules are conical, rather elongate with large kidney-shaped eyespots. Three multiple setae ('q', 'o', 'v',) are present. The labrum is markedly extended beyond the cephalic margin. The postoccipital ridge has a strong caudal expansion on the ventral side. In their general features, the three existing descriptions are quite comparable⁷. Glukhova (1979) states that *Nilobezzia formosa* is very similar to *Probezzeria seminigra* in all but minor details, but that the color of the head capsule and body are distinctly different -- *N. formosa* head capsules are uniformly light stramineous, whereas *Probezzeria* head capsules are much darker and contrasting, darker to lighter from the postocciput towards the gena. In any case, distinguishing the larvae of these genera should not cause any difficulty.

Sexual dimorphism is expressed in fourth instar larvae in particular, not only in size but also to some extent in the shape of the head capsule. Male-destined larvae tend to have higher head ratios but

⁷ The larva of *N. triquetrinotata* depicted by Debenham (1974) differs significantly from the other two known species in several respects, such as in the configuration of anal setae, and the apparently uniform post occipital ridge ("collar"), but the implications of this cannot be evaluated at present, given the dearth of material.

lower head width ratios than larvae which subsequently produce females (Glukhova 1979), that is, "male" larval head capsules are relatively longer but less conically narrowed at the anterior end.

In the anal segment the setation is comparable to that of many Sphaeromiini larvae, in that for *N. formosa* and *N. robusta* at least, there are four pairs of long setae, two pairs of which are arranged linearly along the mid-dorsal and mid-ventral lines. The Australian specimen shows an unusual arrangement of setae, and a preanal constriction in the body wall which I suspect is an artifact of preservation conditions.

Pupa: Debenham (1974) and Palchick (1981) give good diagnostic characterizations for the genus and various species. Interestingly, all four of the Nearctic species are now well described (Palchick 1981) in this stage; in all, 12 species' pupae are described from all zoogeographic regions combined (Table 20). The respiratory horn is 4-5 times as long as wide, with corrugation at the base. Abdominal tubercles are usually not very prominent, either sharp-pointed, or stout and rounded (e.g., *N. brevicornis* or *N. robusta*). Abdominal glandular disks are apparently absent from 11 of the known pupae, present only on *N. schwarzi* (Table 20).

Based on available data, it appears that members of the subgenus *Nilobezzia*, characterized by armed femora and tibiae, do not possess glandular disks, but that the subgenus *Parrotia* Kieffer with unarmed femora may prove to possess glandular disks on at least some of the abdominal sterna V-VII.

Table 20. Summary of all *Nilobezzia* species for which descriptions of immature stages are available.

<u>Nilobezzia</u> Species	Pupa	Larva	Reference
Afrotropical			
nigritibialis I&M	X	-	Ingram & Macfie 1921
robusta (DeM)	X	X	Mayer 1955
Australasian ^{1/}			
arenae Debenham	X	-	Debenham 1974
basispinigera Debenham	X	-	"
fuscitarsus Debenham	X	-	"
triquetrinotata Debenham	X	X	"
virago Debenham	X	-	"
whartoni Lee	X	-	"
Neartic			
brevicornis (Wirth)	X	-	Atchley 1969, Palchick 1981
mallochi Wirth	X	-	Palchick 1981
minor (Wirth)	X	-	Wirth 1962b
schwarzii (Coq.)	X	-	Wirth 1962b Palchick 1981
Oriental			
badia (Joh.)	X	-	Mayer 1934b
diffidens (Joh.)	X	-	"
Palaeartic			
formosa (Loew)	-	X	Glukhova 1977, 1979

^{1/} M. Elson-Harris has apparently described 2 *Nilobezzia* larvae and pupae from Australia in her M.S. thesis (Kettle 1981; Kettle and Elson-Harris 1981) and it is about to be published (Elson-Harris and Kettle 1986b in press)

4.7.3 Larval Habitat Review

The only specific data on *Nilobezzia* larval habitats published is that of Atchley (1969), Glukhova (1979) and Palchick (1981). In addition, pupae have been obtained and reared from about 20 sites (combined for all other species). For the genus as a whole, the rearing and habitat records are evenly divided between river/stream sites and lake/pond sites, but on a species-by-species basis, a definite preference may become evident.

Thus, *N. formosa* has been taken only in rivers, both in midchannel as well as along the margin, in considerable numbers (Glukhova 1979); *N. posticata* is associated with the "potamon" (larger rivers) in east central Europe (Havelka 1978). The Australian *N. aranea* and *whartoni* were taken repeatedly at creeks and rivers. The Rio Grande River in New Mexico and Texas has yielded *N. minor* on several occasions. Undoubtedly, most of these records derive from lentic subhabitats along the margins of these rivers.

A tolerance of, or preference for, saline or mineralized alkaline habitats is evident in several *Nilobezzia*, notably *N. brevicornis* and *N. minor* in the southwestern U.S., and *N. virago*, possibly *N. aranea*, in Australia. Those sites, where these species were recorded in such habitats, occur in rainwater-deficient areas, usually at inland saline sites, but coastal haline (salt marsh) sites are also known. Wirth (1952:444) listed both *brevicornis* and *minor* as halobionts on the basis of repeated association of adults with the saline habitats. However, in the ecological sense, the species as a whole (i.e., taken over their entire range) may be halophilic or -tolerant, but they cannot be con-

sidered halobiotic *per se*, because such species are by definition extremely stenoecious, meaning they are characteristic of and limited to that habitat type (Thienemann 1954:34). Yet, *N. minor* has been reported from freshwater environments, particularly outside of the southeast, and *N. brevicornis* is known from habitats which were slightly alkaline (Wirth 1962b, Atchley 1969). In other species, halophily is apparently facultative as well, though it may well be that given population will be more-or-less flexible depending on the availability of habitats of various salinities.

As to microhabitat, particularly substrate, preferences, there are strong indications that most members of the genus are hydropelophilic, meaning they occur on soft wet or submerged mud/silt, with or without vegetation. For example, *N. brevicornis* was recorded from alkaline mud 1/2 in. thick over the redox discontinuity (black) layer, with little vegetation and shade, at the margin of a reservoir at Bitter Lakes National Wildlife Refuge, New Mexico (Atchley 1969).

In a river with bottom consisting of a thick (up to 1 m) layer of sand and black silt, *N. formosa* occurred around beds of aquatic macrophytes (Glukhova (1979)). These larvae had consistent accumulations of a black material in their gastrointestinal tracts, suggesting that their feeding activity took place mainly on and in the soft black silt, where many other metazoans (potential prey) would occur, rather than on or among the macrophytes. Several other records suggest that the "mud" substrate is one which *Nilobezzia* may well prefer.

As can be expected with most all members of this family, filamentous algae do provide a suitable habitat for some species, such as the African *N. nigriritibialis* (Ingram and Macfie (1921) and *N. zibanensis* (Clastrier 1962). No generalizations can be made as to shade preferences, because various species have been recorded from a wide range of shaded conditions.

4.7.4 Distribution

4.7.4.1 Geographic Range

Nilobezzia species are well represented in all zoogeographic regions, but their greatest development has occurred in the Oriental region, where about 45% of the 60+ species are found. Members of the genus seem able to exploit habitats in regions where rainfall is not abundant, such as in the southwestern U.S. or parts of Australia. The genus is least diversified in the New World and in Europe, in contrast to the *Probezzia*, which is strictly Holarctic in distribution.

4.7.4.2 Biogeography

It is likely that the center of high *Nilobezzia* diversity and endemism is in the Indian subcontinent and southeast Asian archipelagos, and that the reasons for the relatively low number of species in the Nearctic is due to historical biogeographic factors. The low incidence of collections of *Nilobezzia* in the southeastern U.S. may be related to the small number of suitable lakes and water courses in the region, compared to the west, southwest and northcentral sections of the country (cf. Frey 1963).

4.7.5 Annotated Taxonomic and Biological References

Afrotropical (8 spp.)

- Ingram and Macfie 1921:373-4 (*N. nigritibialis* I&M (as *Dicrobezzia*), detailed pupal descr., no figs., habitat, Ghana)
- Mayer 1955:113-5 (*N. robusta* (DeM.)(as *capensis* DeM. & Hardy), larva, pupa descr., figs. 15-20: larv. head caps., epipharynx, term. segm., pup. resp. horn, abd. tub.; S. Africa)
- Clastrier 1962:120, 122 (*N. (Parrotia) henaneii* Clastrier, *N.(P.) zibanensis* Clastrier⁸, pupal habitat, Algeria)
- Wirth et al 1980:171 (catalogue, eight spp., syn.)

Australasian (9)

- Debenham 1974:62-81 (nine spp. treated (7 new), female, male, pupa (6 spp.), larva (1 sp) descr., figs.; habitat notes, distr.)
- Debenham 1979:547-555 (synopsis of 10 species, citations, types, type loc., synonymies, literature, distr., biology; incl. *N. curticornis* (Kieffer, 1917) n. comb., poss. senior synonym of *N. triquetrinotata* Debenham.)
- Elson-Harris and Kettle 1986b (larval and pupal habitat description and keys to two Australian *Nilobezzia*)

Nearctic (4 spp.)

- Wirth 1952:244 (*N. brevicornis* (Wirth), *N. minor* (Wirth) as *Sphaeromias*; habitat notes, California, USA)
- Wirth 1962b:285 (four N. Amer. spp. descr. or redescr., keyed, figs. male gen., female claws; brief pupal char., locality records, syn.)
- Atchley 1969:54-7 (*N. brevicornis*, male, pupa, larval habitat descr., figs.; new distr. rec. for *N. minor* (Wirth), New Mexico)
- Palchick 1981 (3 spp. pupae descr., fig., chaetotaxy; N. Amer.)

⁸ For reasons unknown to me, these species are not listed in the catalogue of Afrotropical Diptera (Wirth et al 1980).

Neotropical (4 spp.)

- Wirth 1974:50 (four Neotrop. spp., syn., refs., type-loc.). No immatures.

Oriental (27 spp.)

- Mayer 1934b:189-91 (*N. diffidens* (Joh.) as *N. ochriventris* var. *diffidens*; & *N. badia* (Joh.) as *N. flaviventris* var. *badia*, pupal descr., habitat, Sumatra)
- Mayer 1955:115 (similarity of *N. diffidens* and *N. robusta* (see above))

Palaeartic (4 spp.)

- Glukhova 1977:439 (*N. formosa* (Loew)⁹, larva keyed; habitat, S. Europe, USSR)
- Glukhova 1979:108-110 (*N. formosa*, larv. descr., figs. biology, USSR)
- Havelka 1978:445 (distr. 2-3 European spp., habitat of *N. posticata* (Zett.) (as *N. grisea* Zil.-Seb), syn.)
- Remm 1980:86-8 (two new *Nilobezzia* spp., Centr. Asia)
- Remm 1981:27 (synonymy of *Sphaeromias griseus* Z.-S. with *N. posticata* Zett.).

⁹ Havelka (1978) indicates that this may be a synonym of *N. paradoxa* Zil.-Seb.

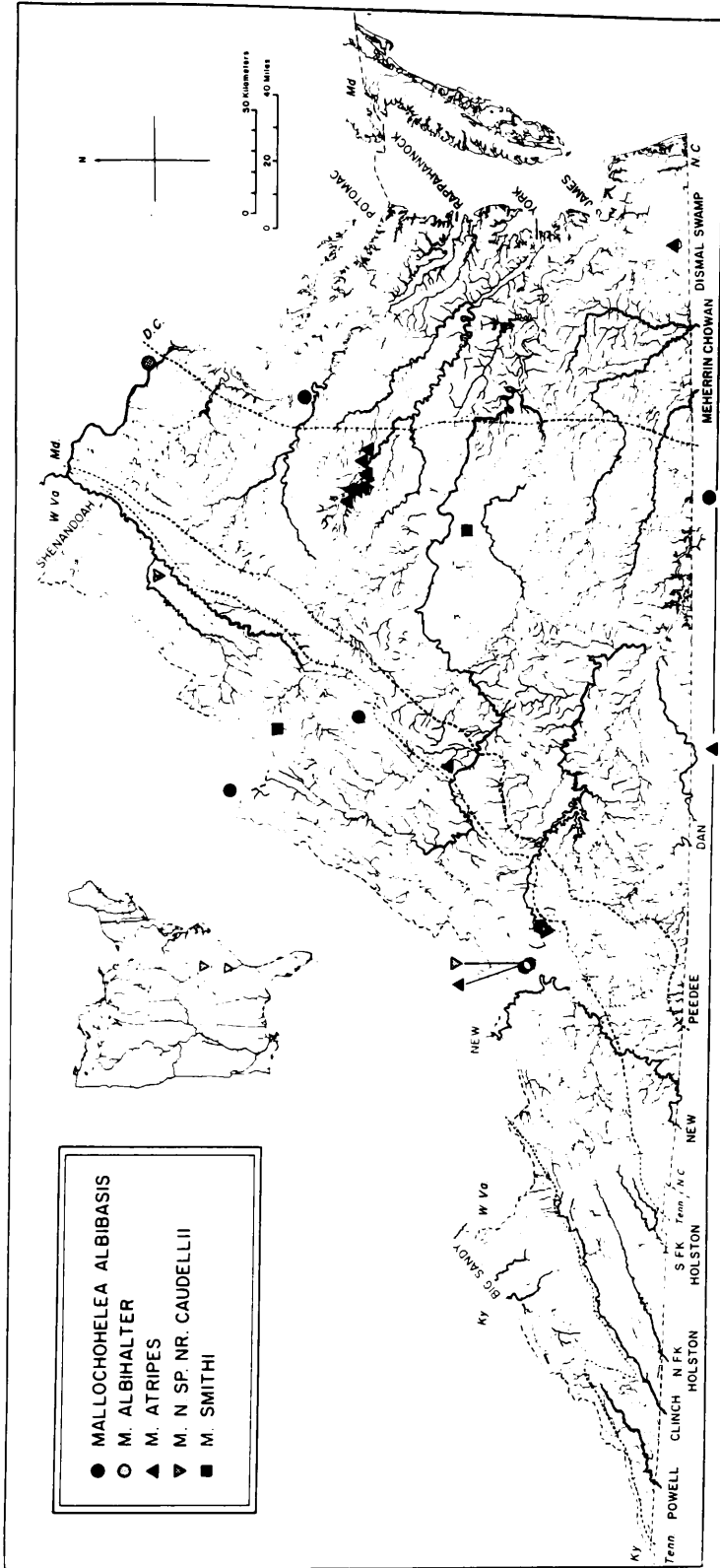


Figure 13. Geographic distribution of the five *Mallochohelea* species of the Virginia region.

CHAPTER FIVE

Ecosystematics and Autecology of Immature Sphaeromiini -- III:

Genus *Probezzia*5.1 Genus *Probezzia* Kieffer

5.1.1 Systematics and Habitus Synopsis

Nomenclature: Because confusion still arises on the part of some aquatic biologists over the proper use of the generic name *Probezzia*, I will discuss this aspect briefly here. The erroneous use of the name *Probezzia* as applied to a section of *Bezzia* with unarmed femora persists to this day among those authors who rely on Thomsen 1937 (1970 reprint) or on keys adopted essentially unaltered from her work, such as in Pennak (1953, 1978). The correct nomenclatural application of the name *Probezzia* has been pointed out by Wirth (1951a, 1952, 1962, 1971), and was incorporated into a major work on aquatic insects (Wirth and Stone 1956), on which most later keys to ceratopogonid immature stages are based (e.g., Edmonson 1959, Webb and Brigham 1982). Table 21 presents the appropriate nomenclature for the taxa assigned to "*Probezzia*" by Thomsen (1937). The larval and pupal morphology given by Thomsen is largely valid to characterize the species involved, but not sufficiently detailed to distinguish them from the many additional species now known. Genera and species of many larval Sphaeromiini and Palpomyiini can now be determined in the

Table 21. Summary of the nomenclatural status of the "Probezzia" in Thomsen (1937).

Name Used by Thomsen	Correct Name	Reference
<u>Probezzia copiosa</u> Thomsen 1935	<u>Bezzia (Homobezzia)</u> <u>bicolor</u> Meigen 1804 (= <u>syn. copiosa</u>)	Wirth 1983b
<u>P. glabra</u> (Coq.) 1902	<u>B. (H.) glabra</u> (Coq.)	Wirth 1983b
<u>P. opaca</u> (Loew 1861)	<u>Phaenobezzia opaca</u> (Loew)	Wirth & Grogan 1982
<u>Probezzia</u> (genus)	<u>Bezzia</u> in part <u>Phaenobezzia</u> in part	

Palaeartic (Glukhova 1977, 1979), but to date, construction of strong generic keys has not been possible because too few of the species are known in the immature stage. In particular, the Nearctic larval stages have not been well enough assessed to allow keys to be significantly improved at this time.

Adult: Distinguishing characteristics for the adult *Probezzia* are provided by Wirth (1951a, 1971) and Wirth and Grogan (1979). Key characteristics I have found useful in sorting out unmounted liquid-preserved specimens of *Probezzia* include: mesonotum dorsally with scattered (20-50+), short, stout, erect spines; wing with a single long radial cell, reaching nearly to wing tip in the female; femora unarmed, and 5th tarsomeres ventrally armed with blunt strong spines. The sharp erect spines on the mesonotum are unique to this genus, and are also present in the males of all species I have seen.

Sexual dimorphism in size is considerable. Males, normally, are much smaller, about 60-80% the size of females. Similarly, the larvae from which males will develop are consistently about 80% the size of "female larvae", i.e., the female larvae are 1.25 x larger than the male larvae (based on data presented for *P. seminigra* by Glukhova 1979). Some species have banded or infuscated wings, though in the male the darkening may be most apparent mainly on the veins. Male genitalia offer few if any definite characters distinguishing the genus, or species within the genus. Leg coloration in the male generally parallels that of the female, and in most species provides our important means of correlating males and females of a species. How-

ever, in *pallida* and *albitibia*, sexual color dimorphism (dichromism) complicates this situation, it is adequately identified by Wirth (1971) resp. Wirth and Grogan (1979). Another complicating factor often encountered in the course of conducting individual rearing efforts, is the fact that coloration of often under developed in specimens which for various reasons do not fully harden before being preserved. Male *Probezzia* have at least a four ventral batonnets on the 5th tarsal segments, which serves to distinguish them from male *Bezzia*.

Eggs and oviposition. Oviposition biology has been described for the Holarctic species *Pr. seminigra* Meig. and *concinna* Meig. -- species which apparently are more common in the Palaearctic than in the Nearctic -- by several European authors (Wesenberg-Lund 1914, 1915 (in Thienemann 1928), Lenz 1934, Rieb 1981). As illustrated and described by Lenz (1934) the eggs are extruded by the hovering female, form a gelatinous ribbon a few centimeters long, containing several hundred eggs. The ribbons are twisted and take on the form of a "stretched ellipsoid," or helix. The eggs are obliquely displaced at an angle with respect to the longitudinal axis of the ribbon. In *seminigra*, this angle is given as 25 deg. by Rieb (1981). Additional new, interesting details provided by Rieb are discussed in the Sphaeromiini tribal overview.

Larva: A larval description for *Probezzia* is available only for *seminigra*, but these are among the most thorough done for any

ceratopogonid species anywhere, and include descriptions of all four instars (Glukhova 1971, 1977, 1979). The most useful macroscopic characteristics for sorting mature larvae include: a) head capsule elongate-conical, anterior end strongly narrowed, labrum by hyaline and conspicuously protruding; b) thoracic segments with irregular concentrations of brown pigment; c) anal segment with a dorsal and ventral row of four setae linearly arranged along the longitudinal axis; and d) the caudal triangular extension of the ventral "collar" (the latter character common to all known Sphaeromiini).

Larvae fitting this pattern were encountered on at least 30 occasions during this study, but no definite associations could be made. Nevertheless, they have been tentatively designated as *Probezzia* sp. The most common of this type of larva occurred at localities where *Pr. pallida* had been collected by other means.

While a detailed description of these larvae is beyond the immediate scope of this study, a brief review of the larval habitus, or macroscopic appearance, is in order. Specimens which I consider to be *pallida* differs from *seminigra* in possessing a brownish head capsule (rather than yellow), with the base of the frontoclypeus a strong brown (Munsell 7.5 yr 3/6, NBS 55), becoming a moderate orange yellow apically (Munsell 7.5 yr 7/8, NBS 71). The cephalic sclerites are accentuated by pigmentation differences (Figure 14 on page 340), and the ocellar spots are strongly constricted on the outer sides, with caudal extensions similar to those of *M. atripes* (Figure 12 on page 274), but smaller. Other presumed *Probezzia* larvae I have seen possess head capsules of the same general shape but are of a more uniform

grayish brown or yellowish brown color which appears to be consistent for each type, and remain distinct and unchanged whether the specimens is an exuvium, alive, preserved in liquid, or mounted on a microscope slide.

In the thorax, distinct brown pigment spots occur laterally in the outer fat layer beneath the hypodermis in the meso- and metathorax, and another concentration in the inner fat layer bordering the tracheae and gut at the intersegmental line between the pro- and mesothorax (Fig.14a). These pigment spots remain reasonably distinct when the larvae are preserved in alcohol. Under certain conditions in preservation, the cuticle can lose some translucency, though the spots remain visible (Fig.14b). The latter specimen was submitted by an individual who had preserved the larva in approx. 90% isopropyl alcohol, which caused cuticle shrinkage, and head capsule retraction into the prothorax. A more appropriate method of larva preservation, which would have prevented these conditions, has been discussed in Chapter 1.

Pupa: Pupae of the genus appear to lack any single distinguishing feature. The exuviae range from a light brownish yellow in color to a darker grayish brown. The prothoracic respiratory horn is slender, short (L/W ratio 3.0-4.0), with the number of spiracular openings at the apex ranging between 4 (*albitibia*) and 16 (*seminigra*). The operculum is consistently 1.2-1.3 times as long as wide, with an acute point at the middle of the posterior margin in all species seen.

Figure 14.a-c. Probezzia sp. prob. pallida, larval head and thorax habitus: (a) live, fourth instar; (b) preserved fourth instar, shrunken due to excessive ethanol:water ratio ($\geq 9:1$); (c) larval cuticle and head capsule from bluegill fish gut. Bar equals 1 mm (a-c same scale).



On the abdominal segments are large sharp-pointed tubercles angled somewhat caudally, but the dorsal tubercles are rather inconspicuous in comparison with the *Mallochohelea albibasis* type (e.g., Fig. 9). The surface of the integument is spinulose in various combinations, which offers some diagnostic value. Ventral adhesive disks (cf. Fig. 12c & d) are found in about half of the 15 species for which pupae are known, including 3 of the 7 described and 2 new species in the Virginia region (Table 22). At the tip of the abdomen, the paired posterolateral processes are narrow, sharp-tipped and divergent, forming angles between the processes ranging from about 10 deg. (sub-parallel) to about 160 deg. (greatly divergent). This character state provides a useful diagnostic feature to help distinguish species, though the sexes differ in their expression of it.

5.1.2 Habitat Characteristics

Among the approximately 16,630 immature ceratopogonids seen in this study from all sources (approx. 46% submitted by other aquatic biologists) about 150 larvae and less than a dozen pupae could be assigned to *Probezzia* sp. These represented at least 37 localities in 11 states from North Dakota to Texas and Florida; 30 (81 %) of these collection localities were in distinctly lotic macrohabitats, the remaining 7 in reservoirs.

Because habitat information is available for many of these sites (which I specifically requested from all those submitting specimens), a brief descriptive review of the more representative and interesting

Table 22. Overview of *Probezzia* pupal abdominal disks' presence or absence, and geographic distribution in Nearctic (based on Wirth 1951, 1971; Wirth and Grogan 1979; Mayer 1934; and present results). Asterisk (*) indicates species present in Virginia or contiguous states.

Species	Abdominal Disks on Segment	Geographic Distribution in Nearctic				
		S.F.	E.	N.E.	W.	N.W.
*albitibia Wirth	(6,7) indistinct or absent			WI-VA		
*n.sp.nr. albitibia	(6,7) indistinct or absent			VA		†
*albiventris (Loew)	6,7 prominent		WI-FL	MI		
atriventris Wirth					TX	
bottimeri Wirth						
concinna (Meigen)	Absent?				(Holarctic-northern)	
flavonigra (Coq.)	6,7					
fuscipennis Wirth	6,7				ME-NY-ON	
infuscata Malloch	Absent				MN-IL-ON	
*jamnbacki Wirth					MI-CN,MD,AS	
ludoviciana Wirth		LA				
nigra Wirth		FL,GA,LA				
*pallida Wirth	6,7 Ontario ¹		WI-FL			
	Absent, elsewhere					
rosewalli Wirth		LA				
*sabroskyi Wirth	Absent	FL	WI-WV			OR
seminigra (Panzer)	Absent		(Holarctic)			†
*smithii (Coq.)	Absent		WI-FL			
unica (Joh.)				NY		
williamsi Wirth	5,6,7			WI-NY		
*n.sp.nr williamsi	Absent	NC				
*xanthogaster	Absent				WI-VA	

¹Present in a series from Rideau R., Ontario, only (Wirth 1971).

data follows. (A more complete review will appear in separate papers on the Ceratopogonidae of lakes and of running waters.)

5.1.2.1 Streams and Rivers

Using the drift net technique I discussed earlier, concentrating on collection of floating pupal exuviae in streams, W.P. Coffman obtained numerous ceratopogonid exuviae among collections for chironomids in several western Pennsylvania streams. I examined 3 cast pupal skins of *Probezzia* sp. taken on 8 July 1975 from French Cr., a 3rd-order stream which passes through a patchwork meadowland-woods ecosystem.

Drifting larval *Probezzia* were encountered by Kennedy et al. (1981), in a mid-stream drift net placed in the New River at Glen Lyn, Giles Co., VA. I was able to examine 3 larvae collected June 16-17, 1976, during a normal flow period. Other such larvae apparently appeared regularly (J. Kennedy, B. Kondratieff, pers. commun.) At this point in its course, the New River is an Order 6-7 river with an average current velocity of ca. 15 cm/sec (near shore) and an average yearly discharge of 141m³/sec. The bed is ca. 70m wide, and the substrate is rubble-gravel, with sandy silt in the deeper channels, interrupted by occasional rock ledges. The margins are of silt and fine sand (pers. obs.; Newbern et al 1981).

Aquatic macrophyte growth in and along the river is considerable. Productivity of the waterwillow (*Justicia americana*) is four to five times greater than any other major aquatic species in the New River (Hill 1981). It is quite conceivable that the *Probezzia* occur in association with the waterwillow beds in the New River; these beds grow

on lightly silted gravel shoals and around islands in the river (cf. Koryak 1978), where conditions could also be appropriate for *Probezzia*.

Apparently, all larvae in the above drift nets appeared during the night. This, combined with the fact that catastrophic drift is not involved, suggests that benthic *Probezzia* larvae actively enter the water column of streams and rivers, and that they do so at night. This they are known to do in lakes, where prepupal larvae have been observed to leave the bottom substrate and swim toward shore at the lake surface, and once they reach the shore, they promptly burrowed into the beach sediment to pupate. (Weerekoon 1953, Williams 1955). The functional significance of such behavior is discussed in Chapter 7.

The rather extensive collection of larval and pupal ceratopogonids from lotic habitats assembled at the Academy of Natural Sciences of Philadelphia (ANSP) contains at least 10 probable *Probezzia* spp.¹, collected at rivers and streams throughout the eastern U.S. Many of these sites were characterized and their flora and fauna discussed in Patrick (1961), Patrick et al (1966), and Roback (1976).

The ANSP collection contains specimens taken in some of the most rapidly flowing water from which *Probezzia* larvae have yet been recovered, notably from Big Stone Cr., Giles Co., VA. Roback (1976) thoroughly sampled this site (as Station 36) for Chironomidae and made representative general collections of associated fauna as well. Big Stony Cr. where sampled is a 3rd-order mountain valley stream at 2900

¹ as determined by WIK.

ft. (884m) elevation, 25 ft. wide, water 2-2 1/2 deep, and with a "very rapid" water flow ("fast breaking flow in montane stream", Roback 1976:149); the bottom substrate is bed rock and loose boulders. The station was described as partially shaded (by riparian vegetation), with no aquatic macrophyte recorded. Water quality, temperature, and a photograph of the station are given in Roback (1976).

Although Ceratopogonidae were not listed among the fauna associated with this station, I personally identified one larva collected there, which was mounted on a slide, plainly labelled "VA, 36-Big Stony Cr. nr. Goldboro, Rts. 685 and 781, VI-12-1971"(ANSP coll.). My familiarity with the stream sampled, and inspection of the photograph of the site, lead me to believe that suitable microhabitats in that stream, and others like it, would indeed present themselves in several places.

Several records suggest a *mid-stream* larval presence in larger watercourses. Three larvae were taken by W.S. Ettinger by Ekman grab in the Schuylkill R., PA, where the substrate was mainly silt, water depth 0.3 to 1.2m. Many specimens were collected by Ponar dredge in the Tombigbee and Black Warrior rivers (mi.216-293) by aquatic biologists with Harmon Engineering, Alabama. At their sites yielding *Probezzia*, the current was slight (<6-15(max.)cm/sec), sediment a fine sand to mud, and water between 3 and 15 m deep.

Diversified, careful sampling in several southeastern streams and small rivers, in South Carolina (J. C. Morse, T. R. White and others, Clemson University) and Arkansas (E. Bender, Edgewood Arsenal; G. Harp, C. Latimer, Ark. St. Univ.) has yielded numerous specimens. Of particular interest is the large assemblage of *Probezzia* larvae (plus

other Sphaeromiini and Ceratopogonidae) present in the Upper Three Runs Creek drainage basin, Aiken Co., referred to earlier. Three distinct larval *Probezzia* types were distinguished among nearly 100 larvae of the genus taken from five sites during the course of one year. The two most common *Probezzia* ranked 52nd and 56th out of 551 species of aquatic insects, in terms of numerical abundance and frequency of collection (Knausenberger 1983, Morse et al. 1983). Subsequent attempts by (Morse et al. (*in litt.*) to collect the adults by light trap and emergence traps yielded nine *Pr. nigra* Wirth (which see).

5.1.2.2 Reservoirs and Lakes

Judging from the ca. 20 larvae and 10 pupae of *Probezzia* sp. which I distinguished among extensive collections received from collaborators working on man-made lakes, the genus is present in modest numbers, but consistently, in such environments throughout the country. Material seen was derived from:

1. Louis and Clark Lake and Lake Francis Case, on the Missouri River in South Dakota (subm. by P. L. Hudson).
2. Lake Sakakawea, Mercer Co., North Dakota, also on Missouri River (subm. by P. A. Guthrie).
3. Lake Anna, on the North Anna River, Louisa Co., in the outer Piedmont of Virginia (subm. by J. R. Voshell and G. M. Simmons).
4. Smith Mountain Lake, on the Roanoke (Staunton) River, in the western Piedmont of Virginia (subm. by E. Prince)

5. Lake Norman, in the western Piedmont of North Carolina (subm. by T. W. Bowen)
6. Lake Keowee, Oconee Co., South Carolina, also in the western Piedmont (subm. P. L. Hudson).

These reservoirs ranged in pH from an average of 6.6 to 8.4, and the specimens were encountered from 0 m to 27 m in depth. In those lakes where samples were taken at the shoreline, *Dasyhelea cincta* group and *grisea* group species were frequently associated with the *Probezzia* spp. Samples taken by dredge or artificial substrate (Lake Anna), consistently yielded other Sphaeromiini, esp. *Sphaeromias longipennis*, and various Palpomyiini.

Bluegill fish taken in Smith Mtn. Lake had larval *Probezzia* in their guts, in which numerous head capsules were found quite intact (Fig. 15c). The fish were taken in June 1975 around artificial reefs constructed of tires and placed at 20 ft. depth. Several other fish species were found to have ceratopogonid larvae, including *Probezzia*, in their guts as well (E. Prince, pers. comm. 1975).

5.1.2.3 Pollution Tolerance.

Tolerance to chemical pollution is suggested by the presence of fair numbers of two distinct types of preserved *Probezzia* larvae in Phillips Cr., which drains a large portion of Edgewood Arsenal, near Pine Bluff in the Arkansas River flood plain. This creek drains a large tract of land that is contaminated by DDT, mustard decontamination products (prim. lime and thiodiglycol), arsenic, and other potential decontaminants (E. S. Bender, *in litt.*, Pearson, et al 1976). Most specimens

were taken in a pool with water about 25cm deep. About 12 other ceratopogonid taxa were collected on the Arsenal property, particularly in Yellow Lake.

5.1.3 Autecological Discussion

5.1.3.1 Habitat Requirements

- Macrohabitat.

Dominantly rheotopic, subdominantly lacustrine in affinities.

Probezzia species exhibit one of the most consistent patterns of macrobiotope association in the entire family Ceratopogonidae. Members of this genus characteristically inhabit riverine and lacustrine habitats, specifically larger streams, upper and middle reaches of rivers, and sizable lakes, respectively.

A clear preference for lotic macrobiotopes is evident from Table 23, based on a compilation of all available rearing records. An "abundance index" incorporating numbers of specimens and frequency of collection (number of localities yielding a given species) provides a basis for comparison. The rationale for this abundance index is provided in Chapter One (Sect. 1.3.4.1).

Only *williamsi* (and n. sp. nr. *williamsi*), among the species whose habitat is known from rearing, appear to be more common in lakes. Circumstances evidence points to the likelihood that *flavonigra* may turn out to be mostly lake dweller as well. *Probezzia pallida* is the most commonly collected species in the genus, having been reared in significant numbers from at least 16 lotic margins. The three next

Table 23. Relative abundance of *Probezzia* spp. in lotic and lentic environments, with microhabitat summaries based mainly on explicit rearing records.

Probezzia Species	Lotic		Lentic		Microhabitat Notes
	No. Sites ¹	Abundance Index ²	No. Sites	Abundance Index	
<i>albitibia</i>	9	16.4	1	1.4	Depositional areas and margins of smaller streams (2nd-3rd order); sand consistent component of substrate; somewhat shaded; not primarily associated with rooted aquatic plant cover.
<i>sp. nr. albitibia</i>	1	2.2	0	-	Sandy mud at margin of small stream, among roots of riparian vegetation; slight shade.
<i>albiventris</i> ⁵	1	3.16	0	-	Margin of Wisconsin R.
<i>concinna</i> ¹	1	+	0	+	Various lakes and streams in Europe.
<i>flavonigra</i> ^{4,5}	0	-	2	+	Twice swept at lake margins in Canada.
<i>fuscipennis</i> ⁵	1	3.0	0	-	Margin of Fishing Brook, NY.
<i>infuscata</i> ⁵	2	6.9	0	-	River margins, Wisconsin.
<i>jambacki</i> ⁵	2	3.5	1	1.0	Stream margin and sand bar; sandy beach of lake.
<i>nigra</i>	1	1.0	0	-	Marshy margin of small stream.
<i>pallida</i>	16	164.7	3	18.0	Sandy-silty margins of large streams; phytophilic in lakes; reservoir floatam.
<i>sabroskyi</i> ⁵	1	1.4	0	-	Stream margin.
<i>seminigra</i> ¹	9	++	3	+	Sandy-silty expanses, esp. along rivers, often taken near emergent plants.
<i>smithi</i>	5	20.6	1	1.4	Depositional stretches, margins of streams, near emergent plants.
<i>williamsi</i> ⁷	1	1.0	2	19.3	Pupae in beach sand of lake, larvae in submerged pondweed <i>Potamogeton natans</i> ; some pupation on Typha.
<i>sp. nr. williamsi</i>	0	-	1	1.4	Floating on lake surface among floatam.
<i>xanthogaster</i>	9	53.2	1	1.0	Coarser substr., incl. gravel, moderate shade, no immed. emerg. veg.

^{1/} Separate localities yielding specimens, combining literature and present study records.

^{2/} $(N_1)^4 \times F \text{ Coll}^1$, where N_1 = number of individuals (total), $F \text{ Coll}^1$ = frequency of collection, from separate localities.

^{3/} Numbers of specimens not given in most cases; sources: Rieth 1915, Thuenemann 1928, Meyer 1933, 1934; Glukhova 1971, 1979; Havelka 1978; Rieb 1981.

^{4/} Not actually reared.

^{5/} Source: Wirth 1951, 1971.

^{6/} Does not include numbers in Lake Mendota (Nittkowski 1918)—2.20m at 0-2 m depth.

^{7/} Source: Williams 1955 (as *sabroskyi*).

most abundant, *xanthogaster*, *smithii* and *albitibia*, are also markedly more common in running waters, than in lakes. These four species are also the most common of the seven described species present in the Middle Atlantic states (Table 22 on page 343).

An analysis of stream order² with respect to species occurrence presents an interesting perspective to *Probezzia* distribution along lotic waters (Table 24). Thus, first-order streams, such as spring runs or woodland brooks, are not occupied by species in the genus. However, a concentration of records occurs in the 3rd and 4th-order streams, i.e., in lotic systems approximated by "large streams and small rivers." Consistent but fewer records for the genus as a whole occur in rivers of 5th and 6th order or above.

Indications are that some segregation by species among water courses of different orders is taking place. For example, *albitibia* appears more likely to occur in smaller streams than *smithii*.

This stream order related occurrence apparently conforms to the predictions of the river continuum theory, as described by Vannote et al (1980). This theory predicts that physical heterogeneity and food resource heterogeneity should be maximized in streams of 3rd to 5th orders. It follows, from biological diversity theory, that maximum biological diversity will also occur in streams of these orders.

² An objective method for classifying streams advocated by Abell (1961) and Kuehne (1962), and endorsed by Hynes (1970:14) for use in biological studies. Extreme headwater streams are ranked as first order; they have no tributaries. Where two streams of the same order join, they form one of the next higher order.

Table 24. Ecological partitioning of *Probezzia* along stream order and lentic habitat continua, using only those taxa collected from at least four localities. Symbols indicate relative abundance index values¹: + = 1-10; ++ = 11-29; +++ = >30.

Probezzia Species	Habitat									
	Lentic System					Continua				
	Stream Order					Lentic System				
	2	3	4	5	≥6	Pond	Littoral	Sublittoral	Lake Zone	Profundal
albitibia	++	+++	+							+
jamnbacki		+								+
pallida	+	++	++	+	+				++	
seminigra	+	+	++	++	+				++	
smithii	+	++	++	++						+
williamsi									++	
xanthogaster	+	+	++	++	++	+				
spp. undet.	+	+++	++	+	+				++	+
Relative Abundance	6	12	12	8	7	1	11	6	6	2

¹(N_I)¹ x F_{Coll}, where N_I = no. individ., F_{Coll} = frequency of collection (separate localities).

In the case of the genus *Probezzia*, it does appear to be present in greatest abundance, in terms of frequency of collection if not necessarily in numbers per unit area, in 3rd and 4th order streams, as shown.

Despite the consistent association of *Probezzia* species with the general lotic habitat, one cannot say that they are rheophilic in the strict sense. Instead, the term "rheotopic" would better characterize the nature of the association, that is larvae of this genus normally occur under conditions often encountered along and in a stream bed, but the larvae do not have inherent current requirements (such as those often associated with the respiratory physiology or feeding mechanisms of rheostenic stream invertebrates, e.g., black fly or caddisfly larva). Rather, the *Probezzia* seen able to colonize the relatively uniform and often depauperate sediments in lenitic, or depositional, stream segments where current is reduced. Thus, eddy pools, sand bars, widened stretches, and shallow-sloped littoral sediments are where larvae may be encountered. Ideal conditions for some species, such as *seminigra*, seem to be provided in rather large soft sand-silt flats across which flow slow, shallow, more-or-less meandering trickles.

Under unusually favorable conditions such as large expanses of sandy-silty substrate along particular stretches of larger rivers, extensive breeding has been known to occur. This has been so, for example, on the Potomac River at Scott Run (Wirth and Grogan 1979:853), Rideau R., Ontario (Wirth 1971) and several Russian rivers (Krivosheina 1957, Glukhova 1971, 1979). However, in the present study comparable habitats were not located.

▪ Microhabitat distribution

Probezzia larvae are very often clumped in their distribution, and pupae also tend to occur in rather large assemblages, in both of the two main habitat types which they occupy. Among the factors contributing to this distribution pattern would be:

1. oviposition habits of the gravid female;
2. self-sorting by larvae according to substrate texture, aquatic plant presence or absence, and/or nutritional resources;
3. physical sorting by wind, waves, current, geomorphic features of the waterbasin, etc.;
4. life history and seasonal events, such as overwintering habits, or prepupation and pupation behavior.

Deposition of the egg ribbons by the gravid females takes place near shore in quiet waters, though apparently not necessarily near aquatic plants. It seems unlikely that choice for a particular substrate type is a factor in oviposition. Rather, the population (e.g., small stream versus lake inhabiting) from which the female originated will, if optimum habitat choice behavior applies (Antonovics 1971, Powell and Taylor 1979, McLeod et al. 1981), determine the general ecological area which the fly seeks out. The larvae should prove maximally fit to survive in this environment. Thus, stream inhabiting *Probezzia* can exploit a range of coarse to fine-textured sediments, as well as aquatic hydrophyte beds and algal clumps, and probably are better able to cope with fluctuating water levels.

Initial aggregations of larvae often occur near the point of egg ribbon deposition. Glukhova(1979) found that large concentrations of

earlier instar *P. seminigra* larvae (with a complement of older larvae as well) frequently occurred in and near the roots of aquatic plants growing on soft sand-silt substrates. From such foci, the larvae may then move out to other substrates in which they have been commonly encountered.

Probezzia larvae are more likely than any other ceratopogonids, besides the *Culicoides selfia*-group (Fredeen 1981, Atchley 1970), and some *Mallochohelea*(this study) species, to be encountered in mid-channel sediments of moderately to rapidly flowing streams(e.g., the Big Stony Creek specimens mentioned earlier; see " Streams and Rivers" on page) Because these larvae are particularly vigorous swimmers, this may enable them to negotiate currents with success. Some species, such as *P. xanthogaster* and *albitibia*, have definitely been found on coarser sediments in significant current. Yet, because there is a thin zone, the boundary layer, above all surfaces on stream bottoms, where the current is negligible even in areas of rapid current(e.g., Jaag and Ambuhl 1964), it appears likely that this is where the larvae move about most of the time, true to their "burrowing" habit.

The question whether and how microhabitat distribution is affected by the texture of the substrate cannot be answered very well without controlled and comparative field observations, but it is possible from indirect evidence to infer that deliberate substrate selection and colonization takes place. Krivosheina(1957) found the population density of ceratopogonids to be small in a pure sand layer over silt along the margin of the Oka river, but *seminigra* was the only species to be developing in significant numbers there. Larvae of the same species

appeared on shoals of fine silt and sand within two weeks after the shoals were exposed by the falling water level of the Komarovka river (Glukhova 1979). In the New River, Virginia, *Probezzia* were considerably less common than I would have expected for a river with a silty-sandy margin as it has. Despite sampling on a bi-weekly and monthly basis for nearly two years, I reared only two specimens of *P. pallida* from there. It is my impression that the tidal flow nature of the river because of weekly water level management at Claytor Lake reservoir is detrimental to the development of *Probezzia* and other ceratopogonids. This is due to the likely scouring action taking place at the margins, which often can lead to a depauperate fauna (Ward 1976). On the other hand, as mentioned above, beds of aquatic macrophytes(esp. waterwillow) may be the source of larvae collected in that river by drift net.

With respect to the action of current, wind, and waves, it is clear that these play an important role in concentrating larvae and pupae at natural points of convergence such as in quiescent eddy pools immediately below rapid stretches, behind logs, among beds of hydrophytes, at the downstream ends of sand bars, and the like. Strong erosional wave action is definitely negatively correlated with the presence of pupae. However, slight wave action resulting from wind can cause higher densities of larvae on the leeward side of pools or lakes, as I have repeatedly observed.

Pupae are commonly encountered in flotsam concentrated by wind or current action, and this is one of the most productive way of obtaining them. Indeed, in discussing stream-inhabiting Ceratopogonidae and

substrate preferences, it is important to bear in mind that many observations made in the past have been based on collections of pupae, a good many of which may not have been particularly near to their actual larval habitat. Nevertheless, it is extremely useful to observe carefully existing current patterns and the like while collecting members of this family in particular, because this will invariably augment the success of collections.

- Larval and pupal behavior

No direct observations on trophic relations have yet been made with *Probezzia* larvae. However, in Loch Lomond, Scotland, Weerekoon (1953) observed red gut contents in *Probezzia seminigra* and *Mallochohelea ?nitida* larvae, which may very likely have resulted from preying on *Chironomus*, other bloodworms, or possibly certain Oligochaeta. Judging by the narrowed anterior end of the head capsule (which emphasizes the prognathous expression of the mouthparts), the relatively fine teeth on the epipharynx, and knowledge of the food habits of related groups, one can reasonably infer that the larvae are piercer-predators, and engulfers of small animals. Undoubtedly, they are also able to exploit animal food resources in the aufwuchs community on plants and other substrates. Because microturbellaria and oligochaetes are pioneer colonizers of sediment in small streams as well as other bodies of water (Schwoerbel 1981a, b), it is likely that *Probezzia* and other predaceous Ceratopogonidae prey on these animals, helping to explain the larval occurrence on these sorts of sediments.

- Larval movement

Probezzia larvae swim with typically very rapid oscillations, about twice as rapid, even as fourth instars, as most *Culicoides* do. An approximation of the frequency may be given by the fact that a *P. albitibia* which I observed was blurred into a "whirl" with two nodal points. The "flicker fusion frequency" at which the human eye can no longer resolve flickering images into individual entities, is around 20 cycles/sec. Becker(1961) estimated that *C. circumscriptus* oscillated at ca. 9 cycles/sec. Glukhova(1977, 1979) characterizes *P. seminigra* as "very rapidly swimming". However, despite the high frequency of the oscillations, the actual speed of propulsion through the water is not dramatically greater for *Probezzia* than it is for, say, *Culicoides*. *Probezzia* larvae may readily swim considerable distances in lakes, particularly at the approach of pupation. In Lake Douglas, *P. williamsi* swam to shore in large numbers overnight, from a submerged pondweed bed 40 feet out in the lake(Williams 1955).

Pupae of *Probezzia* spp. have been commonly collected on emerged plant stems and debris, in sediments above the water line, and, commonly, among flotsam, on the water's surface, usually concentrated by wind or water current. While ceratopogonids are not known to be able to emerge from free-floating or submerged pupae, it is likely that they are able to emerge successfully if pupae are in an air-water-emerged object "intersectional line³". The preponderance of solid-substrate pupation sites probably ensures greater pupation success, particularly

³ A term proposed by Bates(1949) in connection with mosquito larval and pupal habitat and behavior.

in streams, than for many other nematoceros dipterans, or other insects which emerge from the open water.

5.1.3.2 On the functional significance of the pupal "glandular disks"

The differential occurrence or absence of membranous patches or "glandular disks" on the ventral abdominal segments of various *Probezzia* (see Table 22 on page 343 and Figure 11 on page 272), suggest a comparable differential in functional significance. The imputed significance of these disks is to enable the pupae to scale smooth-sided objects, and to attach them securely to the substratum above the water level in preparation for eclosion (e.g, Wirth, 1962a, 1971; Wirth et al. 1974; Wirth and Grogan 1979). Possession of these disks or patches may, therefore, be the phenotypic expression, in that species, of increased fitness for pupation on emerged plants or stones. This would lead one to expect the species to pupate more commonly on non-sediment substrates than in sand or mud. Alternatively, the patches could contribute to ecological segregation when several *Probezzia* species occur in the same microhabitat. Such co-occurrence is apparently rather common (see below in the discussion).

Another possibility is that the disks enhance the likelihood of successful emergence because the pupae would be less easily dislodged when, say, plant stems bend due to wind or waves. In habitats with fluctuating water level or significant wave action, the scaling behavior would avoid the scouring of the margins which otherwise tends to take place. Waters (1962) pointed out that even slight increases in depth and velocity of a stream would be expected to have a marked effect on larvae associated with the surface film and with wet areas near

the water's edge. Pupae attached to emerged objects would be less likely to appear in stream drift.

In any case, pupae of both types (with and without disks) have been commonly found on both types of substrates (emerged objects vs. sediments) substrates. The disks do not appear to be essential to successfully scale emerged objects. This is often accomplished by the larvae, in fact, which can take advantage of surface-film tension (pers. obs.; Williams 1955, Weerekoon 1953). I have observed pupae of *Bezzia*, *Culicoides*, *Dasyhelea*, *Isohelea*, & *Stilobezzia* attached to the interior of the glass rearing vials (Figure 6 on page 68). Attachment was always on the venter of the abdomen or cephalothorax, and the pupae invariably scaled the wall in a thin film of water such as condensate.

Nor does possession of the disks prevent the pupae from burrowing in exposed sediments near the waterline. Very little detailed data on substrate conditions in relation to ceratopogonid presence is to be found, nor do the data of this study allow evaluation for behavioral correlations between adhesive disk presence and plant substrate occurrence, and the like; most *Probezzia* in this area do not possess the disks, anyway, and no such correlations are apparent for the *Mallochohelea* species either. The likelihood of a geographical correlation can almost certainly be excluded, however.

Other morphological features of the pupae which may have a bearing on behavior include: the shape of the abdominal tubercles, the differential divergence of the posterolateral processes at the terminal

end of the pupae, and the differential extent to which denticulation is developed on the integument. The assumption here is that such characters are phenotypic expressions of particular adaptations to various types of substrates and habitats in the transition between fully aquatic to semiterrestrial conditions. For example, it has been suggested plausibly that *C. melleus* and certain other intertidally breeding species have relatively small tubercles, and divergent terminal processes to enable them to burrow up and down in the intertidal sand in response to water level changes (Dyce and Murray 1966, Linley 1966). Similarly, the variously divergent terminal processes and the presence of more or of less denticulation in *Probezzia* pupae could be related to a preference for or adaptation to sediment of particular particle-size range. Predominately lake-dwelling species would be expected to be distinguishable from lotic species on this basis. I would expect pupae primarily occurring in soft mud sediments to have more nearly parallel terminal processes and more denticulation than those which pupate mostly in coarser sediments. However, I have not been able to verify this with the limited series available to me.

5.1.3.3 Species co-occurrence.

Probezzia species appear to have a propensity for being associated with others of the same genus. I have collected three species from three sites along the Jackson River (Alleghany Co., Virginia) in a single sampling session; at least two species co-occurred at each of three sites. Similarly, at the Scott's Run and Holmes Run sites in northern Virginia, Wirth (1951a, 1962b, 1971; Wirth and Grogan 1979)

Table 25. Co-occurrence of Probezzia species at three Virginia streams. Symbols indicate ranges in number of specimens collected or reared: + = 1-5, ++ = 6-10; +++ = > 11.

<u>Probezzia</u> Species	Jackson R. Alleghany Co.	Scott's Run Fairfax Co.	Holmes' Run Fairfax Co.
<u>albitibia</u>	-	+++	+
<u>pallida</u>	++	++	+
<u>smithii</u>	+	+	-
<u>xanthogaster</u>	+	-	+

obtained four species, three at each site, usually on the same day or in the same week (Table 25).

5.1.3.4 Adult habits.

Insectivorous feeding behavior is known for 3 adult female *Probezzia* biting midges, in which mayflies, phantom midges, mosquitoes, true midges, and the conspecific males are the prey (Downes 1978):

Species	Prey	Location
<i>xanthogaster</i>	<i>Chaoborus flavicans</i>	Ontario
<i>venusta</i> (= <i>seminigra</i> ?)	<i>Ephemerella ignita</i>	Scotland
<i>concinna</i>	Chironomidae(5 spp. in 5 genera)	Alberta

Oviposition behavior is discussed under "Eggs and oviposition." on page 238 and in the tribal discussion.

5.1.4 Distribution

5.1.4.1 Geographic Range

This is a dominantly if not exclusively Holarctic genus, with perhaps 5 species in the Palaearctic and at least 20 in the Nearctic. Only one-half of the species are recorded from the south of the 40th parallel, and the five known only from the south (Table 22 on page 343) are comparatively uncommon. The present known distribution of *Probezzia* species in the Virginia region is shown in Figure 15 on page 365. The respective species are discussed individually below.

5.1.4.2 Biogeography

As a genus, *Probezzia* has clear boreal affinities, and very possibly its center of endemism, diversity and distribution is in the Great Lakes region of North America. The greatest number of species in the greatest abundance appear in the Wisconsin to New York region, and southern extensions typically are found to coincide with the Appalachian Mountain chain. To some extent, this conclusion may represent disproportionately distributed collection activity, but it is unlikely that the overall pattern will be altered significantly. Apparently, however, the genus is diversifying towards the south, and it is to be expected that several new species besides the two in this study will be encountered in the southern states in particular.

5.1.5 Annotated Taxonomic and Biological References

- Nearctic
 - Muttkowski 1918:408 (*Pr. pallida* behavior in lake, Wisconsin)
 - Wirth 1951a:25-34 (clarified nomenclature, revised and keyed N. American imagoes)
 - Williams 1955:94-6 (larval, pupal biol. observ., 3 spp., lake margin; Michigan)
 - Wirth 1971:729-739 (new spp., distr. records; key; biol. notes for 10 reared spp., N. Amer.)
 - Wirth and Grogan 1979:882-891 (diagn. female, male, descr. & figs., pupae of 4 spp. in lower Potomac Valley, Virginia, Maryland)
 - Downes 1978:4, 25, 36 (adult prey habits of *Pr. concinna*, Alberta)
 - Bowen 1983a:84 (3 spp. in lake, North Carolina)
 - Knausenberger 1983:305 (*Probezzia* larvae in streams, South Carolina)
- Palaeartic

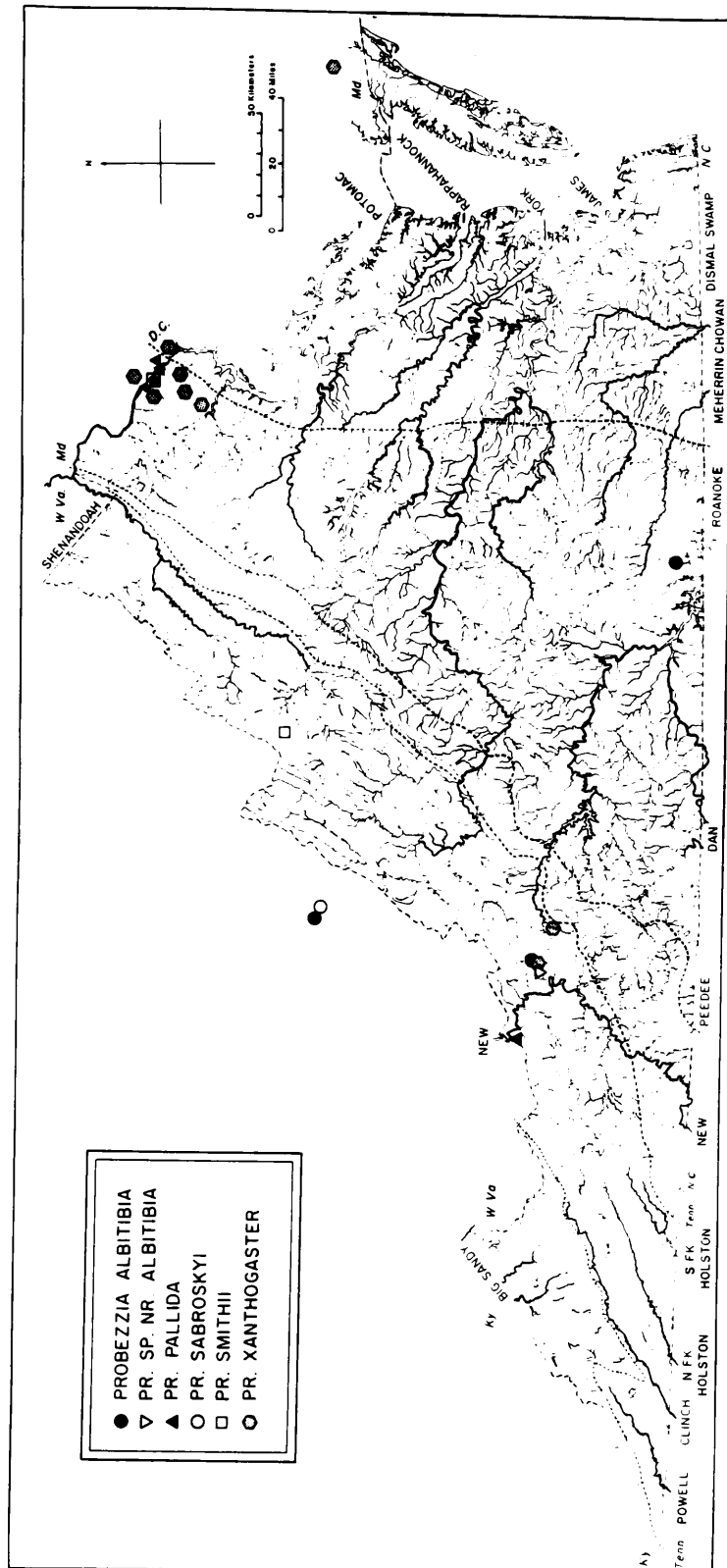


Figure 15. Geographic distribution of the six *Probezzia* species of Virginia and surrounding states.

- Rieth 1915: 404, 407, 408 (pupa of *seminigra* (Panzer) (as *Bezzia venusta* Meig.), descr.; fig. respir. horn; habitat; Germany)
- Thienemann 1928:600-1 (as *Dicrobezzia* spp. (*D. concinna* Meig. treated as variety of *venusta* Meig after Kieffer 1925:118); summarized nomenclature, published info. on developmental stages, habitat records, Europe)
- Lenz 1934:120, 122 (*seminigra* as *D. venusta*, oviposit., photo egg ribbon; Germany).
- Mayer 1933:292 (reared, habitat, N. Germany; *P. seminigra* as *Dicrobezzia venusta*).
- Mayer 1934:243-4; 272, 275 (*seminigra* and/or *concinna* as *D. venusta* var. *concinna*; notes on oviposit, pupa, fig. operculum; habitat; Germany)
- Weerekoon 1953:88, 91 (*seminigra* (as *venusta*), larval biol., in lake; Scotland)
- Krivosheina 1957:69-72 (larval habitat in rivers and floodplain pools, ponds; European USSR).
- Glukhova 1971:176-7 (*seminigra* (as *venusta*), larval descr. & figs.; USSR)
- Glukhova 1977:442 (*seminigra*, larva keyed; habitat notes; figs. larv. head caps., hypopharynx, larval anal segm.; USSR)
- Glukhova 1979:98-104 (*seminigra*, descr., figs., 4 larval instars, notes on habitat and biology; USSR, Europe)
- Havelka 1978:447 (list, Eur. spp.)
- Rieb 1981:114 (ovipos. of *seminigra*, France).

5.2 #130. *Probezzia albitibia* Wirth

(including notes on #131. *Probezzia* sp. nr. *albitibia*)

5.2.1 Synopsis of Systematics and Habitus

This is a member of a species group which possesses broad dark transverse bands on the wing, or in which various portions of the wing are infuscated. The possible n. sp. nr. *albitibia* (all males) is very similar to *albitibia* s.s. except that the former has banded tibiae, while in the latter they are uniformly infuscated except at the extreme bases. There also appear to be differences in the genitalia, but this awaits careful study.

Eggs and larvae have not been described. An individually-reared larva of *Pr.* sp. nr. *albitibia* was 5-6 mm long when it pupated 2 days after collection. Based on a laboratory sketch, the larva had an overall brownish cast, with a distinct dark pattern dorsally on all thoracic and abdominal segments. The head capsule was of the subconical elongate type, with rather elongate ocelli somewhat resembling the shape of a telephone receiver. The larval exuvium was lost subsequently in the rearing dish, so no further observations were possible.

Pupa with relatively long (L/W ratio 3.8-4.1) respiratory horn, smooth-surfaced, with 4-8 spiracles at the apex. Posterolateral processes on female terminal segment of *albitibia* s.s. described as widely divergent and bare (Wirth and Grogan 1979), but in specimens examined in this study, slightly to moderately divergent. Minor discrepancies of this sort suggest that all the reared and associated specimens at hand may be *Probezzia* sp. nr. *albitibia*.

Glandular disks are indistinct on the specimens examined. Wirth and Grogan make no mention of glandular disks in their description of

albitibia s.s., but Wirth (1971) states that they are present, though not prominent, on abdominal segments 6 and 7. Very close inspection of the pupal exuviae of the specimens at hand reveals elongate areas ventrally on segments 6 and 7 which are only weakly differentiated by less pigmentation, absence of denticulation and, in most specimens, on integument with slight longitudinal "wrinkles". The color of the pupal integument is a darker brownish than the other *Probezzia* seen, except *pallida*.

5.2.2 Habitat Characteristics: Present Study

Pr. albitibia. Reared by FVB from damp sandy mud on a small sediment islet (bar) in a stream (Miles Cr.). Another specimen was reared by WIK from a pupa taken in sandy clay along a 3rd order stream bank with epipellic algae in small depressions, under the sparse canopy of a sycamore tree (Tom's Cr.).

Pr. sp. nr. albitibia. A series of larvae and pupae was taken along a stream from sandy mud with a prominent coal ash residue component, within the root sphere of willow and with a moderate overstory (WIK 253).

5.2.3 Autecological Review

- Habitat Preferences.

Apparently rheotopic, most often associated with smaller and cooler streams and creeks with a well-formed bank. Sand is generally present in the sediment, with silt and clay in varying proportions. Wirth (1971) provided 4 lotic collection records, Wirth and Grogan (1979)

added 2 more from the Potomac Valley region. Nine of the 10 records available, including the latter 6, are from watercourses, and only two of these would be considered large enough to be called rivers.

Apparently only one lentic habitat record exists to date for this species, along the sandy beach of Douglas Lake, Michigan, from where R. W. Williams reared 3 females and 1 male (Wirth 1971).

It is likely that the preferred habitat tends to be somewhat shaded, and not heavily vegetated. However, no definitive information is available now whether the larvae occupy a mud/sand substrate *per se*.

▪ Rearing Observations.

The larvae swim in a very rapid vibratile manner which appears to be characteristic of the smaller sphaeromiine larvae. The frequency of oscillations was at least 20/sec (the approximate flicker fusion frequency), because the larva appeared blurred as it swam. The 4th instar is merely 5-6 mm in length.

One larva pupated within 24 hrs of collecting and yielded a male imago 3 1/2 days later. All three reared pupae (2 M, 1 F) required only about 3-4 days until eclosion, which is less than the 4-6 days required by other species in the tribe.

▪ Species Associations.

Eight other ceratopogonid taxa were encountered with *Pr.* sp. nr. *albitibia* (all Coll. 253), namely chiefly *Culicoides haematopodus* (2 M, 1 female with p. ex., 3 M, 3 females RC), *C. baueri* (2 M with p. ex.), *Clinohelea bimaculata* (1 F by RC), *Bezzia nobilis* (4L, 2P; 1 M, 1 F by IR), *B. dorsasetula* (1 F by RC), and unidentified *Culicoides*,

Stilobezzia and Sphaeromiini larvae or pupae. Only *B. nobilis* occurred with *Pr. albitibia* s.s. at one of the two sites.

▪ Seasonal Occurrence.

Most of the records occur in early June at the more southern localities and in early July farther north. A few records in late August suggest a possible bivoltine life cycle.

5.2.4 Distribution

▪ Geographic Range

From Wisconsin to Maine, south to Virginia, between 50° and 36° N. South of Michigan, there are no records besides those in Pennsylvania, Maryland, West Virginia and Virginia. *Probezzia albitibia* Wirth is now recorded from at least 13 states, two provinces and the District of Columbia: CT, DC, MA, MD, ME, MI, NY, ON., PA, QU., VA, WV, and WI.

In the Virginia region, the counties are: DC; MD: Montgomery, Prince George's, Worcester; VA: Fairfax, *Mecklenburg, *Montgomery; WV: Pocahontas. See Figure 15 on page 365.

▪ Biogeography

Extends south of New York only in a relatively narrow band paralleling the Appalachian Plateau, Ridge and Valley and Piedmont physiographic provinces. In the southernmost localities, especially in the Maryland and Virginia Piedmont, occurs in cool streams or rejuvenated rivers. Technically the Potomac Valley records belong in the inner Coastal Plain, adjacent the Fall Line. The Mecklenburg Co., VA, record is in the outer Piedmont.

5.2.5 Collection Records

Reared *Pr. albitibia*. Virginia: Mecklenburg Co., Miles Cr. at U.S. Rt. 1, stream sand bar; 6-VI-1969, 3 F, 1 male (FVB 94).
Montgomery Co., Blacksburg, Tom's Cr., left bank 30 m upstream from Shadowlake Rd. bridge, under sycamore; 10-VI-1975, 1 female with p. ex. (WIK-12).

Reared *Pr. sp. nr. albitibia*. Virginia, Montgomery Co., Tom's Cr., Co. Rt. 684, 0.5 mi. W of Kanodes Mill, stream bank; 27-V-1976, 1 male L-A, 2 males P-A; 1 L-P, 1 L? by IR (WIK 253).

5.2.6 Annotated Taxonomic and Biological References

- Wirth 1971:732-3 (female, male descr., distr., notes on rearing records, pupa).
- Wirth and Grogan 1979:884-86 (female, male diagnosis, pupal descr., figs.; rearing biology, habitus notes).

5.3 *Probezzia jamnbacki* Wirth

5.3.1 Remarks

This species does not appear in the material collected during this study, nor it is in the Potomac Valley fauna (Wirth and Grogan 1979), but it has been reported from Maryland at Snow Hill, Worcester Co., on the Delmarva Peninsula (Wirth 1971). Its recorded distribution (5 states, 1 province) ranges from Michigan to Connecticut, south to Arkansas, so it clearly is expected in the biting midge fauna of Virginia.

On three occasions, *P. jamnbacki* has been reared from a specific habitat. Two are from streams (margin and sand bar) in New York, another from a sandy beach at Douglas Lake, Michigan. The pupa lacks ventral membranous patches (Wirth 1971).

Nine of ten capture records fall between mid-May and mid-June. The single exception is at the Douglas Lake site, where a mid-August trapping undoubtedly represents a second generation that season.

5.3.2 Reference

- Wirth 1971:735 (female descr., male gen. fig.; distr., rearing rec., Eastern U.S.)

5.4 *Probezzia nigra* Wirth

5.4.1 Systematics and Habitus Synopsis

Immature stages unknown. Adult female wing entirely infuscated dark brown in fully hardened animals.

5.4.2 Habitat Characteristics: Present Study

This species was collected once by emergence trap and on 8 occasions by light at two locations in the watershed of Upper Three Runs Creek, Aiken Co., SC. The characteristics of this spring-fed creek and its tributaries are described above in the Sphaeromiini tribal discussion. The habitat which the emergence trap covered was a sandy substrate along a marshy section at the margin of the stream. It is likely that one of the two larval *Probezzia* types recovered in significant numbers from the Upper Three Runs stream system is this species.

Wirth (1971) swept this species from the margin of a stagnant silt-bottomed creek (Bayou Macon, West Carroll Parish, LA).

5.4.3 Geographic Range

Previously recorded from LA, FL and GA. This is the first South Carolina record, though it is well within the range from which it would be expected, having been collected in the southcentral sandhills and Savannah River mountains region near the Georgia border. It is to be

expected that this species is most likely to occur at least as far north as the sandhills of the North Carolina Piedmont.

5.4.4 Collection Records

- Other

South Carolina: Aiken Co., Savannah River Plant, Upper Three Runs Creek, 9 May - 31 Aug. 1979, 12-13 May 1980, 8 females by light trap, SRP8/8&8, 19 June-10 July 1980, coll. J.C. Morse and associates.

5.4.5 Reference

- Wirth 1971:736 (descr. adult, distr.)

5.5 #132. *Probezzia pallida* Malloch

5.5.1 Synopsis of Systematics and Habitus

One of the few sexually color-dimorphic ceratopogonids, the female is uniformly pale yellowish but the male has a shining black thorax and darkened abdomen. A thorough diagnostic description of the male is not available though Wirth (1971) did provide an excellent figure of all available stages; this figure is representative for the genus.

Larva unknown¹. However, of the specimens obtained at the Jackson River in this study, at least 2 larvae with pupal respiratory horn pigmentation in the thorax were observed, which had distinctly elongate-conical head capsules, similar to that of fourth instar *Pr. seminigra* (Panzer) (Glukhova 1979) and similar to many unreared larvae I have seen from other sites. The frontoclypeus was distinctly darkest brown basally, lighter distally. The larvae in question pupated before they could be photographed in the laboratory; the larval exuviae were not found.

Male and female pupae were described by Wirth and Grogan (1979). They make no mention of the disk-like glandular structures ventrally on the abdomen, but the specimens I examined do not possess them. Wirth (1971) found them to be absent on all specimens seen by him except those from a series taken at the Rideau River, Ontario. Pupal integument color is a rather dusky brownish.

¹ Malloch(1915:318) stated that Muttkowski was intending to describe the early stages, but I have not been able to locate such a description in the literature.

5.5.2 Habitat Characteristics: Present Study

Numbers of larvae and pupae were obtained from a loose mud and leaf deposit along a large backwater created by an eddy of the strongly flowing Jackson River, a medium-sized tributary of the James River; after pupae were found floating among a concentration of vegetative detritus mid algae mats, new and old leaves, grasses, etc. entrapped by logs 1m from shore. It was likely that these specimens had been transported from upstream after a recent freshet. During an earlier survey along the banks of the New River near Glen Lyn, two specimens of *Pr. pallida* emerged from coarse silt and fine sand sampled at the water line along the margin of the river. The nature of the substrate along that stretch of the New River might have been conducive to greater production of this species and other rheotopic ceratopogonids, but only low numbers occurred there, probably because of the tidal flow pattern caused by the discharge schedule of an upstream reservoir, Claytor Lake.

In New York, Simpson reared a male from a larva collected by Ekman grab in the bottom sediment of the gently-flowing Erie Canal; the larva pupated and the imago subsequently emerged in the laboratory on the 7th day after collection.

5.5.3 Autecological Review

5.5.3.1 Habitat Preferences

Running Waters: Clearly most often associated with rhithral environments; probably phytophilic. Primarily inhabiting depositional

stretches of larger streams and smaller rivers, where the pupae are commonly encountered in sandy margins, sand bars, along backwaters, and the like. Of the 20 records gleaned from the literature and present results, fully 17 (85 %) fit the above characterization (Malloch 1914, 1915a, 1915b; Muttkowski 1918; Wirth 1951, 1971; Wirth & Grogan 1979).

Lakes: The only exceptions to the above are some records from large lakes. For example, *Pr. pallida*² was among the three most common ceratopogonids of six found by Muttkowski (1918). Lake Mendota, Wisconsin, a calcareous lake 39.4 km² in extent. He found the larvae to be common to abundant below the breaker line:

<u>Depth (m)</u>	<u>Number/m²</u>
0-1	2.68
1-2	1.95
3-4	0.24
3-7+	rare

The optimal larval ceratopogonid habitats in this lake were the stretches of emergent and recumbent vascular plant among shattered rock below the shore proper (which was "always barren"). Rock and

² While there is no reason to doubt the determination (Muttkowski (1918) stated that "all commoner species were successfully reared"), it seems likely that this involves more than one species, probably including *Pr. williamsi* Wirth 1971, known from lake environments in Michigan and Wisconsin.

boulders of various sizes made up about 60 % of the littoral bottom. Plumes of the green alga *Cladophora* commonly were attached to the rocks and gravel. Interestingly, *Pr. pallida* was absent from sand substrates and rare in mud or gravel *per se*.

The Lake Mendota collections also included *Sphaeromias longipennis* and *Bezzia glabra*, especially the latter of which showed a particular preference for *Cladophora* and other filamentous algae. *Ceratophyllum*, *Myriophyllum* and *Potamogeton* spp. dominated the plant beds.

Along a recently flooded river bottom in the Tennessee River basin, Snow et al (1957) reported finding pupae among woody flotsam along a wooded portion of shoreline, with *Culicoides biguttatus*, *C. spinosus* and *Monohelea macfieii*. The pupae were collected on April 26, 1955. This is the earliest seasonal record for this species, preceding by over two weeks a record of 13 May from Drew Co., Arkansas (Wirth 1971).

Another unequivocal record of *pallida* breeding in lakes is provided by Bowen (1983a, b; pers. comm. 1978-79), who reared 24 males and 10 females from pupae taken by skimming flotsam off the surface near the margin of Lake Norman. This is a large (132 km²), man-made, oligo-to-mesotrophic lake in the western Piedmont of North Carolina. Collections of pupae were made between 15 May and 7 July in 1978-79.

Other pupae from Lake Norman yielded *Pr. sp. nr. williamsi* (det. WIK), still others were not reared and could not be determined. At least one more species was among the indeterminable pupae, and several *Probezzia* sp. larvae were obtained by dredging from this lake. Two larvae for which records are at hand were 3rd and 4th instar specimens

taken at Duke Str. No. 3, at 9 m depth near the shoreline, on 3 Jan. 1978 (see also discussion under generic heading).

From this information, it can be reasonably concluded that lake-dwelling *Probezzia* overwinter as mature larvae, and that they form a component of the true sublittoral benthic community. Apparently about the time of spring turnover, the larvae leave the bottom and migrate toward shore, probably swimming at the surface (Weerekoon 1953), where pupation takes place among shore vegetation.

The intraspecific variation in habitat which is apparent from the above observations on *P. pallida* presumably is an expression of optimal habitat choice behavior, which has been demonstrated to be responsible for genetic variation in ecologically diverse environments in many insects and other animals (e.g., Powell & Taylor 1979). Thus, in a given population of *P. pallida* one would expect different genotypes to select the lake habitats than those, a smaller proportion, which have maximized fitness in the riverine habitat. At present, however, there is no direct information as to the existence of the two habitat phenotypes in a single geographically proximate population of this species.

5.5.3.2 Larval and Pupal Habits

This species appears to have clear phytophilic associations in its larval stage, rather than a pelo- or psammobiotic preference, on the basis of evidence of observations in the present study and on Muttkowski's numerous collections among filamentous algae and submerged, floating and emergent vascular plants. While nearly all other

available habitat information is based on pupal collection from sediments at the margin of running waters, this is not necessarily evidence for the actual nature of the larval habitat. Instead, these sediments are most likely sought out by the larvae nearing pupation, from the adjacent plant beds and algal mats.

The sediments provide a relatively stable substrate in which to accomplish pupation and eclosion. On the other hand, these pupae also are likely to be capable of climbing up the stems of erect plants. Muttkowski makes the rather surprising claim that this species is capable of emerging from the water surface, a claim which is contradicted by personal observations and those of Weerekoon (1953) and Linley (1972) for other ceratopogonids. Yet, it is possible for eclosion to take place reasonably well at an "intersectional line", i.e., at the interface of water, emerged object and air.

Nothing specific is known of the larval feeding habits.

5.5.3.3 Adult Activity Period.

Adult emergence in this study required 3 to 4 days from the time of pupal collection. In the case of prepupal larvae, eclosion took place within 6-7 days after collection. Records in the present study and literature point to an early summer emergence peak, in which the preponderance of the dates fall between late May and late June in most parts of its range.

5.5.3.4 Species Associations.

Two other *Probezzia* species were obtained at the same site as *pallida* in this study, namely *smithii* and *xanthogaster*. Seven other biting midges were reared as well. They are, in order of abundance:

Culicoides haematopotus (8 females, 13 males L-A, 1 male P-A); *Bezzia* sp. *pulverea* gr. (2L, 2 females L-A, 1 female RC), *Stilobezzia antennalis* (1 female L-A, 2 L), *S. sybleae* (1 male L-A, 1 L), *Phaenobezzia sabroskyi* W&G (1 male P-A, 2 L?); and *Phaenobezzia opaca* (1 female P-A).

5.5.4 Distribution

- Geographic Range

Probezzia pallida is primarily eastern Nearctic, from North Dakota and Ontario to Florida with southwestern extensions as far as Arizona. It is now known from at least 13 states: AZ, AR, CT, IL, KS, MD, *NC, NY, ND, ON., PA, VA, and WI. Counties from which it is known in the study area include: MD: Montgomery Co.; NC: *Mecklenburg; VA: *Alleghany, Fairfax, *Giles. See Figure 15.

- Biogeography

Occurred in this study in a metarhithral river in a broad valley, ridge and valley physiographic province. Apparently occurs mainly in Open habitats in younger stream systems, but not in mountain streams. A concentration of records extends in a broad belt from ND to IL to the east coast. South of there, the records suggest association with cooler streams with reasonably rapid flow, though lakes will also produce this species. Likely has some boreal affinities, though less so than *Pr. xanthogaster*.

5.5.5 Collection Records

Reared. VIRGINIA: Alleghany Co., Jackson R., Natural Well, vicinity of Co. Rt. 638 bridge, ca. 2500ft. (760m) elev., 4-VI-1977, 4 females and 1 male with pupal exuviae by IR (WIK 383, 385). Giles Co., New River near Glen Lyn, above Appalachian Power Co. plant, margin of river, 6-V-1971, 1 male by RC, coll. E.C. Turner, Jr. NEW YORK: Erie Canal, Sta. 19, Weedsport 0.4 mi. W. of Rt. 34 bridge, 18-VI-1974, 1 male reared from pupa, coll. Karl W. Simpson (#74-046). NORTH CAROLINA: Mecklenburg Co., Lake Norman, Sta. 8.7 1-VI-1978, 4 females with p. ex., coll. T. Boyer.

5.5.6 Annotated Taxonomic and Biological References.

- Muttkowski 1918:407-8, 475-80 (larval biotope, Lake Mendota, Wisconsin)
- Snow, Pickard and Moore 1957:34 (pupae taken in Tennessee River basin)
- Wirth 1971:731, 736 (figs. of male, female, pupa; notes on sexual dimorphism; rearing records, distribution)
- Wirth and Grogan 1979:888 (male, female imago diagn., pupa descr., figs., biol. notes, distr.)
- Bowen 1983a, b(occurrence in lake, North Carolina)

5.6 #133. *Probezzia sabroskyi* Wirth

5.6.1 Synopsis of Systematics and Habitus

As clarified by Wirth (1971), the species referred to by Williams (1955) in his paper on sphaeromiine immatures' biology are *williamsi*, not *sabroskyi*.

Fully developed eggs still inside the female were partially extruded and examined. They were creamish-white, packed in parallel rows in which the eggs overlapped each other like shingles. About 350 eggs of 0.34 to 0.36 mm in length were present, apparently to be laid in ribbons; eggs were of the characteristic cigar-shape, rather uniformly straight, with a broadly acute end opposite the micropylar end, which is subtly differentiated from the remainder of the chorion as a smooth, slightly constricted "cap". Chorion possesses a "grainy" appearance.

Larvae of this species are not yet described. While a complete pupal description has not been published, apparently there are no ventral adhesive disks present (Wirth 1971).

5.6.2 Habitat Characteristics: Present Study

An egg-replete female was collected by a black light trap which had been placed in a small open bog (Cranberry Glades, ca. 1020 m elev.) within 15 m of the upland forest margin. The light trap was in line of sight of and 150 m away from Charles Cr., though screened by ca. 50 m of light understory and tree trunks in the bog forest be-

tween Flag Glade and Round Glade. It is conceivable that the creek may have been the source of this specimen.

5.6.3 Autecological Remarks

The only published reference to habitat is that of Wirth (1971), who reared this species from a stream margin in Alleghany St. Pk., NY, 3 June 1963. It is quite conceivable that *Pr. sabroskyi* will be found to prefer smaller streams in more shaded situations.

A very rich complement of about 300 specimens of biting midges, constituting 24 species, was collected in the same light trap sample with this species. Among them were 11 *Culicoides*, 4 *Palpomyia*, 3 *Bezzia*, 2 *Forcipomyia*, and 1 each of *Atrichopogon*, *Dasyhelea*, *Monohelea* and *Stilobezzia* species. This species assemblage is representative of the large biting midge populations which can develop in the relictual upland bogs of the Appalachian Plateau and Ridge and Valley Provinces.

5.6.4 Geographic Range

Probezzia sabroskyi is irregularly distributed from Oregon to New Brunswick, south to Illinois, and West Virginia, with an anomalous record from Florida. It is now known from at least 12 states and provinces: CT, FL, IL, ME, MI, NB., NY, ON., OR, PA, WI, and *WV(Pocahontas Co.).

5.6.5 Biogeographic Distribution

A species with a predominately boreal distribution, including the record at the Cranberry Glades, which is in the Canadian Life Zone, a subdivision of the Alleghanian Biotic Region.

5.6.6 Collection Record

Adult Field-Trapped

West Virginia: Pocahontas Co., Cranberry Glades Botanical Area, at entrance to Flag Glade near old boardwalk. 24 to 25-VI-1976, 1 female by blacklight trap (BL-46=274 BL).

5.6.7 Reference

- Wirth 1971:736-37 (distr., systematic notes on imago, pupa)

5.7 #134. *Probezzia smithii* (Coquillett)

5.7.1 Synopsis of Systematics and Habitus

A dark species. Wing infuscated on the distal two-thirds, the veins brown. Thorax and abdomen black. Femora and tibiae on all legs dark brown.

Eggs and larvae unknown. Pupal respiratory horn 3x as long as broad, surface smooth, apex with 9-12 spiracles; posterolateral processes less divergent than *Pr. albitibia*. No abdominal adhesive disks present. Mature pupa small, unusually dark brown to black, especially in the cephalothorax, due to the black thorax and legs of the imago,

showing through the pupal integument, which itself is a light grayish brown-yellow.

5.7.2 Habitat Characteristics: Present Study

Pupa encountered floating among algae and leaves concentrated behind a log 1m from shore in a large back eddy of a rapidly flowing small river, the Jackson River.³ The river had experienced a recent freshet due to brief but heavy showers, which scoured the margins farther upstream. The collections were taken in early June.

An unusual record is provided by two females reared from pupae taken in a freshwater sponge bed between shore and 2 ft. depth in North Bar Lake, Michigan, in August (leg. G. A. Jackson).

Two females were collected at a light trap sited at another metarhithral (order 4) stream, the North Anna R., in a narrow valley, 400m downstream from the Lake Anna reservoir dam, in late July. This site yielded a rich complement of 12 biting midge species, and is discussed more fully above under *Macropeza pamunkeiana*.

5.7.3 Autecological Review

5.7.3.1 Habitat Preferences.

Chiefly associated with metarhithral(esp. Order 4 and 5) environments (5 of 6 records). One record (17 %) is from a lentic situation, in the littoral zone of the lake (referred to above) formed in a river pupae taken from river margins in Wisconsin (Wolf R.) and northern

³ approx. an Order 4 (metarhithral) stream.

Virginia (Potomac R.) by Jones and Wirth and Jones, resp. (Wirth 1971, Wirth & Grogan 1979).

An adult collection record reported by these authors can be taken to support the assumption of a rhithral preference for this species, in that a male was collected at light by Schwarz and Shannon on Plummer's Island in the Potomac R. Also, the collection of the two females at a stream-sited light trap on the N. Anna R., mentioned above, supports the assumption.

Specific larval habitat data is not available, but *Pr. smithii* is likely to inhabit littoral zones of aquatic macrophytes and algal growth over shallow stretches of silty-sandy substrates, such as those occupied by other *Probezzia* spp. The sponge-associated record in N. Bar Lake is quite consistent with the character of the presumed habitat, in that the "irregular growth form of sponges affords a favorable substrate for a wide variety of metazoans" (Pennak 1978).

5.7.4 Geographic Range

Nearctic east of the 100th Meridian, from Kansas and Wisconsin to New Jersey and Virginia, south to Louisiana and Florida.

5.7.5 Biogeographic Distribution

The six records available from the Virginia-Maryland area are along rivers ranging from the western part of the Ridge and Valley physiographic province to the outer Piedmont and inner Coastal Plain near the Fall Line. See Figure 15 on page 257.

5.7.6 Collection Records

•Reared. Michigan: Benzie Co., North Bar Lake, 0-2ft., 8-VII-1975, 2 females with p. ex., leg. George A. Jackson (Michigan Dept. Nat. Res., Water Qual. Appraisal Sect., Lansing, MI). Virginia: Alleghany Co., Jackson R. 16 km upstream of Covington at Natural Well, ca. 760 m elev., 4-VI-1977, 1 female with p. ex. by IR (WIK-385).

• Adults Field-Trapped: Virginia: Louisa - Spotsylvania Co. lines, on N. Anna R., VA Rt. 601 at Smith's Mill Bridge, 400m downstream of L. Anna dam, 28-VII-1977, 2 females by UV baffle light trap, coll. C. R. Parker (BL-53).

5.7.7 Annotated Taxonomic and Biological References

- Wirth 1971:737 (synonymy, distr., habitus notes on female, male, pupa)
- Wirth & Grogan 1979:889-90 (synonymy, redescr. female, &, descr. pupa; biol. notes on rearing)

5.8 *Probezzia* sp. nr. *williamsi* Wirth

5.8.1 Synopsis of Systematics and Habitus

Two somewhat teneral males of this probably new species were reared from pupae. The specimens key closest to the *Pr. williamsi* and *Pr. seminigra* (couplet #11) in Wirth's (1971) key. The hind and mid tibiae are infuscated on the basal 1/3 to 1/2 (*williamsi* with dark sub-basal tibial bands; *seminigra* dark only on extreme bases and apices); the hind and mid femora are infuscated on the distal 1/3 to 1/2, and the fore femora and tibiae are completely yellow; 5th tarsomeres blackish.

The pupa of this species possesses no abdominal adhesive discs, whereas *williamsi* has them on segments 5, 6 and 7.

5.8.2 Habitat Characteristics: Present Study

The pupae were found floating among flotsam on the lake surface of a large reservoir, between the 8m depth contour line and the shore (Bowen 1983; pers. commun.).

5.8.3 Collection Record

- Other: North Carolina: Mecklenburg Co., Lake Norman reservoir, west-central NC, 1 June 1978, 2 males reared from pupae taken by skim sample, coll. T. W. Bowen.

5.8.4 Annotated Taxonomic and Biological References

- Williams 1955:94 (*williamsi*, as *sabroski*[sic], larval biology, Michigan)
- Wirth 1971:737 (*williamsi*, male female descr., figs. distr.)

5.9 #135. *Probezzia xanthogaster* (Kieffer)

5.9.1 Synopsis of Systematics and Habitus

A lighter, yellow and black species; wings and veins milky white, thorax blackish, abdomen yellowish; legs mostly yellowish white, with distal third of femora dark brown. See above references for fuller diagrams.

Eggs and larvae have not been described. Pupal respiratory horn smooth in both sexes, 3.4 to 3.8 times as long as broad at apex, with 8 - 12 spiracles. No abdominal adhesive disks are present. The posterolateral processes are greatly divergent in both sexes, forming an angle of ca. 160 deg. in the female, ca. 140-150 deg. in the male, with surface bare. Although the terminal segment description by Wirth and Grogan corresponds well enough with observations made in this study, their figures are quite at variance, showing posterolateral process which are denticulate, parallel in the female and only moderately divergent in the male.

The "*Probezzia xanthogaster* Kieffer" pupal exuvium illustrated in Thienemann (1928) represents a species in the *Bezzia* (*Homobezzia*) *bicolor* Group, as defined and revised recently by Wirth(1983a).

5.9.2 Habitat Characteristics: Present Study

Reared from three streams or small rivers, ranging from 2nd/3rd order (Tom's Cr.) to 4th/5th order (Jackson and S. Fk. Roanoke rivers). The Jackson River site was at the water's edge along a large back-eddy in the swift river, substrate loose silty mud, riparian

leaves and *Elodea* (WIK 383). Tom's Cr. site at edge of stream in gravely mud adjacent a rush clump (WIK 243). Similarly, the S. Fk. Roanoke R. (GH-1) consisted of gravel in a sandy-silty matrix at the waterline, with no immediate aquatic vascular vegetation, but leaf accumulations were present.

All sites were only moderately shaded by overhanging trees or bushes. The Roanoke River shore flora consisted of boxelder, sycamore, elm and hickory, at Tom's Creek sycamore, and at Jackson R., willow. All three of these streams flow through open meadow environments.

5.9.3 Autecological Review

5.9.3.1 Habitat Preferences.

Predominately a rheotopic species, and presumably hydropelophilic, in the depositional zones of streams to moderate-sized rivers. Nine of 10 available rearing records (7 of which are summarized by Wirth and Grogan 1979) derive from such habitats. Only one record is from a pond margin, in New York, sampled by Wirth.

From the evidence of the sites for which specific information is known, this species is more likely than the other *Probezzia* to be found in coarser substrates, including gravel, sand and silt, occurring in the bed and along the margins of streams and smaller, shallow rivers. Upstream sites, as spring runs, brooks, mountain or woodland streams are unlikely to provide suitable breeding substrates, because either of shaded conditions which prevent periphyton and aquatic macrophytes from becoming established, or the lack of appropriate bottom and shore sediments in a high-energy environment, or both.

On the other hand, the lower reaches of large, deep rivers do not appear to provide optimal habitats either, where deep soft substrates are likely to be inhabited by other organisms, including other ceratopogonids such as *Bezzia nobilis* or *Palpomyia novitibialis*, which may have a competitive advantage. Because of the lentic nature of a large river margin, though, suitable microhabitat are found to be available for at least limited breeding of this species which has also been recorded from a pond.

5.9.3.2 Larval and pupal habits.

Available information does not permit one to rule out a phytophilic association, but this is likely to be a facultative substrate. Feeding habits are not specifically known. Pupae have not been collected on plants. The pupae reared required 3 to 4 days to adult eclosion.

5.9.3.3 Adult Activity.

Probezzia xanthogaster was observed by Downes (1978) capturing swarming male *Chaoborus flavicans* at Black Lake, Stanleyville, Ontario, the prey being the same size as the host.

This species appears to be on the wing about two weeks earlier than *Pr. pallida*, beginning in early May in Virginia and peaking in early June. Very few of the over 30 recorded capture dates fall in July anywhere in its range. A second emergence appears not to occur.

5.9.3.4 Species associations.

Collected with other characteristic stream dwellers, such as *Culicoides baueri*, *C. spinosus*, and *Probezzia pallida*, but also with such generalists as *C. haematopotus* and *Bezzia nobilis*.

5.9.4 Distribution

- Geographic Range

Probezzia xanthogaster (Kieffer) is restricted to the northeastern U.S. and adjoining Canadian territory from Wisconsin to Ontario and south to Illinois and Virginia. It is now recorded from at least 10 states and 2 provinces: DC, IL, NJ, MD, MI, NY, ON., PA, QU., VA, and WI. In the study area, the distribution is: MD--Montgomery Co., Worcester Co.; VA--*Alleghany Co., cities of Alexandria, Fairfax, *Montgomery, and *Roanoke Cos. (see Figure 15).

- Biogeography

All new records in this study occur in the western ridge and valley province, and the Alleghanian biotic region, though distributed among three river basins: New, Roanoke and James (refer to Figure 15 on page 257. This, combined with an early activity period in this latitude suggests a species with more boreal affinities. The published records in the region concentrate in the lower Potomac River basin in the outer Piedmont; an interesting collection involving 10 females was recorded on the coastal plain, at Salisbury, MD on the Delmarva peninsula, in mid-May.

5.9.5 Collection Records

- Reared: Virginia: Alleghany Co., Jackson R., 16 km upstream from Covington, at Natural Well, ca. 760m elev., 4-VI-1977, 1 female with p. ex. by IR (WIK 383-2). Montgomery Co., Blacksburg, Tom's Cr. at Shadowlake Rd., 50m upstream from bridge, at margin, 4-V-1976, 1 male by RC (WIK 243, Loc. 5). Roanoke Co., S. Fork Roanoke River, margin,

20-V-1971, 1 male reared by RC, coll. E. C. Turner, Jr. and C. Kessinger (GH-1).

5.9.6 Annotated Taxonomic and Biological References

- Wirth 1971:738 (synonymy, new records, notes on color, male genitalia)
- Downes 1978:9 (prey of imago)
- Wirth and Grogan 1979:890 (notes distr., diagnosis & figs. female legs, male genitalia; pupa descr. & fig., rearing records)

CHAPTER SIX

Ecosystematics and Autecology of Immature Sphaeromiini -- IV:

Genus *Sphaeromias*

6.1.1 Introduction

The genus *Sphaeromias* is represented in all zoogeographic regions except the Neotropical one, and is most diversified in the Oriental and Afrotropical regions (Havelka 1978, Wirth 1965b, 1973, 1974; Wirth et al. 1974, 1980). However, essentially all the biological information on the genus deals with a handful of species, all in north temperate regions of Europe or North America.

The limnological literature contains more references to *Sphaeromias* than most any other ceratopogonid group, which is probably largely because it has been encountered regularly in the benthos of lakes. References to the genus are much more frequent in the European literature than in the North American (see "Annotated Taxonomic and Biological References" on page 405). Undoubtedly, this is a reflection of the fact that European aquatic biologists have generally placed greater emphasis on immature aquatic insects, including rearing, than was the case in North America until quite recently.

Nevertheless, specific ecological studies on this genus are practically non-existent. The generic overview which follows briefly summarizes from an ecosystematic perspective the available biological

literature in the context of the data gathered in this study. This is followed by a comprehensive discussion of the biology and systematics of the immature stages of the fairly widespread North American species *S. longipennis* (Loew), compared and contrasted, as appropriate, with other species of the genus.

Microhabitat Attributes.: Four main substrate types can be identified for the most common *Sphaeromias* species, in approximate order of frequency of occurrence:

1. Littoral submersed aquatic plant beds or emergent wetlands, often in dense stands, including emersed, floating or recumbent macrophytes, with abundant organic matter in the form of coarse detritus primarily.
2. Unconsolidated shores with wet aerobic mud, enriched by finer organic detritus or epipellic algae and other aufwuchs.
3. Soft-mud and detritus-rich bottoms of lakes and ponds (unconsolidated bottoms).
4. Mature filamentous algal mats/blankets.

Rather consistent attributes of these sites include: exposure to sunlight, with little or no overstory, though immediate shade may be provided by emergent plants; presence of open expanses of water; nutrient-rich conditions created by haptobenthic, epipellic or epiphytic aufwuchs, and/or detritus.

Species in the genus are unlikely to occur in current-influenced habitats, bogs, or marshes where no open water is present. Also, with the possible exception of *pictus*, *par*, and *bifidus*, shaded sites such as in swamp forests, are unlikely to be inhabited.

The most common members of the genus are rather eurytopic within the limits of the above habitat characterizations. Inasmuch as the substrate can be considered the "common denominator", wherever apt substrate conditions occur, the larvae may well occur also. The female apparently oviposits onto and from plant surfaces at or on the water. Thus, this determines the "point of origin" of the larvae.

Because they are strong swimmers and trophic generalists, they exhibit apparent behavioral plasticity, which increases the likelihood that they will be encountered in a diversity of microbiotopes within a given general wetland system. For a fuller discussion of the subject, refer to the section "Habitat Preferences" on page 424.

Characteristic synecological assemblages (or taxocenoses) of ceratopogonids can be identified for particular habitat types. For example, a halotolerant phytophilic association of eight key species, including *longipennis*, occurs in water of fluctuating salinity on algal mats and floating macrophytes. Further elucidation of this aspect is found in "Synecological Species Associations" on page 453.

Larval feeding behavior: Based on the fact that all known *Sphaeromias* larvae possess moderately robust epipharyngeal mouthparts, and on extension from larval feeding observations made on *longipennis* and *fasciatus* (see "Trophic relationships" on page 448), members of this

genus may reasonably be characterized as trophic generalists. Thus, they are able to function either as collectors (presumably mainly by detritivory and deposit feeding), as herbivores-grazers (on the aufwuchs coating plants, detritus, and other surfaces; and facultatively either as swallowers or piercers.

Life history.: While no detailed studies are available on the life cycle of any *Sphaeromias* species, considerable indirect evidence based on larval collections and adult trapping results at many locations suggests a univoltine life cycle for most species. Overwintering of the larvae nearly always takes place in the fourth instar. Related observations are reviewed below under " Life-history related events and seasonal variation " on page 433 and " Adult Habits" on page 452 .

Biogeographic Observations.: The apparent center of endemism and diversification is in the Afrotropical and Oriental regions, especially southern Africa and the Indian Subcontinent. In Europe and North America, the common species are apparently rather eurythermal, being found at a wide range of latitudes. At the same time, they may be boreal in their historical affinities, based on the fact that the majority of the locality records derive from north of 35°.

6.1.2 Synopsis of Systematics & Habitus

Nomenclature There is considerable discrepancy in the European literature as to the gender which the specific epithet assumes with this

genus, the feminine "-a" ending being used in alternation with the masculine "-us" (e.g. Havelka 1978, Hennig 1950, Mayer 1934c, Thienemann 1954.). This situation is perhaps attributable to the fact that for several decades the species were assigned to the generic name *Xylocrypta* Kieffer 1899. In any case, the genus *Sphaeromias* erected by Curtis in 1829, the type species of which is *albomarginatus* Curtis(= *fasciatus*)(Wirth 1962b), is clearly intended to be masculine. Grammatically, a noun ending in *-ias*, in the nominative singular, is always masculine, on the analogy of such nouns as *tamias* and *neanias* (pers. commun., T. O. MacAdoo, 1985)¹.

Worldwide, the genus *Sphaeromias* contains at least 37 species² (Wirth et al. 1974), which would make it the third largest genus in the Heteromyiini and Sphaeromiini, after *Nilobezzia* (ca. 60) and *Mallochohelea* (ca. 50). In the New World, however, the genus is re-

¹ The form of the name *Sphaeromias* appears to be at variance with normal Greek or Latin construction. While I have not been able to examine the original description or subsequent early use of the name, it would appear to be more properly spelled "*Sphaeromyia*", after the manner of *Forcipomyia* Meigen 1818, a form in which the Greek suffix *-myia* ("fly") is widely used in the family Ceratopogonidae and other Diptera. This construction is in the feminine gender. In Latin, an accusative plural construction would add an *-s*, and it is easy to see how a later writer (perhaps unschooled in Latin) may have picked this up as "*Sphaeromyias*". Wirth et al.(1980) listed this as a variant spelling. I do not know what the reasons for the loss of the *-y-* in subsequent constructions would have been, but usages of the generic name have at times also rendered it as *Sphaeromyas*, without the "i" (as by Johannsen 1905:107, or Kieffer 1906 (in Wirth 1962b)). In any case, it is clear that *Sphaeromias* takes the masculine, as systematists have properly treated it in recent decades (my thanks to Dr. MacAdoo for his classical languages expertise).

² I have not been able to verify this number from the catalogues and other sources available to me.

presented by only two Nearctic species, *bifidus* and *longipennis*. A relatively large amount of information is available on *longipennis*, which was first described in 1861 and has been commonly collected. The second species, *bifidus* was not discovered until 1979.

The greatest amount of biological data, including the developmental stages, is to be found for the European species. There are now apparently five valid species there: *candidatus* (Loew), *fasciatus* (Meigen), *floralis* (Meigen), *ornatipennis* Goetg., and *pictus* (Meigen), based on Havelka (1978) and synonymies recently published by Remm (1981) and referred to in the references section for this genus (see "Palaeartic" on page 405).

Adult. This genus contains among the largest of all Ceratopogonidae. The species are robust, grayish pollinose species with wing lengths between 4 to 5 mm. They have no genital sclerotizations or ventral hair tufts on segment VIII. Of the seven North American sphaeromiine genera, *Sphaeromias* is the only one which lacks these characters. The relevance of this to oviposition behavior is discussed above under the tribal heading and below in connection with *S. longipennis*. Good generic diagnoses of the male, and in particular the female, are provided by Debenham (1974), Wirth (1962b) and Wirth and Grogan (1979).

Immature Stages. The eggs are apparently deposited in small hemispherical, gelatinous masses up to 5 mm in diameter (see under *S. longipennis*). Young larvae are rather similar to *Culicoides* in general habitus. Mature larvae are large, ranging from 13 to 19 mm

in length, with short conical head capsules ($< 500 \mu\text{m}$) which are disproportionately small in comparison to the body. The head is a light yellow with small reniform eyespots. The postoccipital collar is usually darker in color, and has a characteristic triangular mid-ventral caudal expansion. The epipharynx is the most robust of the tribe, with two pairs of relatively strongly sclerotized combs.

The body segments are comparatively large, white with blackish or brownish pigment concentrations. Setae on the anal segment are short and relatively inconspicuous, with two groups arranged linearly in rows of 2 to 3 along the mid-ventral and mid-dorsal lines.

Three European species have been described (*candidatus*, *fasciatus*, *pictus*) in the larval stage, notably by Glukhova (1971, 1977, 1979), including head capsule chaetotaxy and epipharyngeal features. Mayer (1934c) provided detailed descriptions of mouthpart characters for *fasciatus*. Larvae of *longipennis* from Illinois, New York and Maryland were briefly described and illustrated by Malloch (1914, 1915, 1917), Thomsen (1937) and Wirth & Grogan (1979), respectively. The mouthparts of *longipennis* have not been adequately described, though Malloch (1915) did sketch the mandible and labium. The head capsule chaetotaxy is adequately described by Wirth and Grogan.

Pupae of *Sphaeromias* are also relatively robust and large, 7-9 mm long and dark brown in color. The respiratory horn is elongate, flattened, smooth-surfaced, and broadest at the apex, where 20-50 spiracular openings are concentrated in several rows, making it difficult to count them. On the abdomen, the ventral membranous patches are absent.

6.1.3 Generic Autecological Summary

For only five (14 %) of about 37 *Sphaeromias* species worldwide is anything direct known about the larval habitat, and for a few more an educated guess could be made from adult collection records. Only four of the five have been collected often enough to allow conclusions to be drawn about their breeding site characteristics (see Table 26 on page 404). These are the same four whose immature stages have been described (see previous section), including the North American species, *longipennis*. Significantly, these four species also account for at least 90% of all *Sphaeromias* records in the Nearctic and Palaearctic. Thus, the information discussed herein is very representative of the genus in these regions, but it probably should not be extrapolated to the many African and Oriental species, for which practically no habitat data is extant.

The extensive discussion under *S. longipennis* of macro- and microhabitat attributes, larval and pupal behavior, adult habits and synecological species associations probably applies in many respects to *S. fasciatus*, a close ecological homologue in Europe. Available data on all other species is compared and contrasted as appropriate. A brief summary in the generic context follows.

6.1.3.1 Macrohabitat Characteristics

Members of the genus *Sphaeromias* predominantly inhabit open lake and pond margins, a fact which has been well-established, at least in general terms, for quite some time (Zavřel 1926; Thienemann 1928; Mayer 1934a, c; Brundin 1949; Glukhova 1971, 1977, 1979; Wirth and Grogan

1979). Also, they are often among the most commonly encountered ceratopogonids in the lake benthos, particularly in north temperate lakes(e.g., Brundin 1949; Glukhova 1979). Factors governing larval distribution in lakes are elaborated upon in the section "Occurrence of *Sphaeromias longipennis* in Lakes" on page 428.

However, as the breakdown by habitat systems in Table 26 shows, this genus is to be found not only in freshwater lacustrine environments, but also in a rather diverse array of other water bodies and wetland habitats. It is apparent that the most common representatives of the genus, such as *fasciatus* in Europe and *longipennis* here, are comparatively euryoecious.

Thus, for example, brackish coastal habitats have been reported for *fasciatus* by Strentzke(1951), Remmert(1955) and others, though it is basically a freshwater lake species(e.g., Glukhova 1979) while saline and mineralized lakes may develop large populations of *candidatus*, as in the European U.S.S.R.(Glukhova 1979). On the other hand, *S. longipennis* was not known to inhabit brackish habitats until the results of the present study(see Table 33 on page 443). It is possible that the populations of *Sphaeromias* spp. which develop in saline or brackish waters are at least somewhat ecologically segregated from conspecific freshwater populations. Yet, in the cases of *fasciatus* and *longipennis* at least, it appears that their occurrence in mixohaline³ waters is simply a reflection of their facultative

³ Brackish water of marine origin, fluctuating in salinity (Cowardin et al. 1979)

Table 26. World-wide summary of aquatic habitat systems at which immature stages of *Sphaeromias* species have been collected. Biogeographical Regions to which the species belong are abbreviated as: Af -- Afrotropical, Ne -- Nearctic, Pa -- Palaearctic. The symbols represent an arbitrary scale of relative frequency of occurrence: ± = only inferred from adult collection site and conditions; + = small numbers of specimens, few instances of collection (< 3); ++ = intermediate numbers and instances, occasionally large numbers but infrequently; +++ = relatively most frequent in occurrence, often in larger numbers, many instances (> 10).

Sphaeromias Species	Freshwater Lakes/Ponds		Mud Flats Around Ponds	Riverine Margins/ Wetlands	Marshes ^{2/}	Swampy/ Wooded Sites	Brackish/ Estuarine	Saline/ Alkaline Lakes
	Benthic ^{1/}	Littoral						
bifidus -- Ne						±		
candidatus -- Pa	++			+				++
fasciatus -- Pa	++	+++	+				++	
longipennis -- Ne	++	+++	++	+			++	
par -- Af						+		
pictus -- Pa		++		++	+	±		+
sp. -- Ne, Pa	+++	+++	++	++			++	+

^{1/} Below 2 m depth.

^{2/} No open water bodies larger than a few m².

tolerance of moderate salinity, as long as macrohabitat and substrate conditions are otherwise suitable.

Unconsolidated sediments⁴ adjacent open water bodies such as floodplain pools, livestock ponds, and river margins are a significant breeding site, previously not well recognized. Lotic habitats are uncommon for the genus: only *longipennis* and *pictus* have been taken infrequently, from along or in rivers, always at depositional sites. These habitat types are discussed more fully below in particular reference to *S. longipennis* (see " Other Habitat Types and Attributes" on page 440)

Marsh or forested swamp habitats, which normally lack open water expanses and direct sun exposure, do not support *Sphaeromias* populations to a significant extent. Only *S. par* and *pictus* have been collected at such sites, on a few occasions. This habitat type is discussed below in connection with *S. bifidus* and the two above species.

6.1.4 Annotated Taxonomic and Biological References

These references are listed in addition to the ones given under *S. longipennis*. I have attempted to render the species names exactly as used in the original sources.

6.1.4.1 Palaeartic

⁴ Bare mudflats and sandbars, etc. with less than 30% established plant cover (Cowardin et al. 1979)

- Zavrel 1926:276 (larva, pupa of *S. copiosa*⁵ Kieffer (as *Xylocrypta* spp.))
- Thienemann 1928:603, 608 (as *Xylocrypta*: oviposition of *fasciata*, pupae of *copiosa*⁵, *ocularis*⁶)
- Lenz 1934:
- Mayer 1934a:291-93 (*S. picta* (Mg.) larva, pupa descr., collection site, N. Germany)
- Mayer 1934c:244-7; 272, 274 (*S. fasciata* (Mg.) larva, pupa descr.; habitat, biol. observ., Centr. Europe)
- Brundin 1949: many pages, esp. 128-29;262 ("*Sphaeromias* sp." ecol., distr. in lakes, Sweden)
- Hennig 1950:222-3 (summary, list, early descr., larv., pupae, *copiosa*⁵, *fasciata*, *picta*, sp., Palaearctic, Nearctic)
- Strentzke 1951:685 (*S. fasciatus* on Black Sea coast)
- Thienemann 1954:361, 371 (*S. sp.*, *S. picta* (Mg.), lentic biotopes in rivers, N. Germany)
- Remmert 1955:39 (*S. fasciata* in brackish habitats, N. Germany)
- Krivosheina 1957:69, 70, 72 (*S. fasciatus* habitat in lakes, ponds, rivers, USSR)
- Clastrier 1961:223 (*S. par* I&M rearing record, habitat, Gambia, W. Afr.)
- Wirth 1962b:275 (rev. generic concepts, synonymy; pupal diagn.(p. 278))
- Glukhova 1971:102-03 (*pictus* larva descr.; river, pool and lake habitat, USSR)
- Glukhova 1977:104 (*fasciatus*, *pictus* larvae keyed, habitat notes, European U.S.S.R.)
- Glukhova 1979: 51-53, 94-97 (*S. candidatus* (Loew), *fasciatus*, *pictus*, *S. sp.*, key, larvae descr., habitat, overwintering biology in lakes, USSR)

⁵ Synonym of *S. pictus*, per Remm(1981).

⁶ Synonym of *S. fasciatus*

- Havelka 1978:447 (6 European spp.⁷ , list, syn., distr.)
- Remm 1981:27-28 (synonymies, sel. Palaearctic spp.)

6.1.4.2 Other Zoogeographic Regions

- Debenham 1974:53 (generic diagn. with new characters for female, male; diagn. pupa, n. sp., Australia)
- Wirth and Grogan 1979:891 (generic diagn. imago, immature stages, synonymy)

6.2 *Sphaeromias bifidus* Wirth and Grogan 1979

6.2.1 Remarks

Sphaeromias bifidus is only the second species described in the genus in North America since *S. longipennis*(Loew) was recorded in 1861. The former is known only from the Maryland type locality in the Patuxent River floodplain, Prince Georges Co.(see Figure 18 on page 466)(Wirth and Grogan 1979). Immature stages have not yet been discovered.

This species was taken by Malaise trap in a fairly densely shaded (by sweet gum and red maple, mainly) swampy site adjacent a marsh. The above authors speculate that *S. bifidus* may prefer shaded swampy situations, and that it may be found to inhabit swamps in the southeastern coastal plains of the U.S. This interpretation seems plausible in that it would ecologically segregate this species from its congener,

⁷ Two of the six species listed by Havelka(1978) are synonymized by Remm(1981): *S. copiosa*(Kieffer) is a junior synonym of *S. pictus* (Meigen), and *S. griseus* Zil.-Seb. is *Nilobezzia posticata* (Zett.).

longipennis, which, as the discussion below shows, is almost exclusively associated with emergent wetlands and mud shores along open bodies of water fully exposed to sunlight.

In Europe, *S. pictus* (Meigen) has been recorded from swamps in former lake basins, and is thought to be a "relictual lake" species (Glukhova 1979). However, the same species has also been collected in accumulated detritus among dense reeds and rushes at an open lake margin (Mayer 1934a). In the Gambia (W. Africa), *S. par* (Ingram & Macfie) is reported by Clastrier and Wirth (1961) as having been reared from *Rhizophora* (mangrove) peat soil. Such soil usually forms on berms beyond the immediate tidal range but still within old successional mangrove swamps. In all other *Sphaeromias* for which habitats of developmental stages are known, the open marsh/lake environment seems to prevail. I would consider the forested swampy habitat to be secondarily derived, or apotypic.

6.2.2 Reference

- Wirth & Grogan 1979:893-4 (female, male imago descr., biol. notes)

6.3 # 136. *Sphaeromias longipennis* (Loew), 1861

6.3.1 Systematics and Habitus Summary

Adult body large, robust, thorax grayish-brown pollinose, wing length 4.2-5.0 mm. One of the very largest species in the Ceratopogonidae, comparable to the Palearctic *S. fasciatus* Mg. in size. Female and male diagnoses given in Debenham (1974), Wirth (1962), Wirth & Grogan (1979). Of some significance to this species' oviposition behavior is the absence of ventral genital sclerotizations and, especially, of ventral hair tufts on abdominal segment VIII, whereas sphaeromiine species known to oviposit by extruding a gelatinous egg ribbon, while hovering over water, possess well-developed hair tufts. Consistent with this is the fact that *S. longipennis* is thought to oviposit from solid surfaces, such as leaves floating in water.

The eggs have not been thoroughly described, but they apparently are laid in hemispherical gelatinous clusters up to 1/2 cm in diameter, wherein the eggs are arranged radially with their longitudinal axes as the "spokes" (Malloch 1914; Thienemann 1928).

Larvae destined to become females, can attain 18 to 19 mm in length in the fourth instar, the longest of all ceratopogonid larvae. The closest in size to this of any larvae with which I am familiar, is *Palpomyia jonesi* Grogan and Wirth, of which I have seen pre-pupal

specimens⁸ 16-17 mm in length. "Male larvae" of *S. longipennis* pupated after attaining 14 to 15 mm. The size of the larvae and their relatively "robust" body segments, in which the longitudinal muscles are readily visible, serve to readily distinguish them from any other ceratopogonid larva.

Thomsen (1937) misleadingly likens *S. longipennis* larvae to those of *Palpomyia lineata*⁹, stating that they are alike in color and size. Rather, *P. lineata* larvae never exceed 12-13 mm in length, and possess a distinctively different head capsule, being elongate and cylindrical, with a head length: width ratio (HR) of 3.0 : 0.2, and bipartite paired eye spots (Fig. 17a), whereas the head capsule of *S. longipennis* is considerably shorter and ovoid-conical, the HR being 1.8 ± 0.2 ; also, the eyespots are kidney-shaped, among other obvious differences in the head capsule.

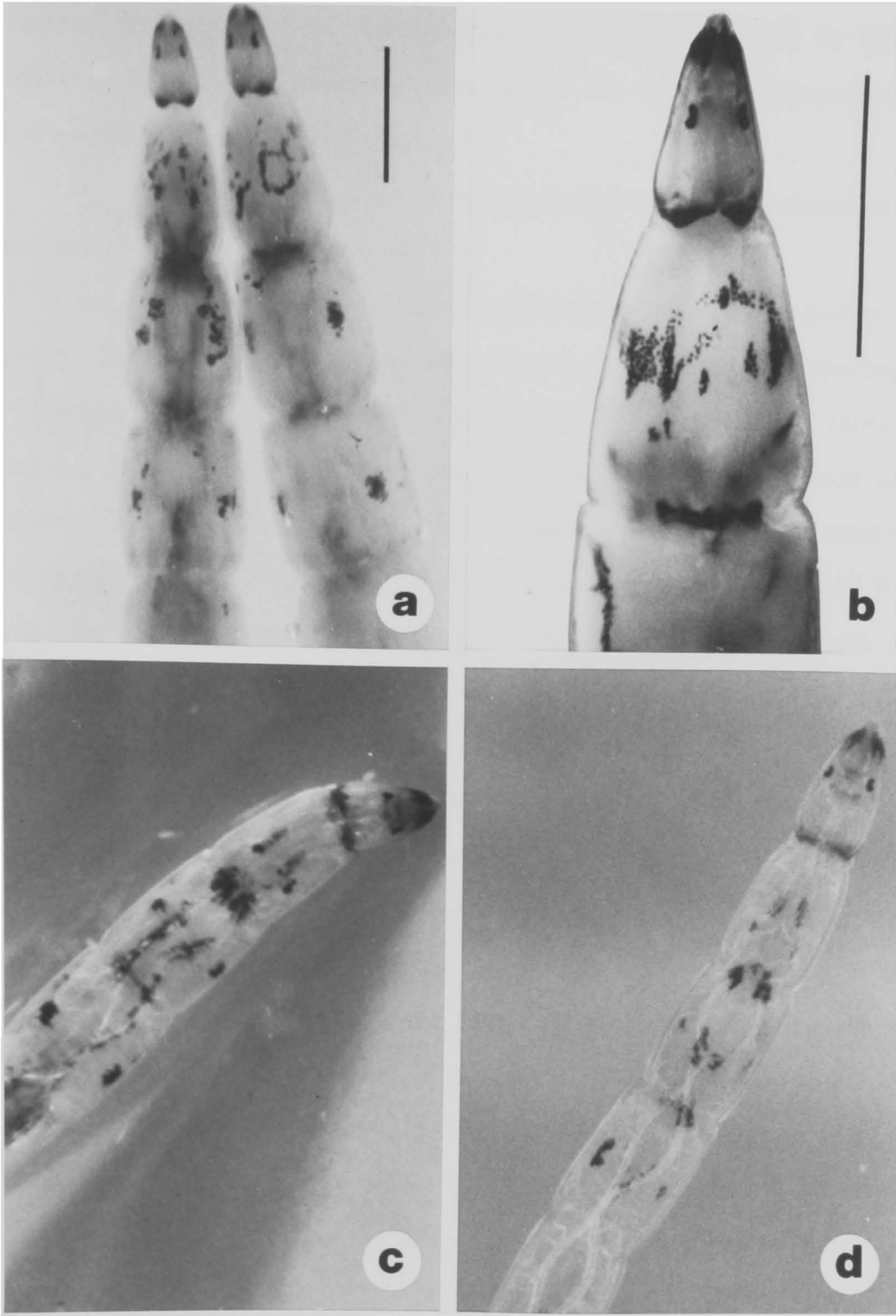
Likewise, the pigmentation is quite different. In *S. longipennis* it is subepidermal, granular, dark brown to black with more or less discrete pigment concentrations which are quite characteristic, and remain easily visible in preserved or starved specimens (see Figure 16 on page 412).

Pigmentation in *P. lineata* has two manifestations (Figure 17 on page 415) elongate and irregular greyish brown subcuticular "streaks" sublaterally on all thoracic segments, and black tracheal trunks ex-

⁸ Collected by R. H. Jones, Washburn Co., Wisconsin, 18-V-1953, from algal mats in a pond.

⁹ As *P. pruinescens* Thomsen

Figure 16 a-d. *Sphaeromias longipennis* larval head and thorax; (a) fourth instar, preserved in ethanol; (b) close-up of mature fourth instar; (c) live third instar specimen, shortly after extraction; (d) same specimen as in (c), with depleted fat body. Bars equal 1 mm (b-d same scale).



tending the length of the entire body. The latter pigment is often somewhat obscured in preserved specimens, the former remains visible and useful in diagnosis (Figure 17).

The chaetotaxy of the larval headcapsule of *S. longipennis* is described in Wirth and Grogan (1979).

I have verified the presence of the flap-like (perhaps better, pouch-like) structures on the cast larval exuvium of this species, "attached to the conjunctiva of each body segment except the first two and the last" (Thomsen, 1937). These structures are apparently associated with tracheae and the vestigial spiracles. I did not find them to be particularly "long and pointed" in comparison to those of *P. lineata*. In fact, these structures are at best difficult to see and characterize, being diaphanous, easily distorted and obscured (not to mention that larval exuviae are rarely available). Exuviae are often crinkled, twisted or folded. I have not systematically studied the several exuviae (ca. 20 spp. in Palpomyiini and Sphaeromiini) available to me, but of the ones I have examined, the results with respect to the "flaps" are given in Table 27.

It does not seem likely these flap-like structures will prove to be consistent and diagnostic for determinations, nor is it practical to depend on exuviae for characters. Cleared larvae of *P. lineata* do not show the flaps. In any case, the significance attached to these structures by Hennig(1950) as potential diagnostic tools for distinguishing larval ceratopogonids does not appear to be borne out.

Pupae are 7 to 8 mm in length, and dark brown in color, especially at the anterior (top) end. This darker color is consistent with the

Figure 17. *Palpomyia* spp. larval head and thorax: (a) fourth instar *P. lineata* (Meigen) killed in boiling ethanol:water (left) and cold ethanol (right); (b) live fourth instar *P. lineata* larva; (c) prob. *P. tibialis* Group (sp. unknown) from benthos of Lake Anna, Virginia. Bar indicates 1 mm (a-c at same scale).

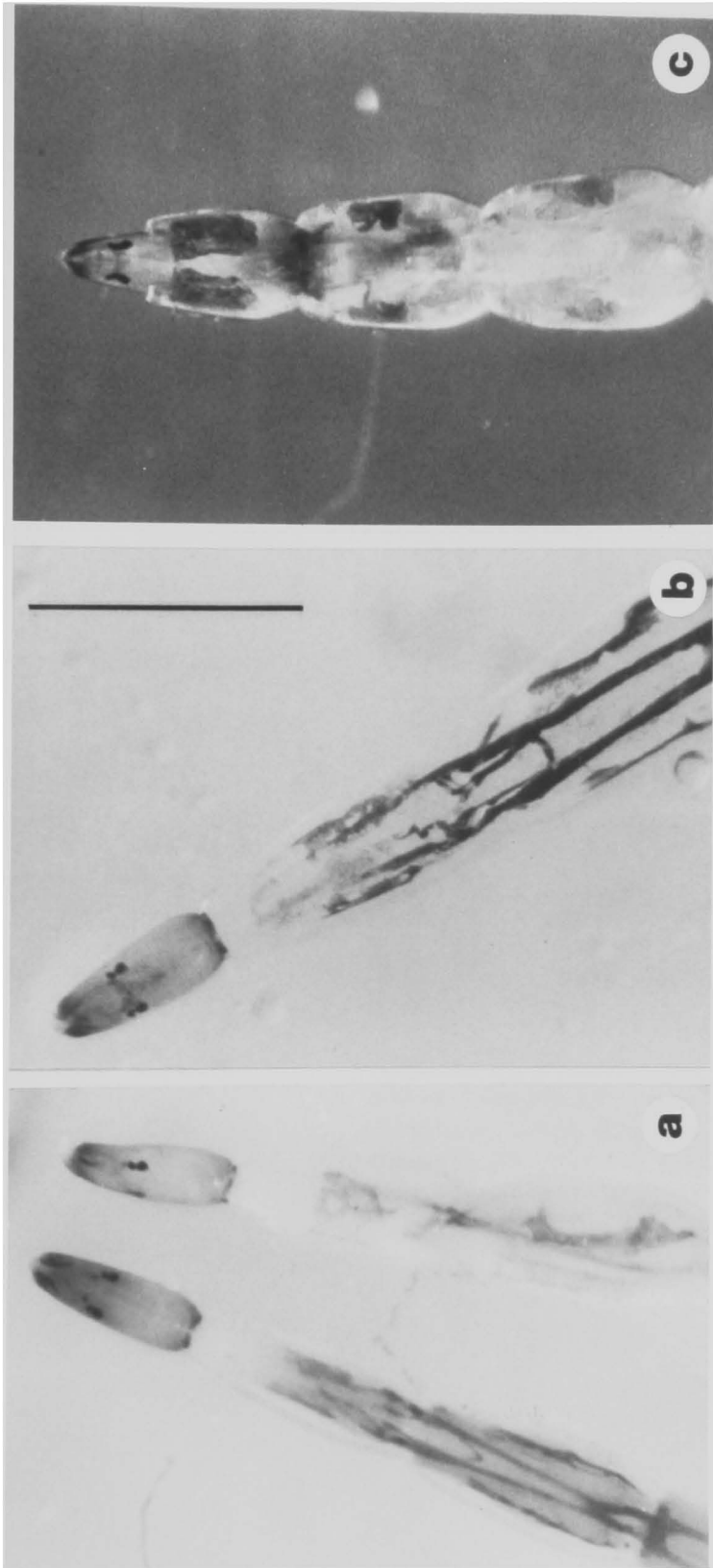


Table 27. Presence or Absence of Conjunctival "Flaps" in Larval Exuviae of Selected Sphaeromiini and Palpomyiini.

Species	Status of Conjunctival Flaps
<i>Sphaeromias longipennis</i>	Present, relatively distinct (0.21-0.25 mm, n=2 exuviae), several flaps
<i>Mallochohelea atripes</i>	No flaps of any consistent form were found in the two exuviae examined.
<i>Palpomyia lineata</i>	Present, 0.24 mm long (0.19-0.30 mm, n=10 exuviae)
<i>P. novitibialis</i>	Obscure, amorphous (n=3 exuviae)
<i>P. weemsi</i>	None found, (n=1 exuvium, in good condition).
<i>Bezzia (B.) nobilis</i>	Apparently absent, but various other "entities" resembling tracheal trunk fragments were present in various shapes and configurations (n=5 exuviae).

propensity of pupae to occupy sites which are exposed, often to full sunlight. Diagnoses are found in Debenham (1974), and Wirth and Grogan (1979), and in the generic discussion herein.

6.3.2 Habitat Characteristics: Results of Present Study

Records obtained in this study include at least 160 specimens reared or extracted from habitat substrates taken in 47 unit collection efforts from 22 localities in five states (GA, MI, VA (7 counties), WI, WV) and Ontario. The substrate and habitat types occupied by *S. longipennis* are summarized in Table 28, including all available published records.

All sites are associated with open water bodies, from pools and ponds to large reservoirs and lakes to shallow, quiet rivers or canals. None of the sites had a significant upper canopy shading it. Full sun exposure for much of the day on bare wet mud characterized 27% of the collections positive for this species. A clear predilection exists for shoreline habitats consolidated by a rich assemblage of aquatic vegetation (35% of collections).

Accumulations of filamentous algae yielded good numbers of specimens, but this is not a predominant substrate. On the other hand, all the "bare mud" type of habitats (e.g. WIK 248, Luster's Gate sites FVB A, C) consistently included an epipelagic algal film, particularly at sites frequented by cattle.

Table 28. Substrates occupied by *Sphaeromias longipennis* immature stages, based on 60 specific substrate collections or rearing records, including 13 literature records (L). The '+' symbols indicate positive records obtained in this study: + = 1, ++ = 2-9, and +++ = 2-10 specimens per unit collection.

Blanket Algae ¹	Emergent Wetlands ²				Unconsolidated Shores ³				Lake Bottom ⁴			Substrate Unspecified		
	Pool/Pond	Lake River	Pool/Pond	Lake River	Pool/Pond	Lake River	Lake River	3-4m	1-2m	Pond	Lake	River	Lake	River
+++br	L	++	+++br	+++	++	+++	L	+	++	++	++	++	L	+
++			+++br	+++	++	+++	L	L	+	++	++	++	L	L
			++	+	+	+++br			+	+	+	+	++	++
			++	L	+	++			+	+	+	+		
			++	L		++			+	+	+	+		
			+	L		++			+	+	+	+		
			+	L		++			+	+	+	+		
			+			++			+	+	+	+		
			+			+			+	+	+	+		
			+			+			+	+	+	+		
			L			L								
2	1	1	12	7	4	12	1	2	3	9	1	3	2	2

¹ Floating filamentous green algae, esp. Cladophora and Spirogyra; rarely blue-green algae included.
² Including emersed, floating, or recumbent macrophytes in littoral zone.
³ Substrates lacking vegetation--less than 20% areal cover (cf. Cowardin et al. 1979).
⁴ Unconsolidated bottom, mud/organic chiefly (cf. Cowardin et al. 1979).
⁵ Brackish or slightly brackish water.

Livestock Pond Mud Sites. Adults were reared from mud-muck flats surrounding cattle watering ponds on a rather consistent basis from early April until mid-June. This is the first association of *S. longipennis* with livestock-modified pond mud. Another livestock site in the Luster's Gate area, however, yielded no specimens in nearly 30 samples: it was a heavily-trafficked hog lot traversed by a fairly rapid stream (FVB site B) with many rocks interspersed among the mud¹⁰. The substrate pH at the positive livestock-access sites averaged 7.55 (n=12), whereas at other mud sites, the substrate averaged pH 5.52 (n=4).

Brackish Sites. An unexpected result was the occurrence of *S. longipennis* in brackish (mixohaline) waters on four occasions, in near-coastal ponds (WIK 138, 299, 347) or channels (WIK 308). The latter site was choked with a rich assemblage of waterworts, pondweeds and smartweeds, in which the water had a salinity of 9.0 ppt at the time of sampling. The salinity for five readings taken at the four habitat waters averaged 2.7 ppt (0.3-9.0), which falls in the oligohaline range.

The average chemical values for habitat substrate and water samples in which *S. longipennis* was present are listed in Table 32 on page 429, according to the habitat types defined by chemico-physical factors: livestock-modified sites; all other sites; and brackish-water sites

¹⁰ Photo of this site in Hair et al. 1966, fig. 4.

only. The number of samples available for analysis in these categories varied.

Lake Bottom Sites. Benthic lacustrine habitats accounted for 12.5% of the specimens and 25% of the positive collections for this species. Except for one sample taken at 0.5 m among emergent rushes and submersed pondweed, all the specimens were well removed from shoreline vegetation. One set of 6 larvae was taken in a very loose, deep, aerated gyttja aggregation about 5 m lakeward from a large bed of submersed floating macrophytes (esp. *Sparganium*, *Sagittaria*). Most of the lake specimens, however, derived from Lake Anna reservoir, taken by J. R. Voshell and colleagues during a post-impoundment benthic colonization study (Voshell and Simmons 1977, 1984). In the latter study, transects were established at 2, 4, and 7 m depth contours at up to 10 stations in the lake proper and in cooling lagoons separated by dikes from the main body of the lake. Artificial substrate baskets¹¹ containing either riparian leaves or 3-M thermoplastic (Conservation) webbing were set out at numerous positions along these transects and were retrieved monthly by SCUBA for about three years. A synopsis of the *S. longipennis* larvae collected during the 1973-74 study year is presented in Table 29. Other samples taken either before (by Ponar dredge), during the feasibility study, or after that

¹¹ For comparative purposes, an areal conversion of the basket samples surface area (ca. 180 cm²) to a "per m²" basis, though not biologically valid, would give a population size equivalent to about 56/ m² for each specimen found in the basket, if the substrate were inhabited uniformly.

Table 29 . Numbers of *Sphaeromias longipennis* larvae recovered from Lake Anna impoundment, with respect to month, depth, and sampling method, for the year beginning December 1973.

=====

Depth m	Sampling Method	Month											Abundance Index ¹					
		XII	I	II	III	IV	V	VI	VII	VIII	IX	X		XI				
	Kick ²	+			+		+	++	+		+							
2	Leaf					2	2	2	1									6.7
2	Web					1	1	1										2.9
4	Leaf	2	3	1	1								1	3	2			25.2
4	Web	1		3														4.0
4	Dredge ³		4															2.0

¹(N_I)[‡] x F_{Coll}, where N_I = No. individuals, F_{Coll} = instances of collection.
²1974-75 only.

³1972-73 feasibility study.

Table 30 . Co-occurrence with *Sphaeromias longipennis* of the 15 most common species of Ceratopogonidae reared from the positive substrate collections made during this study.

	Percentage Occurrence at									
	All sites (n=24)			Livestock-modified sites (n=14)			Non-livestock sites (n=10)			
	<10	10-19	≥20%	<10	10-19	≥20%	<10	10-19	≥20%	
<i>Dasyhelea</i>	-	12.5	-	-	-	-	-	-	40.0	
<i>grisea</i>	8.3	-	-	7.1	-	-	7.1	-	-	
<i>mutabilis</i>	-	-	-	-	-	-	-	-	-	
<i>Culicoides</i>	-	-	45.8	-	-	64.3	-	-	0.0	
<i>crepuscularis</i>	-	-	29.2	-	-	50.0	0	-	-	
<i>haematopotus</i>	-	-	33.3	-	-	50.0	-	10.0	-	
<i>variipennis</i>	-	-	-	-	-	-	-	-	-	
<i>Stilobezzia</i>	-	-	33.3	-	-	50.0	-	10.0	-	
<i>antennalis</i>	-	16.7	-	-	-	21.4	-	10.0	-	
<i>bullae</i>	-	12.5	-	-	14.3	-	-	10.0	-	
<i>sybleae</i> gr.	-	-	-	-	-	-	-	-	-	
<i>Bezzia</i>	-	16.7	-	-	21.4	-	-	10.0	-	
<i>flavitaris</i>	-	16.7	-	-	14.3	-	-	-	20.0	
<i>glabra</i>	-	12.5	-	-	-	21.4	0	-	-	
<i>laciniastyla</i>	-	-	67.0	-	-	71.4	-	-	60.0	
<i>nobilis</i>	-	-	-	-	-	-	-	-	-	

year, during the follow-up phase (by kick-net at 0.5 m depth), yielded small numbers of larvae also. The artificial substrate data for the 1974-75 phase are incomplete for specimens of this family, and are not presented here, though there seemed to be trend towards somewhat increased numbers). The data are discussed below (see "Occurrence of *Sphaeromias longipennis* in Lakes" on page 438).

At least 40 ceratopogonid taxa (35 species) occurred in association with *S. longipennis*, as judged by the emergence from the 24 habitat substrate collections taken in the study area which were positive for this species. The 15 most common species are listed in Table 30. The greater richness of the livestock-modified substrates is immediately apparent from the high occurrence of species which consistently can be associated with organically enriched soft mud substrates. All species except *Stilobezzia syleae* and *Bezzia glabra* could be considered indicators of such habitats.

Among the non-livestock sites, *Dasyhelea grisea* and *B. nobilis* occurred at every brackish site, and the former appeared only there. Fifteen of the 20 species recorded only once occurred at the 10 non-livestock sites, the remaining 5 species at one of the 14 livestock-modified sites. Ten genera in all were recorded with *S. longipennis*:

Genus	#taxa	#sites
Alluaudomyia	1	1
Atrichopogon	1	2
Bezzia	11	24
Clinohelea	1	1
Culicoides	6	24
Forcipomyia	1	1
Mallochohelea	1	1
Palpomyia	6	13
Stilobezzia	6	22

6.3.3 Autecological Discussion

6.3.3.1 Habitat Preferences

Microhabitat Summary: Hydropelophilic (preferring submerged or saturated aerobic mud substrates, usually deep and soft) and epiphytobiotic -- on diverse assemblages of living and decomposing macrophytes, usually in combination with algae or aufwuchs in various manifestations. Comparatively euryoecious, in vegetated and non-vegetated shorelines and near-shore benthic habitats of open water bodies ranging from ditch pools to lakes, distributed from somewhat above the waterline to depths of 4 m or more.

Infrequent or absent at sites substantially shaded by an overhead canopy, (as in swamps or narrow streams), and unlikely to occur in marshy substrates when no open water expanses or free water are present. Not acidophilic.

All habitats observed, whether unconsolidated shore (or bottom), or emergent wetland, had an "enriched" character, in that

autochthonous and allochthonous inputs provide a surplus of nutrients. Thus, for example, the bare or sparsely vegetated mud habitats had an obvious epipelagic algae film no doubt stimulated in good measure by the organic enrichment by cattle frequenting the sites. In the case where cattle had no access, blanket algae, considerable detritus and CPOM (coarse particulate organic matter) were present.

At the vegetated sites, the plant species composition tends to be quite heterogeneous, and detritus is usually abundant. In these littoral environments, many colonizable surfaces exist for epiphytic and haptobenthic algae, bacteria and microflora and - fauna (Allen 1971, Porter 1977, Hutchinson 1981, Burton and Lazorchak 1982), providing abundant nutrition for the *S. longipennis* larvae, which graze as selective omnivores (see below).

6.3.3.2 Macrobiotope

Sphaeromias longipennis might be best characterized as limnophilic, in that essentially only open standing water habitats are colonized. However, as emphasized by the organization of Table S-1, *Sphaeromias* macrobiotopes probably should not be primarily defined in terms of the general physical nature of the aquatic system (e.g., river, lake, marsh or estuary), rather than by the nature and composition of the substrate. The substrate and associated vegetation form the common denominator in wetland habitats and occur in comparable form in all wetland types. These substrates are equivalent to specific "classes" and "subclasses" in the hierarchical wetland classification system of Cowardin et al. (1979). The general order of prominence of *S.*

longipennis occurrence among wetland habitat class and subclass types is given in Table 31.

While emergent wetlands such as stands of sedges, rushes, reeds, cattails, etc., are the primary habitat class for *longipennis* as well as other *Sphaeromias* spp. for which this information is available, the "unconsolidated" substrata (i.e., "bare" mud flats and other sediments with less than 30% plant cover) form a very significant habitat type as well, though this was not previously apparent. The most productive of these substrates have either an algal or plant detritus component. Glukhova(1979) found *S. pictus* to be abundant on a duckweed-covered mudflat produced by receding lake waters. Contrary to expectations , also, the association of *longipennis* with floating algae and submerged plants is not common. However, detailed ecological studies over time, at a specific locality, are needed to lend more precision to such observations.

Emergent vegetation adjacent to rivers and lakes is often very similar in character to that of marshlands and ponds. In fact, wetlands occurring along the banks of rivers but out of the current, do not belong, strictly speaking, to the running water habitat (Hynes 1970).

An evaluation of *S. longipennis* habitat associations according to the "system" (Cowardin et al. 1979), i.e., type of water body (Table 32), shows that there is no apparent discrimination by this species between habitats associated with marsh pools, ponds or lakes, but that river-associated habitats are one-sixth as common as the other two. Both the lacustrine and riverine habitat systems are discussed below.

Table 31. Distribution of *S. longipennis* Among Wetland Substrate Types (Classes/Subclasses).

Class	Subclass	% occurrence ¹²
Emergent Wetland	Persistent	32.2
	Nonpersistent	
Unconsolidated Shore	Mud/Organic	23.0
	Vegetated	2.4
Unconsolidated Bottom	Mud/Organic	20.3
	Artificial Substrate	
Aquatic Bed	Algal	6.8
	Rooted Vascular	
	Floating Vascular	5.1

¹² Proportion of the 60 records available in this study (see esp. Table 28 on page 418). Does not equal 100% because of unspecified substrate records.

The palustrine habitat, which for purposes of this discussion excludes marshland expanses, is encompassed by the treatment of lakes below.

6.3.3.3 Occurrence of *Sphaeromias longipennis* in Lakes

▪ Status of Knowledge: The association of *S. longipennis* with lakes is based largely upon collections taken from the shoreline. For example, Snow and Pickard (1958), in a survey for mosquito and biting midge breeding habitats in the Tennessee River Valley, reared this species from pupae taken among woolgrass (*Scirpus* sp.) clumps along the margin of the Chickamauga Reservoir, TN. Significantly, this and all other habitat records of which I am aware are based on rearings (Malloch 1914, Muttkowski 1918, Thomsen 1937, Wirth 1952, 1971; Williams 1955; Wirth and Grogan 1979). Although the immature stages were described (in a general way) by Malloch (1914, 1915a), a modern description has only recently become available (Wirth and Grogan 1979), so determinations have been dependent upon rearing. This is a practice which has not been commonly engaged in by North American limnologists, probably because of its relative time-inefficiency.

Sphaeromias larvae are among the most lacustrine of the Ceratopogonidae, and undoubtedly are frequently significant constituents of the unidentified "Ceratopogonidae" or "*Palpomyia-Bezzia* complex" faunae in published lake benthic macroinvertebrate lists and discussions. Yet, particularly when the studies include the littoral zone, the presence of the Ceratopogonidae may be quite significant, say, among the five most prominent taxa of the benthic fauna (e.g., Benson & Hudson 1975, Forsythe and Fox 1976, Thorp and Bergrey 1981,

Table 32. Proportional Distribution of *S. longipennis* Among Wetland Habitat Types (systems).

System	Occurrence
Palustrine (Pools & Ponds)	44.1 %
Lacustrine (Littoral & Benthic)	40.7 %
Riverine (Littoral)	15.2 %

Thorp and Diggins 1982, Cowell and Vodopich 1981). In my own experience working with specimens from the areas in which the latter studies were done, *S. longipennis* and other Sphaeromiini (often poss. *Mallochohelea atripes*) were consistently represented. However, I did not have the benefit of close association with the investigators who submitted the specimens.

▪ *Lake Anna and Other Lakes Compared*: The appearance of *S. longipennis* larvae in the benthos of Lake Anna provides valuable new information as to the lake-dwelling habits of this species. Apart from Muttkowski's (1918) study in Lake Mendota, Wisconsin, there is very little published on *longipennis* which is of a benthological/limnological nature. In European lakes, however, *Sphaeromias* spp. have frequently been reported (summaries in Mayer 1934c, Brundin 1949, Thienemann 1954). Numerous more recent records on four species of *Sphaeromias* derived from lakes or large ponds in the western U.S.S.R. were reported by Glukhova 1971, 1979). Historically, in fact, lake-inhabiting Ceratopogonidae have been given more attention in Europe than in North American (e.g., Kutikova and Starobogatov 1977; Zhadin 1960; Winberg et al 1972 in Bowen 1983; op. cit. above).

In rather comprehensive studies on the littoral and profundal (0.2-19 m) benthos¹³ of southern Swedish lakes, Brundin (1949) found *Sphaeromias* species at all depths in all the lakes he studied, from

¹³ All organisms were evaluated, but emphasis placed on the midges.

oligotrophic, oligohumic to eutrophic. In the eutrophic Vaxjo lakes, they were among the dominant taxa with *Procladius* and *Chironomus* spp. (Chironomidae). Their average densities in Lake Innaren (the most intensively sampled, along perpendicular transects, 2 grabs per site, and a total of 313 grabs during the course of a year) ranged from 14/m² to 121/m², depending upon the substrate. They constituted 2-3% numerically of the midge fauna, among > 50 species, including several other ceratopogonids¹⁴. The substrate of the lakes was generally a soft deep gyttja, partially coprogenic, with patches of various macrophytes, such as quillwort (*Isoetes*) mats, in the photic zone. The highest *Sphaeromias* density occurred in the lower littoral zone at 4-6 m, where thick sediments were relatively rich in coarse vegetative detritus and supported watermoss beds and sparse *Nitella* (stonewort) growth.

Larval *S. fasciatus* Mg. have been routinely collected at depths of 0.5-10 m in various freshwater lakes of the European section of the U.S.S.R. (Glukhova 1979), and here again were found at the greatest densities between 4 and 8 m depth. Their densities ranged from 40 to 520 indiv./m² on unconsolidated silt and sand bottoms, or among sparse colonies of *Chara* sp. (musk grass) growing on the bottom. In two of the lakes, *S. fasciatus* constituted 50-100% of a rich benthos.

By contrast, in Lake Anna, a new impoundment which had been full for only about a year at the initiation of the study in question, the bottom was of an entirely different consistency -- a clay-loam with

¹⁴ "*Bezzia* group", "*Culicoides nubeculosus* group".

abundant plant debris -- from that of the natural lakes referred to above. Nevertheless, larval *S. longipennis* and other ceratopogonids were collected at all depths sampled (0.5-7 m) and every month of the year, albeit in relatively small numbers (including data gathered before and after the period shown in Table 29 on page 421). Of the nine ceratopogonids which occurred in the lake, two were about as common as *S. longipennis* : cf. *Mallochohelea* prob. *atripes* (Figure 12 on page 274) and cf. *Palpomyia tibialis* group poss. *subaspera* (Figure 17 on page 415) (tribes Sphaeromiini and Palpomyiini resp.).

Most of the larvae were encountered at 2 and 4 m. The fauna at the 0.5 m depth was much smaller than what one would encounter in a mature, stabilized lake. Likewise, very few larvae occurred at 7 m. There appeared to be a definite differential between the sample type, depth, and larval occurrence.

While the overall numbers collected were quite low, in comparison with the Chironomidae, Ephemeroptera and Trichoptera which dominated the artificial substrates (Reed and Simmons 1976, Voshell and Simmons 1977, 1984) and cannot be subjected to statistical analysis for *S. longipennis* alone, some colonization trends are suggested by an apparent pattern in the distribution of the larvae (Table 29): a) during the winter months, all the larvae occur at 4 m; b) only from April to June do some appear at 2 m, and c) 82% of the larvae occur on the leaf pack samplers.

▪ Factors Governing Larval Distribution in Lakes: The above larval distribution may be a function of one or more of four general factors

which the limnological literature indicates determine depth distribution among benthic invertebrates: colonization and life history patterns; physiochemical conditions related to the trophic state of the lake; resource availability; and biotic interactions (Jonasson 1972; Wetzel 1975; Cowell and Vodopich 1981; Thorp and Diggins 1982).

It is clear from the small numbers of larvae found that the artificial substrates did not provide an optimum habitat condition (which would be a soft organically enriched mud, or aufwuchs-covered stabilized beds of vegetation). Clearly also, *S. longipennis* larvae are not successful pioneer colonizers under the given conditions, in contrast to the situation for the large populations of *S. fasciatus* in the lakes of the European U.S.S.R. mentioned above.

Life-history related events and seasonal variation. Nevertheless, the L. Anna data seem to reflect a life-history mediated sequence of events, in that the *longipennis* larvae occurred at 4 m during the coldest months, but appeared to move to the shallower littoral zone in the spring and summer months. Further, the specimens collected at 2 m in May and June were instar IV larvae nearing pupation (judging by slight swelling in the thorax and incipient prepupation pigment changes) (Fig. 16), whereas most of the larvae at 4 m (Oct.-Feb.) were instar III, and the late summer specimens were instar II. This latter situation also suggests a univoltine life cycle for this species, as is indicated by the adult flight records as well (see below).

Thus, the larvae at the shallower depths were probably moving shoreward to pupate, having left substrates in deeper water, at least

in part. This pattern is consistent with the reasonably well-established ceratopogonine pre-pupation behavior, in which aquatic larvae will leave the substrate and migrate to the shore for pupation either on plant stems, detritus or in the shore substrate immediately above the waterline (Muttkowski 1918, Weerekoon 1953, Linley 1966, 1972, Atchley 1970). The final stage in this movement to the site of pupation and emergence is generally thought to be by swimming at or near the surface of the water.

Pupae of *S. longipennis* were encountered by Williams (1955) on the sandy beach of Douglas Lake (Michigan Biological Station) with a large aggregation of pupal *Probezzia williamsi* Wirth (as *sabroskyi* Wirth). A submersed clump of *Potamogeton natans* 9-12 m out from the shore probably was the source of larvae.

Brundin (1949) observed distinct seasonal variation in the occurrence of *Sphaeromias* spp. in several Swedish lakes. While interpretation of his data is complicated by the fact that several lake types and probably several species (2-3 spp. are likely to occur in Scandinavia) are involved, the smallest profundal and lower sublittoral larvae densities always occurred in the mid-summer months, whereas the upper littoral zone showed increased numbers.

Overwintering of *Sphaeromias* sp. larvae in USSR lakes is discussed by Glukhova (1979:51-3). Between 80 and 100 % of thousands of larvae collected from several depths in Lake Bolshoi Shantropai were in the fourth instar during the months of November to March.

Referring to *S. longipennis* in Lake Mendota, Wisconsin, Muttkowski (1918) suggested that the larvae migrated toward shore "with the ad-

vance of the thermocline." Indeed, during the summer, in many lakes an oxygen deficiency seriously affects the survival of the bottom fauna and the process of decomposition (Jonasson 1972). However, in Lake Anna, the physiochemical conditions related to summer stratification probably were not a factor in larval distribution, because the metalimnion usually formed at 5-7 m; spring turnover in L. Anna begins in April, fall turnover in October (Reed and Simmons 1976).

The distribution pattern of *S. fasciatus* in Lake Pskovsko-Chudsky led Glukhova (1979) to conclude that depth *per se* was not the major determining factor, but distance from the shore, of either the mainland or an island in the lake. Thorp and Diggins (1982) found Ceratopogonidae to be most evenly distributed among 10 depths (0.16-5 m) during January-April, in a thermally destabilized reservoir in South Carolina.

Generally, there is an inverse relationship between invertebrate abundance and water depth (e.g. Brundin 1949, Jonasson 1972, Thut 1969). Compared to deeper zones, shallow water habitats are structurally more complex, and resource availability and habitat heterogeneity are at their greatest. Littoral and adjacent wetland communities often control much of the pelagic and benthic metabolism of lake ecosystems (Wetzel 1975). For example, algal epiphytes on submerged macrophytes may be one of the dominant primary producers in shallow water ecosystems, and may be comparable to or exceed that of phytoplankton (Allen 1971). It is in this environment, where epiphytic, epilithic and epipellic aufwuchs communities abound, that Ceratopogonidae thrive. This is where their eggs are laid as well.

Colonization and dispersal. *Sphaeromias longipennis* appears more likely than most ceratopogonid larvae to disperse from the shore, perhaps because of the ability to exploit soft substrates (among others), which may be due to a probable generalized omnivorous feeding habit. Their large size and strong swimming ability suggest that they may readily disperse planktonically over considerable distances. Because of their long cylindrical shape, one may regard the whole body as a gill (Hutchinson 1981), which suggests the ability to survive in low-O₂ environments, if conditions otherwise are suitable.

They do not appear to be successful colonizers or competitors in restricted environments where competition is intense, such as on the artificial substrates in Lake Anna. On these substrates, the presence of predators, e.g., *Perithemis tenera* at 4 m, or *Enallagma basidens* and *Argia apicalis* (all Odonata) at 2 m (Voshell and Simmons 1978) is likely to have had a critical influence. Thorp and Cothran (1984) showed that dragonfly nymphs can significantly influence the structure of the benthic invertebrate community, which in their study included ceratopogonids as the second most common group after chironomids. Herbivores and omnivores (as *S. longipennis* is) are most likely to be predator-limited and not in competition (Hairston et al 1960).

Regarding substrate selection in L. Anna, the data suggest a possible preference for the leaf pack samplers, where the larvae occurred twice as often as in the conservation webbing baskets. The leaves had been in place for at least a month by the time the leaves were first recorded. By then, the leaves would have been conditioned by microbial decomposition (e.g. Golladay et al. 1983), and it is conceivable that

longipennis grazed on either fungal hyphae or other microbial organisms colonizing the leaves.

It is not likely that habitat complexity differed significantly between the sampler types, and as Voshell and Simmons (1977) suggest, variability between the samplers was probably as low as would be expected due to natural aggregated distribution of macrobenthos or natural substrate. They found a sediment - inhabiting *Chironomus* a detritivore, to be most abundant on the leaf basket, of the 3 artificial substrates evaluated. During the entire feasibility study, apparently only four *longipennis* larvae were recovered from the natural bottom, and those were all from 13 ft. depth, in a single Ponar grab sampler. Inasmuch as *S. longipennis* larvae are not likely to be primary colonizers (see below), and the lake margin had not been stabilized and colonized by emergent and submersed vegetation, it is unlikely that this species was significantly more common, at the time, than the data suggests. On the other hand, it is quite possible that, as beds of aquatic macrophytes developed, the artificial substrates were not fully representative of the actual larval population which most likely was drawn to the macrophytes.

Most of the available work on ceratopogonid colonization strategies deal with recruitment by adults and with larval interactions in isolated or harsh environments, such as water-filled tree holes and other phytotelmata (Snow 1958; Kitching 1971, 1972; Heaps 1981), hot springs (Thienemann 1954), temporary pools (Wiggins 1980, McLachlan 1981) or saline habits (Linley 1969, 1976), and deal largely with *Culicoides* or *Dasyhelea*. Specific observations on substrate colonization behav-

ior over time by larvae of the Sphaeromiini and Palpomyiini appear to be practically non-existent.

I have found only two studies which describe larval ceratopogonid colonization of bottom substrate in normal freshwater habitats. Thus, studying invertebrate re-colonization of small substrate disturbances in the littoral zone of a subtropical lake, Cowell (1984) recorded larvae of the "*Palpomyia-Bezzia* complex"¹⁵ as becoming abundant (>1,000/m²) in experimentally disturbed areas. He classified the larvae as "late opportunitists", showing significantly higher densities 24-30 days after the disturbance. Gersbacher (1937) presented evidence for the progressive development in stream pools of a single major benthic community with different successional stages. On the third (oldest) stage, "Ceratopogonidae" became dominant, being "extremely abundant" where considerable organic matter was deposited, co-occurring with *Hexagenia* (Ephemeroptera) and *Limnodrilus* (Oligochaeta). So it appears that ceratopogonids are unlikely to be pioneers invading new habitat, judging from the indications in the above two studies.

▪ Summary: *Sphaeromias longipennis* in Lakes

A consistent pattern of association of *S. longipennis* seems to exist with deeper water lake habitats beyond the upper littoral zone adjacent the shoreline. While the great majority of *S. longipennis* have been

¹⁵ I determined voucher specimens received from Cowell taken in his study to include, in part, *S. longipennis*, as well as *Mallochohelea* and *Probezzia* spp.

taken along near the waterline of lakes and ponds, this is not fully representative of the true distribution because of a skewed collection efforts, which have been accomplished mainly from the shoreline. Likewise, limnologists have not been able to rear adults or identify the larvae when they are encountered on deeper substrates.

Although *Sphaeromias* species have been found frequently at depths up to 19 m, they cannot be considered a profundal inhabitant in the sense that certain Chironomidae or Oligochaeta may be termed indicator species of the profundal benthos. Instead, the center of dispersal for *Sphaeromias* is the shallow water zone, where the eggs are laid in assemblages of 300-500 per female, where food resources are rich and the habitat is structurally complex. Because the larvae are omnivorous, strong swimmers, capable of colonizing mud and plant substrates, and probably opportunistic, they presumably disperse along the depth gradient away from the shore as long as their environmental requirements (esp. as related to food resources, substrate and perhaps oxygen and temperature) are satisfied. The Lake Anna and other data indicate a possible band of preference around 4 m depth (near the normal limit of the photic zone).

Specific ecological studies are lacking as to factors governing depth distribution of *Sphaeromias*. However, it is probable that the primary factors relate to life history events, particularly the need to pupate on a solid substrate out of the water, or at least the need of the imago to emerge directly into the atmosphere. Larvae overwinter primarily in the 3rd and early 4th instar, and apparently are the reason the greatest larval densities seem to occur at the 4 ± 2 m

depth during the late winter and early spring months. Apparently, there is a single emergence "pulse" in Lake Anna, between May and June.

6.3.3.4 Other Habitat Types and Attributes

▪ Riverine Habitats: As indicated earlier, only some 15% of all *S. longipennis* habitats have been associated with lotic systems of any type. In any case, they occur only adjacent shallow quiet water where persistent macrophyte or algal mat development can occur.

To some extent, the relatively low proportion of riverine habitats may well reflect the overall sampling imbalance. For example, of the over 551 sites I sampled in this study between 1975 and 1978, with no deliberate bias, 28.4 and 71.6% were from lotic and lentic (or semi-terrestrial) environments respectively. So, proportionately twice as many samples were from lotic habitats than yielded *S. longipennis*. This suggests that suitable shoreline habitats for abundant *S. longipennis* production do not exist to the same extent along rivers as they do at lakes and ponds. Exposed sand and mud bars, shoals, bare river banks, and the like, are not major habitats for this species. Although pupae may be taken there in quantity, such as on the Rideau R., Ontario by Wirth (1971), this is most likely due to migration or drifting of larvae from emergent or submersed plant beds.

Only one other species, the Palearctic *S. pictus* Mg., has been collected from river-site biotopes. Thienemann (1954) cited two studies in Germany in which this species had occurred among plants at lenitic (depositional) sites in small coastal plain rivers.

Krivosheina (1957) records it from larger river sand flats where

water-trickles through in rivulets, with *Mallochohelea inermis* (Kieffer) and *Probezzia venusta*. The most extensive breeding occurred in areas where moderate stands of wetland had developed in the flood plains, which is consistent with the "archetypical" *Sphaeromias* habitat.

▪ Livestock-modified substrates: The fairly common recovery of this species from pondside mud flats modified by cattle came as somewhat of a surprise. This is precisely the sort of habitat which *Culicoides variipennis* requires and thrives in (Hair et al 1966, Jones 1961, Schmidtman et al 1983). Normally, bare mud above the water line appears to be a rare habitat for *S. longipennis*, while it is the preferred substrate for many *Culicoides*, *Stilobezzia* and *Bezzia*. The more common ceratopogonid species which occurred with *S. longipennis* at the bare mud sites are compared in Table 30.

Krivosheina(1957) recorded *Sphaeromias* sp. from unvegetated soft mud in and along various shallow ponds and pools in the floodplain of the Oka River(USSR) which floods annually. Some of the pools were temporary, others had cattle access. Several *Culicoides* spp. and *B. nobilis* also occurred there. Ponds with small mud shoals throughout were the most heavily populated.

Samples from at least 226 livestock influenced sites at ca. 30 localities were evaluated during the course of this study. These included the following habitat types: bare or sparsely vegetated mud at pond margins (196); mud at stream margins or in stream flood plain (18); pasture seepages and marshy bottoms (12). While detailed analy-

sis of habitat characteristics with respect to factors determining *S. longipennis* presence or absence is not justified by the relatively small number (ca. 50 indiv.) encountered from such sites, some clear trends can be pointed out: *S. longipennis* was present only at bare mud flat sites adjacent ponds, with exposure to the sun for much of the day. Heavily trafficked or shaded sites, and those subject to flooding produced no *S. longipennis*.

In rating the sites according to a 0 to 3 scale for "degree of animal access", where 0 = no access, and 3 = regular access by numerous livestock (cf. Schmidtman et al., 1983), the positive sites scored 1.40 (S.D. = 0.60, n = 15), whereas representative negative sites scored 2.22 (S.D. = 0.89, n = 54). Thus, excessive animal traffic is apparently inimical to *S. longipennis* development. Yet, for the species to develop in the bare soft mud at pond side at all, some manure enrichment and therefore at least low to moderate cattle access appears to be necessary.

Without exception, the positive exposed mud substrate had a distinctly detectable epipellic algal film, consisting in part of *Cosmarium* sp., *Frustula* sp., *Microspora* sp., *Nostoc* sp. and various undetermined diatoms, which presumably were growing there due to the manure enrichment of the sites. In the case of one non-livestock-influenced mud site productive of this species, the filamentous green alga *Oedogonium* was present as stranded mats.

▪ Selected chemical attributes of substrate and water: Indicative of the relative "euryplasticity" of *S. longipennis* is the fact that

Table 33 . Chemical composition of substrata and water for habitats yielding *Sphaeromias longipennis* (numbers in parentheses are S.D.; n = numbers of samples tested).

Habitat Type	pH		Water		Organic Matter %	Aver. conc. nutrients in substr.					Soluble Salts
	Water	Substrate	Salin ppt.	Cond. umhos/cm		CaO	MgO	P ₂ O ₅	K ₂ O	NO ₃	
Livestock Modified n = 12	-	7.5 (0.3)	-	668 ³ (375)	3.9 (0.9)	1675 (12)	198 (6)	3.4 ¹ (2.7)	90 (26)	57 ² (53)	1451 ² (205)
Non-livestock Modified n = 6	6.6 (0.6)	5.7 (0.4)	-	380 ³ (212)	6.5 (4.7)	631 (218)	140 (57)	23.8 (8.2)	64.4 (33)	13 (4)	675 (214)
Brackish ⁴	6.7 (0.5)	6.3 (0.4)	2.7 (3.6)	14,120 (14,294)	10.9 (4.5)	769 (193)	199 (0)	23.5 (0.7)	88 (43)	11 (3)	7253 (2606)

¹ Excludes two extremely anomalous samples of 138 and 137 mg/l, taken at a site receiving milkhouse effluents.

² Based on only 3 samples available for analysis.

³ Based on only 2 samples available for analysis.

⁴ Represents 4 water samples and 2 substrate samples resp.

habitats of 3 markedly distinct chemical types are apparently acceptable to it (Table 33). Although it is not nearly as ubiquitous and eurytopic as certain other ceratopogonids such as *Bezzia nobilis*, *S. longipennis* is capable of colonizing a far greater diversity of habitats than previous records suggested.

Significantly greater pH, Ca⁺⁺, Mg⁺⁺, NO₃, and extractable soluble salts were exhibited by the livestock-modified mud substrata than by the livestock-free sites. In contrast, the livestock pond sites were distinctly lower in organic matter, reflecting an absence of the detritus often encountered at *S. longipennis* sites. The relatively lower pH of the non-livestock freshwater sediments probably is indicative of the redox chemical reactions taking place in the decomposing plants and sediments of typical *longipennis* site, in which the general effect is to lower the pH in non-marl substrates (Wetzel 1975). The average water pH was close to circumneutral. None of the approximately 100 acidic (pH <5.0) bog and swamp sites sampled in this study yielded *longipennis*. Thus, there is no reason to suspect an acidophilic tendency in this species. In fact, the opposite may be more likely, in that the larvae thrive in hard-water lakes with a pH > 8.0, such as Douglas Lake, Michigan, and Lake Mendota in Wisconsin (Frey, 1963).

• Brackish water sites The nature of the brackish water occurrence of *longipennis* indicates that it is likely a haloxenous species, occurring "accidentally" in suitable physiognomic habitat types which happened to be influenced by water in the oligohaline (0.5 to 5.0 ppt) range. Nevertheless, the essential point remains that this species

is physiologically capable of thriving and developing in such waters. Also, the fact that the soluble salts of the substrate were significantly elevated relative to the freshwater sites confirms that the aquatic salinity was not a temporary condition. *Dasyhelea grisea* and *B. nobilis* co-occurred with this species in all the brackish sites.

The European species *S. fasciatus* has been reported as a freshwater euryhaline (0-8 ppt) species from very comparable oligohaline habitats at the North Sea (Remmert 1955:39; Remane and Schlieper 1971; Thienemann 1954) and the Black Sea (Strentzke 1951). Glukhova (1979) characterized *fasciatus* as chiefly a freshwater lake inhabitant, but reports *S. candidatus* as being capable of developing large populations in highly mineralized lakes (13-16 ppt). She also notes that an unnamed but distinct *Sphaeromias* (new species?) has proven to be quite abundant in a group of brackish lakes in the Ural Mountains region. In Lake Bolshoi Shantropai, its population density in places approaches 12,000/m², in nearly monospecific assemblages throughout the lake. In the littoral zones of these lakes, *Culicoides* species such as *C. riethi* and *C. manchuriensis* thrive.

6.3.3.5 Larval and Pupal Behavior

Locomotion. -- In common with most Ceratopogoninae (except many of the tribe Stilobezziini), *S. longipennis* larvae are capable of freely swimming through the water column with directed forward motion, a capability uncommon among dipterans and aquatic insects in general. Ceratopogonid swimming behavior is highly characteristic. It may be most closely described as anguilliform, i.e., "eel-like", such as that

of certain fish (Webb 1984), leeches (Stent et al. 1978), or nematodes (Kirchner et al 1980). Yet, one could perhaps justifiably coin a term such as "ceratopogoniform" swimming, because there are significant differences (which are beyond this discussion) between the anguilliform mode of propulsion and that of the ceratopogonids. In these larvae a sinusoidal oscillatory wave pattern is established, having two nodal points, often in the mesothorax and in the seventh abdominal segment. The wave amplitude and frequency seem to be proportional to body length.

This swimming behavior occurs in short bursts of movement from substratum to substratum. There, movement occurs in a serpiginous gliding in and on the sediment ("burrowing"), on the surface of aquatic plants or rocks covered with aufwuchs, among algal filaments, or in the wet surface film on substrata above the water's surface. The larval "mode of existence" (Cummins 1973, Merritt and Cummins 1984) on substrates approximates attributes of "sprawling", "burrowing", and "climbing". The latter capability is critical to the successful pupation of many species.

Swimming by *S. longipennis* is particularly vigorous and active. I have observed continuous swimming by a given individual over a 10 m distance from one margin of a sinkhole pool to another. In very shallow water (1-5cm) or when they are near the top of the water column, they swim with their head at the water surface, and with their body at an oblique angle to the surface, as also noted by Wirth and Grogan (1979). In limnetic swimming, this angle is not maintained. The strong swimming ability of *Sphaeromias* larvae undoubtedly con-

tributes to the fact that they are commonly found at considerable distances from the shore in lakes. Dzhafarov (1954) claims *Culicoides* larvae migrated up to 100 m in a small and shallow lake, in successive bursts of 3-4 m. However, *Culicoides* larvae are rarely found at any significant depth away from lake shores.

Sphaeromias larvae of the second to fourth instars have been found in 4 m of water and deeper, in this study and others, particularly during the winter. I collected a near-mature larva in late November from a brackish pool which successfully developed into an adult. As discussed, the larvae migrate towards shore for pupation in the spring. The precise mechanism of this behavior in *Sphaeromias* is not known, but all indications from indirect observations by Williams (1955), Muttkowski (1918) and myself suggest that movement shoreward by pre-pupal larvae at the surface of the water body takes place at night.

Pupation --Pupae are quite capable of floating in the water, the respiratory horns attached to the meniscus, with the long axis of the pupa at an oblique angle to the surface, but I have almost always found them in the sediment just above the water line. In the rearing dishes, the pupae burrowed into the agar by a corkscrew action of the abdomen. This occurred within 4 hours after the pupa had pulled out of the ecdysial split in the larval thorax, before the pupa had fully hardened or melanized. An imago successfully emerged from pupa which was imbedded in the agar only up to the lower third of the cephalothorax. Becker(1961) showed that in *C. circumscriptus* it was the pupae and not the larvae that do the burrowing. *Culicoides melleus* larvae seek cav-

ities and depressions in the sand where their water level and darkness preferences are satisfied. The larvae then pupate and develop a burrow, and are able to move vertically in the sand (Linley & Adams 1972).

The process of larval-pupal ecdysis apparently cannot take place in the free water removed from a substrate. It is unlikely also that pupation by most ceratopogonids can take place under water, although *Culicoides melleus* and probably other intertidally breeding *Culicoides* form an exception to this rule (Dyce and Murray 1966; Linley and Adams 1972). Pupae of *longipennis* may be able to reposition themselves in substrates farther up on shallow banks of the water level rises (Malloch 1914). They also are to be found attached to the sides of rocks, plant debris, or emergent vegetation (pers. obs.; Muttkowski, 1918; Williams, 1955). The pupal period typically requires 5-6 days.

Trophic relationships -- During my individual rearing efforts, one 12 mm larva--collected in late November and placed on agar-- grew to 14 mm, and pupated; a completely normal male emerged in mid-February after a six day pupation. This was my longest (10 weeks) successful rearing span for *S. longipennis* (347-1 IR). In another instance, several larvae from an early August lake bottom collection (WIK-316D), of instars II and III (3-7 mm), survived in culture for 4 months before succumbing. Substrate from this site maintained in rearing cartons until the following April was subjected to extraction; the *longipennis* larvae averaged 11 mm in length. Placed on the agar medium, they grew somewhat, but did not thrive. The last finally succumbed to starvation after 114 days in IR culture, a total of 376 days since collection.

Shortly before they died the larvae had largely consumed their fat stores giving them a more translucent appearance, and considerably reducing the amount of subepidermal pigmentation (Fig. 16d).

The main food source provided the larvae was the nematode *Panagrellus redivivus*. Other organisms were "inoculated" onto the agar with bits of original habitat material. In the case of the successful 10-week rearing, protozoans and microcrustacea were able to thrive in the rearing disk. I did observe the *longipennis* larva consume whole nematodes, but did not actually see it ingest any other organisms. In the rearing dishes of the younger larvae from the lake (Coll. 316D), no secondary growth of other organisms appears to have occurred. From this and related observations with other specimens, I concluded that *Panagrellus* alone does not provide adequate nutrition to the *longipennis* larvae, and quite apparently they were not able to glean sufficient sustenance as collectors on the sparse surface of the agar.

Based on larval gut analyses, Mayer (1934d) divided ceratopogonid larvae into two trophic categories determined by the particle-size and nature of the ingested food: coarse and fine detritus feeders. Among coarse detritus (CPOM)¹⁶ he distinguished fragments of higher plants, spores, pollen, fungal hyphae and indeterminable coarse particles (no size specified). Diatoms, algae other than diatoms, and inorganic

¹⁶ This term I use simply as a convenient translation of Mayer's "Grobdetritus", and not strictly in the modern ecological sense, in which CPOM is defined as particles >1 mm in size (e.g., Cummins and Klug 1979).

sediment (chiefly sand) were treated as separate categories. Fine detritus (FPOM) included two categories, the finer undistinguishable particles and a "broth"¹⁷ distinguished from the former by a even finer particle size and lack of color.

Coarse particle feeding clearly characterized the *Forcipomyia* *Dasyhelea* and the *nubeculosus*-Group¹⁸ of *Culicoides* (*Monoculicoides*), all of which have strongly developed epipharynxes and pharyngeal structures. Other *Culicoides* and the Palpomyiini he evaluated were all FPOM feeders, largely with "broth" in their guts associated with animal cell and tissue fluids, which Mayer considered to be derived from a saprophytic feeding habit on dead but undecomposed insects. However, Thomsen (1937), Weerekoon (1953), and my observations provide strong direct evidence for a predaceous - piercing feeding habit, in part. The mouth-parts of these larvae are considerably less robust than those of the CPOM feeders. The epipharynx of *S. longipennis*, on the other hand, is of intermediate robustness, between that of the scrapers (e.g. *Dasyhelea* spp.) and the specialized carnivores (e.g., *Palpomyia lineata*), which supports the supposition that this species is a trophic generalist.

For *S. fasciatus*, which appears to be a close ecological homologue of *S. longipennis*, Mayer (1934d) found an intermediate condition, in which the majority of the gut contents consisted of FPOM and non-diatom

¹⁷ Possibly equivalent to UPOM (ultrafine POM) of Cummins and Klug (1979).

¹⁸ Closely related to *C. variipennis*

algae, with a small but significant proportion of CPOM. He observed a revealing pattern of layering of the gut contents, where the posterior sections contained exclusively FPOM, the anterior sections CPOM. This suggests a behavioral plasticity in which the CPOM may have been taken up from the decomposing plants among reeds at the lake margin, where Mayer collected the larvae, whereas the FPOM may have been derived from detritivory in the sediment out in the open water of the lake, where the larvae may well have been before returning to the shore.

In addition, a significant proportion (on average, 21 %) of the *S. fasciatus* larval gut contents consisted of sand grains and other particulate inorganic matter. Whether the sand grains in *S. fasciatus* guts are the result of particle selection, or passive ingestion with other detritus particles, it is likely that the sand contributed to the nutrition of the larvae by virtue of an organic coating. Deposit feeders¹⁹ are thought to utilize as food the microbial epigrowth on sediment and detrital particles. An optimally foraging deposit feeder will (a) ingest smaller particles, due to the greater surface-to-volume ratio, and (b) will select particles with an organic coating over particles without such a coating, at least in certain marine deposit feeders (Anderson and Sedell 1979; Cummins and Klug 1979; Taghon 1982).

¹⁹ specifically refers to marine deposit feeders, such as certain polychaetes (Taghon 1982).

Thus, from my observations, and those of Mayer (1934c, d), I would summarize the feeding habits of larval *S. longipennis* as follows: facultatively carnivorous, feeding both as swallowers (e.g., of small nematodes) or as piercers (larger larvae); saprophytic to some extent on dead insects. They also appear to be able to function as collectors, mainly as detritivores, feeding on the sediment, or as herbivores on the so-called "universal pabulum" covering the marginal vegetation (Hutchinson 1981). The supposition that *S. longipennis* is a trophic generalist is supported by the fact that its epipharynx is of intermediate robustness between that of the scrapers (e.g., *Dasyhelea* spp.) and the specialized carnivore (e.g., *Palpomyia lineata*).

6.3.3.6 Adult Habits

Oviposition: The female apparently oviposits from solid objects, laying the eggs in groups, with a gelatinous cover, onto leaves of plants in the water (Malloch 1914, Muttkowski 1918). According to Thienemann (1928), *S. fasciatus* (as *Xylocrypta fasciata*) eggs are "semi-ovoid or hemispherical egg masses up to 0.5 cm in diameter, often deposited in massive assemblages on the surface of leaves floating in the water ... (cf. figs. 25 and 26 in Rieth 1915)." Thus, they are basically identical to those of the *Bezzia* and *Palpomyia* species. This oviposition behavior departs completely from that known for other sphaeromiines, in which the female hovers over the open near-shore water and deposits eggs in ribbons up to 3-4cm in length (see discussion under tribe). Careful field observations are needed to confirm the oviposition behavior of *S. longipennis*.

Flight: Collected only once by light trap in this study. *S.*

longipennis was not collected in any of the Lake Anna - sited light trap samples I examined, although *Mallochohelea atripes* was encountered frequently. Apparently *S. longipennis* is weakly attracted to light. This probably means that the species is more abundant than past adult collection records suggest.

A univoltine adult emergence pattern is suggested by an inspection of the larval size distribution by season as well as by the adult activity reflected in the published trapping records. The earliest instars were all obtained in August and September, and most of the last instar larvae and pupae between April and July, indicating that a single emergence pulse is the norm at all localities, and that the progeny of the emerging adults appear in August. Likewise, the adult capture records give a comparable picture (Table 34).

However, the possibility exists that in the poorly-represented southern latitudes a bivoltine life cycle occurs. The earliest record, in April, stems from Louisiana (Wirth 1971).

In Europe, *S. candidatus*, *fasciatus*, and *pictus* all are considered to be univoltine by Glukhova (1979).

6.3.3.7 Synecological Species Associations

Pooled species co-occurrence data (e.g., Table 30) allow some likely synecological associations of species by habitat to be proposed. Ubiquitous eurytopic species, such as *Bezzia nobilis* and *Culicoides crepuscularis* are as likely as not to occur in nearly every conceivable aquatic habitat where free water is present, with the exception of phytotelmata, and thus do not contribute greatly to the

Table 34. Seasonal flight activity of *Sphaeromias longipennis*.

Month	April ²⁰	May	June	July	August
% of total captures n = 28	3.6	17.8	42.8	32.1	3.6

²⁰ Louisiana record only (Wirth 1962b)

delineation of species - habitat association (taxocenoses)(Schwank 1982a, b).

Halotolerant Phytophilic Taxocenosis: One of these taxocenoses is a halotolerant phytophilic/phytophilic species association, the basic elements of which can be seen in the species assemblage which occurs with *S. longipennis* at the brackish water sites. This habitat type is typified by floating algal mats and Aufwuchs-covered macrophytes and plant detritus in mixohaline and mixosaline (coastal maritime, and inland, resp.) water, wherein the plants themselves are halotolerant but normally grow in freshwater. Including an evaluation of the ceratopogonids occurring at *all* brackish water sites investigated in this study (ca. 75), the eight most characteristic species for this taxocenosis are shown in Table 35. A total of 22 species occurred at least once at this habitat type.

The most typical representatives of the halotolerant phytophilic synecological association are in the genus *Dasyhelea*, members of which, especially in the *mutabilis* group, are more likely than not to be limited to brackish habitats. Significantly, no *Culicoides* appear in this species association, nor are true halophiles(which many *Culicoides* and *Dasyhelea* are) significantly included.

Hygropelophilic taxocenosis. Another species association can be considered characteristic of non-shaded, enriched hygropelic sediments around ponds and other non-erosive shoreline freshwater biotopes. Hygropelic sediments are, specifically, damp non-submerged soft mud

Table 35. Synecological Association (Taxocenosis) of Halotolerant Phyto- and Phycophilic Biting Midges with *S. longipennis*.

Species	Abundance Index ²¹
<i>Bezzia nobilis</i>	208
<i>Dasyhelea grisea</i> group	112
<i>D. cincta</i> group	84
<i>D. mutabilis</i> group	70
<i>Stilobezzia coquilletti</i>	49
<i>St. sybleae</i> s.l.	44
<i>B. glabra</i>	30
<i>Sphaeromias longipennis</i>	16

²¹ See Table 14, etc.

or silt deposits, free of vegetation (Illies 1961, Schwank 1981a, b, 1982a). In the case at hand, the hygropel normally supports a rich microflora, and is usually influenced by an allochthonous source of nutrients (often, but not necessarily animal in origin). From the ca. 250 sites which fit this characterization in this study, the 15 dominant ceratopogonid species are listed in Table 36. At least 65 species in all were recorded from the hydropelic habitat, a species richness three times that of the brackish habitat with the halotolerant phytophilic taxocenosis.

One might say that the hydropelic biotopes represent the "archetypical" transitional (aquatic-semiaquatic) habitat in which the generalist Ceratopogonidae thrive particularly well. The genera *Culicoides*, *Bezzia*, *Stilobezzia* and *Palpomyia*, in that order, are the dominant genera at such habitats in this study area. That *S. longipennis*, is present on these lists at all suggests that it is more of a resource generalist than previous knowledge would have led one to expect, albeit much less of a generalist than the ubiquitous *B. nobilis*. While the considerable amount of sampling done at the farm ponds in the Luster's Gate - North Fork of the Roanoke River area undoubtedly skewed the results for *longipennis* towards this sort of habitat, nevertheless it is undeniably reasonably successful there. The fact that the species has not been previously reported from this habitat despite the considerable amount of *Culicoides*-oriented work that has been conducted there, undoubtedly has to do with the simple fact that non-*Culicoides* are not routinely identified.

Table 36. Synecological Association of Hygropelophilic Species of Biting Midges with *S. longipennis*.

Species	Abundance Index
<i>Culicoides crepuscularis</i>	4,012
<i>C. haematopodus</i>	2,540
<i>C. variipennis</i>	1,051
<i>Bezzia nobilis</i>	1,029
<i>C. stellifer</i>	677
<i>Stilobezzia antennalis</i>	652
<i>Bezzia laciniastyla</i>	321
<i>St. bulla</i>	320
<i>Palpomyia novitibialis</i>	242
<i>C. spinosus</i>	226
<i>St. coquilletti</i>	198
<i>P. subsaspera</i>	104
<i>B. flavitarsis</i>	96
<i>Alluaudomyia bella</i>	90
<i>Sphaeromyias longipennis</i>	81

I have not yet closely evaluated the various hydropelic (submerged sediment) and emergent wetland seres for their taxocenoses, but it is unlikely that *S. longipennis* would enter these to a major extent. This is because of the high species richness and number of habitats in- whereas the number of my personal collections of this species in those habitats was fairly low. It is worth noting, however, that Wirth collected *S. longipennis* (from sand and mud at the Rideau River margin, Ontario) with an unusual concentration of five other sphaeromiine species: *Jenkinshalea albaria*, *Johannsenomyia argentata*, *Probezzia pallida*, *Mallochohelea albihalter*, and *M. smithi*, plus several *Bezzia* and *Stilobezzia* species (Wirth and Grogan 1979). As noted earlier, this pupal collection site may not represent the true larval habitat: it is quite possible that the larvae may have left a near-by aquatic plant bed to pupate in sediments along the river margin.

The fact that the five *Culicoides* are at the top of the hygropelophilic taxocenosis list in Table 35 on page 456 , epitomizes the nature of the generalist *Culicoides* habitat. These species are nearly always among the most prominent *Culicoides* at non-maritime sites throughout North America particularly at hygropelic habitats such as characterized above and in Chapter One (e.g., Williams 1955b; Jones 1961, 1967, 1977; Hair et al 1966; Jamnback, 1965; Rowley 1967; Gazeau and Messersmith, 1970; Kardatzke and Rowley 1971; Battle and Turner 1969, 1971; 1972; Blanton and Wirth 1979; Zimmerman, 1981; Zimmerman and Turner 1983; Schmidtman et al 1983; Kline and Greiner 1985; Vaughan 1985).

Habitat knowledge for the *Bezzia* species is not nearly so well established, but *B. nobilis* is ubiquitous in the Holarctic region (Wirth 1983c), and clearly is the dominant or subdominant species, on the whole, for many of the habitat types assessed during this study. For the *Stilobezzia*, although a good recent review of the species in the Maryland and Virginia region including some new biological data, is available (Wirth and Grogan 1981), ecological observations on this genus are sorely lacking. Similarly, the *Palpomyia* have been reviewed for North America, and habitat data was included where possible (Grogan and Wirth 1979).

6.3.4 Distribution

- Geographic Range

Widespread in eastern North America, from Minnesota and Ontario, south to Texas and Florida, with a disjunct record in California based on a single record from Modoc Co., in the northeast corner of the state (Wirth 1951, 1971). The published record does not allow judgments as to the true distribution west of Minnesota. Only ca. 17% of the nearly 60 localities (combined for all available collection records) from which *S. longipennis* is known, occur south of the 36th parallel, a latitude which roughly divides the U.S. in half.

This study provides a new state record, for West Virginia (Randolph Co.), and seven new county records for Virginia (Accomack, Amherst, Cumberland, city of Hampton, Montgomery, Roanoke, city of Virginia

Beach), in addition to the existing records from Alexandria and Richmond Co. (see Figure 18 on page 466).

This species is now known from 18 states, 1 province, and Washington, D.C.: CA, CT, DE, FL, GA, LA, MD, MI, MN, NC, NJ, NY, PA, OK, ON., TX, VA, WI, WV.

▪ Biogeography

More or less eurythermal. Recorded from all physiographic provinces in the study area, from the eastern edge of the Appalachian Plateau to the tidal areas of the Coastal Plain, with no discernible distribution peculiarities related to biotic region (Figure 18). This is as might be expected from a species which could be termed "geographically indifferent", in that it may occur in most any reasonably stable, open wetlands margins if the microhabitat criteria are satisfied. These criteria depend more upon hydrologic regime (rainfall, type of drainage basin, etc.) and exposure to sunlight than upon climate- or altitude-related factors. Nevertheless, it is likely this species has boreal affinities, based on a strong concentration of records north of 36° . There have been no records north of 48° N in the Nearctic. The five Palearctic *Sphaeromias* spp. are largely restricted to the 40-50° band, with two species having been recorded above the Arctic circle.

6.3.5 Collection Records

▪ Reared Material.

Virginia: • Accomack Co., Assateague Is., Chincoteague Nat'l.

Wildlife Ref., Pond "F", surficial scum and algal layer over aerated

marshy mud among abundant aquatic vascular flora, sl. brackish water, 22-VII-1975, 3 females by RC (WIK 138); same, but 2.5 mi. W of Hallwood on Co. Rt. 692, wide roadside ditch with brackish water (9 ppt.) overgrown by dense sprawling mass of recumbent aquatic vascular plants rooted in aerated rich brown mud, 1-VII-1976; 8 larvae, 2 pupated (WIK 308). • Amherst Co., Otter Lake, Blue Ridge, soft loose detritus-rich mud to 30 cm thick, in 1 m deep water, 2-VIII-1976, 6 larvae IR (WIK 316D). • Cumberland Co., Bear Creek Lake, Cumberland State Forest, soft mud and *Eleocharis* mat in stream downstream of lake, aufwuchs-rich; 30-IV-1977, 1 female with p. ex. by IR (WIK 380). • Hampton (city), Grandview Natural Preserve, floating mass of aquatic vasculars with leaves and organic detritus in coastal marsh pool, sl. brackish, 30-VII--976, 1 female, 1 male by RC (WIK 299); same, sample in adjacent pond, sandy clay and organic detritus with overlying algal layer, sl. brackish, 27-XI-1976, 1 male with l. ex., p. ex., by IR (WIK 347-1). • Montgomery Co., Christiansburg, farm pond south of town, 8-IV-1971 substrate sampled, emerged not before 25-IV-1971, 1 female by RC, coll. C. Kessinger and B. Fay; same, 2.5 mi. W of Price's Fork, pool in deep sinkhole in pasture, clayey mud at pool's margin, sprouts of aquatic plants abundant, 20-V-1976, 18 larvae, 1 male with l. ex., p. ex., IR (WIK 248); same, but water level higher, sandy-clay and slimy muck with blue-green algae at water line, some herbaceous weeds in vicinity give partial shade, 9-VI-1976, 1 pupa, 1 female with p.ex. by IR; 2 males, 1 female by RC (WIK 258); same, Luster's Gate, McPherson pond, cattle watering pond mud with abundant emergent plants, 5 collections 2-IV to 18-VI-1969, 4 males, 2 females by RC (FVB

Site A); same, near Luster's Gate, "powerline pond" small farm pond with little cattle traffic, partial shade by tree; 6 collections from 26-III to 4-VI-1969, 6 females, 5 males by RC (FVB Site C); Pandapas Pond, weedy yellowish mud at pond's edge, 2-IV-1969, 1 male by RC (FVB Site E, Coll. 13A); Tallant's Pond, emergent vegetation and marshy mud at margin, 6-V-1976, 1 female with p.ex. by IR, coll. R. Booth. • Roanoke Co., near Catawba Creek N. Fk. Roanoke R. headwaters divide, dairy cattle pasture pond in depression with wide mud flat, epipellic algae, 22-VIII-1975, 8 females, 3 males by RC (WIK 160). • Virginia Beach, Back Bay, Pocahontas Trojan State Waterfowl Mngmt. Area, black-gray muck along ditch-pool, with blanket algal mats, 15-VI-1975, 3 females by RC (WIK 44). West Virginia: Randolph Co., Spruce Knob Lake (elev. 1,173 m), rich marshy seepage infused by root mat of adj. emergent macrophytes, 23-VI-1976, 1 larva, pupa; 7 males, 4 females by RC (WIK 268B). Wisconsin: Bayfield Co., South Fork Fish Creek, "sand-pool", 30-VIII-1953, 1 female with p. ex., emer. 5-VIII-1953, leg. R. H. Jones; Washburn Co., Yellow River, margin, 17-VI-1952, 1 female, emer. 19-VI-1952, leg. R. H. Jones.

▪ Other Material

Georgia: Clarke Co., Athens, Camelot Pond, 3-IV-1973, 5 larvae (15-16 mm), coll. R. G. Baer (VPI). Michigan: Ellsworth, Ellsworth Lake, 10-II-1954, 5 larvae (15-16 mm), coll., E. W. Surber (misidentified as *Palpomyia tibialis*) (VPI). Ontario: Carleton Co., Mississippi R., thick mat of algae, shallow quiet water (2 sites); 20-VI-1966, 4 larvae, 3 pupae, coll. P. D. Hebert (ROM). Leeds Co., Chaffeys Lock;

"shallow, weedy water", 14-VI-1966, 6 larvae (17 mm pre-pupae), coll. P. D. Hebert (ROM); same but in "thick mass of water weeds", 13-VI-1966, 4 larvae (17-18 m), coll. P. D. Hebert (ROM). *Virginia*:

- Amherst Co., Otter Lake, Blue Ridge, emergent vegetation in 50 cm water, 8-V-1976, 3 larvae (17 mm), coll. T. Schaufelberger (VPI).
- Louisa Co., Lake Anna Reservoir, by dredge and ex leaf and webbing artificial substrate samplers at 2 and 4 m depth, X-1972 to VIII-1976, 27+ larvae, coll. J. R. Voshell and G. M. Simmons, Jr. (VPI); same, 5 larvae, IX-II-1976 (WIK 334, 335, 338);
- Montgomery Co., Pandapas Pond, 13-VII-1971, 2 females by black light trap, coll. R. E. Williams; same, 4 pupae *ex Typha* stand among detritus in shallow water, 2-VII-1971, coll. R. E. Williams.

▪ Summary of Collection Records

- IR (5 sites), ca. 15 larvae attempted: L-A: 2 males, 1 female; L-P:7; P-A: 5 females, 3 males from 11 attempts.
- IR sites: WIK Coll. Nos. 308, 316D, 347, 380; Tallant's Pond (Booth).
- IMM (15 sites): ca. 45 larvae, 3 pupae
- RC (17 sites): 29 females , 23 males
- AFT (1 site): 2 females

6.3.6 Annotated Taxonomic and Biological References

- Malloch 1914:224-25 (as *Palpomyia*; oviposition; descr. and figs. eggs, larv. habitus, pupa, pupation; habits; biotope; Illinois)
- Malloch 1915:323-24 (habitus larva, mandible, labium, pl. 17, as *Palpomyia*)
- Malloch 1917 42 (habitus, larva; as *Palpomyia*)
- Muttkowski 1918:407-8; 475-8 (larval ecology, habits, Lake Mendota, Wisconsin; as *Palpomyia*)

- Thomsen 1937:75-76 (brief descr. and figs. larva, pupa, "flap" on conjunctiva of larval exuvium; biotope, New York; as *Palpomyia*).
- Wirth 1952:244 (adult diagnoses, biotope(based on lit.))
- Williams 1955:95 (notes on pupal biotope, sphaeromiine spp. assoc., Douglas L., Michigan).
- Snow and Pickard 1958:5 (pupal biotope, reservoir, Tennessee)
- Wirth 1962b:278 (male, female diagn., figs.; distr., rearing rec., CA)
- Wirth and Grogan 1979: 897-900 (male, female diagn., figs.; larva, pupa descr., figs., biol. notes; Maryland, Virginia)

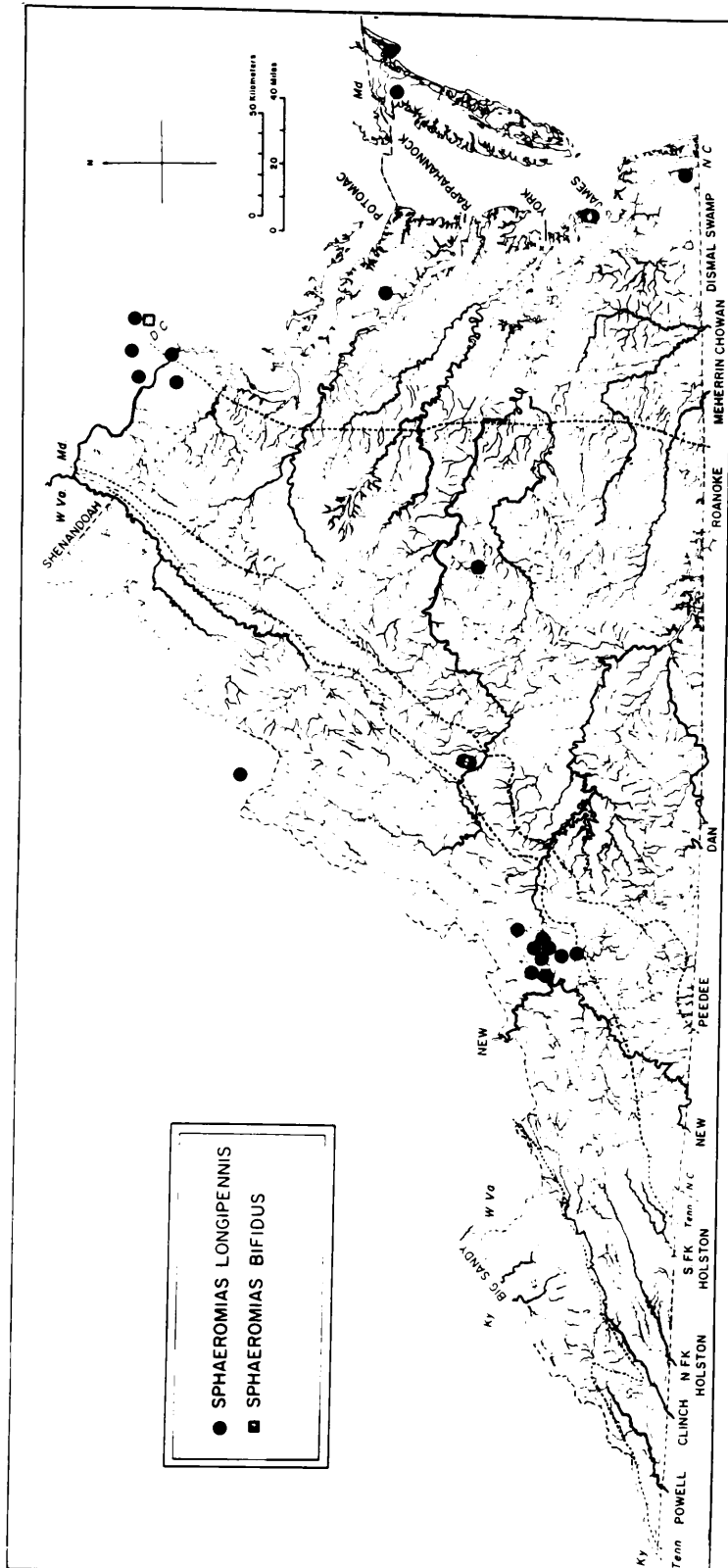


Figure 18. Geographic distribution of the two *Sphaeromias* species in the Virginia region.

CHAPTER SEVEN.

Summary and Discussion -- Section II: Ecosystematics and Autecology

7.1 Summarizing Discussion

In the preceding five chapters (Section II), I evaluated the two tribes of predatory biting midges Heteromyiini and Sphaeromiini in Virginia and surrounding states on the basis of the material resulting from the field collections treated in Chapter 1 (Section I). I have reviewed and characterized salient features of:

- o faunistics and geographic occurrence;
- o egg, larval, pupal and adult morphology and habitus, with attention to possible adaptive significance of certain phenotypic characters;
- o life history and autecology of the individual species, chiefly as related to habitat attributes of the immatures.

Syntheses were presented at the generic and tribal level, incorporating available data on the relevant taxa anywhere in the world. Forty taxa were treated in all (Table 12), following the format presented in the introduction to Section II, part II.5 (see page 201). In the synopses of "Systematics and Habitus", my objective was not to present complete original taxonomic descriptions. Rather, I limited my observations to those insights deriving from the process of determining the specimens, and from the photographic and other records obtained while rearing larvae and pupae, with syntheses from the literature.

Inasmuch as this was not primarily a taxonomic study, and I did not have a broad range of immature specimens available from outside the immediate Middle Atlantic states region, I did not spend much time on questions of general phylogenetic relevance. However, there clearly is enough material extant, were it to be assembled, to make very significant insights possible. I made several references to the potential for such an effort, especially at deriving tribal and generic level diagnoses and concordances between the developmental stages.

7.1.1 Summary of Faunistics and Systematics

From the point of view of adult taxonomy, the Heteromyiini and Sphaeromiini are among the most thoroughly worked out in the family Ceratopogonidae, and the fauna in the Nearctic is relatively well documented. This is particularly true of the Middle Atlantic states region of the U.S. Systematic study of the immatures, in contrast to that of the adults, has been infrequent and mostly in the alpha phase. Very limited amounts of information are available on the habits and life histories of the immature stages in particular. Larvae of the Heteromyiini and Sphaeromiini form a significant component of the so-called "*Palpomyia-Bezzia-Macropeza-complex*", which to date remains difficult to distinguish in this stage, because so few component genera have been reliably described. Recently, significant advances have begun to be made(see Table 37 and Chapter 1, part 1.1.2.2).

The two tribes form a small group of biologically and phylogenetically related but taxonomically diverse species in the subfamily Ceratopogoninae. The larvae of these tribes possess the narrow cylindrical "vermiform" shape characteristic of this subfamily, and most if not all can lead a fully aquatic existence. These tribes constitute some 350 species in 29 genera worldwide, of which 57 species in 12 genera occur in the Nearctic.

In Virginia, 18 species among nine genera in the two tribes had been previously recorded (but not compiled). With the results of the present study, I demonstrate the presence, in the region as a whole, of 22 described species in ten genera, plus at least three additional described species likely to be present. In addition, this study distinguished three undescribed species of Sphaeromiini (Table 12). Twelve species comprise 91% of the specimens and 86% of the collection sites for the 22 species recorded in Virginia and surrounding states. The five most common by far are: *Clinohelea bimaculata*, *Mallochohelea albibasis*, *M. atripes*, *Probezzia pallida* and *Sphaeromias longipennis*.

Of the 13 Nearctic species in 5 genera belonging in the Heteromyiini, the smaller of the two tribes, 8 species in 3 genera are recorded from east of the 100th meridian. In Virginia, six species are now known: 3 *Clinohelea*, 2 *Heteromyia* and 1 *Neurohelea* (Figure 8).

Only seven of the 20 genera in the tribe Sphaeromiini are found in North America. Yet, these genera account for 75% of the 280 species worldwide, and include 44 species on this continent. East of the 100th

meridian, 39 species are known. In Virginia, 16 species in seven genera of this tribe are now known to be present.

Overview of Developmental Stages.

Females of the Heteromyiini and Sphaeromiini are medium to large midges; probably all are predaceous, normally on other Nematocera, and often on their own mates. Mayflies and other insects are also sometimes hosts. Striking secondary sexual characters, found in the female claws and fifth tarsomeres and abdomen, undoubtedly functionally related to the feeding and mating behavior, are used for primary taxonomic breakdown of tribes and genera in this section of the subfamily Ceratopogoninae. However, the adaptive nature of most of the characters has not been specifically determined.

Heteromyiine and sphaeromyiine adults and many of the known pupae and larvae possess often striking characters which are individually diagnostic. But comprehensive tribal and generic summaries for characters of the immature stages have not yet been devised due to the dearth of appropriate descriptions, although excellent progress is being made (cf. Glukhova 1979, Elson-Harris and Kettle 1986a,b). Yet, for the genera which account for most of the species, at least representatives have been described. Of the 29 genera in the tribes worldwide, 5 have representative species which are known in the egg stage, 9 as larvae, and 13 as pupae (see Table 37).

In the Nearctic and Palaearctic regions, of 12 genera, 5 are not known as larvae (Heteromyiini: *Heteromyia*, *Neurobezzia* and *Neurohelea*;

Sphaeromiini: *Johannsenomyia* and *Macropeza*), whereas only two genera remain undescribed as pupae, both in the Heteromyiini (*Neurobezzia*, *Neurohelea*). The known genera account for the great majority of species in the two tribes. On the other hand, the existing descriptions are usually rather sketchy, and the material is widely scattered among three or four zoogeographical regions. Also, the number of species described per genus is small, and, normally, the number of available associated specimens as such is very small.

This situation makes the development of valid keys difficult, because representative series are not available or readily acquired. While 10 of the 12 Nearctic genera have at least one representative pupal description from somewhere in the world, the number of species known as pupae in this region is relatively low. Pupae of at least 17 species (29.7% of the total fauna) are now described, of which fully 12 were treated by Wirth and Grogan (1979). However, nearly all of the available pupal descriptions are less complete than is desirable to arrive at satisfactory distinctions.

Larvae of only three Nearctic species have been described:

*Jenkinshalea albaria*¹, *Mallochohelea atripes* and *Sphaeromias longipennis*. Although the proportion of described immature stages is low for the Nearctic as a whole, the situation is improved in the eastern Nearctic, where the majority of the descriptions have been made. Thus, while only 5.3% of Nearctic species are known as larvae, this proportion

¹ The status of *Jenkinshalea* is somewhat uncertain. See Chapter 3.2.

increases to 12% for the Virginia-region fauna. Similarly, nearly 50% of the pupae in the Virginia region are known in at least a preliminary way.

Heteromyiini Developmental Stages.

Phylogenetic relationships of the genera in the Heteromyiini were proposed by Grogan & Wirth (1979), who suggested that the tribe is monophyletic in origin. They distinguished three groups of genera, on the basis of specific apotypic, or derived, morphological character states in the adults. *Heteromyia* and *Pellucidomyia* fall into the same generic group, as apart from *Clinohelea*. This grouping may also be reflected in differences in the larval habitat preferences of these genera. Thus, the two former genera have a strong phytophilic predilection, apparently, while *Clinohelea* is more apt to be encountered on soft saturated or submerged muds.

Eggs of the tribe Heteromyiini have not been described as yet. Larvae of this tribe are now known for three *Clinohelea* (2 Australasian, 1 Palearctic) and the Australasian *Pellucidomyia leei*. Pupae of seven species are presently described worldwide in the genera *Heteromyia*, 2 *Clinohelea* and *Pellucidomyia* (Table 37). No known heteromyiine pupae have ventral glandular disks.

The pupae of the three known heteromyiine genera are strikingly different at the generic level, but at the tribal level, features they have in common remain to be homologized. Until Elton-Harris and Kettle's (1986a) contribution, existing heteromyiine pupal descriptions have been

too incomplete, thus comparative analysis is difficult. In particular, necessary details of the abdominal armature (tubercles, setae, etc.) and cephalothorax as outlined by Mayer (1957) have generally been lacking. There is no doubt, however, that adequate characters exist in the pupae, and that they could contribute to a strong concordance between pupal and adult systematics.

Sphaeromiini Developmental Stages.

No detailed phylogenetic analyses of this tribe or its genera have yet been published, thus the relationships of the various character states and their derivatives are not clear. However, most of the adult key characters are presumably secondary sexual characters, directly or indirectly related to the insectivorous or mating behavior of these predaceous midges, in that the armature apparently plays a role in grappling prey and in mating, and possibly in oviposition (see below). Elucidating the probable relationship between the behavior and differential phenotypic expression of leg armature, antennae, genitalic and mouthpart characters, for example, will likely remain a fascinating challenge for some time to come.

Eggs: Known for all Nearctic sphaeromiine genera except *Jenkinshalea* and *Nilobezzia*. With the exception of *Sphaeromias*, the eggs of all known sphaeromiine genera are deposited in gelatinous helically-twisted ribbons 3 to 4 cm long, consisting of single overlapping of eggs displaced at particular angles with respect to the long axis of the ribbon. *Sphaeromias* lays its eggs in hemispherical gelatinous clusters up

to 5 mm in diameter. Sphaeromiine eggs are all fundamentally similar, being elongate cigar-shaped to slightly S-shaped, creamish to grayish-brown in color, becoming darker as development progresses. It is probable that attributes of the eggs in this group will contribute to the eventual concordance of the developmental stages' systematic arrangements.

Larvae: Five of the seven Nearctic sphaeromiine genera are known in the larval stage (*Johannsenomyia* and *Macropeza* remain to be described, as mentioned), and a characteristic set of features apparently holds at the tribal level.

A reliable generic key to larvae of this tribe is still beyond reach. Specific characters are to be found in the head chaetotaxy, and pharyngeal details, in particular, the epipharyngeal comb; thoracic pigmentation; shape and color of ocelli and head; and anal setae. Future descriptions should include attention to details of the sensillae and setae in the oral field. Mayer (1934c), Lawson (1951) and Glukhova (1979: 51-53) have shown that significant structural differentiation occurs there.

Based on larval specimens I have seen from collections made in the first half of this century, many larvae from North American lakes and rivers appear to have been misidentified as "*Palpomyia*" species, when they were actually sphaeromiines, and most often *Sphaeromias longipennis*.

Pupae: Although pupae of all Nearctic genera have been described in one way or another, a systematic review is not available, and little attention has been given to tribal classification. Arriving at a consistent set of characters to delineate the tribe may prove to be more difficult, because of the great diversity found among the various genera.

Mayer (1957) focussed on the abdominal tubercles and setae in attempting a concordance of adult and pupal systematics, and managed to develop seemingly natural groups, but these did not distinguish the Palpomyiini. Examination of the anal segment, respiratory horn, operculum, and the various pits, bristle and setae on the cephalothorax usually provides the necessary discriminators.

An interesting feature in the pupae of some species in five of the genera is the presence of ventral membranous patches, often referred to as adhesive glandular discs, on certain abdominal segments. While I could not confirm a relationship of the glandular disks with any phylogenetic/systematic or biogeographic component, they do have an apparent ecological function. The functional significance of these discs is discussed under the *Probezzia* generic discussion (Ch. 5, pt. 5.1.3.2) and summarized below in this chapter.

Sexual Dimorphism.

Dimorphism in size between males and females is variable, but can be quite pronounced in some genera, notably *Probezzia* and *Nilobezzia*. Males are typically smaller than females, and in *Probezzia* much smaller, about 60-80% of the female size. Similarly, the larvae from which *Probezzia* males develop are consistently about 80% the size of "female" larvae. Instar IV *Sphaeromias* larvae destined to develop into female imagoes can attain 18-19 mm in length, the longest of all ceratopogonid larvae. "Male" larvae of *S. longipennis* attain 14-15 mm.

7.1.2 Habitat Characteristics and Ecological Diversity.

Sixteen of the 19 species of Heteromyiini and Sphaeromiini collected in this study were reared from known substrates. Five species were definitively associated with a larval habitat for the first time; for many of the remaining species, the published habitat information had not previously been brought together and interpreted. To the extent possible, literature records for other species were incorporated in the evaluation of generic habitat characteristics.

Macrohabitat and Microhabitat.

In this study, I have distinguished between the "macrohabitat" or aquatic system (e.g., lake, marsh, river) and "microhabitat" or substrate type (e.g., silt, emergent macrophytes), following the general concept of wetland habitat classification of Cowardin et al. (1979). "Microhabitat" applies in the context of the typical ca. 0.1 m² unit-area samples taken in this study.

Macro- and microhabitat attributes are discussed individually under each species, and summarized for the species-rich genera in Tables 14 & 15 (*Mallochohelea*); 23 & 24 (*Probezzia*), and 26, 28, & 31-33 (*Sphaeromias*).

The following substrates most characteristically harbor sphaeromiine and heteromyiine larvae, in approximate order of prominence:

1. Unconsolidated shores of wet aerobic mud; silt or sand, usually enriched by finer organic detritus or epipellic algae and other aufwuchs.

2. Littoral submersed aquatic plant beds or emergent wetlands, including emersed, floating or recumbent macrophytes, with abundant organic matter in the form of coarse detritus, primarily.
3. Mature filamentous algal mats/blankets.
4. Soft-mud and detritus-rich bottoms of lakes and ponds

The transitional ecotone of the littoral zone can be considered the "archetypical" arena in which ceratopogonine larvae of this group thrive, typically above and below the water line. Significant modifying attributes favoring their presence include various sorts of allochthonous (e.g., seasoned plant detritus) and autochthonous (e.g., various forms of aufwuchs) nutrient sources, patchy plant cover, and partial exposure to the sun. The pupae also are rather closely tied to the littoral environment, inasmuch as the adults cannot emerge from the open water surface. Larvae apparently always migrate shoreward at the time of pupation.

The greatest diversity of larvae in these tribes, in terms of co-occurrence of species in both the microhabitat and in the larger systems, consistently occurs in and along mid-reach streams. This is consistent with biological diversity theory, which indicates that physical and food source heterogeneity are maximized in streams of about 3rd to 5th orders (e.g., McLeod et al. 1981, Vannote et al. 1980).

Considerable plasticity in habitat associations is exhibited by most species in the tribes, both in terms of substrate preferences and type of water body occupied. In part, this is due to the physiognomic similarity of wetlands found along lakes, ponds and rivers, where both aquatic plant beds, and bare sediment above and below the waterline are exploited

by larvae and pupae. The "universal" nature of the larval form, allowing them great mobility among many substrate types in and out of the water, also contributes to the impression of "habitat plasticity".

As yet, it is difficult to deduce specific limiting factors for larvae of most species, though some show apparent segregation more clearly than others. Most species for which sufficient collection records are available show fairly consistent habitat preferences. For example, *Mallochohelea albibasis*, one of the most frequently collected of the genus, has only been found in small to medium-sized streams. Likewise, for *Probezzia xanthogaster*, all but one of 10 records are from rivers, the exception being from a pond. On the other hand, *M. atripes* is predominantly known from lakes (Tables 14, 18 and 23, resp.).

Within the tribes and genera, on the whole, there does appear to be some internal consistency in habitat choice, which would follow from the assumption of an ecological and evolutionary common base. In the following few paragraphs, I will attempt to capsulize the commonalities observed in habitat at the tribal and generic level.

Heteromyiini Larval Habitats.

The heteromyiine species for which pertinent information is available appear quite consistent in their habitat requirements: (a) moderate to dense shade under trees or among thick emergent wetland vegetation; (b) soft, water-saturated littoral emersed or submerged mud or sand with high organic matter content, largely coprogenous, usually including coarse particulate vegetative detritus (esp. *Clinohelea* spp.); or (c) a

phytophilic association, such as with mosses or floating/submerged vascular plants, often also in association with organic sediments (*Heteromyia*, *Pellucidomyia*).

These heteromyiine sub-habitats are most often encountered in the forested, shrub, or emergent vegetation sections of palustrine wetlands. They may also be found along depositional and backwater stretches of creeks, streams and small rivers. Larval *Pellucidomyia leei* in Australia have been found on moss attached to rocks in the middle of a rapid stream.

Sphaeromiini Larval Habitats.

Larval Sphaeromiini characteristically inhabit the littoral zone of lakes, ponds, rivers and streams. They do not occur to any significant extent in bogs, marshes lacking open water, or forested swamps. Extreme environments, such as temporary pools (but see *Jenkinsholea*, 3.2.3.1), intermittent streams, or hot springs, are not exploited as a rule, but *Nilobezzia* and *Sphaeromias* species may be abundant in alkaline resp. saline waters. Exotelmata are not utilized, in the temperate zones at least. However, a few tropical species (such as *Mallochohelea*, q.v.) in wet forests have been found in phytotelmata, which often are the only available accumulations of water in those areas, apart from streams.

At the generic level, some generalizations can be proposed as to the "typical" macrohabitat(aquatic system):

- o *Jenkinsholea*: most often lake-dwelling and in lower river course habitats, especially where sand and silt with sparse vegetative cover forms at the margins; ponds and creeks may also be occupied.
- o *Johannsenomyia*: apparently most common in littoral zone of lakes and ponds in Europe, but *Joh. argentata* in the Nearctic is most often (70% of records) encountered along larger streams and rivers, in soft mud, silty or sandy substrates, both well above and below the water line when the slope is shallow.
- o *Macropeza*: possibly has metarhithral affinities, i.e., for larger streams and small rivers.
- o *Mallochohelea*: four of the five Nearctic species for which data is available are clearly rheotopic, i.e., found most often in association with streams and rivers, tending to occur in smaller stream systems (Order: 2 to 4). The most common species in the genus, *M. atripes*, is by far more abundant in lakes than in streams or rivers. Substrate types vary widely, but often will include coarser substrates in lotic systems.
- o *Nilobezzia*: along lakes and slow-moving water courses in thick sediments with little or no plant cover; alkaline or saline waters are characteristic for some species.

- o *Probezzia*: only seven of 21 Nearctic species have sufficient information (collected at least 4 times), and of these, all but one (*williamsi*) are found predominantly in lotic systems, with the tendency being towards larger streams to small rivers (Order: 4 to 6) (Table 23). In Europe, *P. seminigra* also mainly inhabits rivers.

- o *Sphaeromias*: mainly inhabit open margins of ponds and lakes, with exposure to the sun, either in soft bottom sediments, among dense stands of emergent macrophytes, or on bare soft mud sediments above the waterline. Also, *Sphaeromias* spp. tend to be the most commonly encountered ceratopogonids in lake benthos, including the profundal, especially in northern temperate lakes. Lotic and swamp habitats are quite uncommon.

The most common representatives of the genus *Sphaeromias*, such as *S. fasciatus* in Europe and *S. longipennis* here, are comparatively euryoecious. This study demonstrated for the first time that *S. longipennis* can occur in mixohaline water (brackish under marine influence). Also, a livestock-modified mud habitat is recognized in this study for the first time as a comparatively common substrate for *S. longipennis*.

7.1.3 Habitat Partitioning and Life History Tactics

A consistent pattern of species richness in small habitat spaces is suggested by the rearing and extracting results of this study. Typically

the samples (comprising ca. 500-1000 cm³ of substrate from ca. 0.1 m² of surface area) yielded 5-10 species(max. 13) and 20-30 individuals(max. 100's) of ceratopogonids. Normally, the adults would emerge over a period of several weeks. On the other hand, on average about 20% of the samples yielded nothing.

Also, I have been able to identify several characteristic synecological species assemblages for particular habitat types, in which key species consistently co-occur(Tables 30, 35, 36). One of these synecological groupings, for example, involves an association of eight halotolerant phytophilic species, including *S. longipennis*. One question which arises then is, what factors govern the occurrence and co-existence of the species in such a limited space? A few brief indications follow, drawing on representative results of this study.

The absence of a species from a superficially suitable habitat may result from patchiness in distribution, competition, or may be a product of barriers to dispersal or the presence of undetected factors which render the habitat unsuitable. Conversely, the competitive exclusion principle states that the co-occurrence of two or more similar species results from the possession of different niches, meaning the species display ecological segregation(Antonovics 1971). Resource partitioning is thought to be one of the principal factors promoting the co-existence of species. By this mechanism, species' differences in body morphology, for example, would cause them to occupy separate habitats or feed on different food, or be present at different times.

Both species diversity and genetic variability are seen to be associated with habitat heterogeneity (spatial and temporal) and stability/instability. Unstable or ephemeral environments (such as mud shores) are thought to encourage greater species diversity and minimize competition.

With the species occurrence data resulting from this study, I attempted an assessment of *Mallochochelea*, *Probezzia* and *Sphaeromias* habitats on the basis of lentic to lotic habitat "continua". The results (Tables 15, 24, 31 & 32) are suggestive of possible ecological segregation among and within species, although few specific geographical, seasonal or microhabitat partitioning strategies emerged from the available data.

Intraspecific variation in habitat preferences is indicated by some of the results of this study. For example, it appears that populations of *Sphaeromias* spp. which develop in saline or brackish waters are at least somewhat ecologically segregated from conspecific freshwater populations. Also, intraspecific variation is strongly indicated in *Probezzia pallida*, in which there appears to be a definite "lake population" (though in the minority) and a "river population" in the same geographic area. Such cases may possibly be explained by optimal habitat choice behavior theory (Powell and Taylor 1979) (see 4.1.3.1 or 5.5.3.1), according to which different cohorts from within geographically proximate populations of the same species will segregate into different habitats or subhabitats, to maintain genetic variation in ecologically diverse environments. At present, however, there is no direct information as to the existence of two habitat phenotypes in the two species mentioned.

Colonization and Dispersal.

Colonization dynamics clearly play a crucial role in the presence of a species in a habitat. As Sheldon(1984) effectively states, stream insects are constantly in some stage of dynamic colonization governed by an ecological mosaic that includes all components of their biologies, e.g., growth and development; competitive interaction, environmental constraints, as well as a stochastic, random, component.

With respect to habitat selection, the adult female, the larva, and the pupa all play distinct roles. Oviposition behavior is especially significant to dispersal and reproductive strategies. Therefore, available observations on this behavior in the groups under discussion are of particular ecological interest.

Egg deposition has been observed for several Sphaeromiini, but not yet for any Heteromyiini. Two distinct egg-deposition behavior patterns occur: (a) the female oviposits in flight, while hovering over open water, near the shore, head pointing shoreward, in the evening; and (b) while alighted, the female oviposits from and on littoral substrates at the water's surface, in full daylight.

Only one type of oviposition behavior is found in a given genus. The first type of behavior has been observed in detail for five sphaeromiine species among three genera(as reviewed earlier). The second type of oviposition behavior occurs in *Sphaeromias* spp., in which the female is alighted upon the surface where the eggs are deposited, is the norm among the Ceratopogonidae.

However, the hovering habit of oviposition appears to be unique to a closely related group of genera in the Sphaeromiini. It would appear that this behavior pattern is a derivative of the pleisiotypic (ancestral) alighted oviposition habit. All genera known to have the hovering ovipositional habit also possess well-developed long curved pairs of hair tufts near the gonopore on the venter of segment VIII (Fig. 9a). There is evidence that the sternal hair tufts and the legs play a role in guiding and paying out the egg string.

It is therefore reasonable to predict that all species possessing such well-developed hair tufts will be found to oviposit while in flight, in a manner similar to that described.

The in-flight pelagio-littoral ovipositional habit is obviously of high relevance to the nature of the substrate which the larvae will occupy. Larvae of species which so oviposit are among the most fully aquatic of the ceratopogonids, apparently only leaving the water or bottom to pupate. The females normally will oviposit near shore in sheltered places of either lotic or lentic waters. Because of the morphological comparability of such habitats between lotic and lentic systems, it seems unlikely that a given female will determine an oviposition site based on discernment of substrate characteristics. The optimum habitat choice model suggests that, instead, the population or cohort from which the female developed will be the determinant, in that the same or similar place will be sought out as yielded the adults.

Larval dispersal may be active or passive from the initial aggregation of larvae at the point of egg deposition. Some larvae, such as

Sphaeromyias longipennis or *Probezzia pallida*, are particularly vigorous swimmers, and are more likely than most other larvae to disperse from the shore.

On the other hand, the action of wind, current, and waves clearly are important by tending to concentrate larvae and especially pupae at natural points of convergence, such as in eddy pools, behind logs and in snags, among stands of emergent hydrophytes, and the like. Such sites make good collecting points.

An additional mechanism of ecological partitioning may be afforded by variable egg maturation times. For example, egg hatch requires "4 or 5 days" in *Johannsenomyia argentata* (Johannsen 1905), and 3 to 6 days in *Probezzia williamsi* (referred to as *P. sabroskyi*) (Williams 1955). This range in hatching times would tend to reduce the likelihood of too many larvae occurring in too small an area at the same time, thus reducing the risk of depleting immediately available food supplies before the larvae are able to move about effectively. Likewise, it could reduce the risk of an entire egg batch being lost to a catastrophic event.

Diurnal temporal segregation may be one likely method of ecological partitioning by related species. This is evidently achieved by preference for different light intensities in the crepuscular hours by various sphaeromiine species. Recent evidence for this was provided by Rieb (1981), based on observations made along a river margin in eastern France (see Chapter 3, pt. 3.1.2).

Seasonal temporal partitioning has been shown to be a major mode of ecological segregation among groups of taxonomically related stream in-

sects, but also of functionally similar, yet taxonomically diverse groups of species(e.g., Georgian and Wallace 1983). Evidence from this study points to temporal segregation in adult emergence, at least among some species which occur in the same area, such as, for instance, *Mallochohelea albibasis* & *M. atripes*(Table 16). Most species I investigated are vernal in seasonal appearance (May-June peak) and apparently univoltine. Most species apparently overwinter in the larval stage.

Detailed investigations on voltinism and other life history strategies are needed for individual species. As yet, the Ceratopogonidae have defied attempts to fit them into predictive classifications, for example, in the context of temporary pool adaptation(Wiggins 1980).

7.1.4 Adaptive Significance of Certain Morphological & Behavioral Attributes of Larvae and Pupae.

The force of selection is thought to be primarily on the larvae, at least in some insects(Hynes 1984, Wiggins 1966), because the majority of the life span is spent in this stage. It is useful to consider the larva and pupa as instars of the total organism, yet it is possible that independent selection takes place for the adaptations of the different life stages.

Representative Larval adaptations.

Throughout this study, in the context of the various taxa covered, I have drawn attention to four main attributes of the larvae: morphology, habitat, trophic relationships, and locomotion. These attributes con-

tribute most to the evolution and adaptive radiation of this group(e.g., Glukhova 1981). The larvae can be thought to be successful by virtue of their generalist nature and universal adaptability on the whole, which has allowed them to become, paradoxically, "specialists" in the transitional aquatic-semiaquatic ecotone, specifically, habitats associated with shorelines.

While close inspection consistently reveals characters permitting their distinction, larval Ceratopogonidae in general, and the larvae of the tribes Heteromyiini and Sphaeromiini in particular, show comparatively little macroscopic phenotypic diversification morphologically, despite the diversity of the habitats they occupy. Being basically long, thin cylinders, the whole body of these apneustic larvae may be regarded as a gill. The form of the larva has evidently proven so ecologically successful that it has been altered relatively little in its external aspect(habitus). This conclusion is reasonable in light of the relative antiquity of the Ceratopogonidae.

By contrast, larvae of the rare family Nannochoristidae (Order Mecoptera), which apparently have developed a comparable long cylindrical shape, are found only in very restricted gravelly substrates of streams in southern South America(Hynes 1984), which would suggest comparatively recent invasion of this habitat.

Specific morphological adaptations of larval ceratopogonids, particularly with respect to the head capsule, mouthparts, and chaetotaxy, remain to be properly assessed, but will undoubtedly prove to of important ecological significance. Elson-Harris and Kettle(1986a) have drawn at-

tention to an unusual larval feature, that of distinct longitudinal ridges and pleats in the cuticle, known to exist in only three widely separated species: *Pellucidomyia leei* (Heteromyiini; Australia), and two Palpomyiini of the *Bezzia* (*Homobezzia*) *bicolor* group: *B. (H.) bicolor* (Mg.)² in North America(Thomsen 1937), and *B. (H.) xanthogaster*(Kieffer) in Europe(Glukhova 1979b).

The latter two inhabit filamentous algae, but the former was taken from moss on rock outcroppings in the rapids of a stream. The functional significance of such a cuticular character is enigmatic. Because it arose independently in two biogeographically and taxonomically rather unrelated groups, it would be very interesting to investigate this feature further.

With respect to food habits, the larvae of these two tribes appear mainly to be predators(piercers, swallowers), but facultatively many can probably function as either collectors(mainly by detritivory and deposit feeding) or as herbivores-grazers on the aufwuchs coating plants, detritus and others surfaces, especially in littoral regions, which Hutchinson(1981) referred to as the "universal pabulum". *Sphaeromyias* species basically are trophic generalists, reflected in the intermediate robustness of their pharyngeal apparatus, between that of the collecting grazers and more specialized predators.

Larval locomotion by directional swimming can cover considerable distances. Linley(1986)³, investigating swimming behavior of *Culicoides*

² as *Probezzia copiosa* Thomsen.

³ J. Med. Ent. 23(5):473-483

variipennis larvae, found that instar IV larvae(5-6 mm) were capable of directed swimming by rapid sinuous flexion at a sustained speed of ca. 1.7 cm/sec. Larger larvae swim more efficiently than do smaller ones. Thus, larvae such as *Sphaeromias longipennis* would presumably be capable of traveling at considerably greater speed and distances. A second form of locomotion, in probably all larvae of the subfamily Ceratopogoninae, is exhibited in and on semi-solid and firm substrates. Linley(1986, *op. cit.*) has termed this form of locomotion "slow flexing", an eel-like or snake-like gliding over and through surfaces such as sand, mud and plants.

The larvae tend to exhibit limnetic tendencies, particularly immediately prior to pupation, which occurs at what can be characterized as the "air-water-substrate intersectional line", e.g., emersed plants, rocks or mud shores. The capability of directed swimming through the open water column, as well as an effective, serpiginous "sprawling-crawling" locomotion over substrates of all sorts in and out of the water(a waterfilm usually must be present), impart an uncommon "flexibility" to the larvae.

Adaptive Significance of Some Pupal Characters

Apparent morphological diversity in pupae of the Ceratopogoninae is considerably greater than in larvae, despite the fact that the pupal stage lasts merely 3 - 5 days. This would suggest that these pupae are apparently more closely adapted to a particular environment, specifically shorelines, and areas subject to flooding. The pupae of this group cannot actively swim, but can float if necessary; they can and do burrow(into

soft sediments at the shore) and climb emerged objects. The adults apparently all must emerge from a solid substrate above the water line, and cannot successfully emerge from the water's surface.

It is reasonable to assume that pupal characters are phenotypic expressions of particular adaptations to the shoreline environment. This is the context in which I speculated in Chapter 5 (part 5.1.3.2) on the differential functional significance of the so-called "ventral adhesive disks" found on the abdominal segments of certain species of several sphaeromiine genera. Thus, these disks may permit the rather immobile pupae which possess them to more successfully avoid being washed away by wave action or rising water levels, a predominant source of drifting organisms.

Likewise, I would consider the many different manifestations of pupal respiratory horns, thoracic/abdominal tubercles, and other structures to reflect responses to specific conditions in a heterogeneous environment, some of which I referred to in Chapter 5. An additional particularly relevant example might be, for example, the pupae of *Mallochohelea albibasis* group species, which possess large caudally-directed spinose abdominal tubercles and prominent blisterlike protuberances on the thoracic dorsum, but these features are apparently absent in the *M. atripes* species group. The former appear mostly in Order 2 - 4 watercourses, while the latter are primarily lake dwellers. The well-developed tubercles may play a role in attachment to and/or lodging in vegetation or snags in streams.

The exceedingly spiny vestiture of two Australian *Clinohelea* and *Pellucidomyia leei* may likewise be linked with habitat type, especially with respect to vegetation. One possibility is that predation pressure may influence the development of the unusual pupa vestiture (Elson-Harris and Kettle 1986a). That such predation is a reality, especially on unvegetated shores, is exemplified by the recent reports of a carabid beetle (Rieb et al. 1980) and a scatophagid fly (Zimmerman and Turner 1982) preying on ceratopogonid pupae.

Comparative field and laboratory investigations are needed to shed more light on these aspects of organismal adaptation, and would undoubtedly be rewarding.

In general, the Ceratopogonidae appear to possess traits typical of r-selected "fugitive" species normally found in ephemeral or unstable habitats (e.g., mud shores), consistent with the classical and deterministic r- and K-strategy theory (McLeod et al. 1981). They are highly mobile, thus can pass over several microhabitats and so would adapt as generalists. Also, they tend to be polyphagous, and have a fairly high rate of increase.

While this deterministic theory does circumscribe in a very broad way the successful adaptations to shoreline environments by members of the ceratopogonid family, it does not begin to address the complexities of the inter- and intraspecific and ecosystem interactions which take place in these structurally heterogeneous environments. It must also be remembered that even the larvae of the two tribes on which this study focuses are not restricted to shorelines of water bodies as such.

Another theory, a stochastic one(not r- and K-selection), holds that when juvenile mortality fluctuates more than adult mortality, the combination of life-history events expected with the deterministic theory will be reversed (McLeod 1981). The life history events of the of the Ceratopogoninae should be investigated from the perspective of such a theory. In light of the relative lack of pupal mobility in an unstable environment, mortality might be expected to vary more for pupae, particularly, than for adults.

The successful adaptive radiation of these organism must in large part be attributed to (a) the "universal" form of the larvae, (b) their ability to scale, burrow, swim and generally traverse and occupy all manner of niches in and out of the water, and (c) their basically generalist or facultatively predaceous feeding habits, all giving rise to a surprisingly wide range of life styles, habitats and species per habitat. Likewise, the adults and pupae demonstrate "elegant" adaptations to their life space, reflected in behavior and morphology.

The challenges of discerning the isolating mechanisms operating for this relatively ancient primary aquatic family have barely begun to be tackled.

7.2 Conclusions--Section II: Ecoystematics and Autecology

Predaceous biting midges in the tribes Heteromyiini and Sphaeromiini (Ceratopogonidae : Ceratopogoninae) form a small group of biologically and phylogenetically related but taxonomically diverse species, whose adult taxonomy is relatively well established. Systematic and biological study of the immatures, however, has been infrequent, and nearly all has been at the alpha level.

These two tribes contain some 350 described species in 29 genera worldwide, of which 57 species in 12 genera occur in the Nearctic. I reviewed the literature on all zoogeographic regions for species of the Sphaeromiini and Heteromyiini which have at least some descriptive information on oviposition behavior, eggs, larvae, pupae, habitat or biology of immatures. The resulting compilation, given in in Table 37 and including the results of this study, show that the proportion of descriptions available is very low with respect to the total number of species known worldwide, ranging from 2% of the eggs to 18% for the pupae. In the Nearctic, the corresponding proportions range from 3.5 to 30%. Only 9% of the larvae are described.

Such figures are only too characteristic of the enduring problem faced by those who must deal with the indeterminableness of immature insects, particularly holometabolous aquatic ones. I felt it necessary to delve into the specifics of the present "state of the art" vis-a-vis the target insects so as to establish an accurate baseline, and to characterize the relative state of progress in this region compared to others.

Thus, for example, it is quite useful to know that, despite the fact that less than one-third of all Nearctic species are described as pupae, all Nearctic genera of Sphaeromiini have representative species described, even if those species are not necessarily Nearctic themselves; or that only 12 species of the two tribes contribute over 90% of all records of collection, numerically.

But my most important aim in reviewing the world literature was to become acquainted with the extant information, with a view towards synthesis, such as is reflected in the several complex and comprehensive tables presented in this study. This process also considerably broadened the base of information available to me through my own field survey.

The methodology and overall results of this survey, which yielded practically all the material examined in this section, were covered in Chapter One. In the Introduction to Section II, I explained the format and concept for the eclectic treatment undertaken here. In Chapters 2 through 6, I assembled much of what is known about the bionomics, behavior and habitat of the immature stages of some 28 species, 10 genera and the two tribes (Table 12), based on the core of material collected during the field survey. Synopses are provided of the knowledge of the fauna as a whole, including geographic and seasonal occurrence, and of the external morphology of all the developmental stages, with an eye toward discerning adaptive significance, and identifying key gaps in knowledge.

With the results of the present study, I demonstrate the presence, in the Mid-Atlantic region as a whole, of 22 described species in ten genera, and at least three other described species likely to be present,

but not yet recorded here. In addition, this study distinguished three undescribed species of Sphaeromiini (Table 12).

Heteromyiine and sphaeromiine adults and many of the known pupae and larvae possess often striking characters which are individually diagnostic. But comprehensive tribal and generic summaries for characters of the immature stages have not yet been devised due to the lack of appropriate descriptions. Existing descriptions are often rather sketchy, and the material is widely scattered among three or four zoogeographical regions. Also, the number of species described per genus is small, and, normally, the number of available associated specimens as such is very small. This situation makes the development of valid keys difficult, because representative series are not available or readily acquired.

Larvae of the Heteromyiini and Sphaeromiini form a significant component of the so-called "*Palpomyia-Bezzia-Macropenza-complex*", which to date remains difficult to distinguish in this stage, because so few component genera have been reliably described.

Sixteen of the 19 species of Heteromyiini and Sphaeromiini collected in this study were reared from known substrates. Five species were definitively associated with a larval habitat for the first time; for many of the remaining species, the published habitat information had not previously been brought together and interpreted.

The following substrates most characteristically harbor sphaeromiine and heteromyiine larvae: (a) bare shores of wet aerobic mud, silt or sand, usually enriched by finer organic detritus or aufwuchs; (b) littoral

submersed aquatic plant beds or emergent wetlands; (c) mature filamentous algal mats; or (d) soft-mud and detritus-rich bottoms of lakes and ponds. The transitional ecotone of the shorelines can be considered the "archetypical" arena in which ceratopogonine larvae of this group thrive, typically above and below the water line. Significant modifying attributes favoring their presence were described above.

The greatest diversity of larvae in these tribes, in terms of co-occurrence of species in both the microhabitat and in the larger systems, consistently occurs in and along mid-reach streams. This is consistent with biological diversity theory, which indicates that physical and food source heterogeneity are maximized in streams of about 3rd to 5th orders.

Considerable plasticity in habitat associations is exhibited by most species in the tribes, both in terms of substrate preferences and type of water body occupied.

As yet, it is difficult to deduce specific limiting factors for larvae of most species, though some show apparent segregation more clearly than others. Most species for which sufficient collection records are available show fairly consistent habitat preferences.

Within the tribes and genera, on the whole, there does appear to be some internal consistency in habitat choice, which would follow from the assumption of an ecological and evolutionary common base.

Heteromyiine habitats are most often encountered in the forested, shrub, or emergent vegetation sections of palustrine wetlands. They may also be found along depositional and backwater stretches of creeks, streams and small rivers. *Heteromyia* and *Pellucidomyia* fall into the same

phylogenetic generic group, as distinct from *Clinohalea*, which possibly is reflected in differences in the larval habitat preferences of these genera. The two former genera have a strong phytophilic predilection, apparently, while *Clinohalea* is more apt to be encountered on soft saturated or submerged muds.

Larval Sphaeromiini characteristically inhabit the littoral zone of lakes, ponds, rivers and streams. They do not occur to any significant extent in bogs, marshes lacking open water, or forested swamps. Extreme environments, such as temporary pools, intermittent streams, or hot springs, are not exploited.

Several characteristic synecological species assemblages for particular habitat types, in which key species consistently co-occur were distinguished (see esp. Chapter 6). Intraspecific variation in habitat preferences is indicated by some of the results of this study.

Colonization dynamics clearly play a crucial role in the presence of a species in a habitat. With respect to habitat selection, the adult female, the larva, and the pupa all play distinct roles. Oviposition behavior is especially significant to dispersal and reproductive strategies. Therefore, available observations on this behavior in the groups under discussion are of particular ecological interest.

A hovering, pelagio-littoral habit of oviposition appears to be unique to a closely related group of genera in the Sphaeromiini. All genera known to have the hovering ovipositional habit also possess well-developed long curved pairs of hair tufts near the gonopore on the venter of segment VIII (Fig. 9a). There is evidence that the sternal hair tufts

and the legs play a role in guiding and paying out the egg string. All species possessing such well-developed hair tufts may eventually be found to oviposit while in flight, in a manner similar to that described.

In addition to female oviposition behavior and larval dispersal, I addressed other possible mechanisms of ecological partitioning by sympatric species. These include: (a) variable egg maturation times, (b) diurnal temporal segregation, and (c) seasonal temporal partitioning.

Detailed investigations on voltinism and other life history strategies are needed for individual species. As yet, the Ceratopogonidae have defied attempts to fit them into predictive classifications.

Dimorphism in size between males and females can be quite pronounced in some genera, notably *Probezzia* and *Nilobezzia*. Males are typically smaller than females, and in *Probezzia* much smaller, about 60-80% of the female size.

In relation to the question, "to what extent is the diversity among the Heteromyiini and Sphaeromyiini adaptive?", basic to the ecosystematics approach, the following summarizing observations can be made.

Most of the adult key characters are presumably secondary sexual characters, directly or indirectly related to the insectivorous or mating behavior of these predaceous midges, in that the armature apparently plays a role in grappling prey and in mating, and probably in oviposition. Elucidating the probable relationship between the behavior and differential phenotypic expression of leg armature, antennae, genitalic and mouthpart characters, for example, will likely remain a fascinating challenge for some time to come.

The larvae of the tribes Sphaeromiini and Heteromyiini are narrow and cylindrical in the typical "vermiform" characteristic of the subfamily. Most, probably all, can lead a fully aquatic existence.

For many of the genera and species covered, I have drawn attention to four main attributes of the larvae: morphology, habitat, trophic relationships, and locomotion. These attributes contribute most to the evolution and adaptive radiation of this group. The larvae can be thought to be successful by virtue of their generalist nature and universal adaptability on the whole. Their ability to move about efficiently in the open water as well as on substrates of all sorts is undoubtedly a key adaptation critical to their success in the shoreline environments.

The larvae of the tribes Heteromyiini and Sphaeromiini show comparatively little phenotypic morphological diversification, despite the diversity of the habitats they occupy. Yet, significant distinctions can be discerned, especially with respect to the headcapsule, mouthparts, pigmentation and setation.

With respect to food habits, the larvae of these two tribes appear mainly to be predators (piercers, swallowers), but facultatively many can probably function as either collectors or grazers.

In pupae, apparent morphological diversity is considerably greater than in larvae, despite the fact that the pupal stage lasts merely 3 - 5 days. This would suggest that these pupae are apparently closely adapted to a specific environment, i.e., the air-water-substrate intersectional line, due to their relative immobility.

It is reasonable to assume that pupal characters are phenotypic expressions of particular adaptations to the shoreline environment. In this context, I discussed (in Chapters 5 and 7) the possible differential functional significance of the so-called "ventral adhesive disks" and other morphological manifestations of the pupae. Comparative field and laboratory investigations are needed to shed more light on these aspects of organismal adaptation.

Detailing the relationship between taxonomic and ecological diversity with the family Ceratopogonidae will remain a major challenge well into the future, yet there is no doubt that such a pursuit will yield much fruit. Present-day needs in biological inventory and ecological studies emphasize the vital importance of continual advancements in insect systematics at the species level, in particular for the immature stages. In the near future, by combining behavior and other alternative approaches to descriptive systematics, classification and taxonomy may be used widely in predicting ecological aspects of systematically or functionally related species, or both.

Table 37. Species of Heteromyiini and Sphaeromyiini worldwide for which ovipositing behavior, eggs, larvae, pupae, or immatures' habitat or biology have been described, with sources.

Taxa	Sources for Descriptions of					Immatures' Habitat or Biology
	Oviposition Behavior	Eggs	Larvae	Pupae		
HETEROMYIINI (n = 63)						
<u>Climbelelea</u> Kieffer						
Australasian						
<u>dryas</u> Debenham	-	-	Elson-Harris & Kettle 1986a	Elson-Harris & Kettle 1986a	Elson-Harris & Kettle 1986a	Elson-Harris & Kettle 1986a
<u>tasmaniensis</u> Lee	-	-	Elson-Harris & Kettle 1986a	Elson-Harris & Kettle 1986a	Elson-Harris & Kettle 1986a	Elson-Harris & Kettle 1986a
Neartic						
<u>bimaculata</u> (Loew)	-	-	-	Wirth 1951b Grogan & Wirth 1975	Wirth & Grogan 1979 Present study	Wirth & Grogan 1979 Present study
Palaearctic						
<u>unimaculata</u> (Macq.)	-	-	Glukhova 1977, 1979	-	Glukhova 1977, 1979	Glukhova 1977, 1979
<u>Heteromyia</u> Say						
Neartic						
<u>fasciata</u> Say	-	-	-	(This study)	This study	This study
<u>pratti</u> (Coq.)	-	-	-	Wirth & Grogan 1979	Wirth & Grogan 1979	Wirth & Grogan 1979
Neotropical						
<u>clavata</u> Williston	-	-	-	Wirth & Grogan 1977	Wirth & Grogan 1977	Wirth & Grogan 1977
<u>wokei</u> Wirth & Grogan	-	-	-	Wirth & Grogan 1977	Wirth & Grogan 1977	Wirth & Grogan 1977
<u>Pellucidomyia</u> Macfie						
Australasian						
<u>leci</u> Wirth	-	-	Debenham 1974 Elson-Harris & Kettle 1986a	Debenham 1974 Elson-Harris & Kettle 1986a	Wirth 1960 Debenham 1970, 1974 Elson-Harris & Kettle 1986a	Wirth 1960 Debenham 1970, 1974 Elson-Harris & Kettle 1986a

Table 37 (cont'd.)

Taxa	Sources for Descriptions of					Immatures' Habitat or Biology
	Oviposition Behavior	Eggs	Larvae	Pupae		
SPHAEROMIINI (n = 287)						
<i>Hebetula</i> Wirth & Debenham						
Australasian						
<i>tonnoiri</i> (Lee) ^{1/}	-	-	-	Debenham 1974		Debenham 1974
<i>Jenkinshelea</i> Macfie						
Afrotropical						
<i>polyxena</i> deMeillon	-	-	-			Mayer 1952
Nearctic						
<i>albaria</i> (Coq.)	-	-	Wirth & Grogan 1979 ^{2/}	Malloch 1914 Grogan & Wirth 1979a Wirth & Grogan 1979		Wirth 1962a Grogan & Wirth 1977a Wirth & Grogan 1979 Grogan & Wirth 1977a
<i>magnipennis</i> (Joh.)	-	-	-	Grogan & Wirth 1977a		Grogan & Wirth 1977a
Palaearctic						
"sp." ⁴	-	-	Glukhova 1979 ^{2/}	-		Glukhova 1979b
<i>Johannsenomyia</i> Malloch						
Afrotropical						
<i>albidorsata</i> (deM.)	-	-	-			Mayer 1957
Nearctic						
<i>argentata</i> (Loew)	Johannsenomyia 1905	Johannsenomyia 1905 Thomsen 1937 ^{3/}	1st instar: Joh. 1905	Wirth & Grogan 1979		Malloch 1915 Williams 1955 Wirth & Grogan 1979 Bowen 1983a This study

^{1/} as *Nixohelia*

^{2/} See Ch. 3, part 3.3.1

^{3/} In part, at least, *Mallochhelea* sp.

Table 37 (cont'd.)

Sources for Descriptions of					
Taxa	Oviposition Behavior	Eggs	Larvae	Pupae	Immatures' Habitat or Biology
<u>Lanatomyia</u> Debenham (1 sp.)	-	-	Elson-Harris & Kettle 1986b	Debenham 1974 Elson-Harris & Kettle 1986b	Elson-Harris & Kettle 1986b
<u>Leehelea</u> Debenham (2 spp.)	-	-	-	Debenham 1974	Debenham 1974
<u>Macropoza</u> Meigen					
<u>Afrotropical</u>					
<u>aetheopica</u> (I & M) ^{4/}	-	-	-	Mayer 1952	Mayer 1952
<u>bayeri</u> (deM.)	-	-	-	deMeillon 1937	-
<u>natalensis</u> (deM.)	-	-	-	deMeillon 1937	-
<u>Nearctic</u>					
<u>pamunkeiana</u>	-	Knausenberger & Wirth 1980	-	-	(Knausenberger & Wirth 1980)
<u>Palaearctic</u>					
<u>albitarsis</u> Mg.	-	-	(Wirth & Ratana-worabhan 1972)	(Wirth & Ratana-worabhan 1972)	Havelka 1978
<u>Mallochohelea</u> Wirth	-	Thomsen 1937	-	Wirth 1962a	Williams 1955
<u>Australasian</u>					
<u>satelles</u> Debenham	-	-	-	Debenham 1974	-
<u>Nearctic</u>					
<u>albibasis</u> (Malloch)	-	-	This study	Wirth & Grogan 1979 This study	Wirth & Grogan 1979 This study
<u>albihalter</u> Wirth	-	-	-	Wirth & Grogan 1979	Wirth & Grogan 1979
<u>atripes</u> Wirth	-	-	Wirth & Grogan 1979 This study	Wirth & Grogan 1979 This study	Wirth & Grogan 1979 This study

^{4/} as Macroptilium

Table 37 (cont'd.)

Taxa	Sources for Descriptions of					Immatures' Habitat or Biology
	Oviposition Behavior	Eggs	Larvae	Pupae		
<u>Mallochelela</u> (cont'd.)						
<u>flavidula</u> (Mall.)	-	-	-	Malloch 1914	-	-
<u>smithi</u> (Lewis)	-	-	-	This study	This study	
<u>sybleae</u> (Wirth)	-	-	-	Wirth 1952a	Wirth 1952a	
<u>Palearctic</u>						
<u>dentata</u> (Kieffer)	-	-	-	Riech 1915 Thienemann 1928 Lenz 1934 Mayer 1934c Mayer 1952	Thienemann 1928 Mayer 1934a,c	
<u>inermis</u> (Kieffer) ^{5/}	Hamm 1919 ^{6/} Rieb 1981	Hamm 1919 ^{6/}	Glukhova 1971, 1977, 1979	Riech 1915 Thienemann 1928 Lenz 1934 Mayer 1934c	Goetghebuer 1923 Mayer 1934a,c Krivoshchina 1957b	
<u>munda</u> (Loew)	-	-	Glukhova 1971, 1977, 1979b	-	Glukhova 1971, 1979b	
<u>remota</u> Kieffer	Rieb 1981	-	-	-	-	
<u>setigera</u> (Loew)	Rieb 1981	-	Glukhova 1977, 1979b	-	Glukhova 1979b	
<u>Nilobezzia</u> Kieffer	-	-	5 spp. descr. as larvae (world- wide) ^{7/}	ca. 15 spp. descr. as pupae (world- wide) ^{7/}	See Chapter 4, parts 4,7,3 & 4,7,5	
<u>Probezzia</u> Kieffer	-	-	-	14 species descr. in Nearctic ^{8/}	Williams 1955 Wirth 1971 Bowen 1983a,b	
<u>Nearctic</u>	-	-	-	Wirth & Grogan 1979 This study	Wirth & Grogan 1979 This study	
<u>albitibia</u> Wirth	-	-	-	-	-	

^{5/} Including M. nitida (Marquart) as Johannsenomyia

^{6/} as Ceratopogon nitida (Macq.)

^{7/} See Table 20.

^{8/} See Table 22.

Table 37 (cont'd.)

Sources for Descriptions of					
Taxa	Oviposition Behavior	Eggs	Larvae	Pupae	Immatures' Habitat or Biology
<u>Probezzia</u> (cont'd.)					
<u>pallida</u> Mall.	-	-	(This study)	Wirth & Grogan 1979 This study	Muttkowski 1918 Suow et al. 1957 Wirth & Grogan 1979 Bowen 1983a,b This study
<u>smithi</u> (Coq.)	-	-	-	Wirth & Grogan 1979 This study	Wirth & Grogan 1979 This study
<u>xanthogaster</u> (Kieffer)	-	-	-	Wirth & Grogan 1979	Wirth & Grogan 1979 This study
Palaeartic ^{9/}	-	-	-	See Ch. 5, pt. 5.1.5	Wirth & Grogan 1979 This study
<u>concinna</u> Mg. ^{9a/}	Messenberg-Iand 1914, 1915, 1943 Rieth 1915 Munsterjhelm 1920 Thienemann 1928 Lenz 1934	Rieth 1915 Thienemann 1928 Mayer 1934c	-	Thienemann 1928 Mayer 1934c	Krivoshelna 1957a,b Thienemann 1928 Mayer 1934c
<u>semitigra</u> ^{9,10/} (Panzer)	Rieb 1981	Lenz 1934 ^{10/}	Glukhova 1971, ^{10/} 1977, 1979	Rieth 1915 ^{11/} Thienemann 1928 Mayer 1934c	Rieth 1915 Mayer 1934a,c Weerekoon 1953 Glukhova 1977, 1979
4 <u>Sphaeromias</u> spp. Curtis	-	-	-	Wirth 1962b	Brundin 1949 Glukhova 1979b + many others
Afrotropical					
<u>par</u> (I & M)	-	-	Carter, Ingram & Macfie 1921	Carter, Ingram & Macfie 1921	Carter, Ingram & Macfie 1921 Clastrier 1961

^{9/} early records in genus Dicrobezzia
^{10/} as P. venusta (Meigen), resp. Dicrobezzia venusta
^{11/} as Bezzia venusta (Meigen)
^{9a/} P. concinna = jr. syn. of P. semitigra

Table 37 (cont'd.)

Taxa	Sources for Descriptions of					Immatures' Habitat or Biology
	Oviposition Behavior	Eggs	Larvae	Pupae		
<u>Sphaeromias</u> (cont'd.)						
Nearctic						
<u>longipennis</u> (Loew)	Malloch 1914 This study	Malloch 1914	Malloch 1915, 1979 Thomsen 1937 Wirth & Grogan 1979 This study	Malloch 1914 Thomsen 1937 Wirth & Grogan 1979 This study	Malloch 1914 Muttkowski 1918 Williams 1955 Snow & Pickard 1958 Wirth 1962b Wirth & Grogan 1979 This study	
Palearctic						
<u>candidatus</u> (Loew)	-	-	Glukhova 1979b	-	Glukhova 1979b	
<u>fasciatus</u> (Mg.)	Thienenmann 1928	Thienenmann 1928, 12/	Gerke 1879, 13/ Mayer 1934c Glukhova 1977, 1979b	Gerke 1879, 13/ Mayer 1934c Thienenmann 1928	Mayer 1934c Strentzke 1951 Remmett 1955 Krivosheina 1957 Glukhova 1977, 1979b	
<u>pictus</u> (Mg.) ^{14/}	-	-	Zavrel 1926, 13, 15/ Glukhova 1971, 1977, 1979b	Zavrel 1926, 13, 15/ Thienenmann 1928 Mayer 1934c	Thienenmann 1928, 1954 Mayer 1934c Glukhova 1971, 1977, 1979b	
1						
^{12/} as <u>Xylocrypta</u> <u>ocularis</u>						
^{13/} in Hennig 1950						
^{14/} early records as <u>S. copiosa</u>						
^{15/} as <u>Xylocrypta</u> <u>copiosa</u>						

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Appendix A. COLLECTION SITE RESULTS

Appendix Table 3B . Conspectus of Knausenberger's (WIK) and Battle's (FVB) Collection Numbers for sites which yielded the species of Ceratopogonidae listed. Columns are arranged according to method of collection or processing. Mnemonic codes in the column headings refer to specimens obtained in the following ways: "AFT" for Adults Field-Trapped, i.e., captured by various means in the field (ASP, BL, DV, INC, SW, TT); "IMM": Immature Specimens extracted from habitat substrate material; "IR": Individually Rearing immature specimens to adulthood (or attempted); "RC" Rearing Collectively in emergence (Rearing) Cartons at Laboratory. Battle's collections appear only under the RC column heading, following the underlined notation "FVB". See text and Table for further elucidation of abbreviations.

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Rearing (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Rearing Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<u>LEPTOCOPOPIINAE</u>				
<u>Leptocoopos</u> Skuse	-	-	-	DV-14.
<u>L. linleyi</u>	-	-	-	-
<u>FORCIPOMYIINAE</u>				
<u>Atrichopogon</u> Kieffer	-	-	152, 155, 174, 285A, 316E.	BL-22.
<u>A. appendiculatus</u>	-	-	-	BL-9, TT-10, DV-16, INC-48; B-5.
<u>A. fuscus</u>	285A.	-	-	B-1A, B-4, B-5.
<u>A. fusinervis</u>	-	-	-	BL-9, DV-16.
<u>A. geminus</u>	-	-	-	BL-11, DV-12, SW-18, SW-19, INC-48, B-4.
<u>A. levis</u>	-	-	-	-
<u>A. minutus</u>	-	-	21, 173.	B-4
<u>A. cf. peregrinus</u>	-	-	152, 319B.	-
<u>A. sp. 1 nr. peregrinus</u>	-	-	-	-
<u>A. sp. 2 nr. peregrinus</u>	-	-	-	-
<u>A. cf. websteri</u>	-	-	316A.	B-1A, B-4, W-C.
<u>A. sp. undet.</u>	398A, 400B, 401B.	105, 109, 152, 238, 398A, 400B, 401A, 401B, 406A,	122, 171, 173, 207C, 263C, 268B, -C; 274, 285C, 291B, 299, 330B, 400B, 401A, 406A,	TT-3, BL-13, DV-15, DV-16, DV-20, BL-27, SW-31, BL-32, BL-33, BL-34, DV-36, SW-37, SW-38, DV-44, BL-46, BL-50, BL-53, BL-58.
<u>Forcipomyia</u> Meigen	-	-	-	BL-46; B-2, B-4.
<u>F. (Calofoarcipomyia) blauca</u>	-	-	-	-
<u>F. (Euprojoannisia) hirtipennis</u>	-	266B.	266B.	-
<u>F. (Forcipomyia) bipunctata</u>	-	-	44, 94A, 94D.	-
<u>F. (F.) brevipennis</u>	-	-	94A.	-
<u>F. (F.) bystraki</u>	-	-	-	-

Appendix Table 38 . (Cont'd)

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<u>Forcipomyia</u> cont'd.				
<u>F. (F.) fimbriata</u>	-	-	60.	-
<u>F. (F.) pinicola</u>	-	-	60.	-
<u>F. (F.) solonensis</u>	-	-	-	-
<u>F. (F.)</u> sp. undet.	94E.	94E, 108.	85, 94A, 107, 122.	BL-11, DV-12, SW-18, SW-19, BL-50.
<u>F. (Lasiohelea) fairfaxensis</u>	-	-	229B.	-
<u>F. (subg. nr. Lepidohelea) sp.</u>	-	-	-	BL-46.
<u>F. (subg.)</u> sp. undet	148.	113A, 159, 285B.	108, 271B, 131B.	DV-21, BL-26, BL-27, SW-31, BL-32, SW-37, BL-42, BL-53.
DASYHELEINAE				
<u>Dasyhelea</u> Kieffer				
<u>D. cf. atlantis</u>	306.	-	306.	DV-14.
<u>D. cf. brevicosta</u>	-	-	263C FVB:132.	-
<u>D. cincta</u>	-	-	348.	-
<u>D. cincta</u> gr.	325A, 348.	348.	-	-
<u>D. (cincta gr.)</u> sp.8 nr. <u>maculata</u>	130	-	FVB:21, 55.	-
<u>D. grisea</u>	246, 248, 299, 303A, 307.	299, 303A, 306, 307, 343A, 348.	43, 48, 92B, 115, 153, 190, 195, 245, 246, 248, 263C, 288A, 299, 303A, 307, 308, 312A, 343A, 348, FVB:54, 77A.	DV-14, BL-27.
<u>D. grisea</u> gr.	235, 293A, 348.	302, 305, 396A.	78, 305, 348, FVB:138, 50B.	-
<u>D. leptobranchia</u>	7, 357, 395.	395.	357, FVB:21, 36, 52.	-
<u>D. leptobranchia</u> gr.	130, 238, 348, 396A.	238.	-	-
<u>D. (leptobranchia gr.)</u> sp. 9	-	-	263C.	-
<u>D. major</u>	114, 263C, 402.	42, 114, 216, 402.	42, 114, 130, 263C, B-1A, FVB:21, 34.	B-1A.
<u>D. messersmithi</u>	7, 238, 287A, 328, 380.	-	GH-1, FVB:96.	-
<u>D. mutabilis</u>	114, 246, 325A, 361B.	-	64, 65B, 78, 79, 96, 114, 116, 273B, 313B, 313C, 316A, 125A, 331B, 333A, 333E, 333F; B-1A, B-4, B-5, CL-1, FVB:8A, 11B, 12B, 208, 21, 23, 35, 65A, 80, 85, 93, 121B, 122B, 161B, 178B, 180A, 184A.	BL-53, ET-68
<u>D. mutabilis</u> gr. indet.	235, 345.	-	115, 288B, 345.	345
<u>D. (mutabilis gr.)</u> sp. 1	306.	-	259, 306, 313B, 313C.	-
<u>D. (mutabilis gr.)</u> sp. 2	288B.	-	235, 288B.	-

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<i>Dasyhelea</i> cont'd.				
<i>D. (mutabilis gr.)</i> sp. 3	-	-	-	11V-14 SW-31, SW-37.
<i>D. (mutabilis gr.)</i> sp. 4	-	-	27JB.	-
<i>D. (mutabilis gr.)</i> sp. 5	-	-	284	Cranberry GL, WV, 4-VIII-1972.
<i>D. (mutabilis gr.)</i> sp. 7	-	-	FVB:132.	-
<i>D. navatae</i>	-	-	316A, FVB:36	-
<i>D. oppressa</i>	29JB, 387B.	29JB, 387B.	9, 47, 94D, 103, 106, 107, 241B, 259, 261B, 271C, 293A, 293B.	BL-46
<i>D. pollinosa</i>	-	-	96, 210, 302.	-
<i>D. pseudoinclusurata</i>	261B, 261D, 263C, 299.	299.	78, 261B, 261D, 263C, 299.	-
<i>D. cf. spiniforma</i>	-	-	288B.	-
<i>D. stemlerae</i>	398A.	398A.	257A, 316A; FVB:57A.	-
<i>D. sp. nr. stemlerae</i>	357.	-	78.	-
<i>D. traverae</i>	-	-	41, 165, 312B, 313B, 313C, 316C, 316D, 325A, B-2B; FVB:13B, 85	DV-15
<i>D. sp. 6</i> (group undet.)	-	-	FVB:21	-
<i>D. sp. undet.</i>	174, 235, 256, 261B, 284, 287A, 296, 316A, 323A, 328, 345, 392, 395.	67, 94E, 100B, 101, 103, 105, 174, 256, 258, 270A, 316A; B-1, B-2, B-3, B-4, B-5; GH-1, GH-2; GL-1, GL-5; W-A, W-C, W-E.	93, 99, 105, 238, 265, 268B, 268C, 333B, 345.	SW-38, ET-68.
CULICOIDINI				
<i>Culicoides</i> Latreille				
<i>C. alexanderi</i>	-	-	-	BL-1, BL-43
<i>C. arboricola</i>	387A.	-	9, 159.	11V-14
<i>C. baueri</i>	253, 302.	-	95, 113A, .165, 167L, 243, 278A, 302, 361A, 1B-1A, B-1B, B-4, B-5, BSM, GH-1, GH-1, W-A, FVB:2A, 11A, 15A, 19A, 24, 44A, 44B, 48A, 48B, 63A, 63B, 71A, 71B, 72B, 89, 95, 112, 122A, 122B, 126B, 127A, 133, 134, 144A, 144B, 149B, 162A, 165A, 165B, 168A, 168B, 174A, 177B, 180A, 180B, 181A, 183B, 186A, 186B, 188A, 189A, 189B, 191A, 192B.	BL-13.
<i>C. bergi</i>	-	-	67, B-1B, B-5, BSM, GH-1, W-C.	-
<i>C. bermudezsis</i>	301, 307.	301, 307.	301, 307.	INC-48.

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			Adult Field-trapped (AFT)
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	
<i>Uliicoides</i> cont'd.				
<i>C. bickleyi</i>	255,261B.	-	240B, 256, 270A, 270B, 270C, 270D, 270E, 274, 292, 326H.	BL-1, BL-4, BL-9.
<i>C. biguttatus</i>	284, 391.	-	54, 219, 270C, 270E, 284, 289, B-1A, FVB:13B, 26, 50A, 50B, 59B, 60, 65A, 65B, 66, 67.	BL-1, -8, -9, -27, 40, DV-24, -30, ASP-23, BL-26.
<i>C. chiopterus</i>	-	-	-	ET-68, F1-69.
<i>C. crepuscularis</i>	69C, 84, 108, 160, 238, 246, 263C, 319A, 345, 357, 389-1.	50, 105, 108, 113B, 160, 166A, 177B, 391.	50, 52, 65B, 67, 69A, 69B, 69C, 70, 71, 73, 76, 77B, 78, 79, 84, 86, 88, 93, 95, 96, 105, 108, 113A, 113B, 116, 138, 160, 161A, 166A, 177B, 207C, 215, 222A, 222B, 240A, 240B, 241A, 241B, 246, 248, 258, 291B, 292, 325B, 328, 333B, 345, 357, B-1A, B-2A, B-2B, B-4, B-5, BSM, CH-1, GL-1, GL-3, GL-5, W-A, W-C, W-E; FVB: 3A, 3B, 7A, 7B, 8A, 8B, 9B, 11A, 11B, 12A, 12B, 15A, 15B, 16A, 19A, 19B, 20A, 20B, 805, 808, 23, 24, 25, 27, 36, 39, 44B, 45A, 45B, 49A, 49B, 50A, 54, 62A, 62B, 63A, 63B, 64A, 68A, 68B, 69A, 69B, 70B, 71A, 71B, 72A, 72B, 74A, 74B, 76A, 76B, 77A, 77B, 78A, 78B, 79A, 79B, 88, 90, 96, 99, 100, 107, 108, 112, 115A, 115B, 116A, 116B, 117A, 117B, 119, 120A, 120B, 121A, 121B, 122A, 122B, 123A, 123B, 124A, 124B, 125A, 125B, 126A, 126B, 127B, 138A, 139A, 139B, 140A, 142A, 142B, 143A, 143B, 158A, 158B, 159A, 159B, 160B, 161A, 161B, 162A, 162B, 164B, 165A, 165B, 166A, 166B, 167B, 168A, 168B, 169A, 169B, 171A, 171B, 173B, 174B, 175A, 175B, 177A, 177B, 178A, 178B, 179A, 180A, 180B, 181A, 181B, 182A, 182B, 183A, 183B, 184A, 184B, 185A, 185B, 186A, 186B, 187A, 187B, 188A, 188B, 189A, 189B, 190A, 190B, 191A, 191B, 192A, 192B.	
<i>C. debilipalpis</i>	-	-	26, 32, 113A, 313B.	BL-13, SW-41.
<i>C. denticulatus</i>	-	-	-	BL-43, 67.
<i>C. footei</i>	-	-	-	BL-46.
<i>C. furens</i>	297.	115, 137, 297.	115, 134, 137, 222B, 297, 300, 116, FVB: 29, 30, 35.	BL-13, DV-20, SW-31, BL-32, BL-34, SW-37, SW-38, SW-41, INC-48.
<i>C. furensoides</i>	400B.	-	278A; (C Aug. 4, 1972	BL-26, -27, BL-46.
<i>C. guttipennis</i>	3, 12, 156, 293A, 387A, 387B.	12.	9, 47, 69B, 104, 106, 158, 230, 317, 319A, 387A, B-4 B-5, FVB: 141.	BL-26, BL-46, ASP-65.
<i>C. haematopodus</i>	23, 42, 124, 167U, 176, 188, 194, 238, 241A, 245, 253, 261C, 263C, 312A, 313A, 314A.	23, 24, 42, 63, 124, 127, 166B, 167U, 176, 179, 180, 194, 375, 383.	17, 20, 21, 23, 24, 31, 42, 44, 61, 63, 69A, 69B, 70, 77B, 85, 86, 88, 89, 95, 101, 113A, 120, 123, 124, 127, 161A, 161C, 166B, 167U, 167L, 176, 178, 179, 180, 188, 194.	BL-9, DV-20, BL-27, SW-41, BL-46, BL-50, 345-ET.

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			Adult Field-Trapped (AFT)
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	
<u>Culicoides</u>				
<u>C. haematopodus</u> cont'd.	325B, 327H, 332A, 333E, 345, 345, 362, 369, 375A, 377, 383, 384.		196, 221, 222A, 222B, 224, 230, 233, 241B, 241C, 243, 245, 246, 253, 254, 261C, 275, 285A, 288B, 292, 296, 312A, 313A, 316E, 319E, 325B, 327B, 331B, 332A, 333A, 333B, 333E, 345, 364, B-1A, B-1B, B-2A, B-2B, B-4, B-5, 6SM, GH-1, GH-2, GL-1, GL-3, GL-5, M-A, M-C, M-E, FVB: 3A, 3B, 7B, 8A, 11A, 11B, 12A, 12B, 13A, 13B, 14B, 15A, 15B, 16A, 16B, 18B, 19A, 19B, 20A, 20B, 802, 805, 808, 809, 811, 23, 24, 25, 27, 34, 36, 37, 38, 39, 42, 44A, 44B, 45B, 48A, 48B, 49B, 51, 53, 61, 63A, 63B, 68B, 72A, 72B, 75A, 75B, 76B, 78B, 79A, 79B, 80, 84, 86, 87, 88, 89, 91, 95, 96, 97, 100, 101, 102, 103, 104, 107, 112, 113, 115A, 115B, 116A, 116B, 117A, 117B, 120A, 120B, 121A, 121B, 122A, 122B, 123A, 123B, 124A, 124B, 125A, 126A, 126B, 127B, 133, 137B, 138A, 138B, 139B, 141, 142A, 142B, 143B, 158A, 158B, 161A, 161B, 162A, 162B, 163A, 164A, 164B, 165A, 165B, 168A, 168B, 170A, 170B, 171A, 171B, 173B, 174A, 174B, 175A, 175B, 177A, 177B, 178A, 178B, 179A, 180A, 180B, 181A, 181B, 182A, 182B, 183A, 183B, 184A, 184B, 185A, 185B, 186A, 186B, 187A, 187B, 188A, 189A, 189B, 190A, 190B, 191A, 191B, 192A, 192B.	
<u>C. hinmani</u>	293A.	-	37, 107.	-
<u>C. hollensis</u>	114, 118.	114;	114, 118, FVB: 29, 30.	BL-32; INC-49.
<u>C. jannbacki</u>	-	-	18, 21.	BL-1, -4, -8, -9, -46, -27.
<u>C. juddi</u>	-	-	159.	-
<u>C. loisae</u>	-	-	196, M-A, FVB: 81, 97, 117A, 141.	-
<u>C. melleus</u>	298	-	298, FVB: 30.	DV-14, DV-20, INC-48.
<u>C. mulrennani</u>	-	-	277.	ASP-2, -23, 25, -28, -52, BL-4, -22, -27, -30; DV-24.
<u>C. nanus</u>	-	-	158, 328.	-
<u>C. obsoletus</u>	-	-	-	BL-1, -4, -27, DV-20, -30; ASP-23, -45.
<u>C. paraensis</u>	293A.	-	-	ASP-35, -40, ASP-51, INC-61.
<u>C. patapilliferus</u>	-	-	161B.	-

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<u>C. piliferus</u> cont'd.				
<u>C. piliferus</u> s. s.	388, 394.	-	255, 269A, 272B, FVB: 7B, 67, 75A, 75B.	BL-46, BL-1, BL-4, -27; DV-21
<u>C. piliferus</u> gr.	240A, 240B, 255, 270D, 326A, 327B, 400B, 401A.	400B.	100B, 255, 257B, 270A, 270B, 270E, 274, 362, 371B, FVB: 37, 50A, 50B, 59B, 61, 65B, 66, 67, 75A, 75B, 106, 94D, 153, 263B, 274.	BL-46, TT-7.
<u>C. sanguisuga</u>	-	-	94D, 153, 263B, 274.	ASP-2, -33, -52; BL-1, -4, -8, 46.
<u>C. scanloni</u>	-	-	255.	-
<u>C. sphagnumensis</u>	171, 400B.	171, 232B.	171, 328.	BL-26.
<u>C. spinosus</u>	214A, 214B, 245, 357.	-	214A, 214B, 232B, 234, 243, 245, 255, 275, 357, B-1A, BSM, CH-1, FVB: 13A, 13B, 802, 22, 23, 27, 32, 40, 48B, 50A, 50B, 51, 59A, 59B, 65A, 65B, 71A, 75B, 89, 91, 114.	-
<u>C. stellifer</u>	1, 279, 322A, 323A, 325A, 375B.	-	21, 76, 113A, 119, 161A, 161B, 166B, 201C, 214B, 217, 218B, 221, 222A, 222B, 241C, 243, 279, 292, 361A, 381, B-1A, B-2, B-4, B-5, BSM, CH-1, W-A.	BL-13, -34, -50; DV-20, SW-41.
<u>C. testudinialis</u>	-	-	255, 272B, FVB: 50A, 65A, 65B, 75B.	-
<u>C. travisi</u>	-	-	240A, 240B, 261B, 363, CH-1, FVB: 20A, 20B, 50B, 56A, 59A, 62B, 65B, 75A, 106.	-
<u>C. variipennis</u> s. l.	23, 108, 113B, 120, 141, 160, 161C, 163, 240A, 407B, 407C.	23, 44, 108, 113B, 120, 160, 163, 407A, 407B, 407C.	23, 25, 44, 69A, 69B, 74, 76, 77B, 78, 79, 81, 86, 108, 113B, 119, 120, 122, 160, 161B, 218B, 240A, 407B, B-1, B-4, FVB: 3A, 7B, 11A, 11B, 12B, 15A, 39, 44B, 45A, 45B, 47A, 49A, 56A, 56B, 57A, 57B, 58A, 58B, 62A, 63A, 63B, 64A, 64B, 68A, 68B, 69A, 69B, 70A, 70B, 71B, 72A, 72B, 73A, 73B, 74A, 74B, 76A, 76B, 77A, 77B, 79A, 79B, 110, 115B, 117A, 117B, 121B, 122B, 123B, 124B, 138B, 162A, 180B, 183B, 184A, 190B, 191B.	ASP-66.
<u>C. venustus</u>	214B, 285B.	64.	64, 101, 113A, 169, 196, 214B, B-1A, B-1B, B-4, B-5, (L-1, W-C; FVB: 3A, 65A, 115A, 116B, 122A, 122B, 124A, 125A, 125B, 126A, 127A, 114B, 161B, 162A, 167A, 175A, 180A, 181B, 184A, 187B, 191A, 142, 387A.	BL-27.
<u>C. villosipennis</u>	142, 387A, 387B.	387B.	142, 387A.	BL-27, BL-46.
<u>C. sp. undet.</u>	1, 7, 49, 52, 59, 91, 92A, 94E, 100A, 101, 109, 110, 113A, 116, 117, 125, 129, 138, 140, 141, 146, 153, 163, 168A, 170, 173, 174, 177A, 177B, 177D, 178, 182, 183, 186, 191, 192, 196, 200, 207C, 211, 212, 214A, 218A, 218B, 222A, 222B, 225, 232B, 235, 238, 240A, 243, 246, 252, 253, 255, 256,	9, 15, 16, 18, 21, 36, 55, 59, 67, 69A, 69B, 78, 84, 89, 92A, 93, 94A, -D, -E; 99, 100A, -B, 101, 102, 106, 109, 110, 113B, 119, 128, 129, 138, 141, 149, 152, 157, 158, 159, 161A, -B, -C; 162, 165, 166A, 168A, 172, 174, 177A, -B, -D; 182, 183, 186, 190, 191, 192,	255, 257A, 257C, 270A, 270D, 274, 347.	

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<u>Culicoidini</u>				
<u>C. sp. undet.</u> cont'd.	2688, 2698, 2700; D, E, 2728, 278A, 281, 284, 285A, 285B, 292, 296, 300, 302, 319A, 3198, 320A, 322A, 324, 325A, 325B, 326A, 328, 329A, 331A, 331B, 333C, 345, 361B, 364, 374B, 374C, 387C, 393, 401B.	196, 200, 201A, -D, 203, 204, 211, 212, 214B, 215, 218A, -B, 235, 236, 238, 240A, 240B, 241A, 245, 246, 252, 253, 255, 256, 257B, -C, 268B, 270A, -C, -E, 281, 285B, 291, 302, 326B, 343A, 360A, 371B, 374B, 375D, 401B, 406A.	21, 23, 32, 90A, 177C, 181, 187, 211, 263A, 263B, 269B, 273A, 281, 284, 313B, 313C, 316A, 316C, 319E, 320A, 333A, 333B, 333E, 333F, 347; B-1A, B-2B, BSM, W-C, FVB: 13B, 27, 51, 92, 810.	Bl.-64, ET-68
CERATOPOGONINI				
<u>Alluaudomyia</u> Kieffer ^{3/}				
<u>A. bella</u>	234, 268A, 279, 281, 294, 296, 313B, 319B, 319E, 321, 330A, 330B, 331B, 333A, 333B, 333E, 333G, 370A, 370B, 374C, 397C, 404.	21, 177C, 404.	21, 23, 32, 90A, 177C, 181, 187, 211, 263A, 263B, 269B, 273A, 281, 284, 313B, 313C, 316A, 316C, 319E, 320A, 333A, 333B, 333E, 333F, 347; B-1A, B-2B, BSM, W-C, FVB: 13B, 27, 51, 92, 810.	Bl.-64, ET-68
<u>A. sp. nr. footed</u>	-	-	195, 211.	-
<u>A. megaparamera</u>	390.	-	241B, 261C, 393; BSN, GH-1, GH-2, W-C, FVB: 61	-
<u>A. needhami</u>	241C, 319D, 321, 365, 375A, 390, 397A.	375A,	177C, 241B, 243, 246, 333F; B-1A.	-
<u>A. paraspina</u>	370A, 370B, 391.	-	273B, 313B, 405.	-
<u>A. parva</u>	343A.	-	36, 55, 85, 270B, 270E, 278A, 343A, 380.	Bl.-27
<u>A. sp. undet.</u>	211, 269A, 281, 288B, 319C, 319D, 320A, 322A, 323A, 333F, 405.	41, 84, 195, 211, 326B, 346, 370A, 403, 405, B-1, GH-1, GH-2, W-C.	333F.	-
<u>Brachypogon</u> Kieffer	-	-	52B.	INC-61.
<u>Br. canadensis</u>	-	-	270D, FVB: 805	-
<u>Br. sp.</u>	-	-	-	-
<u>Isohelea</u> Kieffer	396A.	396A.	52, 270A, 270B, 270C, 270D, 271B, 278A, 381.	1/
<u>I. sp. 1 nr. serrata</u>	-	-	FVB: 106	-
<u>I. sp. 2</u>	-	-	257A, 260, 275; FVB: 5, 61, 152.	2/
<u>I. sp. 3</u>	-	-	-	1/
<u>I. sp. 4</u>	-	-	-	-

1/ Cranberry Gl., WV, 6 Aug. 1972

2/ Vesuvius, VA, 11 May 1966, J. Humphries, coll.

3/

The genus Alluaudomyia is likely to be re-assigned to the tribe Stilobezziini (e.g., Wirth and Grogan 1981)

Appendix, Table 38 . (Cont'd)

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<u>Isohelea</u> cont'd.				
<u>I. sp. 5</u>	-	-	257B.	-
<u>I. sp. 6</u>	-	-	271B	-
<u>I. sp. undet</u>	257A, 260, 278A, 400B,	257B, -C; 395, 400B, 406B.	257A, -B; 260, 270C, 270D, 271B, 278A.	-
STILOBEZZIINI				
<u>Echinohelea</u> Macfie				
<u>E. lanei</u>	-	-	29.	DV-21.
<u>Monohelea</u> Kieffer				
<u>M. cf. bifurcata</u>	-	-	-	BL-33, BL-34, BL-46,
<u>M. sp. nr. floridensis</u>	-	-	123	-
<u>M. hieroglyphica</u> gr.	-	-	275	-
<u>M. cf. macfiei</u>	-	-	FVB: 106	-
<u>M. obscura</u>	-	-	-	BL-1.
<u>M. stonei</u>	-	-	119, 222B.	BL-11, DV-12, SW-18, SW-19, BL-33, BL-34, BL-53; Cranberry Gl., WV, 6-VIII-72,
<u>M. sp. undet.</u>	-	-	313A.	-
<u>Parabezzia</u> Malloch				
<u>P. alexanderi</u>	-	-	375B; FVB: 804, 34.	-
<u>P. cf. eupetiolata</u>	-	-	FVB: 86.	-
<u>P. sp. prob. huberti</u>	-	-	B-111 11-VII-1971	-
<u>P. sp. undet.</u>	-	-	76.	-
<u>Serromyia</u> sp.				
<u>S. sp.</u>	-	31	-	-
<u>Stilobezzia</u> Kieffer				
<u>S. (Neostilobezzia) lutea</u>	272B, 302, 322A, 388, 396A.	302, 396A.	51, 257A, 272B, 278B, 362, 396A; CH-1	TT-3, BL-46.
<u>S. (N.) stonei</u>	-	-	148, FVB: 46, 61.	TT-7, BL-26, -27.
<u>S. (Stilobezzia) antennalis</u>	23, 83, 92A, 141, 145A, 163, 177A, 217, 239, 246, 248, 258, 285C, 292, 294, 299, 303A, 312A, 319A, 319E, 325A, 325B, 329A, 363, 383.	23, 64, 163, 177A, 187, 246, 299, 303A, 383.	23, 52, 56, 64, 76, 92A, 92B, 93, 95, 105, 129, 141, 145, 163, 177A, 187, 217, 245, 246, 248, 273B, 288A, 292, 296, 299, 303A, 306, 312A, 312B, 319A, 325B, 368A; B-1A, B-2A, B-3, B-4, BSH, GH-1, GI-1, W-A, 49A, 56A, 58A, 62A, 64A, 64B, 70A, 70B, 72B, 74A, 74B, 76A, 76B, 79A, 107, 1163A, 182A.	BL-13, BL-50, BL-64.

Appendix Table 38 . (Cont'd)

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<i>Stilobezzia</i> cont'd.				
<i>S. (S.)</i> sp. nr. <i>antennalis</i>	-	-	324A; FVB:62A,62B,68A,68B,107.	BL-13,DV-16.
<i>S. (S.)</i> <i>beckae</i>	-	-	207C	-
<i>S. (S.)</i> <i>bullae</i>	128,171,173,214B,225,235,278A,278B,288B,290B,319A,322A,328,331A,401A,404.	128,155,171,404.	28,127,128,130,145A,155,156,171,173,225,230,258,278A,278B,288A,288B,313B,316E,320A,328, FVB:6A,9B,13A,B;802,808,24,27,32,34,36,46A, B;50B,65B,74B,75A,79A,85,104,127B.	DV-5.
<i>S. (S.)</i> <i>coquilletti</i>	141,160,163.	67,69B,78,160,163.	67,69B,71,73,74,76,77B,138,160,163,204;B-1A, B-1B,B-2A,-2B,B-3,B-4,B-5,BSM,GH-1,GH-2,W-A, FVB:25,26,45A,B;49A,58A,B;64A,B;70A,B;74A, 79A,163A,178A,184A.	-
<i>S. (S.)</i> <i>diversa</i>	288B,292,354.	-	63,94E,180,288B.	-
<i>S. (S.)</i> <i>glauca</i>	279,288B,296,332A,405.	-	238,279,288A,288B,333D;BSM; FVB:27,36.	-
<i>S. (S.)</i> <i>pallidiventris</i>	-	-	229B,230.	-
<i>S. (S.)</i> <i>sybleae</i>	132,331A,363,383.	383.	20,76,99,130,132,306;B-1A,B-1B; FVB:21, 34,52,56A,72A,182A.	-
<i>S. (S.)</i> sp. gr. nr. <i>sybleae</i>	-	68.	21,68,86,90A,90B,248,278A,319A, 27,58B,68A,70A,B;14A,B;115B,182B.	ASP-45.
<i>S. (S.)</i> sp. A nr. <i>sybleae</i> *	28.	-	20,28,31,41,187,215. FVB:148A.	-
<i>S. (S.)</i> sp. B nr. <i>sybleae</i>	225.	-	20;B-1A,B-1B,BSM,GH-1,W-C. FVB:45B,49A,58A 70A,B;115B,182B.	-
<i>S. (S.)</i> <i>viridis</i>	93,109,176,375B.	-	21,28,93,201A,232B,313B.	-
<i>S. spp.</i> undet.	141,214B,278B,288A,295, 320B,325B,331A,331B,347, 357,380.	28,92A,92B,105,141, 156,176,201A,238,258, 292,331A,380.	176,263B,278B,313B.	-
* = <i>navatae</i>				
HETEROMYIINI				
<i>Clinohelae</i> Kieffer				
<i>Cl. bimaculata</i>	268B.	268B	53,119,160A,176,179,192,201C,253,268B,309, 405; FVB:802,810.	DV-21,-24;BL-27.
<i>Cl. curriei</i>	-	-	122.	-
<i>Heteromyia</i> Say	-	-	313B.	-
<i>H. fasciata</i>	-	-	-	-
SPIAEROMIINI				
<i>Jenkinshelia</i> Macfie	-	-	-	BL-5B
<i>Jen. albaria</i>	-	-	-	-

Appendix Table 38 . (Cont'd)

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<u>Johannsenomyia Malloch</u>				
<u>Joh. argentata</u>	262.	-	39; GH-2.	-
<u>Macropeza Meigen</u>	-	-	-	BL-47, BL-53.
<u>Mac. pamunkefana</u>	-	-	-	-
<u>Mallochebelea</u>	-	-	245, 269C, GH-1; FVB 37, 42, 811	-
<u>Mall. albibasis</u>	-	-	34, 39, 281, 316C. FVB: 85	BL-47, BL-50, BL-53
<u>Mall. atripes</u>	316C, 316D, 335.	335.	255, 359, GH-1	-
<u>Mall sp. nr. caudellii</u>	7.	-	-	-
<u>Mall. smithi</u>	379.	-	245	-
<u>Mall sp. undet.</u>	245, 331A.	-	-	-
<u>Probezzia Kieffer</u>				
<u>Pr. albitibia</u>	12.	-	FVB: 94	-
<u>Pr. sp. nr. albitibia</u>	253.	-	-	-
<u>Pr. pallida</u>	383, 385.	383.	GL-1	GL-1
<u>Pr. sabroskyi</u>	-	-	-	BL-46
<u>Pr. smithii</u>	385.	-	-	BL-53
<u>Pr. xanthogaster</u>	383.	383.	243.	-
<u>Pr. sp. undet.</u>	255.	-	385.	-
<u>Sphaeromias Curtis</u>				
<u>Sph. longipennis</u>	248, 258, 268B, 308, 316D, 347, 380.	248, 258, 302.	44, 135, 138, 160, 248, 258, 268B, 299; FVB: 68, 12B, 13A, 14B, 18A, 62B, 68B, 70A, 74B, 76B, 123A, B	BL-64
Sphaeromiiii gen. undet.	253, 269C, 318A, 322B, 325B, 327B, 329A, 338A, 341, 344, 353, 373B, 398B.	318A, 322B, 338A, 341, 344, 353.	241A	-
SPHAEROMIINI COMPLEX				
PALPONYIA - BEZZIA COMPLEX				
	7, 74, 130, 178, 179, 200, 231, 233, 268B, 282, 284, 285B, 302, 313A, 313C, 316D, 323A,	7, 14, 34, 67, 74, 78, 100B, 138, 147, 166A, 175B, 248, 253, 258, 266A, 268B, 270C, 285B, 291B, 292, 313C, 368C; B-1A, B-1B, B-2A, B-2B, B-5, BSM, GH-1, GL-1, -2, -3, -4, -5; W-A, W-C, W-D, W-E.	-	-

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed				Adult Field-Trapped (AFT)
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)		
PALPOMYIINI					
<i>Bezzia Kieffer</i> sp.	4, 23, 182, 186, 208, 256, 269B, 270C, 272B, 287A, 288B, 325A, 326A, 327B, 353.	18, 36, 156, 166A, 182, 186, 206, 208, 257A, 260, 282, 395A.	-	-	-
<i>B. (Bezzia) bivittata</i> Group					
<i>B. (B.) gibbera</i>	117, 216, 225, 228, 235, 249, 252, 278B, 287B.	69B, 84, 85, 101, 195, 216, 22, 228, 232B, 235, 238, 265, 252, 257C.	60, 252, 268A, 278B.	-	-
<i>B. (Bezzia) expolita</i> Group					
<i>B. (B.) albidorsata</i>	-	-	228, 230	-	-
<i>B. (B.) cf. dentata</i>	225, 226, 288B(sp.nr.)	-	225, 226, 228, 234.	-	-
<i>B. (B.) cf. expolita</i>	262.	-	6H-1	Bl-46.	-
<i>B. (B.) cf. flavicarsis</i>	218B.	-	218B.	-	-
	373A-21R	-	B-4, B-5, 61-1.	-	-
	240B, 351, 357.	-	45, 218B, 270C, 278A, 351, 357, 4671A; B-1, B-4, B-5, 85B, 61-1, 61-2, FVB: 9A, B; 12B, 13B, 13A, B; 17B, 802, 805, 806, 807, 808, 27, 40, 42, 46A, 104.	IV-15, BL-53, BL-64	-
	360A.	-	FVB: 4B, 46A, 51.	-	-
	331B, 370.	369, 375D.	99, 117, 119, 187, 369, 405, FVB: 13A, 46A; 114, 130, 225, FVB: 21, 34, 35, 139A.	-	-
	-	-	(99), 100A, 241A, 245, 252, Montg. Co. V-1968.	-	-
	-	-	122.	-	-
	-	-	FVB: 13B.	-	-
	-	-	FVB: 805.	-	-
	287B.	-	287A.	-	-
	284.	-	-	-	-
	217	-	FVB: 46A.	-	-
	-	-	-	-	Bl-46.
	-	-	FVB: Rd. Spr. 17-V-1968 (VPI Woods)	-	-

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			Adult Field-Trapped (AFT)
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	
<i>Bezzia</i> cont'd.				
<i>B. (B.) nobilis</i> (syn. <i>setulosa</i>)	12, 41, 44, 67, 70, 132, 141, 160, 163, 177B, 183, 190, 191, 192, 207C, 208, 211, 214B, 240A, 242, 243, 245, 248, 253, 258, 285A, 285C, 285D, 288B, 291B, 292, 296, 299, 309, 310, 312A, 314A, 316E, 319E, 320B, 323A, 325A, 325B, 327B, 329A, 329B, 332B, 345, 347, 354, 356, 381, 402.	12, 41, 44, 50, 69A, 87, 105, 108, 109, 128, 132, 141, 144, 160, 161C, 163, 168I, 177B, 183, 191, 192, 211, 240A, 253, 299, 332B, 340, 381, 401B, 402, 407C.	20, 23, 24, 28, 41, 44, 50, 57, 59, 61, 65B, 69A, 69B, 69C, 71, 84, 86, 87, 88, 89, 90A, 92A, 93, 94B, 100B, 105, 108, 109, 113B, 117, 125, 128, 130, 132, 138, 141, 144, 145A, 157, 160, 161A, 161B, 161C, 163, 166B, 168I, 175A, 175B, 176, 177B, 177C, 179, 183, 190, 191, 192, 195, 206, 207C, 208, 211, 214B, 215, 222A, 230, 235, 240A, 243, 245, 248, 258, 285A, 291B, 292, 308, 309, 312A, 314A, 316E, 320B, 325B, 326A, 329A, 329B, 332B, 345, 347, 348, 354, 356, 407B, 407F, B-1, B-2A, B-2B, B-3, B-5, BSM, CH-1, CH-2, CI-1, CI-4, CI-5, W-A, W-C, W-D, W-E, FVB: 9A, 9B, 12A, 12B, 13A, 14B, 16A, 16B, 20A, 20B, 802, 806, 807, 811, 23, 27, 29, 39, 42, 44B, 45A, 45B, 46A, 52, 53, 58B, 64A, 64B, 70B, 74A, 74B, 75A, 76A, 76B, 77A, 77B, 79A, 89, 90, 115A, 116B, 117A, 119, 121A, 121B, 123A, 123B, 125B, 168A, 175A, 184B, 186A, 186B, 1868, 189A, 190A.	SM-31, BI-32, SM-37, SM-38, BI-53, ET-68.
<i>B. (B.) pulverea</i> group				
<i>B. (B.) laciniastyla</i>	217, 225, 240A, 245, 295, 309, 316C, 319C, 319E, 320B, 322A, 325A, 332A, 333A, 333B, 333C, 345, 356, 370A, 370C, 373A, 374A, 374B, 374C, 378C, 384, 225, 370C.	69A, 92B, 240A, 374B, 375E, 378A.	55, 65B, 69A, 69B, 70, 71, 73, 84, 92B, 95, 96, 97, 99, 100A, 133, 190, 195, 207A, 208, 215, 225, 240A, 240B, 295, 313B, 319E, 320B, 333C, 345, 384, B-1A, B-1B, FVB: 9A, 12A, 12B, 16A, 16B, 20A, 20B, 802, 27, 34, 46A, 49B, 55, 64A, 70B, 85, 90, 121A, 126A, 183B, 184A.	BL-64, ET-68.
<i>B. (B.) pulverea</i>	283B, 288B, 291B, 296, 315, 319B, 376.		114, 130, 225, FVB: 21, 34, 35, 139A.	
<i>B. (B.) pulverea</i> complex	314A, 319E, 374B, 374C.	313C, 374B.	319B.	
<i>B. (B.) uncistyla</i>				
<i>B. (B.)</i> sp. 10 <i>pulverea</i> complex				
<i>B. (B.)</i> sp. 11 nr. <i>laciniastyla</i>				
<i>B. (B.)</i> sp. 12 nr. <i>laciniastyla</i>				
<i>B. (B.)</i> sp. 13 nr. <i>spicatus</i>				
<i>B. (B.)</i> sp. 14 nr. <i>uncistyla</i>	332B.			
<i>B. (B.)</i> sp. 15 nr. <i>laciniastyla</i>				
<i>B. (B.)</i> sp. 16 nr. <i>laciniastyla</i>				
<i>B. (B.)</i> sp. 17 <i>pulverea</i> complex				
<i>B. (B.)</i> sp. undet.	217, 312A, 325A, 328, 331A, 331B, 401B.	217.		
<i>B. (Homobezzia) annulipes</i> group				
<i>B. (H.) fascispinosa</i>	375A, 388.			

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<i>Bezzia</i> cont'd.				
<i>B. (H.) varicolor</i> ^{3/}	1, 33, 183, 242, 246, 263A, 263B, 273A, 281, 285C, 285D, 397C, 398B, 403, 404.	33, 162, 165, 183, 246, 370A, 375B, 397C, 398B, 405.	19, 33, 38, 65A, 65B, 67, 77A, 77B, 86, 88, 90A, 105, 125, 157, 161B, 162, 165, 167U, 233, 237, 242, 245, 246, 248, 261D, 263A, 273A, 273B, 281, 285C, 290A, 291A, 291B, 312A, 312B, 314A, 315, 316F, 320B, 356, 365, B-1B, B-2A, B-2B, FVB: 25, 51, 62A, 64A.	BI-64
<i>B. prob. (H.)</i> sp. Indet.	269C, 278A, 292, 309, 312A, 312A, 315C, 319C, 323A, 327B, 330B, 373B.	-	309, 404.	-
<i>B. (H.) bicolor</i> Group				
<i>B. (H.) glabra</i>	3, 41, 65A, 182, 212, 246, 258, 263A, 263B, 281, 285C, 289, 290A, 299, 305, 312A, 316B, 319A, 319C, 321, 333A, 333B, 348, 365, 375A, 380.	41, 43, 92A, 289, 290A, 299, 305, 348, 380.	31, 43, 89, 92A, 92B, 182, 190, 212, 246, 248, 258, 263A, 281, 290A, 299, 305, 312A, 312B, 316B, 333A, 333C, 365; B-2B.	BI-50, BI-53
<i>B. (H.) dorsasetula</i> Group				
<i>B. (H.)</i> cf. <i>dorsasetula</i>	154, 235, 270C, 326B, 357.	154, 156.	236, 253, 270C, 326A, 357.	DV-12, DV-14.
<i>B. (H.)</i> sp. nr. <i>dorsasetula</i>	-	-	138 (326A)	-
<i>B. (H.)</i> cf. <i>obelisca</i>	31, 90A, 268C, 270D, 274, 326B.	155.	31, 52, 111, 147, 155, 263B, 268C, 270D, 278A, 326A, 326B.	BI-46.
<i>Palpomyia</i> Meigen				
<i>Palp. basalis</i>	257B.	-	257B.	-
<i>Palp. canadensis</i>	275.	-	52, 260.	-
<i>Palp. cressoni</i>	240A.	-	316C, 357, FVB: 20A, 51, 68B.	-
<i>Palp. distincta</i> gr.	257A, 270B, 328, 329A.	-	-	-
<i>Palp. flaviceps</i>	257B.	-	257B, 257C, 260, 274.	BI-9, BI-46.
<i>Palp. flavipes</i> gr.	257B.	-	-	-
<i>Palp. hastata</i>	-	-	FVB: 7A, 75B, 114.	-
<i>Palp. lineata</i>	61, 67, 236, 238, 246, 312A, 313A, 330B, 331B, 356, 357, 370A, 370B, 375A, 375B, 377, 391.	236, 370A, 399A, 399B, 404, 405.	63B, 236, 238, 250B, 290A, 316D, 320B, 326A, B-2B, (H-1, H-E, FVB: 25.	BI-46.
<i>Palp. lineata</i> gr.	328.	-	-	-

^{3/} Includes *B. solstitialis*

Ceratopogonid Taxa	Collection Numbers for Sites Yielding Specimens of the Species Listed			
	Individually-Reared (IR) (or attempted)	Immature Specimens (IMM) (or reared)	Reared Collectively in Rearing Cartons (RC)	Adult Field-Trapped (AFT)
<u>Palpomyia</u> cont'd.				
<u>Palp. novitibialis</u>	67, 237, 238, 240A, 292, 294, 319A, 319B, 319E, 323A, 323A, 328, 332A, 333A, 333B, 354, 364, 370C, 374A, 374B, 375B, 376, 391.	237, 374A.	194, 237, 279, 319E, 331A, 357, 359, 405, 8-28, CH-1, FVB: 6A, 6B, 12B, 13A, 13B, 14B, 16A, 16B, 18A, 18B, 38, 107, 119.	-
<u>Palp. n. sp. nr. novitibialis</u>	-	-	126, 285A, 375B, FVB: 3A, 8B, 11A, 45B.	-
<u>Palp. plebeia</u>	326B.	-	{ 49, 51, 54, 69B, 71, 76, 84, 89, 105, 149, 238, 255, 261C, 273B, 277, 279, 285B, 287A, 361A, W-C; FVB: 65B, 123B, 126B.	DV-21, 24.
<u>Palp. cf. pseudorufa</u>	287A	-	63, 85, 270A, 274, 326A, 326B; FVB: 95.	BL-46.
<u>Palp. plebeifella</u>	326B.	-	54, 270A, 270B, 270D, 354.	-
<u>Palp. rubiginosa</u>	-	-	164, 231, 272B, 274, 299; RSM, CH FVB: 36.	DV-16, TT-3.
<u>Palp. rufa</u>	272B, 310.	-	CC 4 Aug. '72.	-
<u>Palp. scalpellifera</u>	-	-	FVB: 37, 104.	B-5.
<u>Palp. stonei</u>	257B.	-	-	-
<u>Palp. subaspera</u>	160, 238, 248, 258, 292, 309, 312A, 353, 407B.	-	160, 176, 195, 248, 312A, 407B; FVB: 47A, 56B, 62A, 62B, 64A, 70A, 70B, 72A, 79B, 115B, 117B.	-
<u>Palp. tibialis</u>	232B, 320B, 370A, 370C.	-	240A, 320B.	DV-16.
<u>Palp. tibialis</u> gr.	288B, 291B, 296, 316C, 316D, 357, 375B.	-	GH-1; FVB: 27.	-
<u>Palp. walteri</u>	326A, 326B, 396A,	396A.	156, 270A, 270B, 270D, 277; FVB: 106.	-
<u>Palp. weemsi</u>	374C, 375B.	-	222B, 240A, 240B, 278B, FVB: 126B.	-
<u>Palp. sp. undet.</u>	257C, 270D, 277, 278B, 375B.	77B, 105, 257B, 258.	268B, 270A, 270C, FVB: 61.	-
<u>Phaenobezzia opaca</u> ^{4/}	{ 246, 261A, 263A, 273B, 312A, 312B, 313B, 375A, 376, 378B.	157, 376, 378A, 378B, 383.	17, 19, 69B, 157, 246, 248, 255, 263A, 265, 273B, 297, 312A, 312B; B-2B.	BL-53

^{4/} Includes Ph. sabroskyi

Appendix, Table 39 . IMM Results: Synoptic tally of WIK collection sites grouped by number of immatures (larvae and pupae combined) retrieved per Site number. Underlined numbers represent the relevant corresponding sites for which no adults were recovered in rearing cartons (RC). See also Table 40. Numbers in brackets are those for which no RC was attempted.

No. of		WIK Collection Site Numbers in Ascending Numerical (and Chronological) Order	
Immatures Extracted	Key Symbol	No. of Sites	
0	-	137	[2, 5, 6, 10, 11, 13, 15, MP-2, 22, MP-3,] 25, 26, 27, 29, MP-4, 35, 37, 40, 46, 47, 48, 53, 62, 66, 71, 72A, 72B, 74, 80, 85, 94B, 94C, 98, 104, 107, 111, 121, 123, 126, 131, 133, 134, 135, 136, 139, 143, 145B, 150, 151, 164, 166B, 168U, 169, 175A, MP-6, 181, 184, 185, 189, 193, 197, 198, 201B, 202, 204, 205, 207A, 207B, 209, 210, 219, 220, 221, 223, 224, 227A, 227B, 229A, 229B, 232A, 241B, 244, 247, 250, 251, 254, 264, 265, 267, 269D, 271A, 271B, 271C, 272A, 276, 280, 283C, 286A, 286B, 291A, 304, 311, 314A, 318B, 327A, 333D, 334A, 334B, 336, 337A, 337B, 338B, 339, 340, 342, 346, 349, 350, 352A, 352B, 355, 358, 359, 360B, 366, 367A, 367B, 368A, 368B, 371A, 382, 386, 397B, 397D, 400A.]
1	±	62	1A, MP-1, 38, 39, 49, 51, 56, 73, 82, 116, 118, 119, 137, 142, 145A, 146, 148, 157, 172, 175B, MP-7, MP-8, 187, 188, 190, 201C, 213, 215, 218A, 222A, 222B, 230, 233, 239, 241C, 249, 259, 261A, 261D, 266A, 266B, 277, 288A, 290B, 300, 303B, 306, 312B, 317, 320A, 330A, 333C, 351, 362, 368C, 371B, 372, 375C, 389, 390, 392, 399, 397A, 397A.
2 - 9	+	163	1, 4, 7, 8, 9, 14, 18, 19, 24, 28, 31, 33, 34, 36, 42, 43, 45, 50, 54, 55, 57, 59, 61, 63, 64, 65A, 65B, 68, 69C, 70, 77A, 77B, 81, 83, 86, 89, 90A, 90B, 91, 93, 94D, 102, 103, 109, 110, 112, 113A, 115, 117, 120, 122, 124, 125, 127, 129, 130, 132, 140, 144, 147, 149, 152, 154, 156, 158, 160, 161B, 161C, 162, 167U, 168U, 170, 173, 177B, 177C, 177D, 179, 180, 184-MP, 194, 195, 196, 200, 201A, 201D, 203, 207C, 214A, 218B, 226, 231, 232B, 234, 241A, 242, 243, 252, 256, 257A, 257C, 260, 261C, 268A, 268C, 269B, 269C, 270E, 273A, 275, 282, 283A, 283B, 287A, 287B, 289, 294, 295, 297, 298, 308, 310, 315, 316A, 318A, 319C, 324, 331A, 331B, 333F, 335, 338A, 341, 343, 344, 353, 354, 360A, 361A, 363, 364, 369, 373A, 373B, 374A, 377, 378B, 379, 381, 385, 387C, 391, 393, 395, 397C, 398A, 398B, 399B, 403, 406A, 406B, 407C, 407F.
10 - 19	++	83	3, 12, 16, 17, 20, 21, 23, 30, 32, 44, 69A, 69B, 75, 76, 87, 92B, 94A, 95, 96, 99, 114, 155, 159, 161A, 166A, 176, 177A, 182, 183-MP, 191, 192, 208, 211, 212, 214B, 217, 225, 237, 252, 262, 263C, 270A, 270B, 270C, 270D, 272B, 274, 279, 281, 284, 285D, 290A, 293B, 305, 313A, 313B, 316B, 316C, 316D, 316E, 322B, 327B, 329B, 330B, 332A, 333E, 333G, 356, 361B, 370C, 374B, 375A, 375D, 376, 380, 384, 387B, 388, 399A, 401A, 401B, 404.
20 - 49	+++	62	41, 52, 67, 78, 92A, 94E, 100A, 100B, 101, 106, 128, 165, 171, 178, 183, 186, 206, 216, 228, 235, 236, 245, 253, 257B, 261B, 263A, 263B, 268B, 273E, 278A, 278B, 285A, 285B, 291B, 293A, 296, 301, 302, 303A, 313C, 314A, 319A, 319B, 319D, 320B, 321, 322A, 323A, 326A, 333A, 333B, 347, 357, 365, 370A, 374C, 378A, 383, 387A, 396, 400B, 402.
50 - 99	++++	26	84, 105, 113B, 138, 141, 163, 174, 238, 240A, 246, 248, 258, 285C, 292, 307, 309, 312A, 319E, 325A, 326B, 328, 329A, 345, 375B, 405, 407D.
Over 100	+++++	12	79, 108, 240B, 288B, 299, 325B, 332B, 348, 370B, 407A, 407B, 407E.
IMM NOT ATTEMPTED		6	MP-5, 58, 60, 88, 97, 167L.
		551	

Appendix, Table 40 . RC Results: Synoptic tally of WIK collection sites grouped by number of adults emerged from rearing cartons (RC) per site. Underlined numbers represent those corresponding sites for which no immatures were recovered. See also Table 39.

No. of Adults Emerged	Key Symbol	No. of Sites	WIK Collection Site Numbers in Ascending Numerical (and Chronological) Order
0	-	127	<u>22</u> , <u>27</u> , <u>35</u> , <u>46</u> , <u>58</u> , <u>62</u> , <u>66</u> , <u>72A</u> , <u>72B</u> , <u>80</u> , <u>83</u> , <u>91</u> , <u>94C</u> , <u>98</u> , <u>102</u> , <u>110</u> , <u>121</u> , <u>131</u> , <u>136</u> , <u>139</u> , <u>143</u> , <u>145B</u> , <u>146</u> , <u>150</u> , <u>151</u> , <u>154</u> , <u>168U</u> , <u>170</u> , <u>172</u> , <u>184</u> , <u>185</u> , <u>189</u> , <u>193</u> , <u>197</u> , <u>198</u> , <u>199</u> , <u>201B</u> , <u>201D</u> , <u>202</u> , <u>203</u> , <u>205</u> , <u>207B</u> , <u>209</u> , <u>216</u> , <u>218A</u> , <u>220</u> , <u>223</u> , <u>227A</u> , <u>227B</u> , <u>232A</u> , <u>239</u> , <u>244</u> , <u>247</u> , <u>249</u> , <u>250</u> , <u>251</u> , <u>261A</u> , <u>262</u> , <u>264</u> , <u>266A</u> , <u>267</u> , <u>268A</u> , <u>269D</u> , <u>271A</u> , <u>272A</u> , <u>276</u> , <u>280</u> , <u>282</u> , <u>283A</u> , <u>283B</u> , <u>283C</u> , <u>286A</u> , <u>286B</u> , <u>287B</u> , <u>290B</u> , <u>294</u> , <u>298</u> , <u>300</u> , <u>303B</u> , <u>304</u> , <u>310</u> , <u>311</u> , <u>314B</u> , <u>318A</u> , <u>318B</u> , <u>319C</u> , <u>319D</u> , <u>321</u> , <u>322A</u> , <u>322B</u> , <u>323A</u> , <u>323B</u> , <u>324</u> , <u>327A</u> , <u>330A</u> , <u>331A</u> , <u>334B</u> , <u>335</u> , <u>336</u> , <u>337A</u> , <u>337B</u> , <u>338A</u> , <u>338B</u> , <u>339</u> , <u>340</u> , <u>341</u> , <u>342</u> , <u>346</u> , <u>349</u> , <u>350</u> , <u>352A</u> , <u>352B</u> , <u>355</u> , <u>358</u> , <u>360B</u> , <u>367B</u> , <u>368B</u> , <u>368C</u> , <u>371A</u> , <u>372</u> , <u>374A</u> , <u>386</u> , <u>390</u> , <u>394</u> , <u>406B</u> .
1	±	56	<u>29</u> , <u>34</u> , <u>48</u> , <u>53</u> , <u>57</u> , <u>94E</u> , <u>97</u> , <u>109</u> , <u>126</u> , <u>133</u> , <u>147</u> , <u>148</u> , <u>174</u> , <u>175B</u> , <u>177A</u> , <u>177B</u> , <u>177D</u> , <u>178</u> , <u>181</u> , <u>182</u> , <u>186</u> , <u>201A</u> , <u>204</u> , <u>212</u> , <u>228</u> , <u>252</u> , <u>257C</u> , <u>269A</u> , <u>269B</u> , <u>269C</u> , <u>271C</u> , <u>289</u> , <u>291A</u> , <u>295</u> , <u>315</u> , <u>317</u> , <u>320A</u> , <u>327B</u> , <u>332A</u> , <u>333D</u> , <u>333G</u> , <u>334A</u> , <u>351</u> , <u>353</u> , <u>367A</u> , <u>368A</u> , <u>369</u> , <u>371B</u> , <u>375B</u> , <u>384</u> , <u>385</u> , <u>393</u> , <u>396</u> , <u>400B</u> , <u>404</u> , <u>406A</u> .
2 - 9	+	172	<u>17</u> , <u>18</u> , <u>20</u> , <u>25</u> , <u>26</u> , <u>30</u> , <u>31</u> , <u>33</u> , <u>36</u> , <u>37</u> , <u>38</u> , <u>39</u> , <u>40</u> , <u>42</u> , <u>43</u> , <u>45</u> , <u>47</u> , <u>49</u> , <u>50</u> , <u>51</u> , <u>54</u> , <u>55</u> , <u>56</u> , <u>59</u> , <u>60</u> , <u>61</u> , <u>63</u> , <u>64</u> , <u>65A</u> , <u>67</u> , <u>68</u> , <u>69C</u> , <u>71</u> , <u>74</u> , <u>77A</u> , <u>81</u> , <u>84</u> , <u>85</u> , <u>89</u> , <u>92A</u> , <u>94B</u> , <u>99</u> , <u>100A</u> , <u>100B</u> , <u>104</u> , <u>107</u> , <u>112</u> , <u>113B</u> , <u>114</u> , <u>115</u> , <u>116</u> , <u>117</u> , <u>118</u> , <u>119</u> , <u>122</u> , <u>123</u> , <u>124</u> , <u>125</u> , <u>127</u> , <u>128</u> , <u>129</u> , <u>135</u> , <u>142</u> , <u>145A</u> , <u>149</u> , <u>152</u> , <u>153</u> , <u>156</u> , <u>159</u> , <u>161C</u> , <u>162</u> , <u>164</u> , <u>166B</u> , <u>167U</u> , <u>167L</u> , <u>168L</u> , <u>169</u> , <u>175A</u> , <u>176</u> , <u>177C</u> , <u>179</u> , <u>180</u> , <u>183</u> , <u>188</u> , <u>191</u> , <u>192</u> , <u>200</u> , <u>201C</u> , <u>207A</u> , <u>208</u> , <u>210</u> , <u>219</u> , <u>222A</u> , <u>224</u> , <u>225</u> , <u>226</u> , <u>229A</u> , <u>229B</u> , <u>231</u> , <u>232B</u> , <u>233</u> , <u>234</u> , <u>235</u> , <u>237</u> , <u>241A</u> , <u>241C</u> , <u>242</u> , <u>254</u> , <u>256</u> , <u>257A</u> , <u>257B</u> , <u>259</u> , <u>260</u> , <u>261B</u> , <u>261C</u> , <u>261D</u> , <u>265</u> , <u>266B</u> , <u>268B</u> , <u>270E</u> , <u>271B</u> , <u>272B</u> , <u>275</u> , <u>277</u> , <u>279</u> , <u>281</u> , <u>284</u> , <u>285A</u> , <u>285B</u> , <u>287A</u> , <u>290A</u> , <u>291B</u> , <u>293A</u> , <u>293B</u> , <u>296</u> , <u>301</u> , <u>302</u> , <u>303A</u> , <u>305</u> , <u>313A</u> , <u>314A</u> , <u>316C</u> , <u>316D</u> , <u>319A</u> , <u>319E</u> , <u>325A</u> , <u>325B</u> , <u>326B</u> , <u>328</u> , <u>329A</u> , <u>329B</u> , <u>330B</u> , <u>331B</u> , <u>333A</u> , <u>333C</u> , <u>333E</u> , <u>343</u> , <u>354</u> , <u>356</u> , <u>357</u> , <u>359</u> , <u>360A</u> , <u>361A</u> , <u>361B</u> , <u>362</u> , <u>363</u> , <u>364</u> , <u>381</u> , <u>387A</u> , <u>401A</u> , <u>405</u> , <u>407F</u> .
10 - 10	++	62	<u>9</u> , <u>19</u> , <u>21</u> , <u>24</u> , <u>28</u> , <u>32</u> , <u>52</u> , <u>70</u> , <u>73A</u> , <u>87</u> , <u>90A</u> , <u>90B</u> , <u>96</u> , <u>101</u> , <u>106</u> , <u>111</u> , <u>120</u> , <u>130</u> , <u>132</u> , <u>134</u> , <u>138</u> , <u>141</u> , <u>144</u> , <u>157</u> , <u>158</u> , <u>161A</u> , <u>161B</u> , <u>166A</u> , <u>187</u> , <u>190</u> , <u>194</u> , <u>196</u> , <u>206</u> , <u>214A</u> , <u>215</u> , <u>218B</u> , <u>221</u> , <u>236</u> , <u>238</u> , <u>253</u> , <u>263C</u> , <u>268C</u> , <u>270C</u> , <u>270D</u> , <u>273A</u> , <u>273B</u> , <u>278B</u> , <u>285D</u> , <u>288A</u> , <u>292</u> , <u>297</u> , <u>308</u> , <u>309</u> , <u>312B</u> , <u>313C</u> , <u>316A</u> , <u>316B</u> , <u>316E</u> , <u>320B</u> , <u>326A</u> , <u>333F</u> , <u>387C</u> .
20 - 49	+++	41	<u>23</u> , <u>41</u> , <u>44</u> , <u>65B</u> , <u>69B</u> , <u>77B</u> , <u>79</u> , <u>86</u> , <u>88</u> , <u>92B</u> , <u>93</u> , <u>95</u> , <u>105</u> , <u>155</u> , <u>163</u> , <u>165</u> , <u>171</u> , <u>195</u> , <u>211</u> , <u>214B</u> , <u>217</u> , <u>222B</u> , <u>230</u> , <u>240A</u> , <u>240B</u> , <u>241B</u> , <u>243</u> , <u>245</u> , <u>255</u> , <u>258</u> , <u>270A</u> , <u>270B</u> , <u>274</u> , <u>278A</u> , <u>285C</u> , <u>307</u> , <u>312A</u> , <u>313B</u> , <u>333B</u> , <u>348</u> , <u>365</u> .
50 - 100	++++	13	<u>69A</u> , <u>76</u> , <u>94D</u> , <u>103</u> , <u>108</u> , <u>113A</u> , <u>160</u> , <u>173</u> , <u>248</u> , <u>263A</u> , <u>345</u> , <u>347</u>
Over 100	+++++	8	<u>78</u> , <u>94A</u> , <u>246</u> , <u>263B</u> , <u>288B</u> , <u>299</u> , <u>306</u> , <u>407B</u> ,
RC NOT ATTEMPTED		71	MP-1 to MP-8; 1, 1A, 2 - 8; 10 - 16; 75, 213, 183-MP, 184-MP, 344, 366, 370A, B, C; 373A, B; 374B, C; 375A, C, D; 376 - 380, 382, 383, 387B, 388, 389, 391, 392, 395, 397A - 400A; 401B, 402, 403, 407A, C, D, E.

Appendix B. Selected Tallies of *Culicoides* and *Bezzia*

Table 41. Synopsis of the 77 *Culicoides* species of the eastern Nearctic Region east of the 100th meridian, including distributional and biological summaries for all species as well as records for the immediate Virginia area as determined in the present study. Abbreviations and symbols are defined at the end of the table.

	Published State Records										Affinities			Widespread			Information Published On				WIK Collections	
	FL	KY	MD	NY	NC	VA	WV	W.I. Gulf	S.W. W.	Bor-eal	Ne	U.S. U.S.	E. Coast	Larval Habitat	Larval Descr.	Pupal Descr.	IR/ IMM	Rearing Carton (RC)	Adult Field Trap			
<u>Culicoides</u>																						
<u>alachua</u>	x				xSC	[x]								N	N	N		
Jannback & Wirth, 1963																						
**alexanderi		xTN	x	x		x			x					N	N	N	-	-	-	+		
Wirth & Hubert, 1962																						
<u>arboricola</u>	x	xKY	x	x	xNC	x				x				Y	Y	Y	+	++	+++	+		
Root & Hoffman, 1937		xTN																				
<u>arubae</u>								x	x					Y	N	Y		
Fox & Hoffman, 1944																						
<u>barbosai</u>	x							x	x					Y	Y	Y		
Wirth & Blanton, 1956																						
<u>baueri</u>	x	xTN	x	x	xNC	x	x				x			Y	N*	Y	+(L)	+++	+	+		
Hoffman, 1925																						
<u>beckae</u>	x					x								N	N	N	-	-	-	-		
Wirth & Blanton, 1967																						
<u>bergi</u>														I*	N	N	-	+++	-	-		
Cochrane, 1973																						
**bermudensis	x				x	xNC								Y	I*	Y	+++ (L)	+	+	+		
Williams, 1956																						
<u>bickleyi</u>	x	x	x	x	xSC	x	x				x			Y	Y	Y	+	++++	++++	+		
Wirth & Hubert, 1962																						
<u>biguttatus</u>	x	xTN	x	x	xNC	x	x				x			Y	I*	Y	+	+++	+++	+		
(Coquillett), 1901																						
<u>bottrimeri</u>														N	N	N		
Wirth, 1955																						
<u>byersi</u>														N	N	N		
Atchley, 1967																						
<u>canadensis</u>														N	N	N		
Wirth & Blanton, 1969																						
<u>chewaclae</u>														N	N	N		
Glick & Mullen, 1983																						
<u>chiopterus</u>	x	x	x	x	xNC	x								Y	Y	Y	-	-	-	+		
(Meigen), 1830																						
<u>crepuscularis</u>	x	xKY	x	x	xNC	x	x				x			Y	Y	Y	++++	++++	+	+		
Malloch, 1915																						

Table 41 . (Cont'd)

	Published State Records										Affinities			Widespread			Information Published On				WIK Collections	
	FL	KY	MD	NY	NC	VA	WV	W.I.	S.W.	Bot-	Ne	E. S.F.	E. U.S.	Coast	Larval Habitat	Larval Desctr.	Pupal Desctr.	IR/ IMM	Rearing Carton (RC)	Adult Field Trap		
	TN	SC	I/	FL	W.	east	U.S.	Desctr.	Desctr.	Desctr.												
<u>denningi</u>								NW		x					Y	Y	Y		
Foote & Pratt, 1954																						
** <u>denticulatus</u>	xKY	x	x							x					Y	I	Y	-	-	+		
Wirth & Hubert, 1962																						
<u>debilipalpis</u>	x	xKY	x	xSC	x						x				Y	N	Y	-	-	++++		
Lutz, 1913		xTN																				
<u>downesi</u>										x					Y	N	N		
Wirth & Hubert, 1962																						
<u>eadsi</u>									x						N	N	N		
Wirth & Blanton, 1971																						
<u>edeni</u>	x														Y	N	Y		
Wirth & Blanton, 1974																						
<u>floridensis</u>	x														N	N	Y		
Beck, 1951																						
<u>flukei</u>										x					Y	Y	Y	-	-	-		
Jones, 1956																						
<u>footei</u>	x	xKY	x	x	x										Y	Y	Y	-	-	-		
Wirth & Jones, 1956		xTN																				
<u>franclemonti</u>															Y	I	Y		
Cochrane, 1974										x												
<u>furens</u>	x	x	x	x	xNC	x									Y	Y	Y	+	+	+++		
(Foe), 1851					XSC																	
** <u>furensoides</u>										x					I*	N	Y	-	-	+++		
Williams, 1955																						
<u>guttipennis</u>	x	xKY	x	x	x										Y	Y	Y	++	+++	++		
(Coquillett), 1901		xTN																				
<u>haematopotus</u>	x	xTN	x	x	xNC	x					x				Y	Y	Y	++++	+++++	++		
Malloch, 1915					XSC																	
<u>hieroglyphicus</u>															Y	Y	Y		
Malloch, 1915																						
<u>hinmani</u>	x	xTN	x	x	xNC	x									Y	N	N*	+(P)	+	-		
Khalaf, 1952																						
<u>hollensis</u>	x	x	x	x	xNC	x									Y	Y	Y	+	++	+		
(Melander & Brues), 1903					XSC																	
<u>hussseyi</u>	x														N	N	N		
Wirth & Blanton, 1971																						

Table 41, (Cont'd)

	Published State Records										Affinities			Widespread			Information Publishes On			WIK Collections	
	FL	KY	MD	NY	NC	VA	WV	W.I. FL Gulf	S.W. W.	Bor-eal	Ne	E. U.S.	S.E. U.S. Coast	Larval Habitat	Larval Descr.	Pupal Descr.	IR/ IMM	Rearing Carton (RC)	Adult Field Trap		
<u>insignis</u> Lutz, 1913	x							x						Y	N	Y		
<u>Jamesi</u> Wirth & Hubert, 1962									x					Y	Y	Y		
<u>Jamnbacki</u> Wirth & Hubert, 1962				x						x				Y	Y	Y	-	+	++++		
<u>Jonesi</u> Wirth & Hubert, 1960														Y	N	N		
**juddi Cochrane, 1973	x			x										N*	N	N	-	+	-		
<u>kirbyi</u> Glick & Mullen, 1983				x									x	N	N	N		
<u>knowltoni</u> Beck, 1956	x						x							N	N	N		
<u>loisae</u> Jamnback, 1965	x			x	x	xNC	x							Y	N	Y	-	+	-		
<u>Loughnani</u> Edwards, 1922	x							x						Y	N	N		
<u>melleus</u> (Coquillett), 1901	x			x	x	xNC	x							Y	Y	Y	+	+	++++		
<u>mississippiensis</u> Hoffman, 1926	x													Y	N	N		
<u>mulrennani</u> Beck, 1957	x			x	x	x	x							N*	N	N	-	+	++++		
<u>multipunctatus</u> Malloch, 1915		xTN												Y	Y	Y		
<u>nanus</u> Root & Hoffman, 1937	x	xTN	x	x	xSC	x	x							Y	N	Y	-	+	-		
<u>neopulicaris</u> Wirth, 1955														Y	N	Y		
<u>niger</u> Root & Hoffman, 1937	x			x	x	xSC	x							Y	N	Y	-	-	-		
<u>obsoletus</u> (Meigen), 1818				xTN	x	xNC	x							Y	Y	Y	-	-	++++		
<u>oklahomensis</u> Khalaf, 1952														Y	N	N		
<u>ousairani</u> Khalaf, 1952	x	xTN	x				x							Y	N	N	-	-	-		

Table 41. (Cont'd)

	Published State Records										Affinities			Widespread			Information Published On				WIK Collections	
	FL	KY	MD	NY	NC	SC	VA	WV	W.I. FL Gulf	S.W. W.	Bor-eal	Ne	E. U.S.	S.E. U.S.	E. Coast	Larval Habitat	Larval Descr.	Pupal Descr.	IR/ IMM	Rearing Carton (RC)	Adult Field Trap	
	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Y	N*	N*	N*	+	+	+
<u>paraensis</u> (Goeldi), 1905	x	x	x	x	x	x	x	x								Y	N*	N*	+	+	+	++++
<u>parapiliferus</u> Wirth & Blanton, 1974	x	x	x	x	x	x	x	x				x				Y	N	Y	-	+		-
<u>pechumani</u> Cochrane, 1974	x			x		[x]										N	N	N
<u>piliferus</u> Root & Hoffman, 1937	x	x	x	x	x	x	x	x				x				Y	I*	Y	++	++	++	+++
<u>pusillus</u> Lutz, 1913	x								x							Y	N	N
<u>salihi</u> Khalaf, 1952										x						N	N	N
<u>sanguisuga</u> (Coquillett), 1901		x	x	x	x	x	x	x				x				Y	Y	Y	-	++	++	++++
<u>scanloni</u> Wirth & Hubert, 1962	x	x	x	x	x	x	x	x				x				Y	N	Y	-	+		-
<u>snowi</u> Wirth & Jones, 1956	x	x	x	x	x	x	x	x				x				Y	N	Y	-	-	-	-
** <u>sphagnumensis</u> Williams, 1955																Y	N	N*	++	++	++	++
<u>spinus</u> Root & Hoffman, 1937	x	x	x	x	x	x	x	x				x				Y	N*	Y	++	++	++	+
<u>stellifer</u> (Coquillett), 1901	x	x	x	x	x	x	x	x				x				Y	Y	Y	+++	+++	+++	+++
<u>stilobezioides</u> Foote & Pratt, 1954																N	N	N
<u>subletted</u> Atchley, 1967																N	N	N
<u>testudinalis</u> Wirth & Hoffman, 1962	x	x	x	x	x	x	x	x				x				Y	N	Y	-	+		-
<u>tissoti</u> Wirth & Blanton, 1966	x			x		x	[x]									Y	N	Y
<u>lorreyae</u> Wirth & Blanton, 1971	x															N	N	N
<u>travisi</u> Vargas, 1937	x	x	x	x	x	x	x	x				x				Y	I	Y	-	+	+	-

Table 41. (Cont'd)

	Published State Records							Affinities		Widespread			Information Published On			WIK Collections					
	FL	KY	MD	NY	NC	VA	WV	W.I.	S.E.	Bor-	Ne	E.	S.E.	E.	Larval	Larval	Pupal	IR/	IR/	Adult	
	TN				SC	I/		FL	W.	U.S.	U.S.	Coast	Habitat	Descr.	Descr.	Descr.	IMM	RC)	Field	Trap	
<u>utownna</u>																					
Jamback, 1965																					
<u>varipennis</u>	x	xTN	x		xSC	x	x														
(Coquillett), 1901																					
<u>venustus</u>																					
Hoffman, 1925																					
<u>villospennis</u>																					
Root & Hoffman, 1937																					
<u>wisconsinensis</u>																					
Jones, 1956																					
Number of species	47	KY:11	40	45	NC:20	38	19	12	12	15	9	16	7	7	Y:57	Y:23	49	20	33	27	
	TN:20				SC:20	44	29	4/							Y+I:59	Y+I:32	52	4/			
						54									61	4/	36	4/			

1/ Including species not yet recorded from Virginia [in brackets].

2/ Holarctic

3/ South of 42° N

4/ With new records from this study

5/ With species not yet recorded but likely to be encountered in future collections.

Abbreviations

Descr.: Taxonomic description available in published literature
 E. : East
 FL : Florida
 I : Incomplete larval or habitat description
 IR/IMM: Individually-Reared and/or Immature specimens obtained in present study
 KY : Kentucky
 L : Larva(e)
 MD : Maryland
 N : Not yet known or published
 Ne : Nearctic
 N.W. : Northwest boreal distribution

NY : New York
 P : Pupa
 RC : Reared Collectively by Emergence Rearing Cartons in Laboratory
 SC : South Carolina
 S.E. : Southeastern U.S.
 S.W. : Southwestern U.S./Mexico
 TN : Tennessee
 W. : West U.S./Canada
 W.I. : West Indies
 WIK : Records of investigator in this study (W.I. Knausenberger)
 Y : Yes, i.e., habitat or taxonomic description available in published literature

Symbols

x : species recorded in area indicated
 [x] : future collection in Virginia may be expected (See Table 11 and text).
 * : present study yielded material sufficient to fill existing gap in knowledge
 ** : new records from present study
 - : collection or processing method did not yield this species
 + : 1-9 specimens of this species obtained
 ++ : 10-19
 +++ : 20-49
 ++++ : 50-99
 +++++ : 100+
 ... : species not recorded for Virginia

References: Atchley (1970); Atchley and Wirth (1979); Battle and Turner (1971); Blanton and Wirth (1979); Bowen (1983); Cochrane (1973, 1974); Gazeau and Messersmith (1970b); Glick and Mullen (1983); Guirgis (1984); Lambach (1965); Jones, H. (1974); Jones, R.H. (1961a); Kline and Axtell (1976); Linley (1965a, 1970a,b); Tanner and Turner (1975); Wirth (1965, 1974); Zimmerman (1981).

Table 42 . Summary of adult feeding habit and host records for 54 described Culicoides species known or expected to occur in Virginia. For comparison, the status of larval habitat knowledge is indicated also. Symbols in table body indicate whether the records are well-established (++) , based on circumstantial evidence only (+) , or not yet established at all (□) . Asterisks at left indicate species not yet collected in Virginia or West Virginia.^{1/} Footnotes at end of table.

SPECIES	Feeding Host or Habit												
	1	2	3	4	5	6	7	8	▲ 9	10	11	▲ 12	▲ 13
	Anthropophilic pest ^{2/}	Man-biting recorded	Large-mammal hosts ^{3/}	Small-mammal hosts ^{4/}	Bird hosts recorded	Ornithophilic ^{9/}	Turtles	General Feeders ^{5/}	Non-bloodsucking	Autoœnous	Host unknown	Diurnal ^{6/}	Larval habitat ^{10/}
<u>Culicoides</u>													
* <u>alachua</u>											□		□
<u>alexanderi</u>		++											□
<u>arboricola</u>		++	+	++	++	+							++
<u>baueri</u>		++				+							++
<u>beckae</u>						+					□		□
<u>bergi</u>					++	+							[++]
<u>bermudensis</u>									++	++			++
<u>bickleyi</u>		++	++		++			++					++
<u>biguttatus</u>	[++]	++	++		++			++					++
<u>chewaclae</u>						+					□		□
<u>chiopterus</u>		++			++								++
<u>crepuscularis</u>		++	++		++	++							++
<u>debilipalpis</u>		++	++	++	++			++					++
<u>denticulatus</u>									+		□		++
* <u>downesi</u>					++	++							++
<u>flukei</u>									+		□		++
<u>footei</u>											□		++
<u>franclemonti</u>										+	□		++
<u>furens</u>	++	++	++		++			++		7/		++	++

Table 42 . (Cont'd)

	1	2	3	4	5	6	7	8 ▲	9	10	11 ▲	12 ▲	13
SPECIES													
<u>Culicoides</u>													
<u>furensoides</u>									±		□		[++]
<u>guttipennis</u>	++	++	++	++	++			++					++
<u>haemato-</u>													
<u>potus</u>	[++]	++			++	++		++					++
<u>hinmani</u>	[++]	++		++	++			++				++	++
<u>hollensis</u>	++	++	±										++
<u>husseyi</u>											□		□
<u>jamnbacki</u>											□		++
<u>juddi</u>									±		□		[++]
<u>kirbyi</u>								±			□		□
<u>loisae</u>									±		□		++
<u>melleus</u>	++	++		++	++			++					++
<u>mulrennani</u>	++	++	++	++	++			++					[++]
<u>multipuncta-</u>													
<u>tus</u>											□		++
<u>nanus</u>											□		++
<u>niger</u>		++	±		++	±							++
<u>obsoletus</u>	[++]	++	++										++
<u>ousairani</u>					++	++							++
<u>paraensis</u>	++	++		++	++			++				++	++
<u>parapiliferus</u>											□		++
* <u>pechumani</u>									±		□		□
<u>piliferus</u>		++	++	++	++			++					++
<u>sanguisuga</u>	++	++	++	++	++			++					++
<u>scanloni</u>		++			++	++							++
<u>snowi</u>		++											++
<u>sphagnumensis</u>					++	++							++
<u>spinosus</u>		++	++	++	++			++					++
<u>stellifer</u>		±	++		++								++
* <u>stilobezzi-</u>													
<u>oides</u>					++	++							□
<u>testudinalis</u>								++					++
* <u>tissoti</u>	8/	++										++	□
<u>travisi</u>		++	++	++	++	±		++					++
<u>variipennis</u>		++	++	++				++				++	++
<u>venustus</u>			++										++
<u>villosipennis</u>		++			++	++							++
* <u>wisconsin-</u>													
<u>ensis</u>									±	±	□		++
TOTALS	8	28	15	11	26	17	1	15	8	4	18	5	
		[12]											

(Continued--footnotes)

Table 42 . (Cont'd)

- =====
- 1/ See Text and Table 41 for further details. Information herein compiled from: Atchley (1970); Battle and Turner (1971); Blanton and Wirth (1979); Cochrane (1973,1974); Hair and Turner (1968); Glick and Mullen (1983); Humphreys and Turner (1973); Jamnback (1965); Schmidtman et al. (1980a,b; 1981); Tanner and Turner (1974,1975); Mullens and Schmidtman (1981); Zimmerman (1981); Zimmerman and Turner (1983); and results of this study.
 - 2/ Consistently (++) or occasionally ([++]) achieve pest status under differing biogeographic conditions.
 - 3/ e.g., sheep, goats, cattle, horses, etc.
 - 4/ e.g., lagomorphs, rodents
 - 5/ Three or more host categories
 - 6/ Regularly (sometimes facultatively) feed in mid-day sun
 - 7/ Facultative autogeny in first ovarian cycle
 - 8/ Anthropophilic pest chiefly in Florida (Blanton and Wirth (1979))
 - 9/ Bird host preferred
 - 10/ [++]: species whose habitat was unknown or not well defined before this study.

Table 43 . Relative abundances of *Culicoides* species in Rockingham Co., Virginia, compared by trapping method, in order of abundance (adapted from Jones, H. 1974 unpublished thesis, with addition of three species -- juddi, piliferus, spinosus -- identified by present writer from Jones' collections).

	Light Trap <u>1/</u>	Emergence Trap <u>2/</u>	Biting Man <u>3/</u>	Combined	% of Total
<u>Culicoides</u>					
1. <u>sanguisuga</u>	243	5	136	384	37.0
2. <u>stellifer</u>	147	26	15	188	18.1
3. <u>biguttatus</u>	158	0	0	158	15.2
4. <u>guttipennis</u>	16	0	126	142	13.7
5. <u>bickleyi</u>	0	59	0	59	5.7
6. <u>baueri</u>	59	0	0	59	5.7
7. <u>haematopotus</u>	12	7	0	19	1.8
8. <u>venustus</u>	13	2	0	15	1.4
9. <u>villosipennis</u>	13	0	0	13	1.4
10. <u>obsoletus</u>	9	2	0	11	1.1
11. <u>arboricola</u>	4	0	1	5	0.5
12. <u>testudinalis</u>	5	0	0	5	0.5
13. <u>paraensis</u>	3	0	1	4	0.4
14. <u>bergi</u>	3	0	0	3	0.3
15. <u>debilipalpis</u>	3	0	0	3	0.3
16. <u>juddi</u>	2	0	0	2	0.2
17. <u>parapiliferus</u>	1	1	0	2	0.2
18. <u>travisi</u>	1	1	0	2	0.2
19. <u>crepuscularis</u>	1	0	0	1	0.1
20. <u>piliferus</u>	0	1	0	1	0.1
21. <u>spinosus</u>	1	0	0	1	0.1
22. <u>variipennis</u>	1	0	0	1	0.1
TOTAL	655	104	279	1,038	100.0

1/ Results of 13 trap nights, 11 locations, 4 May - 25 Sept.

2/ Nine of 51 traps yielded Culicoides.

3/ Results of 38 evening and 3 morning sessions of ca. 1 hr. each (crepuscular) with a total of 10 people from June to October.

Table 44 . List of unnamed Bezzia species number assignments, with brief designation of some key characters, for the specimens encountered in this study.

Species Nos. and Brief Key Characters	Coll. Site	Number of	
		♀	♂
<u>Bezzia</u> (<u>Bezzia</u>) <u>bivittata</u> Group			
<u>B.</u> (<u>B.</u>) sp. nr. <u>gibbera</u> (Coquillett)	WIK 225 RC, IR	1	1
	WIK 226 RC, IR	3	2
	WIK 228 RC	-	1
	WIK 234 RC	1	1
<u>Bezzia</u> (<u>Bezzia</u>) <u>expolita</u> Group			
<u>B.</u> (<u>B.</u>) sp. 1 (nr. <u>mallochi</u> Wirth) - male genitalia as <u>mallochi</u> , but 9th sternum with deep, wide U-shaped excavation; aedeagus with hastate tip cf. <u>dentata</u> Malloch and <u>media</u> (Coq.) ; and fore femora: apical 1/3-1/5 pale; fore tibiae: basal 1/5, apical 1/3 pale, otherwise typical.	WIK 100A RC	3	1
	WIK 241A RC	1	-
	WIK 245 RC	-	1
	WIK 252 RC	-	1
	FVB Rd. Spr. 17-V-1968	1	1
	FVB 20A	-	1
<u>B.</u> (<u>B.</u>) sp. 2 (nr. <u>mallochi</u> Wirth) - 9th sternum trapezoid-shaped (0.73 as wide cephalad as caudad), with straight edges; "paramere" evenly tapered to narrowly rounded smooth tip; leg color as <u>B. albidorsata</u> Malloch.	WIK 122-1 RC	-	1
<u>B.</u> (<u>B.</u>) sp. 3 (nr. <u>media</u> (Coq.)) - Csa as 1/4 circle; fore and mid tibiae uniformly pale, basal 1/4 of hind tibiae pale.	FVB 13B	1	-
<u>B.</u> (<u>B.</u>) sp. 4 (nr. <u>flavitaris</u> Malloch) - complex bilobate telomere, basimere as <u>B. mallochi</u> ; leg pattern also as <u>B.</u> <u>mallochi</u> .	FVB 805	-	1

Table 44 . Cont'd.

Species Nos. and Brief Key Characters	Coll. Site	Number of	
		♀	♂
<u>B. (B.)</u> sp. 5 (nr. <u>flavitaris</u>)	WIK 287A RC	-	1
- 9th sternum as in <u>B. expolita</u> (Coq.), basimere non-lobate, stout; squat triang. telomere; "parameres" and aedeagus differ from any in Dow and Turner 1976; leg coloration unique, e.g. apical 1/5 of hind femur pale.	WIK 287B IR	1	1
<u>B. (B.)</u> sp. 6 (nr. <u>flavitaris</u>)	WIK 284-2 IR	-	1+l.ex. +p.ex.
- genitalia unique: basimere partially fused to 9th sternum, which is tapered caudad into 2 narrow "peaks" separated by deep "v" notch, extend to 0.7 basimere length; telomere 0.96 length of basimere, cleft tip, recurved, with thumb-like lobe at base; legs as <u>B. flavitaris</u> in color and armature.			
<u>B. (B.)</u> sp. 7 (nr. <u>mallochi</u> Wirth)	WIK 217-4A IR	-	1+p.ex.
- aedeagus triangular, "parameres" very broad, uniform in width caudal portion; tibiae uniformly light-colored.	FVB 46A ?	2	1
<u>B. (B.)</u> sp. 8 (nr. <u>flavitaris</u>)	WIK 274 BLT	4	5
- male 9th sternum strap-like (transverse); basimere more like <u>B. pulverea</u> type; telomere as <u>B. perplexa</u> , but is curved and has larger spoon-like excavation.			
<u>B. (B.)</u> sp. 9 (nr. <u>flavitaris</u>)	FVB Rd.Spr. 17-V-1968	-	1
- basimere fused to 9th sternum, which has prominent heavily sclerotized forceps-like caudal extension, to 0.5 of basimere; telomere relatively short			

Table 44. Cont'd.

Species Nos. and Brief Key Characters	Coll. Site	Number of	
		♀	♂
(0.46 of basimere) with slight inward curve apical 1/3.			
<u>Bezzia</u> (<u>Bezzia</u>) <u>pulverea</u> Group			
<u>B.</u> (<u>B.</u>) sp. 10 (<u>pulverea</u> complex)	WIK 200 RC	2	-
- male genitalia as in Plate 28C (Dow and Turner 1976) - bifid telomere; legs with solid dark hind femora, banded fore femora - otherwise as Plate 25L.	WIK 194-1 RC	1	-
	WIK 201C-1 RC	-	1
	FVB 96	1	2
	FVB 89	1	-
<u>B.</u> (<u>B.</u>) sp. 11 (nr. <u>laciniastyla</u> Dow and Turner)	WIK 112 RC	1	-
- spermath. subspherical, subequal in size; Csa heel reduced; mid-tibiae apical 1/5 yellow, fore femora not banded, otherwise same leg coloration.			
<u>B.</u> (<u>B.</u>) sp. 12 (nr. <u>laciniastyla</u>)	FVB 18B	1	-
- Csa distinctive: broadly bifurcate apically, processes equally developed; spermathecae subelliptical, unequal, with short distinct necks; femora ventrally not spinose.			
<u>B.</u> (<u>B.</u>) sp. 13 (nr. <u>spicata</u> Dow and Turner)	FVB 27	-	1
- genitalia as <u>spicata</u> , but telomere with strongly projecting "thumb" opposite hook; legs as <u>laciniastyla</u> type.			
<u>B.</u> (<u>B.</u>) sp. 14 (nr. <u>uncistyla</u>)	WIK 332B-21 IR	-	(1)1.ex. + pharate adult
- telomere intermediate <u>spicata-uncistyle</u> shape, but with distinct spicules at tip adjacent hook-like process; "parameres" and aedeagus more			

Table 44. Cont'd.

Species Nos. and Brief Key Characters	Coll. Site	Number of	
		♀	♂
prominent than others in <u>pulverea</u> "group"			
<u>B. (B.)</u> sp. 15 (nr. <u>laciniastyla</u>) - large flap-like process on telomere, 3x size of <u>lacinia-</u> <u>styla's</u> .	WIK 255 RC	-	1
<u>B. (B.)</u> sp. 16 (nr. <u>laciniastyla</u>) - Csa sickle-shaped with nar- rowly rounded, backward- directed tip; spermathecae elongate-obovate; fore femora uniformly light yellow orange, otherwise leg color as in <u>laciniastyla</u> .	WIK 231-1 RC	1	-
<u>B. (B.)</u> sp. 17 (<u>pulverea</u> complex) (cf. <u>magnisetula</u> Dow and Turner and <u>apicata</u> Malloch)	FVB 34 L. Norman, N. Carolina	2 -	- 1
- numerous heavy interocular setae, both sexes; spermath. subellip. dark brown in con- trast to light yellow abdomen (as <u>apicata</u>); Csa retrorse at tip, with acute hook directed inward; as <u>B. "pulverea group"</u> type, but "parameres" and aedeagus resemble those of <u>atlantica</u> , Wirth and Williams.			
<u>Bezzia (Homobezzia)</u> spp. Group			
<u>B. (H.)</u> sp. nr. <u>dorsasetula</u> Dow and Turner - all dimensions 15-25% larger; leg banding differs, esp. apical light bands on all tibiae.	WIK 122 DV	1	-

Csa = coxosternapodeme, or "genital sclerotization" of authors (Saether 1977).

Appendix C. GEOGRAPHY AND BIOGEOGRAPHY

Table 45. Geographic checklist of all described species in the family Ceratopogonidae known or expected to occur in Virginia and five adjoining states, as well as in the District of Columbia. Based on published records, and augmented by results of the present study. Extralimital distribution records are indicated as a frame of reference. The "x" denotes presence based on literature records; the 'Δ' highlights new records based on present results; '?' indicates a record that has not been recently verified or one that remains equivocal until taxonomic uncertainties are cleared up. To the left of certain species names the symbol '☆' indicates species which are as yet unrecorded in the region covered here, but which reasonably can be expected to occur in one or more of these states. See footnotes and text for additional explanatory detail.

SPECIES	Published Records ^{1/}							This Study's Records ^{2/}				
	DC	KY	MD	NC	TN	VA	WV	Other ^{3/}	NC	VA	WV	Other ^{4/}
CERATOPOGONIDAE												
LEPTOCONOPINAE												
<u>Leptoconops</u>												
<u>linleyi</u> Wirth and Atchley, 1973					X		Δ	MA, FL				K
(continued)												

- 1/ New records from this study indicated by the symbol Δ .
- 2/ Distinguished according to investigator by one-letter designations: B = F.V. Battle's collections; K = collections by present writer.
- 3/ Concentrating on records in the eastern Nearctic east of 90°W, when the record suggests possible presence or wider occurrence in the mid-Atlantic region; ranges given from north to south. Abbreviations elaborated in Appendix.
- 4/ Records from states receiving minor attention in this study (AL, KY, MD).

Table 45. cont'd.

SPECIES	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
FORCIPOMYIINAE														
<u>Atrichopogon</u> ^{1/}														
A. (<u>Atrichopogon</u>) <u>appendiculatus</u> (Goetghebuer)						Δ		Δ				K		
(A.) <u>fuscus</u> (Coquillett), 1901			X		Δ			Δ				K		
<u>fusinervis</u> (Malloch), 1905					Δ			ME-OH, IL				K?		
<u>geminus</u> Boesel, 1973		X			Δ			ON.-NY-KY				K		
<u>levis</u> (Coquillett), 1901			X	X	X	Δ		NH-FL				K		
<u>minutus</u> (Meigen), 1830			X					MI-VA; Europe				K		
<u>peregrinus</u> (Johannsen), 1908					Δ			MI-NY-OH				K		
<u>websteri</u> (Coquillett), 1901			X		Δ			Cont. U.S.A.				K		
A. (<u>Melohelea</u>) <u>downesi</u> Wirth, 1980			X	X	X	X		NS.-TN						
(<u>M.</u>) <u>oedemerarum</u> Stora, 1939					X	X		ON.-VA; Europe						
<u>Forcipomyia</u> ^{2/}														
F. (<u>Caloformipomyia</u>) <u>glauca</u> Macfie, 1934				X	X	X		NS.-FL, Holarctic				K		
F. (<u>Euprojoannisia</u>) <u>blantoni</u> Soria and Bystrak, 1975					X			SC, Neotropics						

^{1/} Up to two undescribed species of Atrichopogon encountered in this study; several more are known to exist from unpublished surveys.

^{2/} At least one undescribed Forcipomyia species encountered in this study, and several additional undescribed species have been recognized in others' surveys.

Table 45 . cont'd.

SPECIES	Published Records											This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other			
<u>Forcipomyia</u> (E.) cont'd.															
(E.) <u>calcarata</u> (Coquillett), 1905					X			SC, FL							
<u>hirtipennis</u> (Malloch), 1915	X	X	X	X	X	X	X	Holarctic				K			
<u>titillans</u> (Winnertz), 1852					X	X	X	N.E.U.S.A.							
☆ (<u>Forcipomyia</u>) <u>aurea</u> Malloch, 1915								IL							
(F.) <u>bipunctata</u> (Linnaeus), 1767				X	X	Δ		Nearctic, Holarctic				K			
<u>brevipennis</u> (Macquart), 1826	X			X	X			PQ.-AL, LA; Europe				K			
<u>bystraki</u> Grogan and Wirth, 1975							X	MI-FL				K			
<u>elegantula</u> Malloch, 1915	X	X						IL-MS							
<u>fimbriata</u> (Coquillett), 1901	X	X	X			Δ		FL				K			
☆ <u>genualis</u> (Loew), 1866								GA, FL, LA							
<u>pergandei</u> (Coquillett), 1901	X							IL, KS							
<u>picea</u> (Winnertz), 1852				X				ON., MA, AL							
<u>pilosa</u> (Coquillett), 1902	X				?			MI-IL							
<u>pinicola</u> Grogan and Messer-Smith, 1980							X	n/a				K			
<u>solonensis</u> Wirth, 1951							X	n/a				K			
<u>squamipes</u> (Coquillett), 1901				X				IL, AL							
☆ <u>townesi</u> Wirth, 1952								ON., NY-FL							
F. (<u>Lasiohelea</u>) <u>fairfaxensis</u> Wirth, 1951				Δ		X		MI-PQ.-IA, FL				K			
F. (subgenus near <u>Lepidohelea</u>) unnamed species								[Δ]				K			
F. (<u>Metaforcipomyia</u>) <u>pluvialis</u> Malloch, 1923				X	X	X		E. Nearctic, LA, FL							
☆ (<u>Microhelea</u>) <u>fuliginosa</u> (Meigen), 1818								AL; Holarctic, Neotropical, FL							

Table 45. cont'd.

SPECIES	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
<u>Forcipomyia</u> cont'd.														
<u>F. (Saliohelea) leei</u> Wirth and Ratanaworabhan, 1978					X			E. U.S.A. MI, NY, FL						
☆ <u>F. (Thyridomyia) frutetorum</u> Winn., 1852					X	X		IN, FL; Holarctic						
(Th.) <u>monilicornis</u> (Coquillett), 1905			X					NY, FL						
☆ <u>johannseni</u> Thomsen, 1935			X		Δ		X	PQ.-FL						
<u>rugosa</u> Chan and Le Roux, 1970			X					FL						
<u>F. (Trichohelea) baueri</u> Wirth, 1956			X	X				MN-ME-NC, FL						
(Tr.) <u>crinita</u> Saunders, 1964			X	X				ON.-ME-NC						
<u>eques</u> (Johannsen), 1908			X	X				NY-FL						
<u>mcateei</u> Wirth, 1956			X	X										
<u>veroensis</u> Wirth and Messersmith, 1971			X					MD, FL						
DASYHELEINAE														
<u>Dasyhelea</u> 1/														
<u>D. cincta</u> Group														
<u>cincta</u> (Coquillett), 1901			X		X	X	Δ	Continental U.S.A.			K	K?		
<u>major</u> (Malloch), 1915		X		X	X	X	Δ	CN-FL			B, K	K		
☆ <u>pseudocincta</u> Waugh and Wirth, 1976								NY						
<u>D. grisea</u> Group														
<u>grisea</u> (Coquillett), 1901			X		X	X	Δ	Eastern U.S.A.			B, K	B, K		
<u>luteogrisea</u> Wirth and Williams, 1957			?					MD(?), Bermuda, FL						
<u>oppressa</u> Thomsen, 1935			X	X	X	X	X	WI-PQ.-FL			K	K		

1/ Up to 10 undescribed species encountered in the present study alone.

Table 45 . cont 'd.

SPECIES	Published Records													This Study's Records				
	DC	KY	MD	NC	TN	VA	WV	Other					NC	VA	WV	Other		
<u>Dasyhelea grisea</u> Group cont'd.																		
<u>pollinosa</u> Wirth, 1952			X			X		FL; WA, CA; CO									K	
<u>pseudoincisurata</u> Waugh and Wirth, 1976			X			X	Δ	NH-FL									K	K
<u>stemlerae</u> Waugh and Wirth, 1976			X			X		NY-FL									B,K	
<u>traverae</u> Thomsen, 1935					Δ	?	Δ	NY-SC, LA									B	B,K
<u>fasciigera</u> Kieffer 1925			X			X		Holarctic										
<u>D. leptobranchia</u> Group																		
<u>brevicosta</u> Waugh and Wirth, 1976						X	X	NY-VA										K
<u>leptobranchia</u> Waugh and Wirth, 1976			X	Δ				NY-GA									B	B,K
<u>messersmithi</u> Waugh and Wirth, 1976			X			X	Δ	MD, VA, TX										K
<u>navaiae</u> Waugh and Wirth, 1976						X	Δ	MI										B,K
<u>scutellata</u> (Meigen), 1830						X		Holarctic										K
<u>D. mutabilis</u> Group																		AL(B)
☆ <u>ancora</u> (Coquillett), 1902								CN-FL; CA										
<u>atlantis</u> Wirth and Williams, 1957							Δ	NY-FL, Bermuda										K
<u>mutabilis</u> (Coquillett), 1901			X	X	X	X	Δ	Nearctic										B,K
<u>spiniforma</u> Waugh and Wirth, 1976						Δ	Δ	NY										K
<u>thomsenae</u> Wirth, 1952			?			?	?	CA, NM										
Unplaced <u>Dasyhelea</u> species																		
<u>D. brevicornis</u> Waugh and Wirth, 1976			X					NS.-MD										
Subfamily CERATOPOGONINAE																		
Tribe Culicoidini																		
<u>Culicoides</u>																		
<u>C. (Avaritia) obsoletus</u> Group																		
☆ <u>alachua</u> Jamback and Wirth, 1963								SC, FL										

Table 45. cont'd.

SPECIES	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
<u>Culicoides (Avaritia) obsoletus</u> Group cont'd.														
<u>C. (A.) chiopterus</u> (Meigen), 1830	X	X			X	Δ	Holarctic		K		K			
<u>juddi</u> Cochrane, 1973					Δ		NY, FL		K		K			
<u>obsoletus</u> (Meigen), 1818	X	X	X	X	X	X	Holarctic N of 35°N		K		K			
☆ <u>pechumani</u> Cochrane, 1973							NY-FL							
<u>sanguisuga</u> (Coquillett), 1901	X	X	X	X	X	X	AK-CA; PQ.-GA		K		K			
<u>(Beltranmyia) Vargas</u>														
<u>C. (B.) bermudensis</u> Williams, 1956				X		Δ	Coastal NY-FL		K					
<u>crepuscularis</u> Malloch, 1915		X	X	X	X	X	Nearctic	B, K	B, K		B, K			
<u>hollensis</u> (Melander and Brues, 1903)														
<u>sphagnumensis</u> Williams, 1955		X	X			X	Coastal E. U.S.A.		B, K		B, K			
<u>(Culicoides) Latreille</u>						Δ	MI, ON., PQ., NY		K		B, K			
<u>C. (C.) pulicaris</u> Group														
☆ <u>canadensis</u> Wirth and Blanton, 1969							AK-WI-ME							
<u>(Diphaeomyia) Vargas</u>														
<u>C. (D.) baueri</u> Hoffman, 1925		X	X	X	X	X	S.E. U.S.A.	B	B, K		B, K	AL(B)		
<u>bergi</u> Cochrane, 1973					X	X	NY-VA		K					
<u>footei</u> Wirth and Jones, 1976		X	X	X	X	Δ	S.E. U.S.A., PA-FL				K			
<u>haemotopotus</u> Malloch, 1915		X	X	X	X	X	Cont. U.S.A., S. Canada		B, K		B, K	AL(B)		
<u>(Drymodesmyia) Vargas</u>														
<u>C. (D.) hinmani</u> Khalaf, 1952		X	X	X	X		E. U.S.A., S of 42°N				K			
<u>(Hoffmania) Fox</u>														
<u>C. (H.) venustus</u> Hoffman, 1925		X	X	X	X	Δ	E. Nearctic							
<u>(Monoculicoides) Khalaf</u>														
<u>C. (M.) varipennis</u> Coquillett, 1901		X	X	X	X	X	SC, Nearctic				B, K			

Table 45 . cont'd.

SPECIES	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
<i>Culicoides</i> cont'd.														
<i>C.</i> (<u>O.</u>) <i>Poey</i>														
<i>C.</i> (<u>O.</u>) <i>biguttatus</i> Group														
<i>biguttatus</i> (Coquillett), 1901	X	X	X	X	X	X	X	E. U.S.A.	K	B,K	K	K		
<i>loisae</i> Jamnback, 1965	X	X	X	X	X	X	X	E. U.S.A.	B	B,K				
<i>mulrennani</i> Beck, 1957	X	X	X	X	X	X	X	S.E. U.S.A.		K	K			
<i>spinus</i> Root and Hoffman, 1937	X	X	X	X	X	X	X	E. U.S.A.	B	B,K	B,K			
<i>C.</i> (<u>O.</u>) <i>debilipalpis</i> Group														
<i>debilipalpis</i> Lutz, 1913	X	X	X	X	X	X	X	S.E. U.S.A.		K				
<i>furensoides</i> Williams, 1955								MI, NY, WI		K	K			
<i>paraensis</i> (Goeldi), 1905	X	X	X	X	X	X	X	S.E. U.S.A.	K	K				
<i>C.</i> (<u>O.</u>) <i>furens</i> Group														
<i>furens</i> (Poey), 1851	X	X	X	X	X	X	X	Atlantic, Gulf Coasts	K	B,K				
<i>stellifer</i> (Coquillett), 1901	X	X	X	X	X	X	X	Nearctic	B,K	B,K	B,K			
<i>C.</i> (<u>O.</u>) <i>guttipennis</i> Group														
<i>arboricola</i> Root and Hoffman, 1937	X	X	X	X	X	X	X	E. N.Amer.		K	K			
<i>beckae</i> Wirth and Blanton, 1967	X	X	X	X	X	X	X	S.E. U.S.A.						
<i>flukei</i> Jones, 1956								WI, NY, VA						
<i>guttipennis</i> (Coquillett), 1901	X	X	X	X	X	X	X	MN-NY-FL	K	K	K	KY(K)		
<i>ousairani</i> Khalaf, 1952	X	X	X	X	X	X	X	S.E. U.S.A.						
<i>villosipennis</i> Root and Hoffman, 1937	X	X	X	X	X	X	X	E. N. Amer.		K	K			
<i>C.</i> (<u>O.</u>) <i>heliophilus</i> Group														
<i>niger</i> Root and Hoffman, 1937	X	X	X	X	X	X	X	E. U.S.A.						
<i>tissoti</i> Wirth and Blanton, 1966	X							MD, SC, FL						

Table 45. cont'd.

SPECIES	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
<u>Culicoides</u> cont'd.														
<u>C. (O.) piliferus</u> Group														
<u>alexanderi</u> Wirth and Hubert, 1962			X	X	Δ	Δ	Δ	Boreal N. Amer.		K		K		
<u>bicklei</u> Wirth and Hubert, 1962			X		X	X	X	E. N. Amer.		K		K		
<u>chewaclae</u> Glick & Mullen, 1983			X					AL						
<u>denticulatus</u> Wirth and Hubert, 1962			X	X	Δ	Δ	Δ	ON.-MA-KY		K				
<u>husseyi</u> Wirth and Blanton, 1971			X					MD-FL						
<u>jambacki</u> Wirth & Hubert, 1962			X		Δ	Δ	Δ	ON.-NY		K		K		
<u>kirbyi</u> Glick and Mullen, 1983			X					AL						
<u>parapiliferus</u> Wirth and Blanton, 1974			X	X	X	X	X	ON.-FL		K				
<u>piliferus</u> Root and Hoffman, 1937			X	X	X	X	X	WI-PQ.-TN		B,K		K		
<u>scanloni</u> Wirth and Hubert, 1962			X					E. U.S.A.				K		
<u>snowi</u> Wirth and Jones, 1956			X	X	X	X	X	E. U.S.A.						
<u>testudinalis</u> Wirth and Hubert, 1962			X	X		Δ	Δ	E. U.S.A.		B,K		K		
Unplaced <u>C. (Oecacta)</u> species														
<u>melleus</u> (Coquillett), 1901			X	X	X	X	X	Coastal E. U.S.A.		B,K				
<u>nanus</u> Root and Hoffman, 1937			X	X	X	X	X	E. U.S.A.		K		K		
<u>travis</u> Vargas, 1937			X	X	X	X	X	E. U.S.A., SC		B,K		B		
<u>C. (Selfia)</u> Khalaf														
<u>C. (S.) multipunctatus</u> Malloch, 1915				X				IL, AL-TX, Mex.						

Tribe CERATOPOGONINI

Brachypogon

Table 45. cont'd.

SPECIES	Published Records											This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other			
CERATOPOGONINI <u>Brachypogon</u> cont'd.															
<u>canadensis</u> Downes, 1976	X	Δ	X	X	X	X	PQ.-FL		K			K			
Ceratoculicoides															
<u>blantoni</u> Wirth and Ratanaworabhan, 1971	X				X		n/a								
<u>longipennis</u> (Wirth), 1952	X				X		PQ.-FL; WA-CA					SC			
<u>virginianus</u> (Wirth), 1952	X	X			X	X	NY-FL								
Ceratopogon 1/															
☆ <u>culicoidithorax</u> Hoffman, 1926							ON.-NY, NJ								
<u>Isohelea</u> 2/							CT					2/			
☆ <u>serrata</u> (Lewis), 1956															
Tribe STII/OBEZZIINI															
<u>Alluaudomyia</u> 3/															
<u>bella</u> (Coquillett), 1902	X			Δ	X	X	Δ	Nearctic	B	B,K	K	MD(K)			
<u>footei</u> Wirth, 1952	X							ON.-FL		K?					
<u>megaparamera</u> Williams, 1957	X					X		MI-FL		B,K					
<u>needhami</u> Thomsen, 1935	X	X			X	X	Δ	Nearctic		K	K				
<u>paraspina</u> Wirth, 1952	X				X	X	Δ	Nearctic		K	K	MD(K)			
<u>parva</u> Wirth, 1952	X				X	Δ		NS.-FL, AK		K	K				

1/ Several undescribed species of Ceratopogon are known from this region (Grogan, in litt.), but none encountered in this study.

2/ Up to six undescribed Isohelea species encountered in the present study alone.

3/ At least one possible new Alluaudomyia species encountered in the present study.

Table 45. cont'd.

SPECIES	Published Records										This Study's Records				
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other			
<u>Alluaudomyia</u> cont'd.															
<u>variegata</u> Glick & Mullen, 1982	X			X				TX-FL, S.E. U.S.A. MI, GA							
☆ <u>wirthi</u> Williams, 1957					?										
<u>Echinohelea</u>															
<u>lanei</u> Wirth, 1951	X				X	Δ		MA-FL, Panama		K	K				
<u>Monohelea</u> <u>1/</u>															
<u>andersoni</u> Wirth and Grogan, 1981	X							n/a							
<u>bifurcata</u> Wirth and Williams, 1964	X				X	Δ		MA		K	K				
<u>floridensis</u> Wirth and Williams, 1964	X							MS, FL				K ^{1/}			
<u>hirsuta</u> Wirth and Grogan, 1981	X							FL							
<u>johannseni</u> Wirth, 1953	X	X			X			MI-FL							
<u>macfieii</u> Wirth, 1953	X				X	Δ		WI-MS			B				
<u>magnitheca</u> Wirth and Grogan, 1981	X							WI							
<u>nebulosa</u> (Coq.), 1901	X	X			X			MA-FL, TX							
<u>obscura</u> Wirth and Williams, 1964	X				Δ	Δ		MI-NY, MA		K	K				
<u>stonei</u> Wirth, 1953	X	Δ			X	Δ		MA-FL, AL		K	K				
<u>Parabezzia</u>															
<u>alexanderi</u> Wirth, 1965	X	X				Δ		MA-FL		B	K	MD (K)			
<u>bustraki</u> Grogan and Wirth, 1977	X							MD, FL							
<u>eupetiolata</u> Grogan and Wirth, 1977				Δ				NY		B?					
<u>huberti</u> Grogan and Wirth, 1977	X				X			n/a			K?				
<u>neunguis</u> Grogan and Wirth, 1977	X				X			n/a							
☆ <u>petiolata</u> Malloch, 1915								IL							
☆ <u>uncinata</u> (Johannsen), 1943								AL							

1/ Possibly one new species of Monohelea encountered in this study (nr. M. floridensis).

Table 45. cont'd.

SPECIES	Published Records											This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other			
STILOBEZZIINI cont'd.															
<u>Serromyia</u>															
<u>crassifemorata</u> Malloch, 1914			X	X	X	X	MI, IL						K?		
<u>femorata</u> (Meigen), 1804					?		PQ.-VA?, Holarctic								
<u>Stilobezzia</u> ^{1/}															
<u>S. (Eukraiohelea) elegantula</u> (Joh.), 1907			X				KS, LA, FL; Neotr.								
<u>S. (Neostilobezzia) lutea</u> (Mall.), 1918			X		X	Δ	E. U.S.A.						B, K K		
(N.) <u>stonei</u> Wirth, 1953			X		X	Δ	MI-FL						B, K K		
<u>S. (Stilobezzia) antennalis</u> (Coquillett), 1901			X	Δ	X	X	ON.-TX-FL						K B, K K		
(S.) <u>beckae</u> Wirth, 1953			X	Δ	X	Δ	MD-MS-FL; Neotr.						K K		
<u>bullae</u> Thomsen, 1953			X	Δ	X	Δ	PQ.-FL						B, K B, K B, K		
<u>coquilletti</u> Kieffer, 1917			X		X	X	IL-MD-FL; Neotr.						B, K		
<u>diversa</u> (Coquillett), 1901			X	Δ	X	Δ	NJ-FL						K K K		
<u>glauca</u> Macfie, 1939			X	Δ	X	X	MD-FL; Neotropical						K B, K		
<u>navaiae</u> Wirth and Grogan, 1981			X		Δ		NY						K		
<u>pallidiventris</u> (Malloch), 1915			X	Δ	X	X	CT						K		
<u>pruinosa</u> Wirth, 1952					X	X	AZ, CA, FL								
<u>rabelloi</u> Lane, 1947			X				GA, FL; Neotropical								
<u>sybleae</u> Wirth, 1953			X	Δ	X	Δ	MI-NY-FL						B B, K K		
<u>viridis</u> (Coq.), 1901			X		X	X	NJ, FL, TX						K		

^{1/} Up to two new Stilobezzia species encountered in this study (nr. S. antennalis and S. sp. B nr. sybleae).

Table 45. cont'd.

SPECIES	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
Tribe HETEROMYIINI														
Climochelea														
<u>bimaculata</u> (Loew), 1861			X	X	X	X	Δ	NH-FL				B	K	K
<u>curriei</u> (Coquillett), 1905		X				X	X	NF.-FL; AK, CA NY, FL						K
☆ <u>nubifera</u> (Coquillett), 1905														
<u>pseudonubifera</u> Grogan and Wirth, 1975			X	X		X		ON.-NC						
Heteromyia														
<u>fasciata</u> Say, 1825		X	X			X		MA-FL						K
<u>prattii</u> (Coquillett), 1902		X	X			X		ON.-FL						
Neurochelea														
<u>nigra</u> Wirth, 1952				X	X	X		GA; BC.; CA						
Tribe SPHAEROMIINI														
Jenkinchelea														
<u>albaria</u> (Coquillett), 1898		X	X			X		ON.-FL						K
☆ <u>magnipennis</u> (Joh.), 1908								ME-NY, IL; BC.-QU.						
Johannsenomyia														
☆ <u>annulicornis</u> Malloch, 1918								IL, MI, ON.; FL						
<u>argentata</u> (Loew), 1861	X	X	X	X	X	X		ON.-FL						K
Macropeza														
<u>pamunkeiana</u> Knausenberger & Wirth 1980								n/a						K
Mallochochelea 1/														
<u>albibasis</u> (Malloch), 1915		X	Δ			X		PQ.-AL BC.-CA; AZ, TX, FL				B	B, K	
☆ <u>caudellii</u> (Coquillett), 1905														

1/ At least one possible new Mallochochelea species encountered in this study (near M. caudellii(Coq.).

Table 45. cont'd.

SPECIES	Published Records											This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other			
<u>Mallochochelea</u> cont'd.															
albihalter Wirth, 1962	X						WI-PQ.-LA								
atripes Wirth, 1962	X	Δ		X			ON.-FL	B	K						
smithi (Lewis), 1956		X	X	X			WI-PQ.-NC, FL			K					
<u>Nilobezzia</u>															
mallochi Wirth, 1962	X						ON.-MI-MD; OK								
☆ minor (Wirth), 1952							PQ.-TX								
☆ schwarzii (Coquillett), 1901							SC-FL, Neotropics								
<u>Probezzia</u> 1/															
albitibia Wirth, 1971	X				X		WI-PQ.-VA				B, K				
☆ albiventris (Loew), 1861	X						WI-NB.-GA, FL								
jambacki Wirth, 1971	X						ON.-CT								
pallida Malloch, 1914	X	X	X	X			ON.-FL			K					
sabroskyi Wirth, 1951	X					Δ	WI-NB.-PA, IL, FL				K				
smithi (Coquillett), 1901	X				X		WI-NJ-FL				K				
xanthogaster (Kieffer), 1917	X				X		ON.-IL-VA				K				
<u>Sphaeromias</u>															
bifidus Wirth & Grogan, 1979	X						n/a								
longipennis (Loew), 1861	X	X	X	X	Δ		Eastern Nearctic			B, K	K				
Tribe PALPOMYIINI															
<u>Bezzia</u> 2/															

1/ Up to two new Probezzia species encountered in this study (near P. albitibia and P. smithi resp.)

2/ Up to 19 new undescribed Bezzia species encountered in this study alone (most in B. expolita and B. pulverea Groups). The systematic arrangement in this genus is based on revisionary work in progress by Wirth and co-workers (Grogan and Wirth, 1981; Wirth 1983a, b, c; 1984; in litt. 1980-83; Wirth and Grogan 1982, 1983; Wirth et. al. 1984).

Table 45. cont'd.

	Published Records											This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other			
<u>Bezzia</u> (<u>Bezzia</u>) cont'd.															
B. (B.) <u>nobilis</u> Group															
<u>nobilis</u> (Winnertz), 1852	X	X	X	X	X	X	Δ	Holarctic, Neotrop.	B, K	B, K	K	K			
B. (B.) <u>pulverea</u> Group															
<u>laciniastyla</u> Dow & Turner, 1976	X	X	X	X	Δ	Δ	MD, SC, FL: MS, TX	B, K	B, K	K	MD (K)	MD (K)			
<u>pulverea</u> (Coquillett), 1901	X	Δ	X	X	X	X	NJ, MS, LA, TX	K	K		MD (K)	MD (K)			
☆ <u>spicata</u> Dow & Turner, 1976							FL								
<u>uncistyla</u> Dow & Turner, 1976					Δ		ON.-NY-FL; NE				K				
B. (Homobezzia) species															
B. (H.) <u>annulipes</u> Group															
<u>annulipes</u> (Meigen), 1830								Holarctic, boreal							
<u>fascispinosa</u> Clastrier, 1962			X		Δ		ON., Holarctic				K				
<u>pseudobscura</u> Wirth, 1951			X		X		FL								
<u>solstitialis</u> (Winnertz), 1852			X		X		Europe, N. Amer.				K? B, K	K?			
<u>varicolor</u> (Coquillett), 1902			X	Δ	X	Δ	ON.-NF.-FL				K	B, K			
B. (H.) <u>bicolor</u> Group															
☆ <u>bicolor</u> (Meigen), 1804								Holarctic, boreal							
☆ <u>fairchildi</u> Wirth, 1983								FL							
<u>glabra</u> (Coquillett), 1902			X	X	X	Δ	Eastern Nearctic				K	K			
B. (H.) <u>cockerelli</u> Group															
☆ <u>cockerelli</u> Malloch, 1915								NY, boreal Nearctic							
☆ <u>pruinosa</u> (Coquillett), 1905								NY, MI; ON.-B.C., CA							
B. (H.) <u>dorsasetula</u> Group															
<u>dorsasetula</u> Dow & Turner, 1976					Δ	Δ	NY, FL				K	K			
<u>obelisca</u> Dow & Turner, 1976					Δ	Δ	NY				K	K			

1/ [syn. setulosa (Loew), 1861]

Table 45. cont'd.

SPECIES	Published Records											This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other			
Tribe PALPOMYIINI <u>Bezzia</u> cont'd.															
<u>Bezzia</u> (<u>Bezzia</u>) species															
<u>bivittata</u> Group															
<u>andersonorum</u> Wirth and Grogan, 1983	X	X	X	X	X	X	X	n/a							
<u>bivittata</u> (Coquillett), 1905	X	X	X	X	X	X	X	Nearctic	K?			K?			
☆ <u>flavitibia</u> Dow and Turner, 1976								ON., NY							
<u>gibbera</u> (Coquillett), 1905					?			FL, AZ; Caribb.				K?			
<u>gibberella</u> Wirth and Grogan, 1983	X	Δ	X	X		X	X	MI-MD-FL; QU.				K?			
<u>luteiventris</u> Wirth and Grogan, 1983						X	X	VA Only							
<u>setosinotum</u> Wirth & Grogan, 1983	X		X				X	NJ-FL							
<u>spathula</u> Wirth & Grogan, 1983	X		X					MD Only							
B. (B.) <u>expolita</u> Group															
<u>albidorsata</u> Malloch, 1915						X	X	CT-IL-VA				K			
☆ <u>apicata</u> Malloch, 1914						X	X	MI, NY, IL				K?			
<u>dentata</u> Malloch, 1914								IL							
<u>expolita</u> (Coquillett), 1901						X	X	NY-FL				K			
<u>flavitaris</u> Malloch, 1915	X	Δ	X	X		X	Δ	CT-FL	B, K	B, K	B, K	B, K			
<u>imbifida</u> Dow and Turner, 1976	X							MD							
<u>mallochi</u> Wirth, 1951						X	X	VA				B, K			
<u>media</u> (Coquillett), 1904						X	X	CT-VA							
<u>perplexa</u> Dow and Turner, 1976						X	X	PQ.-FL				B, K			

Table 45. cont'd.

	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
PALPOMYIINI cont'd.														
<u>Palpomyia</u> ^{1/}														
<u>P. distincta</u> Group														
<u>plebeia</u> (Loew), 1861	X	X		X	X	X	NF.-WI-FL				B,K	K		
<u>plebeiiella</u> Grogan and Wirth, 1975	X	X	X	X	X	X	WI-TN				B,K	K		
<u>pseudorufa</u> Grogan and Wirth, 1975	X	X	X	X	X	X	MD-FL							
<u>rubiginosa</u> Grogan and Wirth, 1975	X	X	X	X	X	X	WI-PQ.-SC							
<u>rufa</u> (Loew), 1861	X	X		X	X	X	MI-FL		K		B,K	K		
<u>stonei</u> Wirth, 1951				X	X	X	ON.-VA				B,K	B		
<u>walteri</u> Grogan and Wirth, 1979				Δ	X	X	PQ.-LB.-WV				K	B,K		
<u>P. flavipes</u> Group														
<u>basalis</u> (Walker), 1848	X	X		X	X	X	NB.-WI-GA					K		
<u>canadensis</u> Grogan and Wirth, 1979	X	X	?	X	Δ	X	LB.-WV					K		
<u>flaviceps</u> (Johannsen), 1908 ^{2/}	X	X	X	X	X	X	NB.-MI-GA							
<u>hastata</u> Grogan and Wirth, 1975	X			X	X	Δ	NB.MI-GA					K		
<u>scalpellifera</u> Grogan and Wirth, 1975	X	X		X	X	X	NF.-NC					K		
<u>P. lineata</u> Group														
<u>lineata</u> (Meigen), 1818	X	X		X	X	X	Holarctic				B,K	K		
<u>P. tibialis</u> Group														
<u>cressoni</u> (Malloch), 1915	X			X	X	X	PA					B,K		
<u>novitibialis</u> Grogan and Wirth, 1975	Δ			X	X	X	WI-PQ.-VA							
<u>subaspera</u> Coquillett, 1901	X	X	X	X	X	X	Nearctic					B,K		

^{1/} At least one undescribed Palpomyia species encountered in this study (near P. novitibialis).

^{2/} Probably constitutes a complex of two or more species (Grogan and Wirth, 1979:109).

Table 45 . cont'd.

SPECIES	Published Records										This Study's Records			
	DC	KY	MD	NC	TN	VA	WV	Other	NC	VA	WV	Other		
<u>Palpomyia</u> cont'd.														
<u>tibialis</u> (Meigan), 1818			X	Δ	X			ON.-VA, Holarctic	K	K		MD(K)		
<u>weemsi</u> Grogan and Wirth, 1979			X	X	X	Δ	MD-FL	K	B,K	K				
<u>Phaenobezzia</u>														
<u>opaca</u> (Loew), 1861			X	X	X	X	NS.-MI-FL		K	K				
<u>sabroskyi</u> Wirth and Grogan, 1982			X		Δ	Δ	FL, LA		K	K				
Tribe STENOXENINI														
<u>Stenoxenus</u>														
★ <u>johnsoni</u> Coquillett, 1899								NJ, MO, TX						
SPECIES TOTALS BASED ON PUBL. REC.														
	19	13	158	74	61	152	44	-	42	137	83	141/		
NEW REC. OF DESCR. SPP. (THIS STUDY)														
	0	0	1	20	0	28	56	-				n/a		
GRAND TOTAL DESCR. SPP. NOW KNOWN														
	19	13	159	94	61	180	100	-				n/a		

1/ AL=3; KY=1; MD=9; Σ=14.

Table 46. Geographic allocation, among physiographic province and river basins, of all substrate collection stations and localities covered in this study. Entries proceed from west to east, and south to north, within and among physiographic provinces. Collection numbers are grouped according to locality. The initials "FVB" precede collections made by F. V. Battle; all other collections were made by the author. Numbers in parentheses indicate how many sample sites are included in each area listed. Higher elevation localities are identified by the symbols as follows:★★ above 4000 ft. (1220m), ★ 3000-3999 ft. (914-1119m), ◊ 2000-2999 ft. (610-913m). Biotic regions are designated when possible, based on associations of fauna and flora, and on altitudinal and thermic characteristics at the sites per se. Clear distinction in areas of overlap generally is not possible with available data.

Location	Biotic Region ^{1/}
<u>APPALACHIAN PLATEAU PHYSIOGRAPHIC PROVINCE (P.P.)</u>	
West Virginia Only	
NEW/KANAWHA RIVER BASIN	
Pocahontas Co. (see also Ridge and Valley P.P.)	
★ Williams R. (1): 61	Teaysian
★★ Black Mtn. on St. Rt. 150 (1): 62	Canadian
★ Cranberry Glades/Cranberry R. (45): 51-60; 145A-156; 169-173; 273A-273B; 325A-328; 343A,B.	Canadian
Randolph Co.	
★★ Gaudineer Scenic Area (2): 272A,B	Canadian
★ Sinks of Gandy (12): 269A-271C	Canadian
★ Spruce Knob Lake (3): 268A-C	Canadian
Pendleton Co.	
★★ Spruce Knob (3): 266A-267	
<u>RIDGE AND VALLEY (SOUTHERN SECTION) P.P.</u>	
POWELL TENNESSEE RIVER BASIN (R.B.)	
★ Big Cherry Reservoir (2): 90A,B	Alleghanian
CLINCH/TENNESSEE RIVER BASIN	
Clinch Valley Spring (1): 86	Carolinian

^{1/} Including Canadian "Life Zone" (Hoffman 1969:49)

Table 46 cont'd.

Location	Biotic Region
HOLSTON-TENNESSEE R.B.	
◊ Clinch Mtn. Wildlife Mngmt. Area (1): 85	Canadian?
★ White Top Mtn. flank (1): 84	Canadian
Saltville (11): 76-80; 470A-407F	Carolinian
★★ Beartown Mtn. bog (6): 399A-401B	Canadian
<u>RIDGE AND VALLEY (MIDDLE SECTION) P.P.</u>	
NEW RIVER BASIN	
★ Burkes Garden (3): 87-89	Alleghanian
Reed Creek at Wytheville (6 sites sampled approx. 72 times in all)	Teaysian
◊ Dismal Creek (Trib. of Walker's Cr. Giles Co.) (1) FVB 141	Alleghanian
Montgomery Co. (110) (see Appendix Table A-1 for listing of site numbers.)	Alleghanian
◊ Blacksburg/V.P.I. & S.U. area (21)	
◊ Laurel Ridge (3)	
New River floodplain (7)	
◊ Pandapas Pond/Poverty Creek (27) + (FVB site "E":8)	Alleghanian
Price's Fork area (5)	
◊ Shadow Lake Pond (13)	
Sink-hole pool - McCoy area (5)	
Stroubles Cr. (3)	
Tom's Cr. drainage/floodplain (29)	
Giles Co.	
★ Salt Pond Mtn. massif (9; see also James R.B.) 283A-285B; 322A,B	Canadian
★ Little Stony Cr. (upper) (4) 323A,B,; 324; 395	Canadian
◊ Cascades (5) 287A,B; 394, 396A,B	Alleghanian
★★ Butt Mtn. (2) 286A,B	Canadian
★ Big Stony Creek (5) FVB 5; 60, 61; 66,67	Canadian
◊ Sinking Creek + trib. (6) 9, 10; 256 ,257A-C	
★ Sinking Cr. Mtn. (1) 66	
New River at Glen Lyn (about 195 samplings from 6 sites)	Teaysian
West Virginia:	
Summers Co. (1): FVB 114	
◊ Monroe Co. (9): FVB 104-112	
Greenbrier Co. (3): 65A,B; FVB 113	
Fayette Co. (2): 63,64	
Pocahontas Co.	
Watoga St. Pk. 279	
Knapps Cr. at Minnehaha Spr. 157	

Table 46. cont'd.

Location	Biotic Region
SHENANDOAH-POTOMAC R.B. cont'd.	
Shenandoah Co.	
◊ Passage Cr. Massanutten Mtn. (2) 360A,B	
West Virginia: ◊ Pendleton Co. (5): 263A-C; 264; 265	
<u>BLUE RIDGE PHYSIOGRAPHIC PROVINCE</u>	
<u>Southern Section</u>	
HOLSTON-TENNESSEE RIVER BASIN	
★ Whitetop Mtn/Mt. Rogers region (3): 81-83	Alleghanian
ROANOKE R.B.	
Roanoke Co., Roanoke R. vernal pool (3): 73-75	
Northern Section, Blue Ridge, P.P.	
Bedford Co. Goose Cr. at Montvale (1):390	
JAMES R.B.	
Amherst Co. Otter Lake (5) 316A-E	
SHENANDOAH-POTOMAC R.B.	
◊ Fauquier Co. (1) 359	Shenandoan
PIEDMONT P.P.	
<u>Inner Piedmont</u>	
ROANOKE R.B.	
Henry Co. (4): Dan River basin :FVB 80-83	ian
Bedford Co. Smith Mtn. Lk.: 199	
JAMES R.B.	
James R. at Nelson-Appomattox Co. lines: 382	
Buckingham Co., James R. floodplng pond: 381	
Albemarle Co. (2): FVB 40, 41	
<u>Outer Piedmont</u>	
PAMLICO R.B. (North Carolina)	
Granville Co., NC (3): Tar R. basin FVB 89, 90,	
ROANOKE R.B. (NC)	
Caswell, Halifax, Person, Rockingham, Vance and	
Warren Cos. (18): FVB 84-88; 91-92; 801-804	
806-811	
ROANOKE R.B. (VA)	
Pittsylvania Co. (5) Dan R. basin: FVB 99-103	
Halifax Co. (2): FVB 97,98	
Mecklenburg Co. (4): FVB 93-96	Floridian
Charlotte Co. (2): 45, 46	
Appendix C. Geography and Biogeography	

*Be-do
46 at
45 P. 46
45-46*

Table 46. cont'd.

Location	Biotic Region
West Virginia cont'd.	
◇ Dunmore Spr. (4): 273A,B; 330A,B	
◇ Greenbrier R. at Cass (2): 329A,B	
ROANOKE R.B.	
Montgomery Co.	
N.Fk of Roanoke River floodplain & trib. (21) (see appropriate Appendix Tables; Montgomery and Roanoke Co.)	Alleghanian
◇ Cedar Run (about 270 samplings from 8 sites; ca. 220 above 2000')	
S.Fk. Roanoke River at Elliston (125 samplings from 3 sites)	Alleghanian
Luster's Gate area (95 by FVB, sites "A", "B", and "C")	
JAMES R.B.	
★ Giles Co., Salt Pond Mtn. (9): 391-393; FVB 150-155	Canadian
◇ Roanoke Co. roadside marsh (1): 159	
★ Roanoke Co. at Dragon's Tooth (Appalachian Trail): 158	
◇ Craig Co. farmpond marsh (2): 404,405	
◇ Craig Co. Pott's Mtn. cattle watering trough (1): 108	
★★ Craig Co./Alleghany Co., Pott's Bog (6):109-112; 406A,B	Alleghanian?
Alleghany Co., Jackson River (4): 383-386	
Rockbridge Co., Maury River (2): 164,165	
Augusta Co. (also see Shenandoah RB)	
★★ Great North Mtn. (2) 260	
Elkhorn Lake (4) 261A-D	
◇ Ramsey's Draft (2) 47,48	
Highland Co. (also see Shanandoah-Potomac RB)	
◇ Bull Pasture Mtn. 262	
Bath Co.	
Warm Springs (4): 176U-168L	
◇ Roadside marsh 7 mi E of Warm Spr. (2): 166A,B	
SHENANDOAH -POTOMAC	
Augusta Co.	
Mt. Solon, Blue Hole Spring (1): 362	
Verona, chicken house (1): 198	
Christian Cr. (1) FVB 42	
Highland Co.	
★ Streamside marsh 3.0 mi. E of Monterey:49, 50	
Rockingham Co.	
◇ Little North Mtn. flank (5): 140-144	
Massanutten Mtn., Gerundo Compd. (7): 333A-G	
Page Co.	
Spring seep 4 mi. W. of Luray (2) 361A,B	

Table 46 . cont'd.

Location	Biotic Region
<hr/>	
PIEDMONT P.P. cont'd.	
CHOWAN R.B.	
Lunenburg Co. (5) 201A-D; 202	
Brunswick Co. 203	
JAMES R.B.	
Appomattox Co. (4): 314A,B 315, 389	
Nottoway Co. (1): 200	
Cumberland Co. (1) Bear Cr. Lk.: 380	
Powhatan Co. (3) 378A,B; 379	
Chesterfield Co. (6): 375A-D; 376, 377	
YORK R.B.	
Lake Anna reservoir	Carolinian
Louisa Co. (18) 318A,B; 331A-332B, 334-341	
Spotsylvania Co. (1) 342	
RAPPAHANNOCK R.B.	
Spotsylvania-Orange Co. line (2): FVB 38, 39	
POTOMAC R.B.	
Prince William Co. (2): 373A,B	
Stafford Co. (3): 374 A-C	
<u>COASTAL PLAIN P.P.</u>	
CHOWAN R.B.	
Sussex Co. (1): 313A,B	
DISMAL SWAMP BASIN	
Suffolk city (51): 20-29; 32, 33; 40; 124-129;	Carolinian
178-189; 212; 214A,B; 218A,B; 232A-234; 291A-296	
Chesapeake City (16): 30-39, 122, 123,; 128; 183, 235,	
FVB 51	
Camden Co. (17) 225-231; 288A-290B; FVB 52-54	
Gates Co. (7) 219-224	
CHESAPEAKE BAY/ATLANTIC OCEAN DRAINAGE BASIN	
Virginia Beach City	
Back Bay (16): 41-44; 131-133; 190-192; 205-207C	Littoral and Floridian
FVB 55	
Other (8): 134, 193, 204, 208, 209, 215-217	Littoral and Floridian
Norfolk city (9): 175A-177D; 309; 402	Littoral
JAMES R.B.	
Suffolk city (6). Nansemond R.: 114, 115; 130; 174	
310-311	Littoral

Table 46. cont'd.

Location	Biotic Region
JAMES R.B. cont'd.	
Isle of Wight Co. (11). 116-120, 194-196; 211; 312A,B. James City Co. at Jamestown (6): 197; 354-358	Littoral
YORK R.B.	
York Co. (2): 353; FVB 25 Gloucester Co. (3): 26-28	Littoral
CHESAPEAKE BAY DRAINAGE BASIN	
York Co., Poquoson (5): 210; FVB 21-24	Littoral
Gloucester Co.: FVB 29	Littoral
Hampton city (7): 297-299; 347-350	Littoral
PIANKATANK R.B.	
Middlesex Co. (2): FVB 30, 31	Littoral
RAPPAHANNOCK R.B.	
Lancaster Co. (1): 32	Littoral
Stafford/King George Cos.: 37	
CHESAPEAKE BAY /ATLANTIC DRAINAGE BASIN	
Eastern Shore - Delmarva Peninsula	
Northampton Co. (3): 135, 136; 300	Littoral
Accomack Co. (12): 137-139; 301-308	Littoral, other
POTOMAC R.B.	
Northumberland Co. (3): FVB 33-35	Littoral
King George Co. (1): FVB 36	Littoral
Fairfax Co. (3): 371A,B. 372	Littoral
Prince Georges Co., MD (3): 370 A-C	Carolinian

Appendix C. Table 47. Overview of the biogeographic classification scheme proposed for Virginia by Hoffman (1969) in the context of physiographic provinces and river basins. Classified in two parts, according to biotic regions and physiographic provinces, respectively. Entries listed in general order of south to north and west to east.

Part I. Arranged by Biotic Region		
Biotic Region	River Basin	Physiographic Province ^{1/}
AUSTRAL AFFINITIES		
Carolinian (overlaps Floridian, Alleghanian in part)	Roanoke	Coastal Plain
	Chowan	
	Dismal Swamp	Piedmont - Outer
	Atlantic (Eastern shore, S.E. Vir- ginia)	Piedmont - Inner Ridge and Valley - Middle (in part)
	Chesapeake Bay	
	James	
	York	
	Rappahannock	
	Potomac	
	(all but Tennessee, New, Big Sandy)	
Floridian (overlaps Carolinian, Littoral)	Same as Carolinian (above)	Coastal Plain - Upper, Lower Piedmont - Outer (in large river basins)
Littoral (overlaps Floridian)	Atlantic Chesapeake Bay James York Rappahannock Potomac	Coastal Plain - Lower
BOREAL AFFINITIES		
Cumberlandian (overlaps Alleghanian, Teaysian)	Big Sandy	Appalachian Plateau Cumberlandian Mtns.
	Tennessee New/Kanawha	Appalachian Plateau - Unglaciaded

^{1/} Listed in order of amount of surface area of Province included in Region.

Table 47. Part I cont'd.

Biotic Region	River Basin	Physiographic Province
Alleghanian (overlaps Cumberl., Teaysian, Shenandoan, Carolinian in part)	Tennessee Big Sandy New/Kanawha Roanoke James Rappahannock Shenandoah/Potomac	Ridge + Valley - South R. + V. - Middle Appalachian Plateau Blue Ridge Piedmont - Inner
Canadian Life Zone (disjunct, relictual above 1100m, in Alleg., Teaysian)	Tennessee New James Shenandoah/Potomac	Appalachian Plateau Ridge + Valley - South Ridge + Valley - Middle
Teaysian	New/Kanawha	Appalachian Plateau Ridge + Valley - South Ridge + Valley - Middle Blue Ridge - South Blue Ridge - North
Shenandoan	Roanoke James Rappahannock Shenandoah Potomac	Blue Ridge - North

Part II. Classified by Physiographic Province

Physiographic Province Province Subsection	River Basin	Biotic Region
Appalachian Plateau Cumberland Mtns. Unglaciaded	Big Sandy Tennessee New/Kanawha	Alleghanian Cumberlandian Alleghanian (Canadian L.Z.) ^{1/} Cumberlandian Teaysian
Ridge and Valley South	Tennessee	Alleghanian (Canadian L.Z.) Carolinian

^{1/} The Canadian Life Zone concept of Merriam; not a biotic region in the sense of Hoffman (1969:49) though Hoffman does consider it a distinct ecological biome.

Table 47. Part II cont'd.

Physiographic Province Province Subsection	River Basin	Biotic Region
Ridge and Valley Middle	New/Kanawha	Alleghanian (Canadian L.Z.) Cumberlandian Teaysian
	Roanoke	Alleghanian Carolinian
	James Shenandoah/Potomac	Alleghanian (Canadian L.Z.) Carolinian
Blue Ridge South	New	Alleghanian Teaysian
	Roanoke	Alleghanian Carolinian Teaysian
North	James Rappahannock Shenandoah/Potomac	Alleghanian Shenandoan
	Roanoke James York Rappahannock Potomac	Alleghanian Carolinian
Piedmont Inner	Roanoke James York Rappahannock Potomac	Alleghanian Carolinian
	Roanoke/Staunton Chowan James York Rappahannock Potomac	Carolinian Floridian
Coastal Plain Upper Terraces	Chowan	Carolinian Floridian
	James York Rappahannock Potomac	Carolinian Floridian Littoral

Table 47. Part II cont'd.

Physiographic Province	River Basin	Biotic Region
Coastal Plain		
Lower Terraces	Atlantic Ocean/ Chesapeake Bay	Carolinian Floridian Littoral Sabalian ^{1/}
	Dismal Swamp	Carolinian Floridian Sabalian
	James York Rappahannock Potomac	Carolinian Floridian Littoral

^{1/} Informally raised name for a region including the two lower terraces in southeastern Virginia, north up to Cape Henry (Hoffman 1969:52).

Appendix C. Table 48. Geographical tally of Knausenberger's (WIK) substrate Collection Site numbers, by State, County and City, for natural and artificial substrates collected in Virginia and surrounding States from 1975 to 1978. Numbers in parentheses give the total number of collections made in each geographical entity listed. Underlined Site numbers indicate sites which yielded neither emerged adults nor immature specimens of Ceratopogonidae (where both were attempted).

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=====
STATE
  Counties                WIK Collection Site Numbers
-----
KENTUCKY
  Carter Co. (1)          317

MARYLAND (3)
  Prince Georges Co. (3)  370A,370B,370C,

NORTH CAROLINA (22)
  Camden Co. (14)         225,226,227A,227B,228,229A,229B,
  Dismal Swamp (all)     230,231,288A,288B,289,290A,290B

  Currituck Co. (1)      121

  Gates Co. (7)          219,220,221,222A,222B,223,224
  Dismal Swamp (6)      all but 219

VIRGINIA (443)
  Accomack Co. (12)      137,138,139,301,302,303A,303B,
                        304,305,306,307,308

  Alleghany Co. (4)      383,384,385,386

  Amherst Co. (5)        316A,316B,316C,316D,316E

  Appomattox Co. (4)     314A,314B,315,389

  Augusta Co. (10)       47,48,198,260,261A,261B,261C,
                        261D,362,388

  Bath Co. (7)           166A,166B,167L,167U,168L,168U,
                        169L

  Bedford Co. (2)        199,390

  Brunswick Co. (1)      203

  Buckingham Co. (1)     381

  Charlotte Co. (2)      45,46

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Table 48 . (Cont'd)

STATE	
Counties	WIK Collection Site Numbers
VIRGINIA	
Chesterfield (6) Co.	375A, 375B, 375C, 375D, 376, 377
Craig Co. (9)	108, 109, 110, 111, 112, 404, 405, 406A, 406B
Cumberland Co. (1)	380
Fairfax Co. (3)	<u>371A</u> , 371B, 372
Fauquier Co. (1)	359
Giles Co. (31)	9, 10, 66, 256, 257A, 257B, 257C, 283A, 283B, <u>283C</u> , 284, 285A, 285B, 285C, 285D, <u>286A</u> , 286B, 287A, 287B, 322A, 322B, <u>323A</u> , <u>323B</u> , 324, 391, 392, 393, 394, 395, 396A, 396B,
Highland Co. (3)	49, 50, 262
Isle of Wight Co. (11)	116, 117, 118, 119, 120, 194, 195, 196, 211, 312A, 312B
James City Co. (6)	<u>197</u> , 354, <u>355</u> , 356, 357, <u>358</u>
Louisa Co. (18)	318A, <u>318B</u> , 331A, 331B, 332A, 332B, 334A, <u>334B</u> , 335, <u>336</u> , <u>337A</u> , <u>337B</u> , 338A, <u>338B</u> , <u>339</u> , <u>340</u> , 341, 344
Lunenburg Co. (5)	201A, <u>201B</u> , 201C, 201D, <u>202</u>
Montgomery Co. (120)	
Blacksburg/V.P.I. Campus (17)	11, 93, 94A, 94B, <u>94C</u> , 94D, 102, 103, 104, 105, 106, 107, <u>113A</u> , 113B, 213, 237, 238
Misc. sites (7)	249, <u>250</u> , <u>251</u> , 259, 387A, 387B, 387C
New River (7)	252, 367A, <u>367B</u> , 368A, <u>368B</u> , 368C, 369
North Fork of Roanoke R. Val- ly (NFRR) (20)	67, 69A, 69B, 69C, 70, 71, <u>72A</u> , <u>72B</u> , 160, 161A, 161B, 161C, 162, 163, 240A, 240B, 241A, 241B, 242, 403 (Mill Cr.)

Table 48 . (Cont'd)

STATE	
Counties/Cities	WIK Collection Site Numbers
VIRGINIA	
Montgomery Co.	
Cont'd.	
Pandapas Pond area (18)	4, 5, 6, 7, 8, 254, 255, 280, 281, 282, 319A, 319B, 319C, 319C, 319E, 320A, 320B, 321
Price's Fork Road	91, 92A, 92B, 236, 247
Shadow Lake Pond area (13)	1, 1A, 2, 3, 16, 17, 18, 19, 97, 98, 99, 246, 365
Sink-hole pool McCoy Rd., Co. Rt. 652 (5)	248, 258, 345, 351, 363
Stroubles Creek (3)	95, 96, 239
Tom's Creek (25) floodplain	12, 12-MP, 13, 14, 15, 16-MP, 100A, 100B, 101, 243, 244, 245, 253, 346, 352A, 352B, 364, 366, 397A, 397B, 397C, 397D, 398A, 398B-1, 398B-2
Nelson Co. (1)	382
Northhampton (3) Co.	135, 136, 300
Nottoway Co. (1)	200
Page Co. (2)	361A, 361B
Powhatan Co. (3)	378A, 378B, 379
Prince William (2)	373A, 373B
Roanoke Co. (6)	68, 73, 74, 75, 158, 159
Rockbridge Co. (2)	164, 165
Rockingham Co. (12)	140, 141, 142, 143, 144, 333A, 333B, 333C, 333D, 333E, 333F, 333G
Shenandoah Co. (2)	360A, 360B,

Table 48 . (Cont'd)

STATE	
Counties/Cities	WIK Collection Site Numbers
VIRGINIA	
Smyth Co. (13)	76,77,78,79, <u>80</u> ,81,82,407A,407B, 407C,407C,407E,407F
Spotsylvania Co. (1)	342
Stafford Co. (3)	374A,374B,374C
Sussex Co. (3)	313A,313B,313C
Tazewell Co. (11)	85,86,87,88,89,399A,399B,400A, 400B,401A,401B
Washington Co. (2)	83,84,
Wise Co. (2)	90A,90B
York Co. (2)	210,353
<u>Cities</u>	
Chesapeake (15) Dismal Swamp (all)	30,31,MP-5,34, <u>35</u> ,36,37,38,39,122, 123,128,183,183-MP,235
Hampton (7)	297,298,299,347,348, <u>349</u> , <u>350</u>
Norfolk (9)	175A,175B,176,177A,177B,177C,177D, 309,402
Suffolk (57) Dismal Swamp (47)	20,21,21-MP, <u>22</u> ,23,24,25,26, <u>27</u> , 28-MP,28,29, <u>32</u> ,33,40,124,125,126, 127,129,178,179,179-MP,180,181, 182,184,184-MP, <u>185</u> ,186,187,188, <u>189</u> ,212, <u>232A</u> , <u>232B</u> ,233,234,291A, <u>291B</u> ,292, <u>293A</u> ,293B,294,295,296
Other sites (10)	114,115,130,174,214A,214B,218A, 218B,310, <u>311</u>
Virginia Beach (23)	41,42,43,44, <u>131</u> ,132,133,134,190, 191,192,193,204,205,206,207A, <u>207B</u> , 207C,208, <u>209</u> ,215,216,217

Table 48 . (Cont'd)

STATE	
Counties/Cities	WIK Collection Site Numbers
WEST VIRGINIA (82)	
Fayette Co. (2)	63,64
Greenbrier Co. (2)	65A,65B,
Pendleton Co. (8)	263A,263B,263C, <u>264</u> ,265,266A,266B, <u>267</u>
Pocahontas Co. (53) Cranberry Glades (45)	51,52,53,54,55,56,57,58,59,60, 145A,145B,146,147,148,149, <u>150</u> , <u>151</u> , 152,153,154,155,156,169,170,171, 172,173,273A,273B,274,275, <u>276</u> ,277, 278A,278B,325A,325B,326A,326B, <u>327A</u> ,327B,328,343A,343B
Other sites (8)	61, <u>62</u> ,157,279,329A,329B,330A,330B
Randolph Co. (17)	268A,268B,268C,269A,269B,269C, <u>269D</u> ,270A,270B,270C,270D,270E, <u>271A</u> ,271B,271C, <u>272A</u> ,272B

Appendix C. Table 49. Talley by State and County of F.V. Battle's (FVB) field collection site numbers for collections of natural substrate in Virginia and other states in 1969. Numbers in parentheses indicate how many collection efforts were made per county or state. Lines under field collection numbers indicate sites which yielded no emerged adults.

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=====
STATE
  County                                FVB Collection Site Numbers
-----
ALABAMA (9)
  Clay Co. (4)                          128,129,135,136
  Talladega Co. (5)                      130,131,132,133,134
NEW JERSEY (2)
  Burlington Co. (2)                     156,157 (Coll. G. Tanner)
NORTH CAROLINA (24)
  Camden Co. (3)                          52,53,54
  Caswell Co. (5)                         85,86,87,800,801
  Granville Co. (3)                       89,90,805
  Halifax Co. (2)                         810,811
  Person Co. (4)                          88,802,803,804
  Rockingham Co. (1)                      84
  Vance Co. (2)                            806,807
  Warren Co. (4)                           91,92,808,809
VIRGINIA (162)
  Albemarle Co. (2)                       40,41
  Augusta Co. (1)                          42
  Chesapeake (City) (1)                    51
  Giles Co. (12)                           5,60,61,66,67,141,150,151,152,
                                           153,154,155
  Gloucester Co. (4)                       26,27,28,29
  Halifax Co. (2)                          97,98
  Henry Co. (4)                            80,81,82,83

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Table 49 . (Cont'd)

STATE	County	FVB Collection Site Numbers
VIRGINIA cont'd		
	King George Co. (1)	36
	Lancaster Co. (1)	32
	Mecklenburg Co. (4)	93,94,95,96
	Middlesex Co. (2)	30, <u>31</u>
	Montgomery Co. (110) ^{1/}	
	Luster's Gate area (weekly 19-III to 13-XI-1969)	
	"Site A"--"McPherson farm pond" (32)	3,8,12,16,20,45,49,58,64,70, 74,79,117,123,126,127,139, <u>145</u> ,148,160,163,164,166,169, <u>172</u> ,175,178,181,184,187,190, 192
	"Site B"--"hog lot stream" (34)	2,7,11,15,19,44,48,57,63,69, 71,73,77,78,116,121,122,125, 138,143,144, <u>147</u> ,159,162,165, 168,171,174, <u>177</u> ,180,183,186, 189,191
	"Site C"--"power- line farm pond" (29)	<u>1</u> ,6, <u>10</u> ,14,18, <u>43</u> ,47,56,62,68, 72,76,115,120, <u>124</u> ,137,142, <u>146</u> ,158,161,164,167,170,173, <u>176</u> , <u>179</u> ,182,185,188
	Misc. sites (5)	4,9,17,118,119
	Pandapas Pond (8) ("Site E")	13,46,50,59,65,75, <u>140</u> ,149
	Northumberland Co. (3)	<u>33</u> ,34,35
	Pittsylvania Co. (5)	99,100,101,102,103
	Spotsylvania Co. (2)	38,39

^{1/} In this county only, all but FVB Coll. Nos. 118 and 119 had duplicate (A,B) samples per collection site for a total of 213.

Table 49. (Cont'd)

STATE	FVB Collection Site Numbers
County (City)	
VIRGINIA cont'd	
Stafford Co. (1)	37
Virginia Beach (City) (1)	55
York Co. (5)	21,22,23,24,25
WEST VIRGINIA (11)	
Greenbrier Co. (1)	113
Monroe Co. (9)	104, <u>105</u> ,106,107,108, <u>109</u> ,110, 111, <u>112</u>
Summers Co. (1)	114

Appendix D. RECORD FORMS

COLLECTION DATA
Immature Ceratopogonidae Project

SITE DATA

Coll. No. Date. Method: Scoop
M D Y Corer
Collector(s) Art. Subst.
Other
Adults by
Polit. Div. State
Location (verbal).
.
.
Long. . . ° . . ' . . " Lat. . . ° . . ' . . " Elev.
Gen. habitat.
.
Microhab.
.
.
Terrain. Pert. weather data.
VEGETATION CHARACTERISTICS: Biotic prov. Pl. comm.
. Dom. Spp.: Overstory. Canopy: Dense.
Moderate.
Sparse.
None
Understory.
. Other species.
CHEMICAL AND PHYSICAL CHARACTERISTICS: Temp.: Air. . . . Water Substr. . . .
Substr. moisture. . . % Org. matter. . . % Particle size D₅₀(mm). . . . ∅

	pH	Salin.	Cond.	Soluble Salts	NO ₃ ⁻	K ⁺	p ⁺⁵	Mg ⁺⁺	Ca ⁺⁺	D.O.	Total Hardness
		ppt.	µmhos/cm	mg/l (p.p.m.)							mg/l as CaCO ₃
Water				+++++							
Substrate										+++	+++++

OTHER

Figure 19. Collection data form used to standarize the information acquired at the suspected habitats of immature Ceratopogonidae (reduced by 26%).

IDENTIFICATION RECORD FOR CERATOPOGONIDAE PROJECT

WIK Coll.# _____ Date Coll. _____ 19 ____ Date ID ____ 19 ____ Location _____

Taxa	(refer to Collection Record)										Remarks	
	IR Individually-reared Stages					IMM Immatures Preserved		RC Adults <u>ex</u> Rearing Carton	Adults Field- Trapped			
	L	L-P	L-A	P	P-A	L	P					
<u>Forcipomyia</u>												
<u>Atrichopogon</u>												
<u>Dasyhelea</u>												
<u>Culicoides</u>												
Ceratopogonini <u>Alluaudomyia</u>												
Stilobezziini <u>Stilobezzia</u>												
Heteromyiini												
Sphaeromiini												
<u>Palpomyia-Bezzia</u> Complex Palpomyiini <u>Bezzia</u>												
<u>Palpomvia</u>												
CHIRONOMIDAE												
TIPULIDAE												
OTHER												

Figure 21. Identification record form used to combine the determinations of specimens retrieved from each collection site by the various methods of processing and/or collecting (reduced to 74% of original).

Appendix E. ADULT FIELD TRAPPING COLLECTION SITES AND RESULTS

Table 50. Adult Field Trapping (AFT) Collection Numbers cross-referenced with the associated WIK substrate collection numbers, if any, and giving the location, date and time of day at which the adults were captured. Seven methods of capture were employed: ASP--aspirated while biting collector (n=14); BL--New Jersey type suction black-light trap (n=22); DV--back-pack mounted "D-vac" suction trap (n=11); ET--Emergence trap, 1 m² funnel (n=2); INC--New Jersey-type suction light trap with 12-volt incandescent light (n=3); SW--by sweep net (n=12); TT--Malaise-type tent trap (n=4).

Adult Field Trap Coll. No.	Ref. WIK Substr. Coll. Site No.	Location	Date and Time	Results
BL-1	51 to 59	W.Va., Pocahontas Co., Monongahela Nat'l Forest, Cranberry Gl., Round Gl., 350 m NE boardwalk entrance to Glade, on isolated red spruce.	20-VI-75 20:00 - 23:30	++++
ASP-2	51 to 59	W.Va., Pocahontas Co., Cranberry Gl., Round Gl., at boardwalk entrance	20-VI-75 20:50 - 21:00	++
TT-3	51 to 59	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	20 to 21-VI-75 20:00 - 08:00	+
BL-4	51 to 59	W. Va., Pocahontas Co., Cranberry Gl., Round Gl., 350 m NE of boardwalk.	20 to 21-VI-75 23:30 - 06:30	++++
DV-5	51 to 59	W.VA., Pocahontas Co., Cranberry Gl., vegetation around edge of bog forest adjacent boardwalk parking lot.	21-VI-75 09:00 - 09:10	+
TT-6	51 to 59	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	21-V-75 18:30 - 08:30	±
TT-7	51 to 59	W.Va., Pocahontas Co., Cranberry Gl., wet meadow 1 km ca. from State 39 on U.S. Forest Service 102; over stream	21-VI-75 11:30 - 21:10	+
BL-8	51 to 59	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	21-VI-75	+++
BL-9	60	W.Va., Pocahontas Co., Cranberry Gl., 500 m NE junc. Rts. 39 and 150, in open, adjacent Forest Service barrier.	21-VI-75 20:40 - 23:50	++

1/ Total number of Ceratopogonidae (all species combined) captured: - = 0; ± = 1; + = 2-9; ++ = 10-19; +++ = 20-49; ++++ = 50-99; +++++ = >100.

Table 50. Cont'd.

Adult Field Trap Coll. No.	Ref. WIK Substr. Coll. Site No.	Location	Date and Time	Results
TT-10	51 to 60	W. Va., Pocahontas Co., Cranberry Gl., adj. USFS Rt. 102, 0.3 Km from St. Rt. 39, upland meadow, over stream.	20 to 21-VI-75 1:10 - 0:900	+
BL-11	122-BL	Va., Suffolk City, Dismal Swamp, at Intersection of Jericho and Washington Ditches	20 to 21-VII-75 22:00 - 07:30	+++
DV-12	122-DV	Va., Suffolk, Dismal Swamp, Washington Ditch Landing, wooded marshy area adjacent to Lake Drummond.	21-VII-75 12:15 - 12:20	+
BL-13	21 129-BL	Va., Suffolk, Dismal Swamp, Jericho Ln.	21 to 22-VII-75 20:45 - 08:00	++++
DV-14	138-DV	Va., Accomack Co., Assateague Is., (Chincoteague Nat'l Wildlife Refuge, Tom's Cove); salt marsh terrain, rising tide near peak.	22-VII-75 20:45 - 20:50	+++++
DV-15	78-DV	Va., Smyth Co., Saltville, Juncus + Typha marsh adjacent brackish pond.	1-VII-75 16:00 - 16:05	+
DV-16	76-DV	Va., Smyth Co., Saltville	1-VII-75 15:30 - 15:40	++
BL-17	81, 82			<u>1</u> / -

1/ No results due to low temperature and wind (site elev. 5000 ft., Whitetop Mtn., Washington Co., VA).

Table 50. Cont'd.

Adult Field Trap Coll. No.	Ref. WIK Substr. Coll. Site No.	Location	Date and Time	Results
SW-18	122-SW	Va., Suffolk City, Dismal Swamp, Washington Ditch landing at site 122; along 100 m of old boardwalk.	21-VII-75 10:30	±
SW-19	122-SW	Va., Suffolk City, Dismal Swamp, Washington Ditch at boat landing, weather cloudy; Lake Drummond.	21-VII-75 13:00	±
DV-20	138-DV	Va., Accomack Co., Assateague Is., Chincoteague NWR, Wildlife Dr.	22-VII-75 18:30 - 18:35	+
DV-21	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., along boardwalk.	30-VII-75 20:40 - 20:45	+++
BL-22	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	30-VII-75 20:30 - 22:00	+
ASP-23	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	30-VII-75	+
DV-24	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	30-VII-75 20:50 - 20:55	++
ASP-25	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., 100 m N of boardwalk in Round Glade	30-VII-75 21:00 - 21:20	+++
BL-26	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., Flag Glade	31-VII-75 19:00 - 23:00	++++
BL-27	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., Flag Glade	31-VII-75 23:00 - 07:00	+++++
ASP-28	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., Round Glade	31-VII-75 18:50 - 19:15	+
ASP-29	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., Round Glade	31-VII-75 20:30 - 20:45	+

Table 50. Cont'd.

Adult Field Trap Coll. No.	Ref. WIK Substr. Coll. Site No.	Location	Date and Time	Results
DV-30	145A to 156	W.Va., Pocahontas Co., Cranberry Gl., around parking lot to boardwalk	31-VII-75 20:30 - 20:50	+++
SW-31	210	Va., York Co., Poquoson, Estuarine marsh	20-IX-75 19:00	++
BL-32	210	Va., York Co., Poquoson, Estuarine marsh	20 to 21-IX-75 19:30 - 07:30	+++
BL-33	179-BL	Va., Suffolk, Dismal Swamp, Jericho Lane, Entrance gate	28 to 29-VIII-75 20:45 - 06:00	+
BL-34	186-BL	Va., Suffolk City, Dismal Swamp, Crossing of Railroad and West Ditch	29 to 30-VIII-75 20:05 - 07:00	+++
ASP-35	184-ASP	Va., Suffolk City, Dismal Swamp, Interior Ditch boat landing	29-VIII-75 19:05	+
DV-36	207-DV	Va., Va. Beach, Knott's Is., Dack Bay, fresh water marsh	19-IX-75 12:00	+
SW-37	210-SW	Va., York Co., Poquoson, salt marsh	20-IX-75	+
SW-38	229-SW	N.C., Camden Co., Dismal Swamp, Forest Line, at burn	25-III-76	++
BL-39	R/A	Va., Suffolk, Dismal Swamp, W border Washington Ditch upper reaches, bridge on Va. Rt. 604, Desert Rd.	24 to 25-III-76 19:15 - 07:00	- 1
ASP-40	185	Va., Suffolk City, Lake Drummond at Interior Ditch landing	29-VIII-75 19:05	++
SW-41	?	Va., Suffolk City, Dismal Swamp	13-VI-75	+

¹ Night temp. 50-55 F.

Table 50. Cont'd.

Adult Field Trap Coll. No.	Ref. WIK Substr. Coll. Site No.	Location	Date and Time	Results
BL-42	N/A	Va., Montgomery Co., VPI, Prices Fork Research Center	21 to 22-IV-76	+
BL-43	N/A	Va., Montgomery Co., VPI, Prices Fork Research Center	23 to 24-IV-76	+
ASP-45	278A	W.Va., Pocahontas Co., Cranberry Gl. Botanical Area, Flag Glade	24-VI-76 20:00	++
BL-46	274	W.Va., Pocahontas Co., Cranberry Gl. at entrance old boardwalk to Flag Gl.	24 to 25-VI-76	++++
BL-47	N/A	Va., Hanover Co., Rt. 601, Butler Bridge over N. Anna River	1-VII-76	+
INC-48	307	Va., Accomack Co., Saxis Nat'l Wildlife Refuge, salt marsh	1-VIII-76 20:00 - 24:00	+++
INC-49	299	Va., Hampton, Grunland Park, adj. Grandview Natural Preserve, freshwater marsh adj. seaside, raining all night.	30 to 31-VII-76 19:00 - 0:800	+
BL-50	320A,B	Va., Montgomery Co., Pandapas Pond	9-10-IX-76 20:00 - 0:800	+++
ASP-51	290A	N.C., Camden Co., Dismal Swamp, Forest Line at burn	28-VII-76 19:00	++
ASP-52	285	Va., Giles Co., Mt. Lake massif, Butt Mt. Ridge, small farm pond on NW slope	14-VII-76	+
BL-53	N/A	Va., Louisa Co./Spotsylvania Co. line, N. Anna R., Rt. 601 at Smiths Mill Bridge, 400 m downstream from dam, 32 river km to fall line	28-VII-77	++++
SH-54 to 57		No ceratopogonids obtained.		

Table 50. Cont'd.

Adult Field Trap Coll. No.	Ref. VIK Substr. Coll. Site No.	Location	Date and Time	Results
BL-58	331	Va., Louisa Co., North Anna Reservoir, Old Mill Cr., arm L. Anna lagoon 2	11-IX-76 19:30 - 21:30	+
ASP-59	325A-328	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	7-IX-76	++
SW-60	325A-328	W.Va., Pocahontas Co., Cranberry Gl., Round Gl.	7-IX-76	+
INC-61	290A	N.C., Camden Co., Dismal Swamp, Forest line burn	28-VII-76	+++
ASP-62	299	Va., City of Hampton, Grandview Nat'l. Preserve	30-VII-76 18:30	++
ASP-63	373A	Va., Prince William Co., Pr. Will. Forest Park	29-IV-77 18:00	+
BL-64	N/A	Va., Montgomery Co., Pandapas Pond, Coll. by R. E. Williams	13-VII-71 19:00 - 22:00	+++
ASP-65	N/A	Va., Montgomery Co., Pandapas Pond,	3-IX-76 19:00 - 23:00	+
ASP-66	407A	Va., Smyth Co., Saltville brine pools.	30-VI-78 13:00	+
BL-67	94A	Va., Montgomery Co., Hoot Owl Barn, VPI & SU Agronomy Farm	30-IV to 1-V-76	+
ET-68	-	Va., Giles Co., New River floodplain nr. Pembroke, marginal silt	20 to 30-V-76	++
ET-69	LOC. 120	Va., Montgomery Co., Prices Fork-McCoy Road, sinkhole pond.	20 to 30-V-76	++

Appendix F. COLLECTION LOCALITY DESCRIPTIONS

F.1 Locality and Habitat Descriptions for Knausenberger's Substrate Collections 1975 - 1978

F.1.1 Introduction

This list presents all substrate collections made by the author(WIK), and a few Virginia Tech colleagues, between 1975 and 1978, inclusive. It does not include information about sites which were not sampled specifically with this study in mind, but material from which sites may have been evaluated. The rearing records in this study are based almost exclusively on the collections included herein and in the next section("Locality and Habitat Data for F. V. Battle's 1969 Substrate Collections" on page). Over 550 collections are described in this section, in the order in which they were sampled. They are further identified by 191 "locality" numbers, which serve as a cross-reference for collections repeated over time in the same general locality, and help distinguish new sites from repeated sites.

"Locality" is here defined as a geographically and/or ecologically distinct area of limited size(usually less than 1000 m²), which includes one or more collection sites. A group of collections at a given locality shares specific location data and microhabitat characteristics. The collections in each locality were normally taken within 100 m of each other.

Locality numbers are used only in this appendix list, so they appear in no other documentation associated with this project. However, each of the sites indicated on the base map (as was done in Fig. 2). pinpoints a "locality" in the sense just defined. I assigned these numbers *post hoc* to assist me in better characterizing the site data and resulting records, as well as in mapping distributions and the like.

Collection sites which yielded no Ceratopogonidae are described in "telegraphic" form only, indicated by "not productive" or "NP", or are omitted altogether. In this way, time and space were conserved. Yet, this will still allow basic collection data to be associated with other(non-ceratopogonid) organisms, of which representatives, at least, were usually retained for every site which yielded them. In addition, more complete site information is available in the field notes on file at the Department of Entomology, Virginia Polytechnic Institute and State University.

To aid those interested in retrieval of specimens and related information developed in this project, the following notes are presented on the collection numbers and processing codes:

1. Collection numbers were assigned in chronological sequence as collections were made on the various sampling trips.
2. Collection numbers normally were assigned sub-designations, usually -A, -B, -C, etc., if they represented sub-habitats, or different microhabitats of a given collection site, e.g., 166A, 167B or 407A to 407F.

3. Major letter codes. On the specimen labels or laboratory notes, letter codes were appended to the collection numbers as follows:

- IMM--specimens involve immatures separated from that sample, usually Ceratopogonidae(CER), sometimes Chironomidae(CHIR), and occasionally Tipulidae(TIP), e.g., 332A IMM CER. When nothing is given after IMM, then the "default" assumption is Ceratopogonidae.
- IR¹ --specimens subjected to individual rearing attempts; normally the "IR" follows a sequential laboratory record number, e.g., 332A-25 IR, referring to a specific entry for that specimen in the "IR Record". Codes that are usually associated with individual rearing results(often with date of occurrence) are
 - A--Adult(female or male indicated by symbols)
 - L, Lex--Larva or larval exuvium
 - P, Pex--Pupa or pupal exuvium
- MISC--Non-ceratopogonids sorted from the substrate sample or rearing carton emergences.
- RC--specimens reared collectively in rearing cartons

4. Adult field-trapping(AFT) codes. These are secondary codes appended to the collection numbers depending on the type of method by which the adult specimens were trapped(see Table 50):

- ASP--Aspirated specimen, usually biting a person at the time

¹ Over 1500 photographs, mostly color transparencies, were taken during the individual rearing work. These are identified by a) an 'IR' number, b) a film and frame number, as Fxx-xx, and c) taxon of the specimen if possible.

- BL--Black-light trap, New Jersey type
- DV--"D-Vac" suction trap, backpack-mounted, 5 minutes per sample
- ET--Emergence trap placed on habitat substrate
- INC--Incandescent light trap, New Jersey type
- SW--Sweep net sample of 5 minutes
- TT--Tent trap of the Malaise type

The apportionment of the collection numbers by physiographic province, river basin and biotic region is presented in Appendix C, Table 46. A breakdown by political or geographic units is given in Appendix C, Table 48. Substrate chemistry data is listed by collection number in Appendix G, Table 51. Available temperature and water chemistry information is presented in Appendix G, Table 53.

F.1.2 Locality and Habitat Descriptions Section

•Locality 1: WIK Coll. Nos. 1-3 (n=4); 19 May, 1975.

WIK Coll. No. 1: Va., Montgomery Co., adjacent Shadowlake pond, Puddle in marshy depression in grassy approach road, permanent enough for sedges to be present. Substrate taken at line, seeking primarily algae and organic matter with some underlying mud.

WIK Coll. No. 1A: as WIK Coll. No. 1, pure soft mud, distinctly below water surface and 20 cm out from water line.

WIK Coll. No. 2: as WIK Coll. No. 1, wet littoral gravelly mud along stream before enters the pond.

WIK Coll. No. 3: as WIK Coll. No. 1, algae with associated organic material (decaying grass and leaves) from surface and margin of pond proper, under large overhanging sycamore tree.

 •Locality 2. WIK Coll. Nos. 4 to 8: 27 May, 1975. (See also 255; 281; 282; 319A-321).

WIK Coll. No. 4: Va., Montgomery Co., Jefferson National Forest, N. side of Pandapas pond (main part), along feeder stream of pond in sandy mud with leaf matter among *Typha* and *Carex*.

WIK Coll. Nos. 5,6: Not Productive. (NP)

WIK Coll. No. 7: Pandapas Pond, as WIK Coll. No. 4, 100 m from parking lot E, along N edge of pond; yellow=gray clay mud substrate with some algal material, roots quite thick; alder bushes overhanging.

WIK Coll. No. 8: as WIK Coll. No. 4, along N. margin of smaller body of pond; mud-flat exposed to full morning sun, with significant fraction of dark decomposing allochthonous leaf matter, esp. oak and alder leaves.

•Locality 3. WIK Coll. Nos. 9-11; 27 May, 1975. (See also WIK Coll. No. 256).

WIK Coll. No. 9: Va., Giles Co., Sinking Creek Valley, Newport Park, crotch of sycamore tree, overhanging creek, 8 inches from ground, damp bark and leaf material with some moss. Lumbriculid worms present in abundance.

WIK Coll. No. 10: NP.

•Locality 4. WIK Coll. No. 11. No ceratopogonids recovered.

•Locality 5. WIK Coll. Nos. 12-15; 10 June 1975 (See also Coll. Nos. 100A, B, 101; 243-245; 397A-398B).

WIK Coll. No. 12: Va., Montgomery Co., left bank of Tom's Creek, 30 m upstream from Shadow Lake Rd., Bridge (intersection with Meadowbrook Drive), bank of creek under sycamore, algae in spots, mud bank.

WIK Coll. No. 12-MP: as above. Multi-plate samples suspended from tree branch into stream (=MP-1).

WIK Coll. No. 14: adj. site 12, right bank of right curve in stream, where a trickle-delta enters. Very wet reddish-brown clay-loam at water's edge, with well-decayed detritus under dense canopy of hardwoods.

WIK Coll. No. 15: Tree-hole. Not productive.

•Locality 1. WIK Coll. Nos. 16-19; 10 June 1976. (See also WIK Coll. Nos. 1-3, 97-99; 246; 365).

WIK Coll. No. 16: Va., Montgomery Co., Shadowlake Pond; 100 m downstream of pond in unnamed creek (1.5 m wide). Sampled very wet slimy grey-green mud at water's edge. Under dense canopy of overarching rose bushes; willow and sycamore in overstory.

WIK Coll. No. 16-MP: as above. Multi-plate sampler suspended in stream from branch overhanging (=MP-2).

WIK Coll. No. 17: Locality as WIK Coll. No. 16, opposite bank; mud-gravel interspersed with thick willow root mat; water running through; canopy overhead less dense.

WIK Coll. No. 18: Same as WIK Coll. No. 1, generalized sampling in road pool.

WIK Coll. No. 19: Locality 1, on N.W. bank of Shadow Lake, under edge of canopy of rose bush, sampled algae floating on surface.

WIK Coll. Nos. 20-40 (n=23): Great Dismal Swamp National Wildlife Refuge, southeast Virginia, Northeast North Carolina. Other collections taken

from this swamp include WIK Coll. Nos. 122-129; 179-189; 212; 220-235 and 288-296 (which see). Compare also 214A-219.

WIK Coll. Nos. 20-31: 13 June 1975.

WIK Coll. No. 20: Va., City of Suffolk; at west escarpment along edge of Great Dismal Swamp, adj. to Jericho Lane, 300 m E. of Whitmarsh Rd., small open marshy depression, wet much, thin layer of standing water. Extensive clumps of cattail, *Eleocharis* and bulrushes (*Juncus effusus* and *J. militaris*). Same as Matta's (1973) site 15.

•Locality 7: 21-24; 129; 179, 179=MP; 212,292; 293A, B; 294(n-13).

WIK Coll. No. 21: Va., Suffolk City, Great Dismal Swamp, on Jericho Lane 800 m E. of site 20 (1.1 km E. of Whitmarsh Rd.), on south side; narrow divided woodland pool of water, 15-30 m long, 10-100 cm deep, level distinctly down, root mat densely permeates steep mud bank. Water pH 6.7. *Salix nigra* and *Pinus taeda* dominate overstory. Duckweed (*Lemna* and *Wolffia*) common. Coincides with Matta (1973:200) site 5.

WIK Coll. No. 21-MP: as above, multiplate sampler suspended in pool, reaching bottom (=MP-3).

WIK Coll. No. 22.: as above; N side of Jericho Lane, deep rut /ditch, filled with leaf duff, surrounded by moss and ferns.

WIK Coll. No. 23: as WIK Coll. No. 21; wet depression 4 m long and 1 m wide in soil road; perpendicular to Jericho Lane, on N. side, 1 km E of WIK Coll. No. 20 under high canopy of sycamore, red oak, tulip poplar; sample of damp muck with well-decayed organic matter.

WIK Coll. No. 24: Adjacent WIK Coll. No. 23, in small ditch (cross-connecting) perpendicular to Jericho Lane; dense canopy of swamp hardwoods; no standing water; sampled wet, thick leaf deposits with dark brown sandy muck; substrate pH 4.5, organic matter 3.3%.

•Locality 8.

WIK Coll. No. 25: Va., Suffolk, Dismal Swamp, semipermanent ditch-pool adjacent Jericho Lane, 500 m W. of Lynn Ditch on north side; sample of leaf matter and grassy detritus in pool under maple.

•Locality 9: WIK Coll. Nos. 26 & 27.

WIK Coll. No. 26: Va., Suffolk, Dismal Swamp along south edge of Badger Ditch, 1 km east of Lynn Ditch; damp tree hole (ca. 0.1m² in extent) near ground in black gum (*Nyssa sylvatica* March), decayed bits of wood in leaves; swamp bottom subject to flooding but weather had been dry.

•Locality 10. See also #296.

WIK Coll. No. 28: Va., Suffolk, Dismal Swamp. Near north end of Jericho Ditch, 500 m N. of Williamson Ditch, in powerline clearing 150 m E. of Jericho in marshy pool in depression with abundant aquatic vascular plants, sample of muck with plants in shallow water.

WIK Coll. No. 28-MP: Multi-plate samples suspended from bridge into ditch.

•Locality 11. Compare #29, 127, 295.

WIK Coll. No. 29: Va., Suffolk, Dismal Swamp. Adjacent W. margin of Jericho Ditch road, 600 m N. of Williamson Ditch in swamp forest, with tulip poplar and red maple forming moderate canopy. Sample in roadside ditch, of damp dark brown mud 50 m deep over sand. Substrate pH 5.3, organic matter 2.4%. Site of *Echinochloa lanai* Wirth.

•Locality 12: 30, 128, 183, 183-MP, 235.

WIK Coll. No. 30: Va., Chesapeake City, 80 m W. of East Ditch, 40 m along sandy edge of large isolated pool; sample included putrid (H₂S) ooze and algal material; N. of Williamson. Substrate pH 3.9-4.5; O.M. sand 1.0%, surface debris 15%. *Juncus* and *Arundinaria* dominant in field layer.

•Locality 13.

WIK Coll. No. 31: Va., Chesapeake City, ca. 300 m N. of Williamson Ditch on East Ditch, 200 m S. of RR tracks. Thick peat-like material, in deltaic area along flowing streamlet near culvert, among fallen trees and branches. Overstory of younger trees, composition typical. Substrate pH 5.4.

WIK Coll. No. 32-40: 14 June 1975.

•Locality 14.

WIK Coll. No. 32: N. side of Williamson Ditch, 200 m E. of Jericho Ditch, forest bottom, 1.5 m below level of road, overstory primarily red maple; sampled damp leaves, roots, with peaty mud, pH 4.4. Compare WIK Coll. No. 33, 324.

•Locality 15. See also #324.

WIK Coll. No. 33: Approx. 900 m E. of Jericho Ditch, algal and floating plant material off top of small ditch pool adjacent N. side of road.

WIK Coll. No. 34-39: Chesapeake City, Dismal Swamp.

•Locality 16: WIK Coll. Nos. 34, 35.

WIK Coll. No. 34: N. bank of Feeder Ditch, 50 m E. of Refuge Boundary, 300 m W. of dam; compacted dark peaty soil, with roots and moss; exposed to wave wash of passing boats; water very gently flowing. Substr. pH 5.6, O.M. 5.9%.

WIK Coll. No. 35: Feeder Ditch, eroded clay bank subject to boat wave action. No life whatsoever.

•Locality 17: WIK Coll. Nos. 36-38.

WIK Coll. No. 36: 150 m NE of Feeder Ditch junction with Lake Drummond, E. shore of Lake Drummond, in 30 m² depression 10m from shore, with a monospecific stand of unidentified herbaceous plant, receiving more light than average due to fallen red maple; leafy damp muck-soil sample.

WIK Coll. No. 37: Edge of Lake Drummond N. side of feeder Ditch; tree hole in a species of *Salix*, near ground (<20 cm), ca. 0.1 m² inside surface area.

WIK Coll. No. 38: E. shore of Lake Drummond, leaf matter in wet depression caused by toppled trees, semi-dense overstory (incl. *Tilia americana*).

•Locality 18.

WIK Coll. No. 39: 100 m into Lake Drummond from Feeder Ditch inlet; sample of algae and moss scraped from knees of cypress tree water line in 1.5 m deep water.

•Locality 19.

WIK Coll. No. 40: Va., Suffolk City, Dismal Swamp, Washington Ditch, 600 m W. of Lynn Ditch junction, along N. side of wide, bare-banked shallow ditch; some grasses and low herbs; (esp. creeping buttercup, *Ranunculus reptans*) sample of clay-muck, gray mud along gently-sloped bank at water line. Opposite bank heavily shaded. Substr. pH 7.1, O.M. 10.4%.

Locality 20: WIK Coll. No. 41-46. 15 June 1975.

WIK Coll. No. 42: Va., Virginia Beach, Back Bay Landing Rd., Pocahontas Trojan State Waterfowl Management Area, permanent pool algae and surface macrophytes (*Nymphaea* spp.) at head of culvert into somewhat brackish Back Bay waters.

WIK Coll. No. 42: Location as WIK Coll. No. 41, littoral sample under bush, sample among roots, black soil.

WIK Coll. No. 43: Location as WIK Coll. No. 41. Ditch 1000 m W. of WIK Coll. No. 41 and 42, along road; floating algae of several spp. differing in appearance from the algal mat of WIK Coll. No. 41.

WIK Coll. No. 44: Locality as 43; littoral sample in black-gray muck mud, W. side of brackish ditch.

•Locality 21: WIK Coll. No. 45, 46:

WIK Coll. No. 45: Va., Charlotte Co., 50 m upstream of Rt. 642 cross-over bridge, mud-gravel bank in Horsepen Cr. (trib. of Roanoke Creek).

WIK Coll. Nos. 47-50: 20 June 1875.

WIK Coll. No. 47: Va., Augusta Co., George Washington National Forest, Ramsey's Draft Campsite, 0.5 miles from highway U.S. 250 on unmarked gravel road; tree hole in sugar maple about 0.1 m² in size and positioned one foot above ground, containing damp leaf matter.

WIK Coll. No. 48: Locality as 47. Gravel-silt depression forming pool along side of stream under bridge, 1 m² in area and 15 cm. deep.

•Locality 23: WIK Coll. No. 49-50. 20 June 1975. Compare WIK Coll. No. 262.

WIK Coll. No. 49: Va., Highland Co., 3 mile E. of Monterey on U.S. 250 to left of road going west; wet muck seepage area in a recently used sheep pasture; densely shaded area, overstory of elm, red and sugar maple and apple with area exposed to roots of skunk cabbage. Elev. ca. 3200 ft.

WIK Coll. No. 50: Location as WIK Coll. No. 49. Sandy substrate and littoral mud of a shallow streamlet coming out a culvert to right of road going W. No immediate overstory, though bushes protected site from mid-day sun.

WIK Coll. No. 51-60: 21 June 1975.

•Locality 24: WIK Coll. No. 51-55. See also WIK Coll. Nos. 154-156; 173; 274; 278A,B; 326A-327B.

WIK Coll. No. 51: W. Va., Pocahontas Co., Cranberry Glades Botanical Area on forest side Flag Glade forest boundary at old (1950's) boardwalk entrance, boggy forest floor, at forest-to-open glade ecotone, at bottom of gentle rise into typical mixed mesophytic forest; sample of decayed and live sphagnum and other mosses along pool adjacent to mossy fallen tree trunk; under dense overstory of yellow birch and hemlock (*Betula lutea* and *Tsuga canadensis*); skunk cabbage and rhododendron in understory adjacent site. 3375 ft. elev.

WIK Coll. No. 52: Locality as 51, near border of Flag Glade (SW edge) bog, open and wet peaty substrate.

WIK Coll. No. 53: Locality as 51, NE of Flag Glade, open water pool, 0.5 m² in an older thicket; live sphagnum and algae, peat ooze sedges around immediate edge of sample.

WIK Coll. No. 54: Locality as 51, Flag Glade; water and mossy edge substrate at base of large red spruce; decaying leaves of yellow birch.

WIK Coll. No. 55: Locality as 51. Middle of Flag Glade, open, no standing water, in raised clump of reddish sphagnum with some cinquefoil.

WIK Coll. No. 56: Cranberry Gl. Bot. Area, bog forest between Flag and Round Glades; adjacent Yew Creek, a small stream flowing into Flag Glade; sample reddish muck

and leaves in cattail, bracken fern swamp; alder overstory, fairly open; algal film on surface of substrate included.

WIK Coll. No. 57: Location as WIK Coll. No. 56; reddish mud in mud flat subject to occasional flooding, beside Yew Cr. Yellow birch and rhododendron in fairly open overstory.

WIK Coll. No. 59: Locality as 56. On Cowpasture Trail. Sandbar with algal Aufwuchs in a road exposed to a thin sheet of water overflowing from Charles Creek. No immediate overstory or root impingement. Water pH 4.8.

•Locality 26.

WIK Coll. No. 60: W. Va., Pocahontas Co., eastern edge of Cranberry Glades Botanical Area, outside glades per se, 750 m W. of barrier closest to Rts. 150 and 39 junction. Debris under a dense stand of red spruce; substrate damp, permeated with twigs and needles and some red maple leaves.

WIK Coll. Nos. 61-66 (n=7): 22 June 1975.

•Locality 27

WIK Coll. No. 61: W. VA., Pocahontas Co. at Williams River, State Rt. 150 crossing, sandy mud (rich brown) among willow roots and *Carex* spp., about 40 cm. on mudflat on water's edge. Water level at least 20 cm shortly before sample taken.

•Locality 28

WIK Coll. No. 62: W. Va., Pocahontas Co., Black Mtn. under spruce, 4500' approx. No ceratopogonids recovered.

•Locality 29: WIK Coll. No. 63, 64.

WIK Coll. No. 63: W. Va., Fayette Co., 1.5 miles S. on St. Hwy. 41 of S. intersection with U.S. 60; gently flowing unnamed stream sampled along wood debris dam across stream (perhaps beaver-constructed) with mud, water trickling through sample area. Partially shaded by dogwood; *Scirpus* emergent.

WIK Coll. No. 64: Locality as 63, 15 m downstream, left side of above dam; gray-brown mud, sparse organic debris; along slow eddy pool behind dam. Shaded by *Sambucus canadensis*.

•Locality 30: WIK Coll. No. 65A,B

WIK Coll. No. 65A: W. Va., Greenbrier Co., 3.1 miles W. of Lewisburg on U.S. 60; sampled floating algae, duckweed, (*Lemna*) and waterweed (*Wolffia* sp.) on an enriched farm pond to which cattle have occasional access; included a few decaying white oak (*Quercus alba*) and cattail (*Typha* sp.) leaves floating in emergent cattail stand.

WIK Coll. No. 65B: Same as 65A, sample taken in wet littoral gray-black muck with liberal amount of decaying stems and other detritus present; duckweed and algae included in sample.

•Locality 31.

WIK Coll. No. 66: Sinking Creek Mtn., tree stump hole. Not productive.

•Locality 32: WIK Coll. No. 67; 163; 240 A,B.

WIK Coll. No. 67: 22 June 1975. Va., Montgomery Co.; grey-green to black muck along farm pond adjacent to Luster's Gate Farm Pond; freshly-grown stand of water plantain (*Alisma*) prominent.

•Locality 33

WIK Coll. No. 68: 22 June 1975. Va., Roanoke Co., N. side of St. Secondary Rt. 785 0.2 mile W. of Co. Rt. at headwaters of N. Fk. Roanoke R. (ca. 2 mi. E of Montgomery Co. line); streamlet ponding in cow pasture; grey-brown muck with some *Aufwuchs*, among emergent grasses, with seepage.

WIK Coll. Nos. 69-71: 28 June 1975.

•Locality 34: WIK Coll. No. 694C; 161A-C. Compare F. V. Battle's Site B.

WIK Coll. No. 69A: Va., Montgomery Co., 7.5 mi. E. of Luster's Gate on Va. 795, near headwaters of N. Fk. Roanoke R. passing through hog lot. Sample of wet littoral mud among hoof prints, manure-enriched; 5-10 cm from flowing watercourse. Exposed to open sun.

WIK Coll. No. 69B: Location as 69A; sampled drying mud among hoof prints with epipellic algal film, under shade of *Salix fragilis*.

WIK Coll. No. 69C: Location as 69A; along well trodden mud bank in stream passing through hog lot, sample of mud exposed to flowing water; no shade.

•Locality 35: WIK Coll. Nos. 70 - 72; 162.

WIK Coll. No. 70: Va., Montgomery Co., in Farmer Orr's sheep and cattle pasture, across from J. K. Hutton property, 5 miles E. of Luster's Gate, along the larger of the two watering ponds N. of road; long bare shale-rock slopes on 3 sides of relatively unpolluted mud near pond out flow under willow.

WIK Coll. No. 71: same location as above, smaller pond, grass border all around, more manure directly evident, sample in wet hoof prints and other mud and some algal material. Densely shaded by sycamore most of day.

•Locality 36: WIK Coll. No. 73-75. 29 June 1975.

WIK Coll. No. 73: Va., Roanoke Co., APCO Dam on Roanoke River adjacent to Blue Ridge RR overlook rock-bottomed vernal pool in floodplain 2 m by 0.8 m, 5 cm. deep; 1-5 cm deep medium brown silty mud scraped from edge of pool, over and between fist-sized rocks, to 5 cm. above water line. No direct shade.

WIK Coll. No. 74: Locality as 73, small marshy 6x40m pond completely covered by Lemna. Sample of bottom sand in water 1.5 m deep, under dense shade of trees including *Ailanthus altissima* (tree-of-heaven).

WIK Coll. No. 75: Locality as 73, another small rock-bottomed pool, 1x5 m in extent, covered by filamentous algae blanket 5 cm thick at deepest. Full sun in afternoon. Rushes overhanging pool.

Coll. Nos. 76-82 (n=7): 1 July 1975.

•Locality 37. WIK Coll. No. 76-80; 407A-F.

WIK Coll. No. 76: Va., Smyth Co., Saltville ponds, 0.2 miles S. of intersection of Farm Dr. and Lake Dr. at upper end of SE pond, receiving freshwater stream in flow; 10 m W. from road; sample of viscid mud with brownish-red and green surficial layer (H_2S) from wide littoral mudflat in cattail stand. Brackish site. ² Substrate 4736-5440 mg/l soluble salts.

WIK Coll. No. 77A and B: Va., Smyth Co., SE of Saltville; 20 m south of WIK Coll. No. #76, in deltaic inflow of a stream (originating at Palmer Spring) which just passed through cow pasture; two samples 5-10 m in from upland edge of marsh, thick brown organic layer over silt mud, among widely spaced cattails and bulrushes, with thin film of water passing over substrate. Substrate only slightly brackish (sol. salts 750-858 mg/l), water flowing is fresh; substrate was 100 deg. C cooler here than at adjacent site 76, due to stream inflow at ca. 1 cu. ft./sec.

WIK Coll. No. 78: Same locality as WIK Coll. No. 76, adjacent to campground on Farm Drive immediately SW of Saltville proper, along NE edge of NE pond; littoral standing brackish water, marshy area; sampled mud infused with slime-algal layer and sedge/rush detritus. Bulrushes to 1.5 m tall, and cattail, adjacent to site. Brackish substrate (sol. salts 12,800 mg/l).

WIK Coll. No. 79: Va., Smyth Co., Saltville, 400 m W. of Farm Drive on Lake Road, 35 m NW of latter on small peninsula, extending into pond, with

mud flats on both sides; sampled at saline pond margin, with compact, dry-damp mud with evident salt film; bound by root mass of adjacent sedges and glasswort; some algal slime film included. Substrate brackish (sol. salts also 12,800 mg/l).

•Locality 38: 1 July 1975.

WIK Coll. No. 81: Va., Smyth Co., Mt. Rogers Recreational Area, Skulls Gap Picnic Area on Rt. 600. Elev. ca. 3100 ft. (940). Wet to damp depression surrounded by mature maple, oak and pine, moderately dense overstory. Sample of brown-gray clayey mud among rushes and sedges near Rhododendron. Soil 70 deg. F, air 78 deg. F.

WIK Coll. No. 82: Same locality as 81. Damp depression under semi-dense overstory as in 81, but substrate rich, peaty (decayed wood) intermixed with roots, pine and leaf litter and detritus. Hemlock added species in overstory.

WIK Coll. No. 83-89: 2 July 1975.

•Locality 39.

WIK Coll. No. 83: Va., Washington C., Hwy 58, Box 374, 7.5 mi. W from Beartree turnoff on N. side; sampled edge of springfed pond with rich brown littoral substrate above and below water level and some floating algae, no bare bank, vegetation growing to edge (*Potamogeton*, *Carex*, *Nymphaea*, moss on bank; *Typha* emergent).

•Locality 40.

WIK Coll. No. 84: Va., Washington Co., 5 mile N. of Damascus on St. Rt. 91 (7 miles N. of N.C. border line) 0.6 mile S. of Co. Rt. 708, on SE side of road, pool backed up along gently flowing stream in cattle pasture, marshy depression in stream bottom along road; microhabitat sampled at water's edge; substrate mud, light brown, rich organic fraction (cattle droppings influence composition); algae form surface scum in cattle hoof depressions.

•Locality 41.

WIK Coll. No. 85: Va., Tazewell Co., Clinch Mtn., Little Tumbling Creek Wildlife Management Area, Ca. 1.6 km W. of hardtop road (St. Rt. 91) littoral sandy substrate with leaf and twig detritus, elev. ca. 3050 ft. beneath overhanging moss along the swiftly moving stream. Birch, rhododendron, etc. in dense canopy overhead.

•Locality 42.

WIK Coll. No. 86: Va., Tazewell Co., 0.8 km S. of Rt. 91 on Rt. 608; Liberty Cr. stream bank, mud along eddy pool, with grasses and water cress interspersed and filamentous algae, mud brown; stream runs through farm where livestock and waterfowl have access; exposed to full sunlight.

•Locality 43: WIK Coll. No. 87-89: Burkes Garden.

WIK Coll. No. 87: Va., Tazewell Co., 0.5 mil E. on Rt. 666 from intersection with Rt. 623; Burkes Garden floor, tributary of Spring Creek, edge of pool, receding waterline causes conc. of Gerridae, brown mud along pool edge, with trickle of water entering. Elev. ca. 3100 ft.

WIK Coll. No. 88: Va., Tazewell Co., Burke's Garden above dam adjacent to Rt. 623, backwater of stream with cow access, standing water; gray-brown mud on bank, *Eleocharis* and *Juncus effusus* rushes along pool, some grass shading site sampled. Elev. ca. 3200 ft.

WIK Coll. No. 89: Va., Tazewell Co., Burkes Garden adjacent to site #88. Marshy, grass flood plain with cattle hoof prints, sample taken from hoof print.

•Locality 44: 5 July 1975.

WIK Coll. No. 90A: Wise Co., Big Stone Gap, Cherry Lake Reservoir at upper end of lake, boggy area caused by Beaver Dam; samples from pool with large amount of decaying organic matter on bottom, at edge of sphagnum mat with acidophilic vegetation (sedges, etc.). Elev. 3600 ft. (1107.7 m). Collected by D. E. Simonet. Substr. pH 4.7, temp. 65 deg. F (18.0 deg. C); air 74 deg. F (23 deg. C).

WIK Coll. No. 90B: Same as site 90A, duplicate.

WIK Coll. No. 91-96 (n=11): 10 July 1975.

•Locality 45: WIK Coll. No. 91; 247.

WIK Coll. No. 91: Va., Montgomery Co., adjacent to Co. Rt. 685 (Prices Fork Road), 0.9 mile W. of Rt. 657 intersection (Merrimac Road), S. side of road damp to dry substrate of temporary marshy pond, no standing water, cattail root mass, dried alga mats, dense stand of cattail and *Eleocharis* in mud.

•Locality 46: WIK Coll. No. 92A,B; 236.

WIK Coll. No. 92A: Va., Montgomery Co., adjacent to Rt. 685, 0.6 mile W. of Merrimac Rd. intersection, S. side of route; semi-permanent (to permanent) pond at edge of field, base of willow shoot, 50 cm. from standing water in wet gray muck.

WIK Coll. No. 92B: Same as 92A, except somewhat drier muck, 2.5 m from water edge, which is receding.

•Locality 113: WIK Coll. No. 93, 237.

WIK Coll. No. 93: Va., Montgomery Co., VPI & SU Sheep Center, Va. Rt. 314, 0.5 mile S. of Rt. 685, (Price's Fork Rd.) Wet marshy depression in sheep grazing area, heavily grass-choked, sample in bare mud under shade of large red oak; duckweed on surface of leaf-infused mud.

•Locality 47: 94A-E; 113A,B; 238.

WIK Coll. No. 94A: Va., Montgomery Co., "Hoot Owl" sheep barn, VPISU Farms. 0.5 mile from hog farm, at end of Rt. 314S, edge of straw heap, under heap, wet straw, damp gravelly, black mud adjacent to sheep congregation site, N. side of barn.

WIK Coll. No. 94B: Same as 94A, W. side of barn, seepage, cattle hoof depressions and manure evident; sample in and around depressions gray-brown with some algal growth.

WIK Coll. No. 94C: No life whatsoever (semi-dry sawdust mixed with manure in shaded location).

WIK Coll. No. 94D: Same as 94A, NW side of barn; damp to wet interface between straw pile and mud; 10 m from barn.

WIK Coll. No. 94E: Same as 94A, NE side of the barn, 1 m from side of barn, wet gravely mud with algal film, exposed to sheep traffic -- heavy at times, rabbit droppings also evident, exposed to full morning sun.

•Locality 48: WIK Coll. No. 95, 96; 239.

WIK Coll. No. 95: Va., Montgomery Co., Stroubles Cr., 15 m downstream of Va. Rt. 314 crossover (bridge), edge of stream, grass-stabilized bank, mud-infused gravel and muddy root and algal mat, *Ceratophyllum*, watercress on upstream side; detectable odor of pig manure due to spray irrigation of pig farm stabilization pond (oxidation pond) water into field, 200 m upstream.

WIK Coll. No. 96: Same as #95, VPISU farms area -- pasture adjacent to Stroubles; permanent seepage area with cow access along bank; yellow-brown mud with some algal growth in depression.

•Locality 1 (q.v.): 97-99; 11 July 1975: Shadowlake pond.

WIK Coll. No. 97: Va., Montgomery Co., Shadowlake pond, muck substrate heavily laced with sycamore leaves, water level receded 1 m from edge, algal contribution on surface.

WIK Coll. No. 98: Old algal mat. No life at all.

WIK Coll. No. 99: Shadowlake pond, surface of pond, floating algae on NE shore; some organic debris.

•Loc. 5: 100-101: 11 July 1975.

WIK Coll. 100A: Va., Montgomery Co., along Tom's Creek intersection of Shadowlake Rd. and Meadowbrook Dr., 150 m downstream from Shadow Lake Rd. bridge on left side (cf. WIK Coll. 245); sampled edge of creek with horse-hoof depressions in reddish-brown surface and gray-green underlying mud.

WIK Coll. 100B: Same as 100A; contributions to sample from 30 cm. above to 15 cm. below water line of stream.

WIK Coll. 101: Same as 100A but opposite side of stream, rich brown silt-loam, samples from horse hoof depressions.

•Loc. 49, 50: 102-107; 15 July 1975.

WIK Coll. 102: Va., Montgomery Co., S. side of Duck Pond, VPI and SU campus, 50 meters from water edge, Amphitheater, large tree holes 1.5 m off ground, *Salix* tree, in dry, damp, peaty detritus.

WIK Coll. 103: Same site as #102, SW of Amphitheater stage, Center of 1 m wide tree, 30 cm. off ground in hole 6 inches wide and 12 inches long; soaked decayed wood and leaf matter.

WIK Coll. 104: Same as site #103, 10 feet from N. edge of pond 100 m from "Solitude", wet tree hole three feet off the ground filled with debris; leaves and floating wood, weeping willow leaf intrusion, very strong methane, sulfurous odor.

WIK Coll. 105: Va., Montgomery Co., Same as #103 along Duck Pond Spring, 10 m from Pond's edge, where spring and stream come from springhouse, rich, wet littoral area exposed to geese, adjacent to stream; rich in organic matter, dark gray ground, thickly laced with twigs and roots. Large willow shading area.

WIK Coll. 106: Va., Montgomery Co., Amphitheatre-VPI and SU Hemlock tree crotch to left of Economic faculty drive by old President's house, 2 feet off ground, accumulation of hemlock leaves and a few hardwoods, water accumulated at bottom of hole, has appearance of permanently being wet.

WIK Coll. 107: Va., Montgomery Co., Amphitheatre VPI and SU base of large white oak, 5 ft. of debris, tree hold filled with damp, peaty mud mixture. Access to hole to left of main stairway to Hillcrest.

•Loc. 51: 16 July 1975.

WIK Coll. 108: Va., Craig Co., Rt. 664, 1.2 miles N from Rt. 611, 20 m from road, in pasture at base of concrete cattle watering (4 ft. high) basin; wet muddy area of standing water, fluid sandy mud with epipellic algal film over most of it; manure present in water; full exposure to the sun. 16 July 1975.

•Loc. 52. WIK Coll. Nos. 109-112 (See also WIK Coll. Nos. 406A,B.): 16 July 1975.

WIK Coll. 109: Va., Craig Co., Pott's Mtn. bog; elev. 3450 ft. (1061 m); ca. 0.7 mi. E on Potts Mtn. jeep trail from Forest Service (FS) Rd. 176, beginning 0.1 mile SE from intersection with FS 177 (U.S. 311 is 6 mi. to the SW) in Jefferson National Forest, New Castle District, near Alleghany Co. and George Washington Nat'l Forest boundary; relictual, small (ca. 1 acre (4000 m²) open bog, with irregular pond (up to 3 ft. deep), sphagnaceous, in depression in oak-maple forest near top of Pott's Mtn. ridge; sampled at base of dense grass-rush-sedge hummock, 10 ft. in from water's edge, mucky peat interlaced thickly with dead grass and sedge. (Located in Barbour's Creek Roadless Area, as designated by U.S. Forest Service comprehensive land management planning in 1978).

WIK Coll. 110: Same locality as WIK Coll. 109, at SW edge of bog, under bushes and ferns in leafy muck, open water at site. Under overhanging American Hornbeam (*Carpinus caroliniana*).

WIK Coll. 111: Locality as 109, Potts Bog in the open, in sphagnum and grass at base of which sample was taken near the water surface, very wet; about 3 m from open water.

WIK Coll. 112: Locality as 109 NE edge of Pott's bog, alongside a rush clump and muck-sphagnum layer floating on surface, with root and leaf matter included in sample.

•Loc. 47: 18 July 1975.

WIK Coll. 113A: Va., Montgomery Co., VPI Research Farm, 800 m SE from Hoot Owl Barn; cattail swamp, seepage area in pasture with cow tracks, 2.5 m from stream, brown clay muck somewhat firm.

WIK Coll. 113B: Va., Montgomery Co. 1 m from site 113A, long edge of streamlet, in path that cows use, gray-brown muck exposed to sun.

•Loc. 53: WIK Coll. 114, 115; 20 July 1975. See also WIK Coll. 174; 311.

WIK Coll. 114: Va., Suffolk Co., Reid's Ferry, Rt. 10 N, 50 meters west of highway bridge, fluctuating water level, red-brown compact clay, exposed to grazing goats, algal film green.

WIK Coll. 115: Reid's Ferry, Rt. 10N, 15 m W of site 114, under shade of sycamore and cypress, sample scrapings of oxidized top layer and unoxidized clay -- exposed to goat traffic and partially interlaced with some *Spartina*.

WIK Coll. 116-120: 20 July 1975.

•Loc. 54. Compare WIK Coll. 119; 195; 211; 312A,B.

WIK Coll. 116: Va., Isle of Wight, Brewer's Creek, Rt. 620, E. 1.4 miles from Rt. 10, organic detritus along a tidal fresh water stream under aquatic plants, moderate shade under sun in morning, racoon frequented, organic layer over dark-gray clay, substrate bare because of a rise and fall of water level of about 1 foot.

•Loc. 55. Compare WIK Coll. 194.

WIK Coll. 117: Va., Isle of Wight, 1.95 miles from intersection Rts. 10 and 32. tributary of Jones Creek, edge of creek, in a flooded pasture; sample taken of rich gray-brown sandy-clay in root sphere of *Pinus taeda*.

•Loc. 56.

WIK Coll. 118: Va., Isle of Wight, Rt. 668, Titus Creek, between Rt. 669 and 665, tidal brackish waters of the James River, exposed to full sun, many crab burrows, frequented by ducks, on mudbank, scattered detritus of sedge and rushes, dark-gray mud sample.

•Loc. 57. WIK Coll. 119; 195; 211. Compare Loc. 54.

WIK Coll. 119: Va., Isle of Wight, intersection of Rts. 600 and 652, Great Swamp, at edge of cypress swamp in heavily detritus-laced muck, sulfurous odor.

•Loc. 58. Compare WIK Coll. 196.

WIK Coll. 120: Va., Isle of Wight, 0.1 mi. E. off of Rt. 605 and 8/10 mile N. of 603, sand bank, small trickling stream feeding hog pen, runs through partially and collects immediately outside hog pen fence.

•Loc. 59. WIK Coll. 121. Knott Is. (NP). Compare 207A-C.

•Loc. 60. WIK Coll. Nos. 122-129. 21 July 1975.

WIK Coll. 122: Va., Suffolk, Dismal Swamp; off boardwalk at Washington Ditch landing, 10 m from edge of Lake Drummond, high water pool; sampled among leaf matter at edge of pool. Dense overstory of blackgum, maple, wateroak, pine and birch.

•Loc. 61.

WIK Coll. 123: Va., Suffolk, Dismal Swamp, adj. N. side of road along Washington Ditch, 200 m W. of Jericho Ditch, permanent woodland pool with dense overstory - mainly red maple, sample peaty mud among thick dense root mass, no immediate emerging vegetation, frogs resident in pool.

•Loc. 62.

WIK Coll. 124: Va., Suffolk, S. side of Washington Ditch 100 m E. of Lynn Ditch intersection, edge of Flood pool, loose clay - organic substrate with racoon tracks.

•Loc. 63.

WIK Coll. 125: Va., Suffolk, Lynn Ditch (E. side) adjacent to road, 1.6 mile N. of Middle Ditch of Dismal Swamp, side of ditch among large clumps of rush; sampled clay-infused leaves and coarse vegetation with some moss-covered peaty clay and attached fern. Overstory of sweet bay (*Magnolia virginiana*).

•Loc. 64. Compare WIK Coll. 29; 127; 295..

WIK Coll. 126: Va., Suffolk, Dismal Swamp, just outside north boundary of Refuge on Jericho Ditch Rd. Sample of clay-sand-muck with water at pool outside active hog pen (odor evident), under moderate overstory of red oak, sweetgum and pine. Water pH 6.9.

•Loc. 10. See WIK Coll. 28; 296 also.

WIK Coll. 127: Va., Dismal swamp, Jericho Ditch Rd. power lines, N. end, 1 mile from Williamson Rd. at edge of pool in semipermanent pool in rut of road. Compare WIK Coll. #29, 126, 295. Moderate canopy of tulip poplar, sweet gum, and basswood.

•Loc. 12. See WIK Coll. 30; 183; 235. Va., Chesapeake, Dismal Swamp, Williamson Ditch. (Same site as WIK Coll. 30, etc.); bank along permanent pool; sampled along bare section of fine sand substrate; water level does not appear to fluctuate much, based on comparison with other pools over time.

•Loc. 7. See WIK Coll. 21-24; 179; 212; 233; 292-294.

WIK Coll. 129: Va., Dismal Swamp. Same site as WIK Coll. #21, etc. (q.v.); water level 50 cm. higher than when last sampled here.

WIK Coll. Nos. 130-139 (n=10): 22 July 1975.

•Loc. 65. See also WIK Coll. 310.

WIK Coll. 130: Va., Suffolk, Nansemond River estuary adjacent to Friendship Inn Waterview Motel, Rt. 10 and 32 N; tidal mud flats; sample

of soft mud heavily laced with organic matter, concentrating on brown surface layer of gray-black brown muck (layered). Fully exposed to sun. Rose-mallow, waterhyacinth and water smartweeds (*Polygonum*) sp. in vicinity.

•Loc. 66: WIK Coll. 132, 133. See also WIK Coll. #191, 192.

WIK Coll. 132: Va., Virginia Beach City, 1/2 mile inside Back Bay refuge (N. Boundary); east side of Ditch, lined with various rushes, behind coastal dune. Sample of pure sand long brackish water. Exposed to full sun.

WIK Coll. 133: Va., Virginia Beach, 1 mile north of Back Bay Boundary; east side of brackish lake, gully running into lake seaward side, growth of rushes throughout; sample taken along edge of standing water in soft sand-muck, covered with a brown organic scum. Sal. 4.9 ppt. Rush species include: *Juncus scirpoides*, *Scirpus americanus*.

•Loc. 67.

WIK Coll. 134: Va., Virginia Beach, Owl Creek Municipal Boat Ramp -- Rudee Inlet, opposite State Military Reserve, General Booth Blvd.; salt marsh, substrate sampled mucky-brown mud (sapropel) in vicinity of aged R-R tie, marsh grass dense; plentiful crabs, 25 m from upper tidal limit; exposed to full sunlight.

• Locality 68A, 68B.

WIK Coll. 135, 136: N.P.

•Loc. 69.

WIK Coll. 137: Va., Accomack Co., Occohannock Creek, Rt. 178, right outside of W. corporate limits of Belle Haven, E. margin of creek, S. of road; along a weedy finger inlet. Sample in mucky substrate along brackish water area. Sal. 15.2 ppt.

•Loc. 70: WIK Coll. 138, 139. (See also 303-306.)

WIK Coll. 138: Va. Accomack Co., Assateague Island, Chincoteague Nat'l. Wildlife Refuge, Wildlife Drive at Pond F, NW side, adjacent to bike path; brackish fresh water with saltwater regulation, surface scum in marsh, algal layer over 1/2 inch thick, oxidized mud; sago pondweed (*Potamogeton pectinatus*), widgeongrass (*Ruppia maritima*), *Eleocharis* spp., *Scirpus* spp., *Polygonum* spp. among abundant vascular plant growth. Productive site.

WIK Coll. 139. As WIK Coll. 138, Tom's Cove, bare clay tidal flat. Nil.

WIK Coll. Nos. 140-144: 24 July 1975.

•Loc. 71.

WIK Coll. 140. Va., Rockingham Co., Sparkling Springs area, in spring run gully under hardwood forest canopy. Sample sand and leaf bank where creek trickles through. Most of stream running over bedrock with hygropetric moss. Hemlock and Azalea upstream in large patches.

•Loc. 72.

WIK Coll. 141: Va., Rockingham Co., Hasler Farm (Smith sublet) on Co. Rt. 763, 1.6 mi. N from intersection with Co. Rt. 770. Grass-lined

pond with cattle access. Sample of mud and epipelagic algae at pond's margin where semi-permanent seepage saturates substrate. Cattle manure enrichment evident. *Eleocharis*, various grasses and herbs present. No shade by overstory.

WIK Coll. 142: As WIK Coll. 141, 20 m. down dry gully facing pond; small 7x4 in. treehole in chestnut oak, hole opening 5 inches from ground level; damp-moist peaty substrate, ca. 200 cm.³ only taken. Moderately open forest with cattle access. *Culicoides* biting.

WIK Coll. 143. As above, tree-hole in chestnut-oak, semi-dry. N.P.

•Loc. 73

WIK Coll. 144: Va., Rockingham Co., adjacent to Rt. 763; waterpool N swale (depression) in cornfield, area 10 m²; yellow clay substrate, compacted mud; sample taken from edge of water about 2 m from edge of depression; some floating algae included in sample; no immediate vegetation around depression, full exposure to sun. Large hydrophilid beetles found.

Coll Nos. 145A-157(n=14): 31 July, 1975 (Second Cranberry Glades trip).

•Loc. 145A-148. (See also WIK Coll. No. 169, 325A, 325B).

WIK Coll. 145A: W. Va., Pocahontas County, Cranberry River, 700 m E. of turnaround, 0.9 mile W. of boardwalk parking lot, 2.4 miles from W. Va. Rt. 39 on Forest Service Road #102, 3 m wide mudbank on W. side of stream; mud thick brown, wet, rich, deep, with vegetation.

WIK Coll. 145 B. N.P.

WIK Coll. 146: W. Va., Pocahontas Co., Cranberry River, adjacent to #145A 15 meters from river. Clearing in thicket (Cranberry Glades Botanical Area), deltaic marshy area, caused by a small trickle out of older thicket; deep dark brown mud thickly laced with leaves and organic detritus, ooze in patches.

WIK Coll. 147: locality as #145A but 200 m downstream. Adjacent to "logjam"; sandy mud-damp to wet, fairly compact mud gray-brown along stream.

WIK Coll. 148: W. Va., Pocahontas Co., Cranberry Glades - 300 m from turnaround on F.S. Road 102 (2.4 miles from W. Va. 39). Damp leaf matter in rarely travelled track (old Boardwalk); primarily yellow birch, spruce and hemlock moderate canopy; adjacent sphagnum moss bank.

•Loc. 25. WIK Coll. 149-151. (See also WIK Coll. Nos. 56-59, 275-279).

WIK Coll. 149: W. Va., Pocahontas Co., outside western edge of Flag Glade off boardwalk (Cranberry Glades Botanical Area). Open bog forest community; mucky fluid peat puddle; some sphagnum adjacent.

WIK Coll. 150: Cu Creek. No ceratopogonids.

WIK Coll. 151: Cu Creek. No ceratopogonids.

WIK Coll. 152: W. Va., Pocahontas Co., 15 m outside W edge of Round Glade, 200 m N. of boardwalk in bog forest adjacent to Forest Service Road 102 (Cranberry Glades Botanical Area). Puddle edge, peaty-leafy, puddle-mud flat; twigs and debris abundant.

WIK Coll. 153: W. Va., Pocahontas Co., 25 m outside Round Glade, W. edge 100 meters N. of Boardwalk (Cranberry Glades Botanical Area). Mud

puddle in depression caused by uprooted tree; brown mud, leaves and root material.

•Loc. 24 WIK Coll. 154-156. (See also WIK Coll. 51-55, 173, 274, 278A, 326A-327B).

WIK Coll. 154: W. Va., Pocahontas Co., inside Flag Glade, SW edge, 80 m N. of old (1950's) boardwalk entrance. Boggy area in cattail-sphagnum growth, wet peaty depression with abundance of cottongrass.

WIK Coll. 155: W. Va., Pocahontas Co., in Flag Glade, 50 m NE of old boardwalk entrance. Open glade, wet but firm area between hummocks; pure sphagnum and vascular plants.

WIK Coll. 156: W. Va., Cranberry Glades, edge of Flag Glade, 20 m. E. of entrance of (1950's) former boardwalk. Sampled bare exposed areas with thin organic fluid film covering dense mass of roots and runners, bordered by sphagnum waters.

•Loc. 76.

WIK Coll. 157: W. Va., Pocahontas Co., ca. 0.2 miles W. of Menneha Springs, in Knapp Creek, 20 m. downstream of Rt. 39 bridge (100 m E. of juncture of Rts. 39 and 28N-92N). Sand-gravel and mud bank midstream, downstream side of bridge support pillar; water flowing slowly at water line where sampled; stream 30-50 m. wide, no plants; morning shade.

•Loc. 77

WIK Coll. 158: 18 August 1975. Va., Roanoke Co., Chestnut oak tree hole, permanently wet, 1 m from ground level. Appalachian Trail approaching Dragon's Tooth from NE, 0.6 mile from summit. Steep slope of rocks and trees; Brush-North-Catawba Mtn. juncture. Catawba Creek drainage basin.

Coll. Nos. 159-163(n=7) : 22 August 1975.

•Loc. 78.

WIK Coll. 159:. Va., Roanoke Co., off Rt. 785, 1.5

mile W. from Rt. 311 crossing (on E. side of road); Catawba Cr. headwaters, James River Basin. Marshy depression filled with cattail along road surrounded by sloping pasture land; rich, dark brown substrate with cattail debris, other sedges, rushes; cattle have access.

•Loc. 79.

WIK Coll. 160: Va., Roanoke Co., on Rt. 697, between Rt. 785(nr. headwaters of N.Fk.Roanoke R.) and Rt. 311 (Mt. Tabor Rd.). Dairy cow pasture, in pond in a depression, water has receded 1-3 m; exposed mud dark gray brown, algal layer on top.

•Loc. 34. WIK Coll. 161A-C. (See also WIK Coll. 69A-C).

WIK Coll. 161A: Va., Montgomery, Farmers Brown hog lot, North Fork on Roanoke River as in site #69. Water puddle separated from stream by 1 m wide mud bank, strong odor of H₂S.

WIK Coll. 161B: Va., Montgomery, same as #69. Mud with algae film, stream water flowing in thin layer, substrate loose rich mix of algae and aerated mud overlaying a gravel substrate.

WIK Coll. 161C: Va., Montgomery Co., same as #161B except less algal influence and removed from flowing water, but still adjacent to stream.

•Loc. 35. (See also WIK Coll. 70, 71).

WIK Coll. 162: Va., Montgomery Co., upper pond of Orr's sheep and cow pasture on Rt. 785. Pond edge on sheep-cow pasture under willow tree; thickly laced with horsetail debris and algal ooze; cow track depressions sampled also.

•Loc. 32. (See also WIK Coll. 67, 240A,B)

WIK Coll. 163: Va., Montgomery Co., Farmer Agnew's Property, Luster's Gate, Rt. 785, Roanoke Valley. In field, mudhole almost dried up.

WIK Coll. Nos. 164-173(n=13): 25 Aug. 1975.

•Loc. 80. WIK Coll. No. 164, 165.

WIK Coll. 164: Va., Rockbridge Co., 0.4 mi. on Rt. 39 E of Rockbridge Baths, Maury River. Abrupt rocky-gravel bank with root cohesion. Sampled littoral and sublittoral gravel with mud and sand deposited by back eddies. Moderate overstory of sycamore. AT 88 deg. F, WT 76 deg. F.

WIK Coll. 165: Locality as 164. Slowly flowing spring run flowing into Maury R. in a rocky herbaceous channel having little mud. Sample of algal film, aquatic vascular plants and moss with gravely-sand trapped at base of sampled plants: knotweed, cord-and other grasses, jewelweed, mint. Mod. overstory of black walnut and sycamore. AT 88 deg. F, WT: 70 deg. F.

•Loc. 81.

WIK Coll. 166A-168L.

WIK Coll. 166A: Va., Bath Co., 7 miles E. of Warm Spring Rt. 39, .1 m E. of Rt. 629, N. of Highway. Small pond visited by cattle and sheep N. of highway; sampled rich brown-gray mud flat 1/2-2 m. wide at pond's edge, immediate site well shaded by boxelder. Duckweed covers entire pond surface. Air temp. 87 deg. F, water 77 deg. F., substrate 72 deg. F.

WIK Coll. 166B: Locality as 166A. Opposite side of pond with more sun exposure and more livestock traffic. Sample of sandy mud with leafy detritus and manure evident. Within root sphere of large white pine. Air temperatures 87 deg. F., water 85 deg. F., substrate 84 deg. F.

WIK Coll. 167U: Va., Bath Co., intersection of Rt. 220 and 39. Edge of stream, above water line, floating algal masses, gravelly mud, overhanging grasses directly to W. of 220 N off 39W, flow of water about 1/2 of warm stream (WIK Coll. 168U,L). Temperatures: air 87 deg. F, water 71 deg. F, substrate 74 deg. F.

WIK Coll. 167L: Locality as 167U. Substrate at water line, of gravelly mud at base of 1m embankment with overhanging grasses. Temperatures: air 87 deg. F, water 77 deg. F. substrate 81 deg. F.

WIK Coll. 168L: Va., Bath Co., Warm Springs -- below bath houses, 10 m above junction of cold and warm stream; gravelly mud bank, between two

branches of the warm spring including thick mass of dead filamentous algae. No immediate overstory -- some shade; black walnut, ash; no aquatic plant growth in immediate area.

WIK Coll. 168U: N.P.

•Loc. 74. (See also WIK Coll. 145A-148, 325A,B).

WIK Coll. 169: W. Va., Cranberry Glades, in former meander of Cranberry River; sampled rich brown clayey mud surface of wide bank exposed by receding waters; water not flowing here; exposed to sun, sparse overstory, little organic detritus on surface. *Culicoides venustus* site.

•Loc. 82: WIK Coll. 170-172. (See also WIK Coll. 171,172).

WIK Coll. 170: W. VA., Pocahontas Co., 150 m on W. edge of Big Glade (Cranberry Glades Botanical Area), edge of Big Glade; water interface sphagnum sample, water 5-12 inches below average surface level, sample 4 inches below surface.

WIK Coll. 171: W. Va., Pocahontas Co., 30 m from W. edge of Big Glade (Cranberry Glades Botanical Area); along sphagnum mats, in sedge community, bare moist peaty area.

WIK Coll. 172: W. Va., Cranberry Glades; somewhat N. and W. of central Big Glade in pitcher plant colony (introduced *Sarracenia purpurea* Siphoned out water and contents of Ca. 50 plants' pitchers.

•Loc. 24 (See also 51-55, 154-156, 274,278A,B 326A-327B).

WIK Coll. 173: W. Va., Pocahontas Co., W. edge of Flag Glade; adjacent to old boardwalk, entrance of Flag Glade, edge of bog. Base of cattail plants, sphagnum and detritus at waterline.

Collections 174-177 (n=8): 28 August, 1975.

•Loc. 53. (See also WIK Coll. 114,115,311).

WIK Coll. 174: Va., Suffolk County, Reids Ferry, a in #114 on opposite side of river to west of Rt. 32: edge of gully, overgrown with sedge and *Spartina*; sampled thin oxidized organic later of mud, inorganic gray to black subsoil, sand component high; but non-uniform; sample along water line to 1 m up from water. Partial shade. Substrate temperature 25 deg. C, air 30 deg. C.

•Loc. 83: WIK Coll. 175-177D (See also 309, 402).

WIK Coll. 175A: Va., Norfolk City, Norfolk Botanical Gardens, adjacent "Tidewater Garden". Sampled sandy fill in seepage of spring with thin organic mud film with algal film on water, pine needles abundant moderate overstory.

WIK Coll. 175B: Va., Norfolk City, adjacent to "Tidewater Garden" in Norfolk Botanical Gardens. Seepage area of source stream, natural muddy-muck substrate heavily laced with pine needles and other decayed organic matter; sulfurous odor beneath surface layer.

WIK Coll. 176: Va., Norfolk City, "Tidewater Garden Pool" in Norfolk Botanical Garden. Sand-mud substrate at edge of water lily pond; sand-mud substrate; roots, knees, twigs, etc. of bald cypresses.

WIK Coll. 177A: Va., Norfolk City, Annarino Bog Garden in Norfolk Botanical Garden. Sampled wet mud in permanent seepage at base of large laurel oak with *Rhododendron*, white oaks, maples, pines and ferns all have detritus contribution.

WIK Coll. 177B: Va., Norfolk City, Annarino Bog Garden in Norfolk Botanical Garden, under dense shade of red maple and cypress. In mud flat caused by water receding from pool of "bog", not putrid; *Typha angustifolia*, *Polygonum* sp., *Iris* sp., *Elodea* sp., *Myriophyllum* sp., common in bog.

WIK Coll. 177C: Va., Norfolk City, Annarino Bog Garden in Norfolk Botanical Gardens; along gully of "bog," rich, dark-brown mud with several spp. prostrate macrophytes at water line, epiphytic algae covering leaves; *Polygonum* sp. and other covering mud densely in patches.

WIK Coll. 177D: Same as #177A, in ditch on upper source end of bog. Sampled milfoil and *Polygonum* densely growing in thick later of water, moving at a very slow trickle. Moderate overstory of red maple.

WIK Coll. 178-196: August 1975.

•Loc. 6. (See also 20, 232 A,B).

WIK Coll. 178: Va., Suffolk City, same as WIK Coll. #20. Cattail marsh, rip-rap pile. Rich, brown muddy substrate at base of willow and cattail patch.

•Loc. 7. (See also 21-24, 129, 212, 233, 292-294).

WIK Coll. 179: Same as site #21. Boggy area created by receding water. Mud, debris thick with willow leaves, pine needles. Site of multi-plate substrate sample.

•Loc. 84.

WIK Coll. 180: Va., Suffolk City, Dismal Swamp -- N. side of Jericho Lane 0.2 mile W. from Jericho Ditch roadside channel with no free standing water. Substrate consists of damp leafy debris of bamboo grass, ericaceous bush, red maple, *Juncus militaris*. Only shade provided by bamboo. At 30 deg. C (86 deg. F), substr. temp. 33 deg. C (sun), 27 deg. C (shade).

•Loc. 85.

WIK Coll. 181: Dismal Swamp, Suffolk, Jericho Ditch Rd., W. side, 100 m N. of Jericho Lane crossing. Permanent 20 m² forest pool Sample of leaf matter at edge of pool with roots. Understory willow (*Salix fragilis*), coast pepperbush (*Clethra alnifolia*), greenbrier, rushes. Overstory moderately dense, live oak, magnolia, maple. At 30 deg. C, WT 24 deg. C (86 deg. F, resp. 75 deg. F).

•Loc. 86. (Compare WIK Coll. 33).

WIK Coll. 182: Va., Suffolk City, Williamson Ditch 2.1 miles from crossing with east Ditch. Sample on sandy edge of dike along dead end ditch to N. of Williamson Ditch; part of sample fully exposed to sun. Rush, bamboo grass and other herbaceous plants including honeysuckle,

AT: 29-30 deg. C, ST: 25 deg. C (shade, 1" beneath surface) AT 33 deg. C (sun).

•Loc. 12. (See also WIK Coll. 30, 128, 138-MP. 235).

WIK Coll. 183: VA ., Chesapeake City, same as #30 and 128. Muddy sand with coarse *Juncus detritus*; water receded 1 m from former site location when sampled 21 July 1975 (WIK Coll. 128).

WIK Coll. 183-MP: Multi-plate artificial substrate sample placed in pool

•Loc. 87. WIK Coll. 184, 185.

WIK Coll. 184: Va., Suffolk City, Lake Drummond at Dismal Swamp, Interior Ditch dock area. Littoral edge of sand and peaty debris above immediate wash line, in root sphere of red maple. No ceratopogonids recovered.

WIK Coll. 184-MP: Multiplate samplers suspended from dock.

WIK Coll. 185 L. Drummond, 50 m from Coll. 184, in lake. Mosses scraped from buttress of cypress at waterline(cf. Coll. 39). Not productive of biting midges.

•Loc. 88.

WIK Coll. 186: Va., Suffolk City, Dismal Swamp, Interior Ditch Road and West Ditch crossing. Edge of ditch, sampled from thick, brown surface of aerated spongy organic muck with no free-standing water, including algal ooze. No overstory.

WIK Coll. 187-192: 30 August 1975.

•Loc. 89. WIK Coll. 187, 188.

WIK Coll. 187: Va., Suffolk City, Lake Drummond. 2 m from lake edge at end of Railroad ditch facing Lake Drummond; peaty mud with heavy root growth; water receded from highest level by at least 3 m. Under very thick canopy of sweet gum, red maple, and other trees; leaf abundant matter; substrate also in sphere of influence of cypress. Swarm of dolichopodids over and on sample.

WIK Coll. 188: Va., Suffolk City, Dismal Swamp, Railroad Ditch where it fades out into forest, edge of ditch, thick leaf debris and large twig matter, black mud.

•Loc. 90.

WIK Coll. 189: Va., Dismal Swamp, gulley near Railroad Ditch. Accumulation of pine needles, tulip poplar and maple leaves. Overstory dense. Not productive.

•Loc. 91.

WIK Coll. 190: Va., Virginia Beach, Back Bar area, Trojan Waterfowl Management Area, along dike 500 m from landing, on West side, edge of lake. Sample taken of sand infused with clay in top layer, among sedges, cattails, rushes, algae.

•Loc. 66. WIK Coll. 191, 192 (see also 131-133).

WIK Coll. 191: VA., Virginia Beach, Back Bay National Wildlife Refuge, 1200 m North of crossing leading to refuge headquarters. On W. side of

ditch; edge of ditch; bare, damp sandbank with thin later of mud over it; 1/4 inch light colored sand, rest is black sand.

WIK Coll. 192: Va., Virginia Beach, Back Bay National Wildlife Refuge, West of B asphalt road, .7 miles S. of N. boundary of refuge. Adjacent to ditch in sand, damp, peaty depression (2-4 inches peat over sand). Water from ditch added to sample.

Coll. No. 193-196: 31 August 1975.

•Loc. 92.

WIK Coll. 193: Va., Virginia Beach, Rudee Inlet.

Steep clay bank along brackish tidal stream. No life whatsoever.

•Loc. 93. (Compare WIK Coll. 117).

WIK Coll. 194: Va., Isle of Wight, Bill Yeoman's Farm, 0.6 mile N. of St. Rt. 10 from Benn's Church, intersection St. Rt. 32 (James River Bridge Road); sample from bank on edge of permanent pool, mud-clay, frequented by cows (not present recently); algal aufwuchs and loblolly pine needles on substrate; partial shade from overhanging grass.

WIK Coll. 195: Va., Isle of Wight, (same as in #119 and 211) on Co. Rt. 600, near crossing of Co. Rt. 652, at Great Swamp in cypress swamp 25 m from shore -- water receded from about 5 foot depth, substrate, loose yellowish brown mud with large amount of cypress debris on top (along edge of receding waters).

WIK Coll. 196: Va., Isle of Wight, Al White's farm. 0.4 mile from intersection of Rt. 605 and 603, sample taken from area where sandy stream bottom and shallow muddy bank meet (2 1/2 feet from permanent steep stream bank), gently flowing stream, sandy mud bank infrequently visited by hogs from an adjacent pen.

•Locality 95. WIK Coll. 197: (27 August 1975). Va, Jamestown, James R., estuarine beach with rocks. Coll. E.C.Turner, Jr. (NP)

&Locality 96.

WIK Coll. 198: (29 Aug. 1975) VA, Verona. Chicken manure. Coll. G. C. Breeden. Forcipomyia only.

•Locality 97.

WIK Coll. 199: (17 Sept. 1975). Smith Mountain Lake reservoir ; washed sandy margin near boat landing. Not productive of biting midges.

•Loc. 98 (18 September 1975).

WIK Coll. 200: Va., Nottoway, ca. 2.5 miles S. of Crewe on St. Rt. 49, adjacent to Little Nottoway River. fishing pond ca. 3000 m² in size, on private property, 200 m W. of road at "The Falls"; clearing in mixed hardwood forest, pond for wildlife. Sampled sandy edge with mud on shallow slope with spreading aquatic macrophyte sample at water line. Hilly terrain of outer Piedmont.

WIK Coll. Nos. 201-203: 18 September 1975.

•Loc. 99. WIK Coll. 201A-D.

WIK Coll. 201A: Va., Lunenburg Co., Reservoir on Nottoway-Lunenburg Co. line, access via public boat landing road, 400 m from St. Rt. 49, 100 m E. of landing, Nottoway River. Edge of reservoir, narrow mud bank, dark brown mud with thick root growth. AT: 68 deg. F, WT 67 deg. F. Water pH 7.3, cond. 82 micromhos/cm.

WIK Coll. 201B: As 201A, 15 m E. of boat landing; narrow sand bank with mud-gravel component; sampled bare sand, light brown-yellow, erosional(mod. wave-swept); Carex and algal mat adj.; overstory moderate. Not productive of biting midges.

WIK Coll. 201C: Va., Lunenburg Co., 200 m E. of boat landing, 40 m W. of dam of littoral mud bank, width 5 m, thick muck, wet heavily laced with hardwood leaves and herbaceous growth; lighter brown mud 1/2 inch over gray-brown layer.

WIK Coll. 201D: Va., Lunenburg Co.; 50 m E. of landing, open water; general sample of plants floating on surface and below surface.

•Loc. 100.

WIK Coll. 202: Va., Lunenburg Co.; tobacco processing plant, pool at base of pile of tobacco leaf residue. Water pH 8.6, cond. 14,800 micromhos/cm, salinity 8.9 ppt; dark brown coffee color. (Not productive).

•Loc. 101

WIK Coll. 203: Va., Brunswick Co., 50 m NW of intersection of Co. RT. 617 and St. Rt. 137; 2.6 mile W. of intersection with St. Rt. 46, ca. 8 mile W. of Alberta municipality. Pond with heavily vegetated margin: vines, shrubs, pines; sampled above and below waterline in a compact brown-gray clay mud with sand component; plant debris cover on mud, some included in sample.

WIK Coll. Nos. 204-207C: September 1975.

•Loc. 102. (See also WIK Coll. 217).

WIK Coll. 204: Va., Virginia Beach, Princess Anne Road. 0.7 mile E. of intersection on Rt. 149 and 165 south, 50 m upstream of bridge. Border of slow-moving (brackish) stream, bank abrupt 1-2 feet high; surface mud flat, ca. 1 m wide, bordered on both sides by overhanging shrubs; no overhead canopy; sample top of thin oxidized layer over heavy gray-black H&sub2.S unoxidized mud with leaves; epipellic algal component evident. *Eleocharis* at site. Fish actively feeding on mud upon my arrival. Water sal. 5.4 ppt. pH 7.15, cond. 9,000 micromhos/cm.

•Loc. 103

Coll. 205: Va., Virginia Beach, Pungo Ferry Rd. inlet. Margin of coastal freshwater marsh, sandy-clay margin. Not productive of biting midges.

•Loc. 104.

WIK Coll. 206: Va., Virginia Beach, end of public landing road, 6 miles from Va. 615 (Princess Anne Road) intersection, 1.5 miles N. of N. Carolina line, littoral of Back Bay, freshwater to sl. brackish marsh; narrow bare area sampled with a light gray substrate above dark sandy clay

substrate, moderate organic content; mat of *Ceratophyllum* sp. No overstory. Sal. 1.0 ppt., pH 7.1, cond. 1,600 micromhos/cm.

•Loc. 104. Also DV-36 (= 207-DV).

WIK Coll. 207A: Va., Virginia Beach city, 0.8 mile from North Carolina state line, Knotts Island. North end public boat landing, at very northern tip, ca. 300 m from landing, ca. 4 Km N. of St. Rt. 615 on 1255; adjacent to Mackay Island National Wildlife Refuge. Edge of somewhat brackish fresh water marsh, open mud bank 3 m wide, compact clay-muck gray-brown, dense mat of *Eleocharis*. AT 28 deg.C, WT 26 deg. C; water pH 8.9, cond. 25,209 micromhos/cm, salinity 1.2 ppt.

WIK Coll. 207B: Locality as 207A. Algae on small woodland pool. Not productive.

WIK Coll. 207C: Va., Virginia Beach city, Ditch E. of private road 150 m N. of boat landing. Drainage ditch ca. 1 m wide with slowly flowing water, dark gray-brown muck with many pine needles, very wet, not putrid, rich organic layer along water's edge. Moderate canopy to E, open to W. AT 27 deg. C, WT 23.5 deg. C, ST 25 deg. C; water pH 6.8, cond. 1830 micromhos/cm, salinity 1.0 ppt.

Coll. Nos. 208-210: 20 September 1975.

•Loc. 106. (See also WIK Coll. 216).

WIK Coll. 208: Va., Virginia Beach city, south on Oceana Blvd., Va. Hwy. (615) 0.8 mile from US Hwy. 58 and Va. 615 intersection. Freshwater pond in sand dune, ca. 0.5 ha in size, with no apparent outflow. Coarse sand at margin; on bare sand subject to wind's wave action; some algal growth just below sand surface. Full exposure to sun. *Eleocharis*, *Juncus*, grasses sparse. AT 26.2, WT 22.5 deg.C. Water pH 7.3, cond. 59 micromhos/cm salinity 0 ppt.

•Loc. 107.

WIK Coll. 209: Va., Virginia Beach, Broad Bay Pt., brackish river sand bank. (NP).

•Loc. 108.

WIK Coll. 210: Va., York Co., Poquoson vicinity of boat landing, end of route 172, along N. shore of Back Bay river, arm of Chesapeake Bay. Estuarine marshy littoral area, bare muck in mud flat exposed by low tide: dark brown-gray to black, 5m² in extent. No overstory. Stand of vegetation in field layer not dense at side: *Spartina* sp., *Phragmites australis*, *Iva frutescens*, *Distichlis spicata*: AT 29 deg. C, WT 27 deg. C. Water pH 6.6, cond. 28,100 micromhos/cm, salinity 16.1 ppt. Substr. pH 6.0, sol. salts 7,855 mg/l.

Coll. Nos. 211, 212: 21 September 1975.

•Loc. 57. (See also WIK Coll. 119, 195).

WIK Coll. 211: Va., Isle of Wight Co., Intersection of Va. Co. Rts. 652 and 600; cypress bog, Cypress Swamp; thick mat of cypress and pine needles and twigs overlying light brown mud with epipellic at edge of water. AT 28 deg. C, substr. temp. 24 deg. C. Water pH 6.2, cond. 189 micromhos/cm

sal. less than 0.1 ppt. Water level higher than in August (195), lower than in July (119).

•Loc. 7. (See also WIK Coll. 21, *et alia*).

WIK Coll. 212: Va., Suffolk City, Dismal Swamp adjacent to site #21, Jericho Ditch lane. Wide ditch, standing water, covered with green blanket of *Lemna* sp. and *Wolffia* sp.; site with fewer pine needles than before. Mud at site is 2 m wide making a shallow-sloped mudbank; sampled brown organic layer, 1/2 inch thick, overlying dark-gray unoxidized layer with substantial leaf and needle component. Moderate overstory of willow, alder, oak, maple, pine. At 29.8 deg. C, WT 24.3 deg.C, Water pH 6.2, cond. 173 micromhos/cm.

•Loc. 49. 16 Feb. 1976.

WIK Coll. 213: Va., Blacksburg, V.P.I. Duck Pond spring run. Soft rich organic mud under willow.

•Loc. 109. 23 March 1976.

WIK Coll. 214A: Va., Suffolk City, 150 m S. of intersection with County Route 675, Cypress Chapel region on U.S. Route 32 south. Fresh water spring, seep in marshy depression in a field of sandy clay soil, adj. to highway; sampled oxygenated mud overlying a thick mat of dead reed stems; algal film over mud surface. No overstory; *Juncus* and *Typha* stand. At 14 deg., WT 15 deg. C. Water pH 7.0, cond 110 micromhos/cm, total hardn. 40 mg/l as CaCO₃.

WIK Coll. 214B: Va., Suffolk City, same as 214A, 20 m from above site (and away from Route 32), along edge of small standing pool of water; sample of oxygenated clay under dense overhanging rushes and dead vegetation.

WIK Coll. Nos. 215-224 (n=12): 24 March 1976.

•Loc. 110.

WIK Coll. 215: Va., Virginia Beach, Harper's Apartment complex, off Harper's Road, Phantom Blvd. Bottom of large open ditch in a field, 20 m across, 5 m deep, sandy muck with an organic fraction interspersed with a little cattail growth, water flowing slowly adjacent to sample site.

•Loc. 106. (See also WIK Coll. 208).

WIK Coll. 216: Va., Virginia Beach, Oceana Blvd., adjacent to Oceana Naval Air Station. Sample from clean sandy beach along clear blue freshwater pond. Some *Eleocharis* (?*parvula*) and spreading macrophyte (*Eleocharis* prob. *occidentalis*). At 15 deg. C, wt 13.8 deg.C, substr. 12 deg.C. Water pH 7.3, cond. 47 micromhos/cm. Tot. hardn. 15 mg/l.

•Loc. 102. (See also 204).

WIK Coll. 217: Va., Virginia Beach off of Princess Anne Blvd., 75 m to south of road, along shallow inlet. Sampled layered mud on mud flat just above level of water.

•Loc. 111.

WIK Coll. 218A: Va., Suffolk City, Harry Gallmer's Spring, behind house, Cypress Chapel; spring pool approx. 20 cm. deep, upstream and outside hog pen; site frequented by a horse; sampled mucky loose organic matter from pool's bottom, with a grayish-yellow sandy clay loam base. Elevated coastal plain site. Air 18 deg. C; water 16 deg. C, pH 7.0, cond. 100 micromhos/cm. Oligochaetes and *Culicoides* abundant.

WIK Coll. 218B: Va., Suffolk City, same as 218A, alongside spring in mud, heavily laced with herbaceous roots and leaves, aerated layer thick.

•Loc. 112.

WIK Coll. 219: N.C., Gates Co., former Jones Millpond basin (drained long ago), 1 mile E. of Corapeake, N.C., 1 miles S of Va. line. Successional old pond basin, edge of herbal pond; sampled leaf pack, floating partly in water. Sweetgum oak, sycamore, cypress and loblolly pine, beech in overstory, based on leaves in sample; dense 20-30 yr. old stand of trees. Water pH 5.8, hardness 21 mg/l as CaCO₃, cond. 81 micromhos/cm.

•Loc. 113: WIK Coll. Nos. 220-224.

WIK Coll. 220: Leaves and root matter along forest vernal pools. Not productive.

WIK Coll. 221: N.C., Gates Co., Dismal Swamp -- Intersection of Sherill Ditch and Hamburg Ditch, northeast section. Muddy leaf bank, primarily leaves, adjacent to bank, pretty much in the open. Water is not flowing (a bare bank of plain mud at head of culvert just before it goes into Hamburg Ditch).

WIK Coll. 222A: N.C., Gates Co., Dismal Swamp, Intersection of Sherill Ditch and Hamburg Ditch, in Hamburg at a mud bank, 1 m from ditch edge; sampled thin organic mud layer over relatively non-compact sand, adj. to water flowing east in ditch (approx. 30 cm. sec.). Sampled with a corer (3 reps). Air 18 deg.C (4:30 p.m.); water 14 deg.C, pH 5.0, cond. 55 micromhos/cm., total hardness 25 mg/l.

WIK Coll. 222B: N.C., Gates Co., same as 222A, 10 cm. present water line; immediate bank of ditch, mucky sand with significant leaf fraction 10-20 cm. deep before sand layer struck. Rose bushes and vines overhang site.

WIK Coll. 223: Same locality as 221, in northeast sector. Dry forest floor, sample of top soil at beginning of root layer, beneath dry leaf cover. Collembola visibly active.

WIK Coll. 224: N.C., Camden Co., Dismal Swamp, adj. to east culvert at very south end of Sherill Ditch before it joins Hamburg Ditch. Sample primarily sand, at bottom edge of root line of adj. bank's vegetation which is primarily maple, roses, and green briar; sand-clay bank. 5:20 p.m.

WIK Coll. Nos. 225-235 (n=14): 25 March 1976.

•Loc. 114. (See also 226, 227A,B, 288A,B.)

WIK Coll. 225: N.C., Camden Co., Dismal Swamp, off Corapeake Ditch road, 0.7 mile West of intersection with Forest Line Ditch (5.0 mile E of Desert Road Route 604, 2.8 mi. E of Sherill Ditch); 100 m. south of Corapeake, in old logging road, pool 30-50 cm. deep, 10 by 3 m in size, water covered by moss; sample of (sphagnum?) moss and algae. Privet, laurel bushes,

greenbriar border one side of pool. Logging road consists of packed wood chips and peaty material.

WIK Coll. 226: Locality as WIK Coll. 225, but 50 m. farther south from above site, along old logging road; collected algae from standing pool, no overhanging vegetation; pool 10 x 3 m in size, 10-20 cm. deep, with peaty bottom. Microcrustacea abundant. Privet and greenbriar surrounding pool. No canopy. Algae determined: *Oedogonium* sp., *Cosmarium* sp., *Frustula* sp., *Microspora* sp., poss. *Zygnema* sp. Water pH 3.8, cond. 145 micromhos, hardness (total) 19 ppm.

WIK Coll. 227 A,B (close to 225,226). Not productive.

•Loc. 115: WIK Coll. 228-230. See also 289-290.

WIK Coll. 228: N.C., Camden Co., Dismal Swamp, on Forest Line, adjacent 2 mi.² burned area, 1.1 mi. S from Corapeake Ditch, near Kim Saunders ditch intersection, in ditch: algal and water sample: green algae: *Microspora*, *Mongeotis*, *Oedogonium* and *Spirogyra* species; blue-green: *Oscillatoria*; other Synedra, *Stigonema* sp., diatoms: *Nitzschia*, *Asterionella*; other microfauna of copepoda (3) and ostracods (2) abundant. Water pH 3.6, tot. hardn. 27 mg/l, cond. 135 micromhos/cm., D.O. 5.4 ppm.

WIK Coll. 229A: N.C., Camden Co., Dismal Swamp, 1.5 mile south on Forest Line from Corapeake Ditch on S edge of cedar slash burned area (burned fall, 1975). Temporary pool under roots of burned stump, peat burned down to mineral soils in spots: red clay. Sample primarily of floating and suspended filamentous green algae with water (water at least 10 cm. higher in last few days). Dominant green alga present: *Microspora* sp. (prob. monospecific growth). Water pH 3.4, cond. 375 micromhos salinity 0.2 ppt, tot. hardn. 68 ppm.

WIK Coll. 229B: N.C., Camden Co., Locality as 229A. Sampled Damp mineral soil and peat coke, along edge of pool, with thin layer of algae left by receding water; no cover, no vegetation in area, "scorched-earth" appearance.

WIK Coll. 230: N.C., Camden Co., vicinity of 229, in burned area; wet depression of an apparent former path leading NW from S bridge over Forest Line Ditch. Sampled wet peat-muck at edge of pool under spreading exposed roots of burned tree. No free water in sample. Peat had been largely burned down to mineral soil, with coke remnants abundant.

•Loc. 116.

WIK Coll. 231: N.C., Gates Co. and Camden Co. line, Dismal Swamp on Corapeake Ditch Road. 1.5 miles E from Desert Road (Rt. 604) S. side of road, extensive open forest pool with emergent young reeds and cattail in blackgum and red maple swamp; sampled aerobic organic mud, along edge of pool with sphagnum moss; milfoil, dead reeds, water pH 5.9, cond. 65 micromhos. Much microfauna and small beetle activity.

•Loc. 6. See also WIK Coll. 20, etc.

WIK Coll. 232A: Va., Dismal Swamp at escarpment, Jericho Lane; floating dead and live plant matter. Not productive of biting midges.

WIK Coll. 232B: Va., Dismal Swamp, as WIK Coll. 20 at escarpment. Surficial mud at edge of marsh pool, with plant detritus. Water pH 7.8. Microcrustacea abundant.

•Loc. 7. See also WIK Coll. 21, etc.

WIK Coll. 233: Va., Suffolk, Dismal Swamp, Jericho Lane, same location as WIK Coll. 21; water level at least 50 cm. higher than when sampled last summer, reaching saddle of tree which was sampled, with pine needles, moss, oak leaves, and particulate organic matter making up bulk of sample. No duckweed floating on water yet this year. Water pH 7.0, cond. 130 micromhos/cm., tot. hardn. 49 mg/l, salinity 0.

•Loc. 15. See also WIK Coll. 33.

Coll. 234: Va., Suffolk city, Dismal Swamp, 0.4 mile E. from junction of Williamson and Jericho Ditch, N. side of Williamson Ditch, edge of ditch; algal sample in ditch with debris and adj. mud. Water pH 3.8, cond. 89 micromhos/cm.

•Loc. 12. See also WIK Coll. Nos. 30, 128, 183.

WIK Coll. 235: Va., Chesapeake City, East Ditch pool as in WIK Coll. 30, etc. Core samples of sand at water's edge. Water pH 4.0, cond. 80 micromhos/cm.

WIK Coll. Nos. 236-239: 15 April 1976.

•Loc. 46: See also WIK Coll. 92A,B.

WIK Coll. 236: Va., Montgomery Co., 0.6 miles west on Price's Fork Rd. (Co. Rt. 685) from intersection with Merrimac Rd.; marsh pond (permanent). Sample of floating detritus -- cattail reeds, sedge and bulrush leaves adjacent aquatic moss clumps among bulrush stand. Water pH 7.8.

•Loc. 117. See WIK Coll. 93 also.

WIK Coll. 237: Va., Montgomery Co., behind Sheep Center of V.P.I. near University Park Apts., Blacksburg. Sample at edge of permanently marshy depression, in highly organic mud, gray clay base; large amount of grass detritus with oak leaves. No immediate overstory.

•Loc. 47. See also WIK Coll. 94, 113.

WIK Coll. 238: Va., Montgomery Co., "Hoot Owl" Barn, VPI & SU campus. Wet meadow in cow pasture with stream flowing through area, soft gray-green mud, spots with algal growth on top of mud, duckweed, grass, *Calamus*, watercress. Very productive site (15 ceratopogonid taxa).

•Loc. 48. See WIK Coll. 95.

WIK Coll. 239: Va., Montgomery Co., Stroubles Creek, 150 m NE of U.S. 460 underpass on dirt road adj. to Creek; sampled on mud bank, soft mud overlying gravel, at foot of a 2 foot drop in stream bank. Full sun exposure.

Coll. Nos. 240-242 (n=6): 22 April 1976.

•Loc. 32. See also WIK Coll. 67 and 163.

WIK Coll. 240A: Va., Montgomery Co., Mr. Agnew's property, Luster's Gate, Route 785, edge of cattle watering pond, seepage into pond from up slope. Sample organically enriched aerobic surface mud (2 cm. thick over dark stratum) in seepage trickle as it reaches pond. No shade. Productive site.

WIK Coll. 240B: Va., Montgomery Co., same as 240A, 50 yards above cattle watering pond in seepage area, with emergent grasses, less cattle traffic. Sampled cleaner organic mud with large amounts of dead plant matter and well decomposed manure. No plant cover.

•Loc. 118.

WIK Coll. 241A: Va., Montgomery Co., adjacent Route 785, 1.7 miles E. of Luster's Gate. North Fork Roanoke River, left bank, 150 yards. below junction with Mill Creek at Bennett's Mill. River's edge sampled, sandy mud bank 40 cm. wide, adj. to an eddy.

WIK Coll. 241B: Location as above, on right bank, 20 yards upstream of 241A. Microhabitat in accumulation of coarse particulate debris adjacent to log-jam, including light brown sandy mud with twigs bark particles and decayed leaves. Water flowing adjacent to sample area. Overstory walnut and sycamore, strongly shading site.

WIK Coll. 241C: Va., Montgomery Co., below 241B. Edge of stream at log-jammed accumulation of debris; water flowing *through* sample area, including mud-infused oak and sycamore leaves and twigs.

•Loc. 119. See also WIK Coll. 403.

WIK Coll. 242: Va., Montgomery Co., Mill Creek, 200 yds. above Rt. 722, at Bennett's Mill, 3 miles E. of Blacksburg; sample of milfoil and watercress at edge of swiftly flowing stream, spring fed; water still at edge where sampled; oak leaves included.

WIK Coll. 243-246: 4 May 1976.

•Loc. 5. See also WIK Coll. Nos. 12-15, etc.

WIK Coll. 243: Va., Montgomery Co., Tom's Creek, 50 m upstream from Shadow Lake Road Bridge at edge of stream in gravelly mud next to rush clump.

WIK Coll. 244: Location as WIK Coll. 243. Basswood tree hole. Not productive.

WIK Coll. 245: Va., Montgomery Co., at Locality 5, 100 m downstream from Shadow Lake Road Bridge, Tom's Creek (cf. WIK Coll. 100A); horse-access to this area of creek. Sampled along waterline at mud bank (1 m wide), gravelly, under shade of black willow tree.

•Loc. 1. See WIK Coll. 1-3, etc.

WIK Coll. 246: Va., Montgomery Co., Shadow lake Road, Shadow Lake Pond with surface algal scum at leeward margin; water line receded 3 m at site. Sample of algal mat, with bottom mud and sycamore leaves. Wind blowing last few days.

WIK Coll. 247-252: 20 May 1976.

•Loc. 45. See also WIK Coll. 91.

WIK Coll. 247: Va., Montgomery Co., Price's Fork Rd.; temp. marsh pool basin. Not productive. Sampled mealy damp mud and dry encrusted algae in shallow estival pool (now dry) which yielded results in previous years' sample.

•Loc. 120. See also WIK Coll. 258, 345, 351, 363.

Coll. 248: Va., Montgomery Co., 1/2 mile E. of intersection of Co. Route 623 and Price's Fork Road (Co. Rt. 652) coming from McCoy (Longshop), 2.5 mi. W of Price's Fk. Rd., in meadow on N. side of road. "Classic" sinkhole, ca. 8 m deep, 40 m wide at rim, with small pool at bottom, max. 1 m water depth, and ca. 20 m² in size, with mud flat of varying width around edge. Sampled brown clayey mud (with some sand component). Water pH 7.4. Elev. 1900 ft. (580 m.).

•Loc. 121. WIK Coll. 249-251.

WIK Coll. 249: Va., Montgomery Co., ca. .35 miles from Rt. 652 (Price's Fork-McCoy Rd) on route 696, 150 m upstream from bridge; sampled margin of small unnamed stream, rocky-gravelly substrate at stream bank; leaves, pine and hardwood, with thin layer of overlying gravel.

WIK Coll. 250, 251: Unproductive tree-hole sites adjacent WIK Coll. 249. (Coll. 250--hemlock crotch, multiple-trunked; Coll. 251-- scarlet oak crotch of 4 trunks).

•Loc. 122.

WIK Coll. 252: Va., Montgomery Co., at end of Rt. 825, 0.25 miles S. off old McCoy Rd. (Co. Rt. 652 to Rt. 625); right bank of New River at Brush Mtn.-Floyds Mt. gap. Sampled on gently sloping sand-mud bank, subject to daily flooding. *Sagittaria* in area. No overhead shade. Water temp. 17 deg.C, air 20 deg.C, substrate 15 deg.C; water pH 7.8.

WIK Coll. 253-257C: 27 May 1976

•Loc. 123. Compare WIK Coll. 259.

WIK Coll. 253: Va., Montgomery Co., Tom's Creek, 50 m upstream from 1st bridge on Rt. 684, 0.1 mile from Rt. 655, (intersection approx. 1/2 mile W of Kanodes Mill). Stream bank with prominent coal ash residue component; sandy mud within root-sphere of willow, moderate overstory. Substrate pH 8.0.

•Loc. 124. Compare Loc. 2.

WIK Coll. 254: Va., Montgomery Co., near headwaters of Poverty Creek above Pandapas Pond, NE pond, 50 m from NE edge in a sluggish stream bottom; sampled in swampy, leafy mud bank with algal growth, in alder-willow flats. Elev. approx. 2150 ft. (655m).

•Loc. 2. See also WIK Coll. 4-8; 280-282; 319A-321. Compare WIK Coll. 254.

WIK Coll. 255: Va., Montgomery Co., swampy willow bottom 20 m from edge of Pandapas pond (northeast section), deltaic-area with shallow standing

water in dense thicket; gray clayey-mud from ca. 1 m² in tree-hole-like cavity in old stone iron furnace with half-circle 50 cm. opening.

•Loc. 3. See WIK Coll. 9,10 also.

WIK Coll. 256: Va., Giles Co., Newport Park, adjacent to Sinking Creek, sycamore tree hole on stream bank; crotch-hole, 2 m from ground; damp peaty debris, only 300 cm³ obtained. Elev. about 1980 ft. (604m).

•Loc. 125.

WIK Coll. 257A: Va., Giles Co., Co. Rt. 601, Clover Hollow Creek, swift creek descending from Rocky Gap in John's Creek Mtn., 0.5 miles uphill from intersection with County Rt. 602; sampled in stream bottom, of moss covering rocks in stream bed. Birch and mixed hardwoods in mod. dense overstory, some just leafing out. Elev. 2600 ft. (792 m). Water temp. 12 deg.C, air 16 deg.C; pH 7.8, D.O. 9.3 mg/l

WIK Coll. 257B: Va., Giles Co., Rt. 601 below Rocky Gap as 257A; muddy sand and gravel with some leaves, along swiftly flowing brook.

WIK Coll. 257C: Same location as WIK Coll. 257A; leaf pack accumulation with muddy base at margin of flowing water; birch-mixed hardwood, dense canopy.

•Loc. 120. Same locality as WIK Coll. Nos. 248, 345, 351, and 363.

WIK Coll. 258: 9 June 1976. Va., Montgomery Co., sink hole near Longshop; in bottom, circular pool 5 m across. Sampled slimy muck at water line with gray-black algae, above water line; herbaceous weeds with orange-gray sandy clay.

•Loc. 123. Compare WIK Coll. 253.

WIK Coll. 259: 15 June 1976. Va., Montgomery Co., tree on slope overlooking Tom's Creek on Rt. 654 between Kanode's Mill and Price's Fork; adjacent to road, NW side. Beech tree hole with abundant debris; opening 50 cm. X 20 cm., cavity bottom 80 cm. below opening, tree approx. 1.5 m. diam.

Collections 260-262 (n=6): 22 June 1976.

•Loc. 126.

WIK Coll. 260: Va., Augusta Co., Co. Rt. 688, ca. 2.0 miles W. of St. Rt. 42; George Washington Nat'l Forest, adj. to East Dry Fork; on east slope of Great North Mtn., elev. ca. 1066 m (3500 ft.); adj. small tributary stream connecting to E Dry Fork, sampled accumulation of pine needles and hardwood leaves, mud and overlying gravel; dense overstory.

•Loc. 127: WIK Coll. 261A-D.

WIK Coll. 261A: Va., August Co., Elkhorn Lake, ca. 9 miles N. of US 250 on Co. Rt. 715 and Forest Service Road 96 (vicinity of Ramsey's Draft). Staunton city water supply reservoir. Elev. ca. 2100 ft. (630m). Microhabitat: ditch with 1-2 ft. deep accumulation of leaves at base of cliff which faces NE towards lake. Sampled leafy detritus and duff com-

prising mixed hardwoods leaves (oak-hickory association) and brushwood fractions. Water dripping from moss-covered cliff face overhanging.

WIK Coll. 261B: Va., Augusta Co., Elkhorn Lake, same locality as WIK Coll. 261A, northeast-facing cliff face, well-shaded and moist; sample of wet moss adhering to brown loose shale of overhanging cliff face, with water dripping throughout; hanging vines, thick herbaceous growth (at bottom of rock face) provide added shade.

WIK Coll. 261C: Va., Augusta Co. Same locality as WIK Coll. site 261A. Deltaic area where North River enters Elkhorn Lake; adjacent stream eddy, sampled in mudbank of soft, brown sand with coarse organic fraction of black decaying leaves, partially shaded. Temperatures air 21 deg.C (70 deg.F); water 17.50 deg.C (63.5 deg.F), substrate 19 deg.C (66 deg.F), water pH 7.0.

WIK Coll. 261D: Va., Augusta Co. Same locality as 261A. Lakeward from 261C in deltaic sand bar with thin layer of water covering it; sample scraped of fine brown sand between sparse *Polygonum* and *Carex* growth (2/dm²) and rocks.

•Loc. 128.

Coll. 262: Va., Highland Co., US 250 W slope of Bull Pasture Mtn. ca. 2 mile E of McDowell. Small (20 m across) pond in old overgrown pasture: 5+ years since pasture grazed (based on succession of plants). Bottom grab sample 30 cm. from edge, in 30 cm. water, consisting of brown mud and roots of emergent grasses and sedges. outlet adjacent to site. Elev. ca. 2500 ft. (750m). Water pH 6.4, cond. 23 micromhos/cm.

WIK Coll. 263-269 (n=15): 23 June 1976.

•Loc. 129. WIK Coll. 263A: W. Va., Pendleton Co., ca. 1 mile S of Franklin, West Virginia, Rt. 220 North S. Fk. Potomac R. basin. Farm pond 200 m x 30 m, adj. roadside park. Margin with well-established vascular plants; sampled mass of floating algae.

WIK Coll. 263B: W. Va., Pendleton Co. Same locality as WIK Coll. 263A, but sample consisted of floating accumulation of vascular detritus, no algal masses included.

WIK Coll. 263C: W. Va., Pendleton Co. Locality as 263A. Farm pond in open pasture adjacent to Rt. 220; sample in 5 cm. water with abundant emergent herbaceous aquatics, sandy, dark brown mud, lighter brown on top; edge of pond flooded, with infrequent cattle access. *Scirpus*, *Juncus*, *Carex*, and *Eleocharis* spp. in undisturbed stand.

•Loc. 130.

WIK Coll. 264: W. Va., Pendleton Co., on U.S. Rt. 33, 2.7 miles E. of Judy's Gap. Seepage area of rich mud in cattle pasture, but under black walnut tree. No ceratopogonids.

•Loc. 131: WIK Coll. 265-267.

WIK Coll. 265: W. Va., Pendleton Co., 0.5 mile E (N) on US 33 of Spruce Knob Rd. turnoff just beyond Judy Gap; roadside cattle watering pond formed on Laurel Run; cattails and sweet flag emerging, thick growth of duckweed on surface and floating cattail leaves, sample taken composed of surface vegetation and plant detritus; water pH 6.6.

WIK Coll. 266A: W. Va., Pendleton Co., near top of Spruce Knob, above Forest Service Rd. overlook, spring pool in dense hardwood forest; red-brown soil-gravel with leaf mats, water pH 6.8, Water 10 deg.C, Air 21 deg.C; elev. approx. 4600 ft. (1402m)

WIK Coll. 266B: W. Va., Pendleton Co., adj. WIK Coll. 266A; damp forest floor, leaf duff, debris and rich moist brown soil, primarily maple leaves.

WIK Coll. 267: On top of Spruce Knob (ca. 4800 ft., 1460 m). Duff under red spruce with mosses, *Lycopodium*, etc. Not productive.

•Loc. 132.

WIK Coll. 268A: W. Va., Randolph Co., Spruce Knob Lake, Monongahela National Forest, elev. 3871 ft. (1,173m). Small embayment with root-contained clumps of grasses and sphagnum. Sample primarily surface algae with some submerged roots and organic matter on bottom. Water pH 6.4, cond. 22 micromhos/cm. No overstory cover of any sort.

WIK Coll. 268B: W. Va., Randolph Co., Spruce Knob Lake, Monongahela National Forest. Sampled rich, marshy, loose muck, profusely infused with roots from surrounding rushes, site at inlet of seepage into lake; *Scirpus*, skunk cabbage; bracken fern, cinnamon and *Osmunda* ferns. Water pH 6.2. *Sphaeromias longipennis* and *Clinohalea bimaculata* site.

WIK Coll. 268C: Locality as 268A, Spruce Knob Lake. Sphagnum with black mucky substrate and emergent grasses along lake shore.

•Loc. 133: WIK Coll. Nos. 269-271 (n=14). Sinks of Gandy Area.

WIK Coll. 269A: W. Va., Randolph Co., Sinks of Gandy, Gandy Creek, near Osceola, W. Va., elev. ca. 3500 ft. (1070 m); ca. 1.5 mi. W. of U.S. Forest Service Rd. #1, turning sharp left ca. 2 mi. from Spruce Knob Lake on USFS Rd. 1. Sample taken among gravelly mud along stream just before descends into cavern, with some sphagnum included. Canopy dense spruce, hemlock, *Acer* spp.; understory huckleberry and *Acer negundo*: Air 21 deg.C. water 15 deg.C, pH 6.1, cond. 19 micromhos/cm.; hardness 11 mg/l.

WIK Coll. 269B: Locality as WIK Coll. 269A, directly in upper end of opening to sinkhole cave. Wet mud at bottom of crevice in big boulder, 1.5 m down from surface; little organic matter. Substrate in alluvial soil of green-brown color, high mineral component. Canopy moderately dense, includes hemlock, sugar maple, yellow birch. Site has tree-hole-like shaded qualities (but lacking organic woody component); water reaches crevice only when flow very high, but is constantly damp because sunlight likely never reaches into crevice.

WIK Coll. 269C: Locality as WIK Coll. 269A, sample of attached brown moss (*Fontinalis*?) on a substrate of soft brown, alluvial mud; plant moves freely in water but anchored to substrate.

WIK Coll. 269D: No ceratopogonids. (Rel. dry deep crevice in boulders above opening.)

WIK Coll. 270-278 (n=18): 24 June 1976.

WIK Coll. 270A: W. Va., Randolph Co., Sinks of Gandy. Locality as WIK Coll. 269A, ca. 200 m SW from road adjacent to upper end of sink cavern, ca. 3600 ft. Narrow, small bog partially encroached on by spruce forest. Sample of fresh wet sphagnum at base of 5 ft. red spruce tree. Air 20 deg.C (8 a.m.), water 18 deg.C, pH 4.7-4.9 throughout bog.

WIK Coll. 270B: Locality as WIK Coll. 270A. Sample of drier sphagnum, in vicinity of clump of common three-square and young hemlock.

WIK Coll. 270C: Locality as WIK Coll. 270A, in bog. Newer sphagnum, in open with water in depression.

WIK Coll. 270D: As WIK Coll. 270A, bog. Older sphagnum and peaty substrate among sedges, and common three-square beside old log; snowberry growing profusely at site.

WIK Coll. 270E: As WIK Coll. 270A, in bog. Sample in pool with sphagnum and algae under dense cover of older spruce, bottom scum included.

WIK Coll. 271A: W. Va., Randolph Co., Sinks of Gandy, general Location as WIK Coll. 269A. Small ledge on rock face described in WIK Coll. 271B; damp leaf duff with mosses and ferns. No ceratopogonids, but many fungus gnats and other semi-terrestrial insects.

WIK Coll. 271B: Same Locality as WIK Coll. 269A. Exit of sinks where Gandy Creek leaves an impressive cavern opening (20 m high), 0.75 mi. N of (downstream from) entrance to cave, at ca. 3400 ft. elevation. Vertical rock face: sampled damp debris in small (10x40 cm) crevice containing "pin cushion" and filamentous moss and algal/bacterial film; 5 m above running water, with continuous cool damp breeze passing site from cavern entrance. *Isohelea* site.

WIK Coll. 271B: As 271A Location; dry to damp tree-hole-like crevice produced by large roots of yellow birch adjacent cave; sampled damp peaty detritus at base of crevice.

WIK Coll. 272B: W. Va., Randolph Co., Gaudineer Scenic Area, Monongahela National Forest, Cheat Mountain, Virgin Spruce Forest, 4100 ft. elev. Narrow sandy mud bank adjacent small rivulet; approx. 1 cm. deep layer of solid organic matter on top of sand, some moss included in sample; moderate to dense canopy of spruce and yellow birch. Water 13 deg.C, pH 5.4, cond. 38 micromhos/cm.

•Loc. 135. See also WIK Coll. 330A,B.

WIK Coll. 273A: W. Va., Pocahontas Co., Dunmore Springs, 1 mile SE of Dunmore on W. Va. 28, E side. Spring marsh site, spring-fed stream; headwater flow rate, issuing from spring, at ca. 0.05 m³/sec (1 cu. ft./sec). Sample of watercress and blanket algae in flow of spring, 2 m from source. Alder-willow marsh adjacent. Air 22 deg.C (1:15 p.m.). Water 17.5 deg.C, pH 6.6, cond.231 micromhos/cm.

WIK Coll. 273B: Same as WIK Coll. 273A, spring pool on one end of former enclosed "bath" with deep soft sulfurous-calcareous deposit in pool *per se*; sample of algal surface 'scum', aerated bottom sediment and organic

matter among reeds, sedges; willow and alder, cattail, and sedges provide shade.

WIK Coll. 274-278 (n=6): Cranberry Glades Botanical Area (4th trip).

•Loc. 24. See also WIK Coll. Nos. 51-55, 154-156, 173, 278A, 326-327.

WIK Coll. 274: W. Va., Pocahontas Co., Flag Glade, Cranberry Glades Botanical Area, bog; standing water and decaying black organic later in small disturbed area adjacent to boardwalk, sphagnum base included.

•Loc. 25. WIK Coll. 275-277. See also WIK Coll. Nos. 56-59, 149-151. Compare WIK Coll. 327.

WIK Coll. 275: W. Va., Pocahontas Co., Cranberry Glades, bog forest, Yew Creek; natural dam, created by accumulation of twigs, leaves, debris covered by layer of brown mud; sample taken just above water level. Air 20.5 deg.C (7:10 p.m.), water 14 deg.C, pH 6.3, cond. 28 micromhos/cm, Canopy dense, except exposure facing northwest.

WIK Coll. 276. Hemlock crotch-gap site. Produced no biting midges.

WIK Coll. 277: Same Locality as WIK Coll. 275, mud flat adjacent to Yew Creek in bog forest clearing. Rich brown mud with organic matter, sampled along clumps of emergent aquatic macrophytes.

•Loc. 24. See also 51-55; 274, 173, 274, 326-327.

WIK Coll. 278A: W. Va., Pocahontas Co., Flag Glade; entrance of former boardwalk, bog opening, sphagnum and sphagnum roots, older growth at base of cattail, water pH 5.2.

WIK Coll. 278B: Same as WIK Coll. 278A. Sphagnum and decayed black organic matter (water table at or near surface) in vegetation-free spots where substrate was a peaty slurry, which was sampled ; pH 4.7.

•Loc. 136. WIK Coll. 279: 25 June 1976. W. Va., Pocahontas Co., Watoga State Park, reservoir edge; organic layer of floating leaves and aquatic vascular plants included *Sagittaria* and *Polygonum* spp. and algae; water 10 cm. deep at collection site; Stream enters lake 10 m. adjacent; trees overhanging, but at site canopy sparse. Water pH 6.4.

WIK Coll. 280-285 (n=11): 14 July 1976

•Loc. 2: See also WIK Coll. 4-8; 319A-321.

WIK Coll. 280: Va., Montg. Co., Pandapas Pond area. Pool in gravel substrate of stream bottom dry at the time. Not productive.

WIK Coll. 281: Va., Montgomery Co., Pandapas Pond, beaver dam-like accumulation of twigs and debris damming outlet of upper (NE) pond into main pond; sampled algal *Aufwuchs*, 10 cm. submerged aquatic filamentous vascular plants soft, aerated light-grey mud, twigs and leaf organic base. Water pH 6.6., cond. 84 micromhos/cm., temp. 24 deg.C (air 25 deg.C).

WIK Coll. 282: Same Locality as WIK Coll. 281, stream side; light yellowish-brown sandy mud along slow-moving streamlet (80 cm. wide); with little organic debris, sampled thin layer of light brown mud, scum on surface; red maple, alder, rhododendron, shagbark hickory in moderate overstory. Air 25 deg.C; water 17 deg.C, pH 6.8, cond. 128 micromhos/cm.

WIK Coll. 283-285 (n=8): 14 July 1976.

•Loc. 137.

WIK Coll. 283A: Va., Giles Co., Southwest flank of Salt Pond Mt., Rt. 714, 1.6 miles W of Co. Rt. 613, adjacent Hemlock Branch at road; gently flowing spring-fed run, 3 m from source; sampled thick brown mud and floating algae, mountain laurel overhanging on one edge. Air temp. 21 deg.C, water 11 deg.C, pH 6.9, cond. 13 micromhos/cm. Elev. 3620 ft. (1114m).

WIK Coll. 283B: Location as WIK Coll. 283A; microhabitat: moss on vertical rock face directly above and overhanging the running water. Mountain laurel (*Kalmia latifolia*) shading moss.

WIK Coll. 283C: Loc. as WIK Coll. 283A. Moss covering rocks in Hemlock Branch, no ceratopogonids.

•Loc. 138. Compare WIK Coll. Nos. 322-323.

WIK Coll. 284: Va., Giles Co., Rt. 714, 3.7 miles W of Rt. 613, Salt Pond Mountain, man-made pond adjacent to hunting lodge in Little Stony Creek basin of Salt Pond Mt.; sampled among marshy grass and sedge-choked pond edge; rich, brown, red mud overlying dark grey anaerobic muck, 10-20 cm. down. Elev. ca. 3000 ft. (923m). Water pH 6.4.

•Loc. 139.

WIK Coll. 285A: Va., Giles Co., West flank of Salt Pond Mt. toward White Rocks campground (Rocky Mtn.), 150 m SE of Co. Rt. 721, 0.7 miles from Co. Rt. 613 (uphill); series of two cattle ponds, upper one spring fed with emergent macrophytes along edge, cattails in center of pond, approx. 10x15 m; sample taken in gray-brown mucky mud with interspersed sedges and grasses and other herbaceous growth, in part from cattle hoof depressions. Elev. ca. 3000 ft. (923m).

WIK Coll. 285B: Location as WIK Coll. 285A, in spring seepage area above and adjacent to ponds, sample from rich aerated loose mud, gray-brown to dark brown. Shaded by maple. Water pH 7.0.

WIK Coll. 285C: Same as WIK Coll. 285A; floating algal sample (brown *Oscillatoria*, green *Oedogonium* sp.) including brown "scum", green bubbly, fresh algae with coated grass stems, cattail stems, leaf debris; water pH 6.9.

WIK Coll. 285D: As 285A, lower pond, firmer edge; continuous growth of *Carex*, sedges; sampled floating submerged clumps of filamentous green algae, (*Oedogonium* sp.) adjacent to edge. Water pH 5.3. Reason for lower pH unclear).

Collections 286A-287B: 22 July 1976.

•Loc. 140.

WIK Coll. 286A: Va., Giles Co., Butt Mountain (Eggleston Quadrangle, USGS 7.5' topographic series) 1/2 mile E of Lookout tower on Rt. 714 (Va. Forest Service 5401), 100 m S of road, small spring fed pond with undisturbed emergent aquatic vegetation, bottom sludge from 10-15 cm. under water, 15-40 cm. from edge, some emergent vascular plants in vicinity,

consistency loose, brick red in color, steep slope. Long. 80 deg.37'03" Lat. 37 deg.21'55", Elev. 4140 feet (1274 m). (No ceratopogonids, but worthwhile site to return to.)

WIK Coll. 286B: Va., Giles Co., same as WIK Coll. 286A, on landward side of pond, wet seepage area, brick red mud richly infused with vascular plants, 10 m from spring outlet, ca. 25 deg.slope, on edge of pond. (No ceratopogonids).

•Loc. 141. See also WIK Coll. 324; 394-396.

WIK Coll. 287A: Va., Giles Co., Cascades, on Little Stony Cr., approx, 50 m below falls, on cliff wall on left as you look downstream, 1.5-3 m up from foot of cliff; elev. 3100 ft. (954m). Very moist, shaded cliff wall with moss, liverwort and fern growth in crevices; water dripping, apparently from an aquifer; microhabitat sampled; mosses, etc. vertically, or nearly so, attached to rock face, wet from slow but steady drip (up to 3 cm. thick layer of moss).

WIK Coll. 287B: Same as WIK Coll. 287A, but immediately at falls, on right as you face Cascades; cliff face under constant influence of spray from falls; mosses scraped from crevices and small ledges, no more than 1 cm. thick layer of moss.

Collections 288A-296 (n=13): 29 July 1976; Dismal Swamp National Wildlife Refuge.

•Loc. 110. See WIK Coll. 225, 226 also.

WIK Coll. 288A: North Carolina, Camden Co., 4.5 miles E on Corapeake Road from Desert Road, 100 m S of road, Long. 76 deg. 21'10", Lat. 36 deg.33'22", Elev. 20m. (Same as site 225); formerly 1-foot deep pool, no more standing water; sampled damp green sphagnum moss covering bottom in partial shade of bayberry and fern.

WIK Coll. 288B: Same Locality as WIK Coll. 288A (and WIK Coll. 226). Drying pool, approx 50 m S of 288A, no standing water; sampled top layer of algae and decaying organic muck and sphagnum moss under fern and shrubs; substrate is soft muck, peat, decayed wood chips approx, 30 cm. deep. Very productive site, esp. of *Dasyhelea* and *Stilobezzia* spp.

•Loc. 111. WIK Coll. 289-290. See also 228. Site of ASP-51; INC-61.

WIK Coll. 289: North Carolina, Camden Co., Dismal Swamp Refuge, in Forest Line ditch, 1.0 mile S of Corapeake; sampled algae floating in ditch (water 2 feet deep) among fallen logs; algae free-floating, attached in part to twigs and bark of logs. Adjacent area logged in past 5 years but not burned. Water pH 5.8.

WIK Coll. 290A: North Carolina, Camden Co., 1.5 miles S of Corapeake Ditch on Forest Line Road, in ditch adjacent to S. edge of burn of ca. 2-3 mi.²; algal sample in water and adhering to logs: *Ulothrix*, *Spirogyra*, *Microspora*, *Tetraspora* sp. Water pH 4.5.

WIK Coll. 290B: As WIK Coll. 290A, in ditch under dense shade of shrubbery and old bridge logs; edge sample of sulfurous smelling mud, rich brown with leaves and twigs. Air 30 deg.C, water 24 deg.C.

•Loc. 142.

WIK Coll. 291A: Va., Suffolk Co., Dismal Swamp, Va. Rt. 604, Desert Road (branch of upper Washington Ditch) 1.0 miles S of intersection with White Marsh, first bridge over swamp in-flow. Sampled *Ceratophyllum* floating along receded edge of stream; stagnant water with cypress, paw-paw, alder overhead. Water pH 6.6.

WIK Coll. 291B: Va., Suffolk Co., Locality as 291A. Along edge of water, 1 m down from normal level i.e., down ca. 30 cm. in height), damp sandy mud with organic dark brown layers, and *Polygonum* Overstory moderately shading.

•Loc. 7

WIK Coll. 292: Va., Suffolk, Jericho Lane, 50 m W of site 21; sampled at edge of receding pool in ditch, soft gray mucky substrate, algal patches on water surface, black layer 3-5 cm. below surface; moderate canopy of sweetgum, red maple, loblolly pine. Air 92 deg.F (34 deg.C); water 90 deg.F (33 deg.C), pH 6.7, cond. 163 micromhos/cm.

•Loc. 143. Compare WIK Coll. 23, 24.

WIK Coll. 293A: Va., Suffolk, Dismal Swamp, 400-500 m N along spur ditch perpendicular to Jericho Lane, tree hole in *Ulmus (rubra?)* at edge of ditch, 60 cm. from ground, hole diam. 10 cm.; damp contents dark brown, peaty, 20 cm. down from opening. Collector: H. Mathews.

WIK Coll. 293B: Va., Suffolk, Dismal Swamp, 15 m W of site 293A. Slit in sweetgum, 1 m up from ground level; damp orangish peaty duff, some sand included from edge of bottom. Collector: H. Mathews.

WIK Coll. 294: (Compare WIK Coll. Nos. 23, 24). Va., Suffolk, Dismal Swamp; Jericho Lane, 1 km. E of escarpment: Depression in bottom of 1-2 m wide ditch, 20 m. S of J.L.; sampled damp, rich black-brown mud with oak and maple leaf component discernible. Dense canopy.

•Loc. 11. See also WIK Coll. 29, etc.

WIK Coll. 295: Va., Suffolk, Dismal Swamp, 0.2 mile N of Williamson Ditch on Jericho Ditch; semi-permanent road-rut pool, yellow-gray sandy clay with many young red maple seedlings and moss in patches on edge, and isolated sedges; overstory moderately dense of maple, sweetgum, yellow poplar, white oak; water pH 7.7, D.O. 4.0 ppm, cond. 311 micromhos/cm.

•Loc. 10. See also WIK Coll. 28, 127.

WIK Coll. 296: Va., Suffolk, Dismal Swamp, powerline clearing on Jericho Ditch, 30 m E of road, 0.4 mile N of Williamson. Sampled mat of plants (monospecific) on soft deep gray layer of apparently well-aerated mud at edge of pool of water; rushes adjacent. Water pH 6.7, cond. 95, micromhos/cm., D.O. 6.0 ppm. No overstory.

WIK Coll. 297-299: 30 July 1976.

•Loc. 144.

WIK Coll. 297: Va., Hampton, Buckroe Beach area, E of Hampton, off Va. Rt. 169, on landward side of barrier beach; salt marsh pool, loose gravelly-sandy clay at base of *Spartina* clump; crab holes throughout, salinity 12.5 ppt (35 percent seawater), pH 7.5.

•Loc. 145.

WIK Coll. 298: Va., Hampton, Gosnold's Hope Park on Southwest branch of Back River (across river from Langley AFB). In loose clump of tall reeds (*Spartina* sp.) near low tide mark (ca. 50 cm below high tide line, 2 m from edge); clayey sand grey-brown to orange aerated surface mud over black layer. Water salinity 19 ppt, pH 7.8.

•Loc. 146. See also WIK Coll. 347-350.

WIK Coll. 299: Va., Hampton, Grandview Natural Preserve, pool 150 m from entrance (1st on left) under dense growth of redbay bushes on one side. Floating mass of aquatic vasculars overlying a partly decomposed wood pier section, 5-10 cm. under water surface, leaves and mucky organic debris adjacent to thick marsh growth. Water salinity 0.3 ppt, cond. 620 micromhos/cm, pH 7.2. Very productive, especially of *Stilobezzia* and *Dasyhelea* spp.

WIK Coll. 300-302: 31 July 1976.

•Loc. 147.

WIK Coll. 300: Va., Northhampton Co., Cape Charles, Fishermans Inlet, island on Atlantic side of Va. 13, in marsh land, mostly inundated by high tide; sampled by corer among emergent marsh vegetation along the edge of dry land spot, in 5-12" deep water, fine sand over dark gray clay. Water salinity 24 ppt. Glasswort is dominant plant (*Salicornia*) at site.

•Loc. 148.

WIK Coll. 301: Va., Accomack Co., Hacks Neck, a Chesapeake Bay inlet, ca. 4 mile W of Pungoteague town, edge of saltmarsh in shade of bushes at margin, among dense growth of reeds, emergent erect vasculars; sand-mud with mussels and crab holes in 5-10 cm. deep water. Salinity 14.5 ppt.

•Loc. 149.

WIK Coll. 302: Va., Accomack Co., 1 mile E of Pungoteague on St. Road 180, 2 miles W. of Feller; woodland stream, slow-moving, 1-2 m wide, rich brown mud, loose and aerated, overlying sand with black decomposed leaves, ash (*Fraxinus* sp.) primarily, with loblolly pine *Pinus taeda* in upper over-story at site. Elev. 30' (9.1m). Salinity 0 ppt, cond. 280 micromhos/cm, pH 7.4.

WIK Coll. Nos. 303-309: 1 August, 1975.

•Loc. 70. WIK Coll. 303-306. See also WIK Coll. 138, 139.

WIK Coll. 303A: Va., Accomack Co., Assateague Island, Chincoteague National Wildlife Refuge; pools of impounded water sl. brackish to salty, ditch along "Pool F" in full sun, water level down drastically because of insufficient rain; sampled algae and floating-leaved plants from surface of water and lower, beneath upper older algae. Water salinity 29 ppt, pH 7.8. Salinity subject to great fluctuations.

WIK Coll. 303B: Same as WIK Coll. 303A, ditch along "Pool F", morning shade from bayberry; water usually slightly brackish but sea water recently added; sand sample, expressly avoiding algae floating adjacent;

sampled sand above and below water line, white-grey sand fairly non-compact, over black sand.

WIK Coll. 304: Assateague, Tom's Cove, coastal salt marsh, heavy clay among rushes. Not productive.

WIK Coll. 305: Va., Accomack Co., Assateague Island, large roadside ditch, slightly brackish, adjacent to Pond "A" shore; soft mucky sand, water with concentrated algal bloom; sampled floating vascular plants coated with algae, some duckweed included. Water salinity 3 ppt, cond. 5,000 micromhos/cm.

WIK Coll. 306: Va., Accomack Co., Assateague Island-adj. bicycle path on causeway between ponds "F" & "A". Damp bottomlands of usually freshwater pond; water drained (evaporated?), substrate a rich, brown, peaty sand among bulrush with 3-square and spike rush, other herbaceous growth; fully exposed to sunlight except for undergrowth, cattail interspersed. Many *Dasyhelea*.

WIK Coll. 307: Va., Accomack Co., Saxis National Wildlife Refuge, Rt. 697 off Rt. 695, 0.5 mile N of town of Saxis. Small road-side ditch, along little-traveled dead end road; saltmarsh growth thick along ditch; sample: decaying plant stems, and black sulphurous mud, slimy. not dense, with algal scum on top, under 5 cm. water. Water sal. 11.0 ppt, pH 7.2. Very productive.

WIK Coll. 308: Va., Accomack Co., Eastern Shore on Rt. 692, 2.5 miles W of Hallwood; 1-2 m wide brackish roadside ditch; dense sprawling (approx. 5 cm. tall) contiguous mat of waterworts (*Elusine*), *Potamogeton* spp. and *Polygonum* spp. throughout ditch, rooted in a very soft aerated brown mud; substrate sample of mud with roots. Salinity 9.0 ppt, pH 6.8.

•Loc. 83. See also WIK Coll. 175, 402.

WIK Coll. 309: Va., Norfolk Co., Norfolk Co., Norfolk Gardens-By-The-Sea entrance, 50 m from Rt. 192, Azalea Garden Road. Dense swampy depression (swale) along road, connected to Lake Whitehurst; sampled rich brown-black mud with leaf pack material (under swamp cottonwood tree whose leathery leaves persist) at water's edge (water receded, exposing mud flat 1 m wide on average) some loose spongy-muck (recently exposed) included; duckweed present sparsely. Water pH 6.1, cond. 190 micromhos/cm.

WIK Coll. 310-318(n=17): 2 August 1976.

•Loc. 65. See also WIK Coll. 130.

WIK Coll. 310: Va., Suffolk Co., Nansemond River 1/2 mile down from Lake Meade Reservoir Dam, adjacent to Rts. 32-10-460, Suffolk Plaza, W side of road, east shore. Tidal mud flat, rich brown loose mud interlaced with reeds and stems among dense growth of tall herbaceous plants (esp. *Polygonum* spp. and *Typha* sp.). Water Salinity 7.5 ppt, pH 6.7.

•Loc. 53. (See also WIK Coll. 114, 115 and 174).

WIK Coll. 311. Va., Suffolk Co., Reid's Ferry. Not productive.

•Loc. 152. Compare WIK Coll. 116, 119, 195, 211

WIK Coll. 312A: Va., Isle of Wight Co., Suffolk City line, Rt. 603 over arm of "Great Swamp" above a branch of Lake Prince Reservoir; sampled thin

layer of brown-grey mud along water line, among a network of roots, stems, twigs, leaves with non-filamentous algae in some areas; mud black and unaerated underneath cypress and prostrate stems of *Polygonum* (not sampled).

WIK Coll. 312B: Same as WIK Coll. 312A; sampled floating filamentous algae (dark-green), *Ceratophyllum*, twigs, leaves, debris around fallen cypress branch and *Salix* seedlings.

•Loc. 153.

WIK Coll. 313A: Va., Sussex Co., Rt. 621 (dirt) 1.5 miles W of U.S. 460 between Waverly and Wakefield, 1.7 miles N of 604, in Coppahaunk Swamp; stand of large oaks, cypress, sweetgum, loblolly pine along edge. Sample of rich brown mud with leaves (esp. oak) and twigs along W. road embankment, at base of yellow birches. Water pH 6.8, cond. 120 micromhos/cm.

WIK Coll. 313B: Same Locality as WIK Coll. 313A, net of bladderwort over leaf pack, adjacent to stagnant pool E of road, with some leaves; water in pool red-brown. Diverse herbaceous flora, but not immediately at site; sparse overstory. pH 6.4, cond. 900 micromhos.

WIK Coll. 313C: Same Locality as WIK Coll. 313A; around base of sedge clump, red-brown mud with decaying matter and leaves from which clump protrudes.

•Loc. 154.

WIK Coll. 314A: Va., Appomattox Co., Rt. 626 bridge over Appomattox River, SE of Holliday Lake State Park, river 12 m. wide here; streamside flat area adjacent slowly flowing water, sampled soft brown mud and coarse filamentous algae (sparse) over lighter grey sand and gravel, above and below waterline in shallow water of small embayment; water pH 8.0, cond. 80 micromhos/cm, D.O. 5.9 ppm. Moderately rolling Piedmont terrain.

WIK Coll. 314B: As 314A. Fresh clump of loose Spirogyra attached to rocks under 5-20 cm. water. No results.

•Loc. 155. Compare WIK Coll. 389.

WIK Coll. 315: Va., Appomattox Co., Holliday Lake State Park in Buckingham-Appomattox State Forest; littoral of an arm of lake W of access road; grey-brown loose mud, substrate with twigs, etc. in small trickle coming into lake. Overstory of dense alder and white pine. Water pH 7.6, cond. 65 micromhos/cm.

•Loc. 156. WIK Coll. 316A-E.

WIK Coll. 316A: Va., Amherst Co., Otter Lake, adjacent to Blue Ridge Parkway; near James River. Sample consist of stripped bark (and debris beneath) of dead pine lying partly in lake above and below water line. Lake water pH 7.6, cond. 49 micromhos/cm., D.O. 3.9 ppm.

WIK Coll. 316B: Same Locality as WIK Coll. 316A, Otter Creek bottom, directly above inlet to Otter Lake, where velocity is diminished by beginning to back up; fine filamentous algae (loose aggregations) held in place by rocks under 2-5 inches of water. Water pH 7.4, cond. 40 micromhos/cm. D.O. 7.1 ppm.

WIK Coll. 316C: Same Locality as WIK Coll. 316A. Thick bed of burreeds and rushes forming "spurious island" on right upper edge of Otter Lake, mud to 1 m thick, held together (over boulder bottom) by root systems, esp. of *Sparganium* spp. Sample of this floating mud-plant aggregation taken from beneath water surface.

WIK Coll. 316D: Adjacent WIK Coll. 316C, 5 m toward stream inlet. Substrate of soft loose detritus-rich mud up to 30 cm. thick. Sampled from this substrate by dredge from bottom, in water 1 m deep.

WIK Coll. 316E: Va., Amherst Co., near Otter Lake, on beaver dam adjacent to Otter Creek, 50 m upstream from entrance into lake. Old stabilized beaver dam mostly overgrown with rooted aquatics; sampled soft grey-brown mud on impounded side, some algal tufts included, partly under alder, above and below water level, gentle fall-off; Eastern Burreed (*Sparganium americanum*) included; dead tree trunks still standing in backed-up area.

•Loc. 157.

WIK Coll. 317: (12 August 1976) Kentucky, Carter Co., adjacent entrance to Carter Caves; ca. 300 ml sample from tree-hole, species unspecified, 1 m from ground, 10x10 in. opening. Collected by J.G. Knausenberger.

•Loc. 158: WIK Coll. 318A,B. Compare WIK Coll. Nos. 331 to 342 and 344, esp. 334-342.

WIK Coll. 318A: 2 August 1976. Va., Louisa Co., Lake Anna, Station F near power plant, in main reservoir, leaf sampler retrieved from 2 m depth. Collector: J. R. Voshell.

WIK Coll. 318B: Lake Anna, Station B, cooling lagoon, bottom dredge sample from 2 m depth. Not productive.

WIK Coll. Nos. 319-321: 3 Sept. 1976.

•Loc. 2: WIK Coll. Nos. 319-321 (n=8); See also WIK Coll. 4-8, etc. Pandapas Pond.

WIK Coll. 319A: Va., Montgomery Co., Pandapas Pond, 20 m E of landing area; edge of pond at deltaic alluvial fan of small streamlet; sample concentrated on aquatic vegetation especially dwarf spikerush (*Eleocharis parvula*) and filamentous algal clumps (*Spirogyra* sp., etc.) with substrate of brown-yellow sandy mud, from under 5-20 cm. of water; cattails immediately adjacent (within 1 m) provide only shade. Water pH 7.2, cond. 80 micromhos.

WIK Coll. 319B: Va., Montgomery Co., Pandapas Pond, 5 m E of 319A. Edge of pond, same short spikerush as in 319A; damp surface mud in dense mat above water level, 50-100 cm. from pond's margin, on edge of rise 30 cm. high, which supports larger spike-rush and sedge growth.

WIK Coll. 319C: Same Locality as WIK Coll. 319, 5 m E of 319B at edge of pond, under shade of overhanging *Viburnum* sp.; sampled from thin layer of floating algae (*Nitella* sp. and some *Spirogyra*) with epipellic algal film overlying leafy semifluid mud with ferrous oxidized component and H₂S odor (slight); twig-leaf component included with dark grey mud "contaminate" (mud substrate de-emphasized in this sample). Shaded by overhanging branches from north.

WIK Coll. 319D: Near WIK Coll. 319A, 15 m E of landing area. Sample of milfoil overlying very wet mud (approx. 80% moisture) among dense littoral

cattail growth, with mud sampled in strips no more than 1" deep, light brown-yellow over dark grey unoxidized layer.

WIK Coll. 319E: Locality as WIK Coll. 319, 50-100 cm. away from 319D, conditions nearly identical, but mud less wet (60% moisture) and no milfoil or algae on surface; sampled aerated mud layer, among cattail stems and roots.

WIK Coll. 320A: (cf. WIK Coll. 281). Pandapas Pond, at junction of upper and lower ponds (cf. WIK Coll. 281), on beaver dam-like accumulation of twigs and mud, water level has markedly receded by ca. 50 cm. height. Sampled slightly moist moss and loose mud with fibrous root matter ca. 1 m above water level, twigs included, especially pine debris; overstory slight, chiefly Virginia pine.

WIK Coll. 320B: Same area as WIK Coll. 320A, adjacent to dam at junction of upper and lower pond; sampled 0-10 cm. above water on small peninsula, 1 m long mud flat exposed by lowered water level; under moderately dense shade of alder with alder, red maple, pine needles; leaf and root component included in sample.

WIK Coll. 321: Va., Montgomery Co., Upper Pandapas Pond, extensive beds of *Nitella* sp., under partial shade of *Salix* sp. in ca. 5-10 cm. water, with small amount of light-grey soft mud substrate included.

•Loc. 138. WIK Coll. Nos. 322-323 (n=4): 6 Sept. 1976. See also WIK Coll. 283, 284.

WIK Coll. 322A: Va., Giles Co., Jefferson National Forest, Salt Pond Mountain, just outside the east edge of Little Meadows in bed of Feeding Creek, an intermittent branch of Little Stony Creek, 1.5 km on forest road from Co. Rt. 714. Sampled deep brown mud with small gravel-sand component, damp in area of normal stream source, adjacent to large rocks, water not flowing at surface but substrate kept wet by underground flow. Hemlock and rhododendron overstory. Elev. 3200 ft. (985 m). Water pH 6.8, cond. 25 micromhos/cm, 14 deg.C (air 21 deg.C, 3 p.m.).

WIK Coll. 322B: Same as WIK Coll. 322A, N side of forest road; pool in Feeding Creek stream bed, to 30 cm. deep, under dense shade of hemlock and rhododendron, water not flowing; sampled bottom mud (grey-brown) from pool, with some loose substrate at water's edge - aerated mud.

WIK Coll. 323A: Same Locality as WIK Coll. 322A, Little Meadows in stream flowing from Little Meadows Hunting Lodge pond outlet toward Little Stony Creek, 5 m from road. Rich brown organic mud flat on edge of stream (80 cm. wide). No significant herbaceous vegetation at site *per se*, but marshy growth adjacent; open exposure except early a.m. and late p.m.

WIK Coll. 323B: As 323A. Small patch of isolated yellowish-green sphagnum on rock in stream. Not productive.

•Loc. 141. Compare WIK Coll. 287A,B and 394-396B.

WIK Coll. 324: (6 Sept. 1976) Vicinity of WIK Coll. 322A, Little Stony Cr. at Upper Cascades Falls. Rock face with mosses, *Lycopodium*, *Galax*, under overhanging rocks; adjacent to right bank of falls, but not very wet, because no water is actually trickling through microhabitat.

WIK Coll. 325-330 (n=11): 8 Sept. 1976. Cranberry Glades (5th and last trip)

•Loc. 74. WIK Coll. 324A,B. See 145-147. Also ASP-59, SW-60.

WIK Coll. 325A: W. Va., Pocahontas Co., Cranberry Glades Botanical Area, Monongahela National Forest, 50 m NE of Cranberry River, 1/2 mile NE of Forest Service Road barrier; grass-sedge community in opening of bog-alder community, sample site unshaded except by adjacent understory; sampled rich brown mud between two small rivulets; spike rush and miscellaneous grasses.

WIK Coll. 325B: Same area as WIK Coll. 325A; mud flat along edge of nearly lentic Cranberry River before enters Cranberry Glades. Sampled adjacent to log-jam, grey-brown mud (with many raccoon and some bear tracks), 5 cm. below water level and to 50 cm. above, very shallow slope; loose consistency with sand component. Water pH 7.2, cond. 73 micromhos/cm.

•Loc. 159. WIK Coll. 326-327. Also WIK Coll. 343.

WIK Coll. 326A: Cranberry Glades Botanical Area. Big Glade, edge of open glade beyond grass-sedge community, among green-white drier sphagnum, wet peaty interface sampled.

WIK Coll. 326B: Adjacent WIK Coll. 326B, edge of glade, adjacent to alder community in grass sedge community which is 5-20 m wide along edge at site area; sampled under thin layer of fresh sphagnum: cool peaty substrate with wet, damp decaying organic matter. Densely shaded by sedge community.

WIK Coll. 327A: Yew Creek outside Big Glade, in bog-alder community. Clump of water starwort (*Callitriche*) in stream flow. No results.

WIK Coll. 327B: Near WIK Coll. 327A, outside Big Glade, in bog-alder community. Along Yew Creek, littoral mud substrate, clayey brown-grey mud with loose damp rich-organic component; upper layer, sample from 10 cm. below to 10 cm. above water level. Compare WIK Coll. Nos. 327A,B with WIK Coll. Nos. 56-56, 149-151, and 275-277 (Loc. 25).

•Loc. 24. See WIK Coll. 51-55, etc.

WIK Coll. 328: W. Va., Pocahontas Co., Cranberry Glade Botanical Area, Flag Glade; depression 15x10 cm deep, in open glade, 15 m from edge in vicinity of old boardwalk, dark old sphagnum and peaty substrate with algal film on surface, free water at site.

•Loc. 160.

WIK Coll. 329A: W. Va., Pocahontas Co., Cass, right bank of Greenbrier River, adjacent to Cass R. R. parking lot. Rich leaf-infused (black, decomposing leaves) brown mud under black Locust and white oak, along eddy backwater; sample from 10 cm. below surface to 20 cm. above edge with algal growth on damp mud. Productive *Bezzia laciniastyla* site.

WIK Coll. 329B: Same Locality as WIK Coll. 329A, downstream end of 5 x 20m midstream island (water of Greenbrier low enough to ford on stepping stones). Sampled from tongue of deposited mud with significant leaf fraction; grey-brown loose, thick mud, shallow incline, sample taken primarily below water level at edge. Full sunlight exposure.

•Loc. 135. See also WIK Coll. 273.

WIK Coll. 330A: W. Va., Pocahontas Co., Dunmore Springs, in spring run, 30 m from source; sampled attached floating moss and a small amount of watercress. Water pH 7.7, cond. 223 micromhos; water temperature 16 deg.C, air 25 deg.C.

WIK Coll. 330B: Same as WIK Coll. 330A, within enclosure of former bath pool; slow spring flow, source of cold water at one end, with sulfurous soft grey calcareous deposit in that part of pool (little vegetation there). Sampled among cattail and reed marshy area with algal filamentous surface layer over cattail reeds and bottom mud organic ooze, under bayberry bushes. Water pH 7.4, conductivity 310 micromhos; water temp. 19 deg.C, air 25 deg.C.

•Loc. 158: 331A,B; 11 Sept. 1976.

WIK Coll. 331A: Va., Louisa Co., North Anna Reservoir, Millpond Creek, arm of Lagoon #2; along edge in nearly pure stand of *Spartanium* sp. with isolated clumps of a *Juncus* sp.; shallow area 5 m wide, 15 m long; sampled coarse sand-clay substrate grey-brown in water standing 5-10 cm. (moderate turbidity). Water pH 7.2, cond. 87 micromhos/cm.

WIK Coll. 331B: Same as WIK Coll. 331A; sample of muddy, wet organic detrital scum, stems and other vegetative material above water level at base of *Sagittaria* and Common Threesquare (*Scirpus americanus*).

WIK Coll. Nos. 332A-333G (n=9): 12 Sept. 1976.

•Loc. 158.

WIK Coll. 332A: Va., Louisa Co., VEPCO property, near lagoon #1 boat ramp, close to power plant on N side of approach road. Cattail marsh in small depression with no standing water, thin rich brown clayey layer 1/2 inch over dark grey clayey sand; covered by thick growth of *Eleocharis*, *Spartanium*, and *Sagittaria*. Adjacent marsh, growth rel. xeric, *Lespedeza* and pines.

WIK Coll. 332B: Across road from WIK Coll. 332A; firm coarse sandy edge of discharge channel to lagoon 1, with significant mica-flake component; full sunlight exposure except morning; sample at water's edge and some in shaded area near clump of grasses, thin soft layer over compact layer, with some soft mucky sand. Very productive of *Bezzia setulosa*, almost monospecific emergence.

•Loc. 162: Coll. Nos. 333A-G. 12 September 1976.

WIK Coll. 333A: Va., Rockingham Co., Grundo Campgrounds, about 5 miles E of Harrisonburg on U.S. Rt. 33, littoral of pond 100 m in diameter. Exposed bank of normally submerged shore substrate, yellow-brown clay layer 1/2" thick with thin algal film in small depressions; over compact dark grey clay (aerobic); sample partly at base of *Juncus* clump, above water's edge except small amount 5 cm. below. Pond in oak-mixed hardwood forest. Water pH 8.8, cond. 130 micromhos/cm.

WIK Coll. 333B: Same as WIK Coll. 333A; 5 m from present water's edge in bottom of only inlet to the larger of the two ponds at Grundo. Damp, deep, mucky leaf bed (oak leaves); sample of thin surface layer which has light brown mud on leaves (remainder dark grey with h&sub2.S odor), water "sponged" up in leaf bed has pH of 6.5.

WIK Coll. 333C: As 333A area, N side of pond, exposed to sunlight except late afternoon; sampled cluster of muskgrass (*Chara* sp.) attached and floating out to 2 m from edge and 1 m deep such growth found all around edge).

WIK Coll. 333D: As 333A locality, etc. Isolated mass of floating *Potamogeton* sp. (pond weed, with thin leaves) on E margin of pond, 1 m out from shore. Not productive.

WIK Coll. 333E: Same as WIK Coll. 333A; E shore of pond, clayey substrate with leaves and gravelly sand and other organic matter including twigs, all above water level, but damp.

WIK Coll. 333F: Same area as WIK Coll. 333A; edge of smaller pond, among roots of *Salix* and stems of *Typha*; sample of grey-brown mud in shallow water in shade of *Salix* and riparian herbs. with some organic detritus and algal growth.

WIK Coll. 333G: Same location as WIK Coll. 333F, edge of upper smaller pond, among roots of *Salix* and stems of *Typha*, but sample with much more organic debris than mud, in shallow water.

•Loc. 158: WIK Coll. Nos. 334-342 (n=12); 344. All on: 11 Sept. 1976.

WIK Coll. 334A & B: Va., Louisa Co., Lake Anna reservoir, Station A, Lagoon 1, W of Harris Point, baskets 1 and 2 respectively; lake benthos, composite leaf packs in basket samples at 4 m depth.

WIK Coll. 335: Va., Louisa Co., L. Anna, Station C basket sample from Lagoon #.

WIK Coll. 336-337B: No results.

WIK Coll. 338A: Va., Louisa Co., L. Anna, basket sample leaf pack from station F at 2 m depth.

Coll. Nos. 338B-340: No results.

WIK Coll. 341: Va., Louisa Co., L. Anna, mix of washings from many 3-M mesh substrates in baskets throughout the lake Bottom.

WIK Coll. 342.: No results.

•Loc. 159. (See also WIK Coll. 326A, etc.).

WIK Coll. 343A & B: (8 Sept. 1976). W. Va., Pocahontas Co., Cranberry Glades Natural Area, Big Glade; WIK Coll. 343A: open bog expanse in largest glade; composite sample of isolated, old *Sarracenia purpurea* pitcher plants and stems (no roots) and contained debris; WIK Coll. 343B: contents of 130 pitcher plants' fluid extracted non-destructively with 50 ml bulb syringe.

WIK Coll. 344: (11 Sept. 1976). Va., Louisa Co., Lake Anna Reservoir, 3-M webbing substrate from miscellaneous stations. Collector: G. M. Simmons, Jr.

•Loc. 120. See also 248, 258, 351, and 363.

WIK Coll. 35: (7 Oct. 1976) Va., Montgomery Co., Longshop-area sink-hole. Sinkhole mud-flat at edge of pool, drying mud expanse with dense growth of annual emergent macrophytes (no det.).

•Loc. 160 12 Oct. 1976. Compare 364, 366.

WIK Coll. 346: Va., Montgomery Co., Longshop, Va., Prices Fork-McCoy Rd. (Va. 652); Tom's Creek, 50 m upstream of Va. 655 bridge; drift net in riffle 25-50 cm. deep; water slightly higher than grass line.

•Loc. 146: 347, 348; 27 November 1976.

WIK Coll. 347: Va., Hampton City, Grandview Park Natural Preserve (compare WIK Coll. 299) end of Beach Road, at Hawkins Pond slightly brackish coastal pool adjacent to water-logged pier plank section and bayberry hedge; sample at water's edge of beige-grey clay with organic detritus and sand with algal component (fragmented green algae, etc.) during warm wet spell after cold (30 deg.-40 deg.F) salinity 0.7-0.8 ppt. dry period.

WIK Coll. 348: Va., Hampton City, Grandview park Natural Preserve, end of Beach Road, across path from WIK Coll. 347, eastward toward dunes in pool larger, deeper (1 m deep); macrophytes floating and attached with surface "crust" of congealed once-dry algal mats; sample taken 50 cm. from margin in 30 cm. of water, floating encrusted macrophytic algae (prob/ *Nitella*) with algal/bacterial film. Isolated daisies still blooming, also goldenrods. Salinity 3.2 ppt (site revisited Mar.3, 1977: water level up 30 cm. algae no longer floating, salinity 1.2 ppt).

•Loc. 120: 28 February 1977. See also WIK Coll. 248, etc.

WIK Coll. 351: Va., Montgomery Co., sinkhole near Rt. 652, between Price's Fork and Longshop; at water's edge, under dense covering mat of dead grasses, loose brown-grey mud, 5-20 cm. from water's edge and some underwater substrate; patches of snow remain in protected areas, following hard winter.

•Loc. 163: 20 Feb. 1977.

WIK Coll. 352A & B: Flood plain pool in Tom's Creek Valley. Not productive.

•Loc. 164: 2 March 1977.

WIK Coll. 353: Va., York Co., City of Williamsburg, left bank of Queen's Creek at Rt. 143 bride (Jefferson Highway) crossing, bank of sluggish

tidal stream, slightly brackish; adjacent to *Spartina* marsh, very soft green-grey mud bank 1-2 m wide, water level down, with patches of green-brown algal, surface scum, surface scraped and water added, dark grey layer 1 inch beneath surface, laurel-type oak overhanging site, March 2, 1977. Water pH 6.7, salinity 0. ppt, cond. 1100 micromhos.

•Loc. 164: WIK Coll. 354-358: 3 March 1977.

WIK Coll. 354: Va., James City Co., "neck of Land" on Colonial Parkway opposite Jamestown Island, body of water (The Thorofare) confluent with James River; marshy flat with small tortuous channels under slight tidal influence, thickly grown over mixed *Spartina* community sample taken 30 m from upland edge, in tiny channel 10-20 inches wide, of thick grey-brown aerated mud heavily infused with organic fibrous debris, roots, etc. from edge and under 1-2 inches of water; Red maple buds just beginning to expand.

WIK Coll. 355: Sand bank near confluence of Glebe Gut and James R. Not productive.

WIK Coll. 356: Va., James City Co., Jamestown Island, Island Drive Long Loop, Colonial National Park; marshy edge of large open woodland pool (connected to Passmore Cr.) with rush and sedge clumps; sampled abundant submerged old reeds, and floating vascular plants covered with algal-bacterial film; no bottom substrate per se included. Salinity 0.2 ppt, cond. 470 micromhos. Water temp. 20 deg.C at surface, air 16 deg.C. Exposed to sun.

WIK Coll. 357: Va., James City Co., Jamestown Island adjacent to short loop of Island Drive, section connecting S and N arms of large loop. Extensive broad ditch pool, shallow water or no standing water, with isolated cattail reeds at sample site; sedge growth dense, *Calamus* among growth, sampled thick, fibrous loose mud and detritus below upper dry layer. Dense overstory of red maple and loblolly pine. Water pH 6.5, salinity 0.2 ppt, cond. 500 micromhos; WT 6-8 deg.C; air 14 deg.C.

WIK Coll. 358: Old sedge, grasses and reeds under 3 inches water. Not productive.

Coll. Nos. 359-362. 6 March 1977.

•Loc. 166.

WIK Coll. 359: Va., Fauquier Co., Thompson Lake, G. R. Thompson Wildlife Mngmt Area, Rt. 688 approx. 1.5 miles S of US 17, in NW part of county, foothills of northern Blue Ridge Mtns. Long 77 deg. 58'W. Lat. 38 deg. 58'N. SE edge of lake in cattail growth, adjacent alder bushes; sampled in sandy substrate under 10 cm. water with alder, cattails, etc., submerged debris, grey-brown sandy mud with coarse grain sand. Water pH 6.8-7.0, cond. 50 micromhos/cm.

•Loc. 167.

WIK Coll. 360A: Va., Shenandoah Co., George Washington National Forest, Elizabeth Furnace Recreation Area, Passage Creek, 2.5 miles S of Rt. 55, long. 78 deg.00-30' Lat. 38-39 deg. 30-00' Elev. 1000 ft. Edge of stream, widened section (3-8 m) above rapids, back eddying at site (good

trout stream, 1.5 miles upstream of hatchery); leaf pack with mud and sand, 0-20 cm. from edge under 5-15 cm. of water. Water pH 6.7, 75 micromhos. Oak forest with scattered white pine.

WIK Coll. 360B: No ceratopogonids (sand bar in stream, WIK Coll. 360A).

•Loc. 168.

WIK Coll. 361A: Va., Page Co. Rt. 615, 0.1 mile S of intersection with Rt. 211, 4 miles W of Luray. Spring seepage in slowly running trickle, a thin layer of water over a dark brown marshy mud substrate; significant fiber content produced by Japanese honeysuckle, primarily, and grasses. Water pH 6.6.

WIK Coll. 361B: Same as WIK Coll. 361A, cattail marshy area with no standing water, marsh approx. 50 m², overgrown on sides and into edges by honeysuckle; spongy wet thick fiber mat among cattails, covered with dead cattail leaves and sedges and marsh grasses.

•Loc. 169.

WIK Coll. 362: Va., Augusta Co., Mossy Creek, 100 m S of intersection 747 and 731 on 731 at Mt. Solon (Blue Hole Spring). (No. 504 in Collins et al. 1930). Marshy area near spring outlet with cattails, watercress, and isolated clumps of rushes and mint, 300 m² area, loose dark brown-grey mud, bound by roots, sample is mud with roots pulled away, but much root fiber present in sample; mud is aerated, light in texture.

WIK Coll. 363-364: 23 April 1977.

•Loc. 120. See also WIK Coll. Nos. 248, 258, 345, and 351.

WIK Coll. 363: Va., Montgomery Co., sinkhole P.F.-Longshop; water receded, only 5 cm. deep, leaving exposed mud flats with extensive algal coating and sprouting seedlings, along small willow 50 cm. from water; mud thick and deep, grey with light brown upper layer, 1 cm. thick.

•Loc. 170. See also 346 and 366.

WIK Coll. 364: Va., Montgomery Co., Tom's Creek basin flood plain, 0.8 miles NE of RT. 655 from Longshop (intersection with Rt. 652-Price's Fork and McCoy Road), 100 m downstream from a sewage lagoon, in a slow moving stream; very deep muck (50-100 cm) heavily laced with leaves and twigs, relatively loose and only mildly sulfurous; under heavy shade in bottom lands; deciduous woods beginning to leaf.

WIK Coll. Nos. 365-369 (n=7): 24 April 1977.

•Loc. 1. See WIK Coll. Nos. 103, etc.

WIK Coll. 365: Va., Montgomery Co., Shadow Lake pond off Rt. 651 toward Tom's Creek from Glade Road, pond edge; sampled extensive beds of blanket algae (*Spirogyra*); *Callitriche* (Water starwort) interspersed with sycamore leaves off pond surface. April 24, 1977.

•Loc. 170. cf. WIK Coll. 346, 364.

Coll 366: Va., Montgomery Co., in Tom's Creek at Longshop; 24 hr. drift net sample BioQuip 1000 cm² opening, 1 m net length); light frequent rain

during past 24 hours, no significant rise in stream level. Site elev. 1690 ft. April 23-24, 1977.

•Loc. 171: WIK Coll. 367-368 (n=5). Compare WIK Coll. 252.

WIK Coll. 367A: Va., Montgomery Co., right bank, New River at end of Brush Mt. 37 deg.14'00"N, 80 deg.37'25"W); sampled fine, dark brown-gray sand on edge, in backwater quiet area behind prostrate tree above and below present water level; significant organic matter component, water level down for weekend (river has tidal flow because of reservoir management upstream) bank 20 cm - 1 m wide; willow leaning overhead. (Elev. 1660') Water chemistry: pH7.0; total hardness 71 mg/l CaCO₃; alkalinity (methyl orange) 44 mg/l; conductivity 124 micromhos/cm; water temp.: 16 deg.C, air 18 deg.C.

WIK Coll. 367B: New River, sandy mud in root sphere of willow. Not productive.

WIK Coll. 368A: Va., Montgomery Co., New River near WIK Coll. 367A, foliose: mosses and liverworts adhering to nearly vertical sandy bank stabilized by root mass of adjacent trees, from 0-30 cm above current water level; subject to frequent flooding; in shade of overhanging trees; some moss taken from underside of leaning tree, 10 cm above water.

WIK Coll. 368B: Algal Aufwuchs on bark of log partially submerged in New River. Not productive.

WIK Coll. 368C: Va., Montgomery Co., New River, lotic; sampled in flowing water, various macrophytes, algae, root fibers, etc. trapped by and attached to logs, etc. jutting into current to 1 m from edge, 30 cm. from bottom.

•Loc. 172.

WIK Coll. 369: Va., Montgomery Co., adjacent to New River 30 m from edge, approx, 5 m above river level, small rivulet (30 cm. wide) in ditch leading from a floodplain vernal pond to the river, along a meadow-wet woods margin; sampled rich red-brown mud with much herbaceous debris, old stems and leaves esp.; ditch sides overgrown with *Equisetum*, *Impatiens* sp. seedlings, under black locust and oaks. Water pH 7.1, total hardn. 53 mg/l, cond. 101 micromhos/cm.

•Loc. 173: WIK Coll. 370A-C: 27 April 1977.

WIK Coll. 370A: Maryland, Prince Georges Co., Lakeland Pond, College Park, shallow pond of about 1 hectare surface area: sampled along flooded pond margin, of *Spirogyra* and other algae (largely old growth) floating with suspended debris and leaves, among sedges, rushes and water lily pads *Nuphar*, *Nymphaea*). Water pH 6.4, cond. 12 micromhos.

WIK Coll. 370B: Same as WIK Coll. 370A; largely submerged or floating dead stems, leafy detritus, more or less decayed debris and some live plant material (emergent aquatics) in partial shade of *Salix* sp.

WIK Coll. 370C: Same as WIK Coll. 370A, Petersen grab sample entirely of substrate under 10-15 cm. of water; loose grey-yellow, aerated mud with much air space produced by interspersed tubers of water lilies (*Nymphaea tuberosa*).

WIK Coll. Nos. 371A-374C: 29 April, 1977.

•Loc. 174: WIK Coll. 371-372.

WIK Coll. 371A: As 371 B. Sand bar in small stream. Not productive.
WIK Coll. 371B: Va., Fairfax Co., Pohick bay regional Park; small stream 30 meters up from inlet into Potomac River, in small hardwood covered ravine; sampled leaf pack in flowing water, avoided sand, but mud interspersed between leaves, immediately below a small log jam.

WIK Coll. 372: Same as WIK Coll. 371B, 2 m from edge of Potomac River, behind log ridge exposed to high water (extensive fish kill evident along river). Damp leafy depression surrounded by shrubs and alders; decomposed leaves and twigs with sandy mud component, in drainage run from adjacent marsh.

•Loc. 175.

WIK Coll. 373A: Va., Prince William Co., Prince William Forest Park, South Fork of Quantico Creek (long 38deg.30'45"N, lat. 77 deg.15'30"W); stream 5 m wide in sections; sampled stream side of large sand bar (color rich yellow-brown) along pool upstream of narrowed rapids section; sample in downstream "shadow" of tree stump roots with some organic debris and leaves incorporated. Water pH 6.4.

WIK Coll. 373B: Same as WIK Coll. 373A, ox-bow pool behind sand bar, open at one end to stream shallow standing water over 10-20 cm. bed of last seasons leaves; sampled thick muck leaf bed with algal growth over leaves.

•Loc. 176.

WIK Coll. 374A: Va., Stafford Co., Quantico Marine Base on Laguna Reservoir; shale and a rust-red sandy-clay substrate with a mica component; forest locally predominately pine-planted; shale underlies large sections of area. Grab sample in 30 cm of water near shore, no vegetation, pH 6.5.

WIK Coll. 374B: Same as 374A; sampled substrate mud along margin above and below waterline with a minimum of included vegetation.

WIK Coll. 374C: Same as 374A; bottom substrate with much plant and algal material on and in water 40-50 cm. from shore at 5-20 cm. water depth.

WIK Coll. Nos. 375A-382 (n=12): 30 April, 1977.

•Loc. 177. WIK Coll. 375-377.

WIK Coll. 375A: Va., Chesterfield Co., Pocahontas State Park and Forest, Beaver Lake Reservoir on Swift Creek. Floating algae and aquatic macrophytes such as water lily (*Nymphaea odorata*). Sample ca. 1 m from edge, 50 m lakeward from dam on left bank.

WIK Coll. 375B: Same as WIK Coll. 375A. Sample along margin in clay-sand substrate, light grey to cream white; surface scrape including no plants, some roots. Maple and pine overhanging site.

WIK Coll. 375C: Same as WIK Coll. 375A; Sample 1 m from edge; including thick, loose mass of roots and mud, partially suspended in water, among emergent aquatics.

WIK Coll. 375D: Same as WIK Coll. 375A. Sample immediately above man-made dam in a beaver-dam like accumulation of twigs, leaves, needles,

mud with water flowing steadily through; and thick mats of milfoil and *Polygonum* root mass. No immediate overstory.

WIK Coll. 376: Same as WIK Coll. 375A; immediately below, in swift Cr. at foot of dam spillway. Mudflat 1 m² in extent, with sparse vegetation (seedlings) in center where sampled, water flowing thru in thin (2-3 cm) layer; sampled light grey-yellow clay with significant brown organic component, stabilized by some root growth. Water pH 5.9, cond. 58 micromhos; temp. 13 deg.C; air temp. 8 deg.C at 8:00 a.m.

WIK Coll. 377: Same as WIK Coll. 375A; 100 m downstream from Beaver Lake reservoir dam (at water level). Sampled left bank, light grey sandy gravelly clay, scraped with leaves, in backwater of large boulder; water slowly flowing at site; rich, organic detritus deposited on bottom; water distinctly brown.

•Loc. 178.

WIK Coll. 378A: Va., Powhatan Co., 25 miles W of Richmond (capital); Branch Creek, 2nd order tributary of Fine Creek, which then flows into James River; 1.5 miles on 615 from intersection with Co. Rt. 603. Beaver-dam like back-up, sizable pool adjacent stream with dead trees upright. Sample in bed of water starwort (*Callitriche*) floating on surface. Lentic site.

WIK Coll. 378B: Locality as WIK Coll. 378A; bottom substrate grab, loose-compact, clayey, grey-brown mud, under 30 cm. water; little or no organic matter included. *Callitriche* bed on water surface shading bottom.

•Loc. 179.

WIK Coll. 379: Va., Powhatan Co., Deep Creek Bridge on US 60 approx, 5 miles W of Cumberland Co. line. Sampled among floating mat of filamentous algae; no bottom substrate included. Pupae isolated in field.

•Loc. 180.

WIK Coll. 380: Va., Cumberland Co., Bear Creek Lake, Cumberland State Forest, long: 78 deg.16', Lat. 37 deg.32'. Sample along margin of spring run 50 m downstream of spillway; of soft mud and *Eleocharis* mat; rich *Aufwuchs* community on stems and bottom; water flowing in thin layer over sample site. Lentic site.

•Loc. 181.

WIK Coll. 381: Va., Buckingham Co., Co.Rt. 605, approx, 2 miles N of US 60, floodplain E side of James River, crescent-shaped pool, 300 m long by 40 meters wide. Sampled at downwind end of pool in accumulation of leaves 0.5-1.0 deep. Some immediate shade by American lotus leaves, *Polygonum*, otherwise fully exposed to sun. Substrate temp. 30 deg.C.

•Loc. 182.

WIK Coll. 382: Va., Nelson Co., on Appomattox Co. line, adjacent to US 60, left bank of James River, inside of left turn in river. Sample of light brown sand with minor organic component adjacent dead long on sand. In small cove protected by a spit of sand, under dense overhanging willow. Cows have access to site.

WIK Coll. Nos. 383-386: 4 June 1977.

•Loc. 183. WIK Coll. No. 383-386.

WIK Coll. 383: Va., Allegheny Co., Jackson River approx. 10 miles up river from Covington at Natural Well. Approx. 200 meters upstream from Co. Rt. 638 bridge, large backwater eddy pool on left bank adjacent to swiftly flowing water. Site along shore adjacent to dead overhanging log which provided protection from revolving current, allowing deposition; sample taken at water level along edge of pool, farthest back from flowing eddy; clayey loose mud and leaf deposit with some *Elodea* growth. Top layer of sediment thin, brown-grey over black unaerated sulfurous layer; sparse willow canopy. Water pH 6.7, cond. 79 deg. micromhos, temp. 16 deg.C; air temp. 21 deg.C.

WIK Coll. 384: 2 m along bank from WIK Coll. 383, more exposed to flowing water, at base of 2 ft. high steep bank; sampled from thick mud deposit with significant gravel-sand components and few leaves; mud uniform dark brown in color at base.

WIK Coll. 385: Va., Allegheny Co., Jackson River, at eddy pool described in WIK Coll. 383. Sample taken 1 m from shore on surface of water 1 m deep, in eddy flow; of floating drift detritus accumulated between two logs (concentrated by entrapment); including algal scum, new and old leaves (especially willow) twigs, grasses, pupal and larval exuviae plentiful, especially of Chironomidae.

WIK Coll. 386. N.P.

Coll Nos. 387A-388 (n=4): 5 June 1977.

•Loc. 184.

WIK Coll. 387A: Va., Montgomery Co., Laurel Ridge, E flank of Brush Mountain, in powerline clearing, 1 km uphill from Tom's Creek, access via Laurel Ridge development road. Small tree stump hole diameter in stump 30 cm. high, 60 cm across (possibly oak); oak, small clumps of raspberry canes and other shrubbery in immediate vicinity. Sample of ca. 50 ml water and some peaty sediment, pH 7.5.

WIK Coll. 387B: Same stump hole as WIK Coll. 387A; sampled moss lining inside hole, above waterline.

WIK Coll. 387C: Va., Montgomery Co., 50 m NE of WIK Coll. 387A & B. Larger and deeper stump hole 30 cm. across. Sample of ca. 700 ml water taken. pH 6.8.

•Loc. 185.

WIK Coll. 388: Va., Augusta Co., Elliot Knob (15 miles W of Staunton) in Great North Mountain ridge line at Iron Spring, Long. 79deg.19'W Lat. 38 deg. 10'N. Elev. 4100 ft. 126 m. Spring pool, 50 ft. (15m) diameter¹. Loose organic muddy sand sampled, with significant vegetative

¹ This is spring #493 of Collins et al. 1930. Springs of Virginia Div. Water Resources and Power, Bull. No. 1. It occurs in syncline

component of grass fibers and other detritus. Vegetation on Knob stunted, contorted by prevailing wind. Coll. by Frank L. Carle. Water pH 5.6, temp. 49 deg.F, air temp. 72 deg.F.

Coll. Nos. 389, 390: 16 June, 1977.

•Loc. 186.

WIK Coll. 389: Va., Appomattox Co., Buckingham, Appomattox State Forest, Holliday Lake 4-H Camp, near amphitheater. Sampled shoreline mud and sand substrate among aquatic macrophytes, adjacent meadow. Water pH 6.2, cond. 800 micromhos.

•Loc. 187.

WIK Coll. 390: Va., Bedford Co., Montvale Wayside adjacent to US 460 at intersection of Co. Rt. 607 on eastern slope of Blue Ridge (Foster Knob) at goose Creek. Sample on face of an old mill dam, beneath mill race; of wet moss and grasses exposed to more or less strong film of water, at least along margin of clumps and loose rock crevices. Branches of moderate canopy overhanging. Water pH 7.6, cond. 550 micromhos; hardness 270 mg/l as CaCO₃. Rich dipteran fauna.

WIK Coll. Nos. 391-393: 25 June 1977.

•Loc. 188.

WIK Coll. 391: Va., Giles Co., Mountain Lake Biological Station, 100 m N of main building in cattail pond. Sample of detritus and algal mat. Elev. 3750' (1154 m). Water cond. 140 micromhos.

•Loc. 189. WIK Coll. Nos. 392, 393.

WIK Coll. 392: Va., Giles Co., Salt Pond Mtn. massif adjacent War Spur Ridge at virgin hemlock stand. Sample in War Spur Creek, of hygropetric moss adjacent to and in swift stream. Under very dense Rhododendron thicket. Water pH 6.6, cond. 50 micromhos, 17 deg.C, air 24 deg.C.

WIK Coll. 393: Va., Giles Co., Salt Pond Mountain, spring run approx. 100 m downstream from Dividing Spring, in upper reaches of War Spur Creek; at bride on trail to virgin hemlock stand, approx. 200 m NE from parking lot. Elev. 3700". Sample of rich brown silt-sand mud in plant debris and leaf pack accumulation on upstream side of a log spanning stream (5' wide). Shallow, slow moving, water trickling through area sampled; canopy moderate, hardwoods; slight incline, extensive fern stand adjacent; Water pH 6.5, cond. 115 micromhos.

Coll. Nos. 394-396B (n=4): 3 July 1977.

•Loc. 141. WIK Coll. Nos. 394-396B. (See also 287A,B and 324).

WIK Coll. 394: Va., Giles Co., Little Stony Creek, 1 mile downstream from lower Cascades falls elev. ca. 2300 ft. Sample on left bank;

of Romney shale, with a flow of 2 gal/min., total hardness of 169 mg/l as CaCO₃, bicarbonate alkalinity of 165 mg/l, etc.

brown-beige sand, along bank of relatively quiet eddy. Pool downstream of rapid section, under dense hemlock and *Rhododendron* with root moss holding bank together. Water pH 6.8, cond. 18 micromhos, hardness 25 mg/l CaCO₃, temp. 18 deg.C; air 25 deg.C.

WIK Coll. 395: Va., Giles Co., Cascades at least 50 m below falls, on E cliff wall (left as you look downstream) elev. ca. 2800 ft. (845 m.) Taken 3 meters up from foot of very moist shaded cliff wall, sample of moss, leafy liverwort and fern growth in crevices. Water dripping from above, apparently from an aquifer; mosses, etc. in 1-3 cm. thick layer, attached to nearly vertical shale rock face, wet from slow but steady drip. Water pH 6.1, cond. 102 micromhos.

WIK Coll. 396A:; Va., Giles Co., 1 km. downstream of lower Cascades Fall, on let (E) side, at least 10 m above stream at foot of overhanging cliff with water dripping liberally from 5 m onto rock screen. Elevation: ca. 3000 ft. (910m). Sample of rich, green mat of hygropetric flat mosses and liverworts very damp to wet with water trickling immediately adjacent. Overstory moderate to dense, only filtered sunlight reaches site. No water sample taken.

WIK Coll. 396B: Same as WIK Coll. 396A. "Crustose" moss (i.e., continuous layer of thin moss) on bark and smooth wood of aged fallen tree under direct influence of dripping water, adjacent to and on the rocks of site 396 A.

•Loc. 5. WIK Coll. Nos. 397A-398B (n=6) (See also WIK Coll. 12-15, etc.).

WIK Coll. 397 A,B,C, and D.: Va., Montgomery Co., Tom's Creek, near bridge at Shadowlake Rd.; 15 m downstream of bridge adjacent small willow tree; drift net positioned in narrowed section funneling most of stream discharge through 0.5 m. section (net of no. 363 Nitex bolting cloth on 30x45 cm. frame). Four 24 hour samples taken as follows:

- A: July 3-04, 1977.
- B: July 14-14, 1977.
- C. Aug. 10-11, 1977, following thunderstorm.
- D. Aug. 19-20, 1977; *Oscillatoria* algal clumps trapped in net.

Water pH 7.3-7.8, cond. 407-435 micromhos, total hardness 210-223 mg/l, temp. 20-24°.C. Elevation ca. 2400 ft.

WIK Coll. 398A: Va., Montgomery Co., Tom's Creek at Shadowlake Road bridge; placement and recovery of basket containing artificial substrate of 3-M black plastic webbing, suspended in at least 40 cm. water, just touching bottom. Put out April 26, 1977, retrieved August 11, 1977.

WIK Coll. 398B: Same as WIK Coll. 398A, but basket in midstream, resting on and attached to bottom, under 3 ft. of water. Retrieved August 17, 1977.

WIK Coll. Nos. 399A - 401B (n=6): 16 August 1977. Collector: Frank L. Carle.

•Loc. 190. WIK Coll. Nos. 399A-401B.

WIK Coll. 399A: Va., Tazewell Co., Wythe Ranger District, Jefferson National Forest, Beartown Mountain wilderness area (proposed), southwest of Burkes Garden. Elev. ca. 4030 ft. (1230 m.). Long 81 deg.27'W, Lat.37 deg.5'N.

Sample from beaver pond and bog in Roaring Fork Creek tributary drainage. Microhabitat: open bog margin among *Juncus* sp. rushes, with *sphagnum* and filamentous algae. Water pH 5.5, cond. 110 micromhos. Biogeographic data: Alleghanian Biotic Region, Canadian Life Zone, Ridge and Valley Province; Canadian Alpine and Northern Hardwood forest community.

WIK Coll. 399B: As WIK Coll. 399A, open bog pond. Sample of bottom sediment/ooze among root development of a young sedge (*Carex*) clump; sediment of organic peaty nature consisting of very fine particulates (>90% passes through 80 mesh, at least 20% through 270 mesh).

WIK Coll. 400A: Same as WIK Coll. 399A, open bog. Sample of sphagnum with sedge clump.

WIK Coll. 400B: Same as WIK Coll. 399A, open bog. Sample of sphagnum clump with no sedge in immediate area.

WIK Coll. 401A: Same as WIK Coll. 399A, spring above Beartown Mountain bog. Sandy-gravel substrate which is covered by older loose-slimy sphagnum peaty detritus. Water pH 6.4, spec. cond. 85 μ mhos, temp.

WIK Coll. 401B: Va., Tazewell Co., adjacent to spring in WIK Coll. 401A. Sample of fresh sphagnum with peaty sandy substrate and other organic matter.

•Loc. 83. (cf. 309, 175)

WIK Coll. 402: 17 August 1977. Va., City of Norfolk, Gardens By-The-Sea, adjacent to approach road. Depression in swampy mud flat adjacent shrub thicket. Sample of dark brown mud (no immediate emergent vegetation cover, though overstory is moderately dense) with strong organic detritus component (bark, twigs, leaves), with water standing in pools; Collector: Janice Knausenberger.

•Loc. 119. (See also 242).

WIK Coll. 403: 5 September 1977. Va., Montgomery Co., Mill Creek at Bennett's Mill, 1.7 mi. E of Luster's Gate on St. Secondary Rt. 785; 12th drift net sample in rapidly flowing water immediately downstream of spring in flow (with water cress). Water pH 8.0, spec. cond. 360 micromhos, total hardness 200 mg/l, temp. 15 deg.C. Elev. ca. 2000 ft. (605m).

Coll. Nos. 404-406B: 15 October, 1977.

•Loc. 191. WIK Coll. Nos. 404, 405.

WIK Coll. 404: Va., Craig Co., Jamison's Farm Pond, Co. Rt. 600, 5 miles SW of Paint Bank (at least 1 mile NE of W. Va. border). Elev. ca. 1800 ft. (545 m). Sampled along *Juncus militaris* clump 1 by 3 m in extent (stands 1 m high, dense, pure) Sample consisted of accumulated

debris and some mud component and dense, loose root mass material. No overstory.

WIK Coll. 405: Same as WIK Coll. 404, rich macrophyte growth, emergent and floating and submerged (not further identified); little mud included in sample. Plant material forms intertwined dense mats.

•Loc. 52. (See also WIK Coll. Nos. 109-112).

WIK Coll. 406A: Va., Craig Co., Pott's Mountain, Pott's bog, in Barbour's Creek Wilderness Study Area; New Castle Ranger District of Jefferson National Forest Bog. Bog roughly circular-oval, 80 m long, 50 m wide with irregular pond in center; surrounded by mixed deciduous oak-maple forest. Sample of wet peaty and young-growth sphagnum about 15 m from edge of bog, SE side toward drainage.

WIK Coll. 406B: Same as WIK Coll. 406A. Sample in soft, root-infused mud with lily adjacent.

Collections 407A-F: 30 June 1978.

•Loc. 37. (See also WIK Coll. No. 76-80).

WIK Coll. 407A: Va., Smyth Co., Saltville saltmarsh ponds; NE pond, on Farm Drive, immediately outside town, 0.5 miles NE of Washington Co. line. Margin of large saline pond with large nearly monospecific population of *Culicoides variipennis*, with *Chironomus*, Ephydriidae, Corixidae present. Sampled clay-silt muck directly at water's edge; equal quantities taken above and below water line with small fragmented organic fibers; water receded to create extensive mud flats. Sunny, no overstory, but adjacent stands of saltmarsh bulrush, especially *Scirpus robustus* and *Salicornia europaea* L. (slender glasswort) in immediate area. Water pH 7.8-8.2; salinity 6.3-7.7 ppt; spec. cond. 5900 micromhos; temp. 32 degC; air 30 deg.C.

WIK Coll. 407B: Same as WIK Coll. 407A, southeast pond adjacent to Lake Drive, approx. 90 m W of Farm Drive. Shallow large pool with 1 m wide connection to freshwater pool to S less saline, water receded to leave 3-10 wide mud bank. Sample of uniformly gray brown, relatively solid substrate (thin layer of fluid mud over packed clay) at water's edge, with sparse component of filamentous algae (esp. *Spirogyra*); no vegetation at site. Geese frequent site, causing some enrichment. With a microscope, a rich microflora and microinvertebrate fauna is evident. Water pH 8.0-8.2, salinity 2.2 ppt., spec. cond. 2700 micromhos, total hardness 383.5 mg/l, temp. 36 deg.C; air 31 deg.C.

WIK Coll. 407C: Same as WIK Coll. 407A, NW pond adjacent to Farm Drive, edge parallel to Lake Drive, 100 m from Farm Drive. Brackish pond with open, gently sloping approx. 2-3 m wide bare mud flat. Sampled at water's edge, clayey brown over gray substrate with fresh algal mats on water's surface. Water turbid due to activity of geese, whose droppings also visible. Sparse understory of bulrush: American threesquare *Scirpus americanus*. Water pH 8.6, salinity 0.4, spec. cond. 550 micromhos, total hardness 185 mg/l.

WIK Coll. 407D: Same as WIK Coll. 407A, pond N of Lake Drive, approx. 200 m from Farm Drive. Sampled thick black grey muck at edge of pond. Thick stands of *Scirpus* spp., *S. acutus* Muhl (Hardstem Bulrush), Collector: R. Zimmerman.

WIK Coll. 407E: Va., Smyth, narrow curved lagoon approx. 100 m NE of intersection between Rt. 91 and Lake Drive. Edge of saline lagoon pond, bare exposed mud 1 m wide, bank shallow slope (receded water line). Sampled deep thick black muck and overlying thin (1-5 mm. thick) layer of light brown-red mud (deposited by recent high waters) at edge of water. Water odor strong of H₂S.

WIK Coll. 407F: Same as WIK Coll. 407A, NW pond adjacent to Farm Drive, 50 m from road. Sampled dense *Eleocharis* mat substrate of damp mud, removed by a 2 meter shallow slope from receded water line of brackish pool.

F.2 Locality and Habitat Data for F. V. Battle's 1969 Substrate Collections

F.2.1 Introduction

Substrate collection sites sampled by F. V. Battle (FVB) in 1969 from North Carolina, Virginia and West Virginia are described here in ascending chronological and numerical order. Except for sites A to E, the wording of the site descriptions is largely Battle's own. The "800" series samples from North Carolina are intercalated between collections 20B and 21, in chronological order. Groups of collections are identified by date and locality number. "Locality" is defined in the same sense as in the list of WIK collections (see "Locality and Habitat Descriptions for Knausenberger's Substrate Collections 1975 - 1978" on page). Locality numbers were assigned to identify related sites and with the intention of mapping sites based on locality(as was done in Figure 2).

Dashed lines separate sets of collections taken on different dates. Thus, dates of collection are normally given only at the top of each set of collections.

All FVB collections which produced Ceratopogonidae are included. Thus, this listing includes many sites omitted by Battle (1970) and Battle and Turner (1970a, 1970b, 1971, 1972), who included only those sites which yielded Culicoides. However, the present list duplicates the previous compilations in part, for the sake of completeness and convenience, and because certain corrections and additions could be made from original sources. Unproductive sites are merely mentioned, or omitted altogether.

See Appendix C, Table 49, for the itemization of collection numbers by political or geographical units, and Table 46 for the apportionment by physiographic province, river basin and biotic region. Available soil chemistry data are presented in Appendix G, Table 52. This data is computerized for analysis of Ceratopogonidae habitat types to be presented elsewhere.

F.2.2 Montgomery County Seasonal Study Areas: Sites A, B, C, D, and E.

Localities B-1 to B-3 (FVB Sites A-C): 17 May - 29 August, 1968 and 19 March - 13 November, 1969.

•Locality B-1.

FVB Site A: Va., Montgomery Co., at Luster's Gate, McPherson pond. Small farm pond in middle of pasture, surrounded on three sides by relatively steep slopes. Collections made in small "flood-plain" with water-filled hoof prints, droppings, and lush growth of short weeds (sic). Exposed to full sunlight. (Battle 1970:147). (1968: 11 collections; 1969: 64 collections).

•Locality B-2.

FVB Site B: Va., Montgomery Co., 7.5 mi. E of Luster's Gate on Va. 785, near headwaters of N. Fk. Roanoke R., Farmer Brown prop.; hog lot stream with shallow rocky bed and shallow sloped mud-flat margins. Rocks and mud along stream's edge supported a lush growth of green algae slime and spikerush. Polluted by manure, exposed to full sunlight (Battle, 1970: 147; Hair et al. 1966, fig. 4). (1968: 11 samples; 1969: 68 samples).

•Locality B-3.

FVB Site C: Va., Montgomery Co., near Luster's Gate. Powerline pond. Small farm pond slightly elevated above adjacent pasture, with steep shoreline; little manure pollution, with partial shade provided by large tree at pond's edge. (Battle 1970: 147) (1968: 11 samples; 1969: 58 samples).

•Locality B-4. 17 May - 29 August 1968 (11 samples).

FVB Site D: Va., Montgomery Co., 4.0 mi. E. of Luster's Gate. Weedy mud along small swift stream, adjacent road. This site not sampled in 1969. Site since eliminated by road construction. (Battle 1970: 148) (1968:11 samples)

•Locality B-5. 2 April - 16 July 1969 (16 samples, 8 visits).
FVB Site E: Va., Montgomery Co., Jefferson National Forest, Pandapas pond (also known as Pandapoulas or Polyscientific pond), on Poverty Cr. between Gap and Brush Mountains, adj. U.S. 460. Small lake in forested valley. Marshy area created by overflow of small stream before flowing into pond. Caramel-colored clayey mud covered by dense underbrush and tree canopy. (Battle 1970: 148).

F.2.3 Substrate Collections in Sequence of Sampling

Sites A, B, C and E collections are not separately itemized below. These are: *FVB Coll. Nos.* 1-3; 6-8; 1-16; 19-20; 43-50; 56-59; 62-65; 68-79; 115-117; 120-127; 137-140; 142-149; 168-192.

FVB Coll. Nos. 1-3: Sites A, B, C (See above).

•Locality B-6: 19 Mar. 1969 (also this locality --- *FVB Coll. Nos.* 17A,B)
FVB Coll. 4A & B: Va., Montgomery Co., VPI woods, Price Mtn.; mud from roadside spring beside abandoned road; road generally flooded; considerable snow present.

•Locality B-7: 20 Mar. 1969 (also this locality --- *FVB Coll. Nos.* 60, 61, 66, 67)

FVB Coll. 5: Va., Giles Co., near Goldbond, (Big Stony Creek), 12 miles N.W. of U.S. 460. Mossy mud at edge of stagnant stream flowing into Big Stony Creek. Elev. 3000 ft. (If mileage indication is accurate, then this location is near Interior, not Goldbond -- *FVB*). Compare station 36 of Roback 1976: 154-5).

FVB Coll. Nos. 6-8: Sites A, B, C. (which see).

•Locality B-8: 26 Mar. 1969
FVB Coll. 9A & B: Va., Montgomery Co.; mud along pool in abandoned road near Poverty Creek.

FVB Coll. Nos. 10-16: Sites A, B, C, and E.

•Locality B-1: 9 Apr. 1969 [as 4A,4B]
FVB Coll. 17B: Va., Montgomery Co., VPI woods, Price Mtn.; sample of mud from road-side spring. Snow melted. (*Coll. 17A* not productive).

FVB Coll. Nos. 18-20: Sites A, B, C.

FVB Coll. Nos. 800-811 ("800" series): 17 April 1969. North Carolina.

•Locality B-9: *Coll.* 800, 801. Not Productive (NP).

•Locality B-10: Coll. 802, 803.

FVB Coll. 802: N. C., NC 57 (not 62), 10 miles W. of Roxboro, Person Co. Wet, fluid mud in stagnant overflow, shaded area at shore of small pond, weeds around the perimeter.

FVB Coll. 803: Locality as Coll. 802. Reddish mud from edge of tiny creek, about 12 ft. back up in dense growth of small trees before creek empties into small pond mentioned in Coll. 802.

•Locality B-11

FVB Coll. 805: N.C., Granville Co., U.S. 158, Tar River. Sandy mud high in organic matter at water's edge.

•Locality B-12: Coll. 806, 807.

FVB Coll. 806: N.C., Vance Co., U.S. 158 east of Henderson. Wet sandy mud from edge of roadside stream.

FVB Coll. 807: (Locality as 806) Red mud in stagnant marsh adjacent to roadside stream sampled above.

•Locality B-13: 808, 809.

FVB Coll. 808: N.C., Warren Co., U.S. 158, 2 mi. E. of Norlina. Mud at edge of effluent into small lake, water very stagnant, much green algae present.

FVB Coll. 809: (Locality as Coll. 808). Mud from pothole subjected to periodic flooding from nearby stream.

•Locality B-14: 810-811.

FVB Coll. 810: N.C., Halifax Co., U.S. 158, 8 mi. W. of Roanoke Rapids. Mud consisting mostly of leaves at edge of stagnant backwash from creek; very shady due to dense growth of trees.

FVB Coll. 811: N.C., Halifax Co., U.S. 158, 8 mi. W. of Roanoke Rapids. Sandy muck beneath bridge at edge of standing pool connected to small creek.

FVB Coll. Nos. 21-39: 18 April 1969

•Locality B-15.

FVB Coll. 21: Va., York Co., U.S. 17, 3 mi. N. of Newport News city limits. Weedy brackish mud at edge of roadside stream.

•Locality B-16: Coll. 22,23.

FVB Coll. 22: Va., York Co., U.S. 17, adjacent to York High School. Damp mud in low-lying shaded area; substr. pH 7.0, 4.2% organic matter.

FVB Coll. 23: Location as Coll. 22. Sandy mud at edge of clear stream, shaded. Substr. pH 7.6, 1.5% organic matter.

•Locality B-17

FVB Coll. 24: Va., York Co., U.S. 17. Yorktown. Black substrate in peat bog, pH 7.2, 14.5% org. matter.

•Locality B-18

FVB Coll. 25: Va., York Co., U.S. 17. Black mud at the edge of clear, swift stream flowing out of bog; pH 4.0, 9.3% organic matter.

•Locality B-19: 26, 27.

FVB Coll. 26: Va., Gloucester Co., U.S. 17; 4 mi. S. of Gloucester. Dark gray sand at edge of brackish water in drainage ditch from swamp.

FVB Coll. 27: Va., Gloucester Co., U.S. 17. Slimy mud supporting algal growth, edge of standing water in little lagoon formed in small roadside stream.

•Locality B-20.

FVB Coll. 29: Va., Gloucester Co., Mobjack Bay off Va. 623. Black mud in tidal marsh.

•Locality B-21: Coll. 30,31.

FVB Coll. 30: Va., Middlesex Co., Piankatank River at Va. 3. Sand among *Spartina* reeds at river's edge, under tidal influence.

Coll. 31. NP.

•Locality B-22: Coll. 32, 33.

FVB Coll. 32: Va., Lancaster Co., Va., Rt. 3, Irvington. Sand in weedy(sic) growth, polluted roadside marsh in run-off from cattle pond (this collection made outside the pasture).

FVB Coll. 33.N.P.

•Locality B-23.

FVB Coll. 34: Va., Northumberland Co., U.S. 360, 1 mi. E. of Callao. Red mud from root system of emergent aquatic plants in marsh-like overflow at edge of small woodland pond.

•Locality B-24.

FVB Coll. 35: Va., Northumberland Co., Va. 202, at Westmoreland Co. line, Hampton Hall Creek, tributary Yeomico River. Mud at tidal creek's edge.

•Locality B-25.

FVB Coll. 36: Va., King George Co., Va. 3, 2 mi. E. of King George. Red mud in marsh adjacent to muddy lake; water flowing into lake from marsh very slowly.

•Locality B-26.

FVB Coll. 37: Va., Stafford Co., Muddy Creek at Va. 3, 10 miles W. of King George. Mud at edge of swift creek (Rappahannock River Basin).

•Locality B-27: 38, 39.

FVB Coll. 38: Va., Spotsylvania Co., Orange Co. line, Va. 3, Wilderness Run. Mud supporting slight growth of algae in standing water in ditch emptying into small clear branch flowing into Wilderness Run.

FVB Coll. 39: Location as Coll. 38. Reddish mud at edge of clear branch flowing into Wilderness Run. Substr. pH 5.8.

•Locality B-28A: 40,41.

FVB Coll. 40: 19 Apr. 1969. Va., Albemarle Co., Ivy Creek Branch on U.S. 250, 6 mi. W. of Charlottesville, Va. Dark mud at edge of swift clear stream. Substr. pH 7.1.

FVB Coll. 41. NP.

•Locality B-28B.

FVB Coll. 42: 19 Apr. 1969. Va., Augusta Co., Christian Creek at U.S. 340, 4 mi. W. of Stuart's Draft, Va. Thick mud at creek's edge, 100 ft. downstream from horse lot; substr. pH 7.8.

FVB Coll. Nos. 43-50: Sites A-E.

FVB Coll. Nos. 51-55: 3 May 1969.

•Locality B-29.

FVB Coll. 51: Va., City of Chesapeake, Northwest River at Va. 629. Thick black mud in root system of tree extending into river (very slow, black water in river). Substr. pH 5.2.

•Locality B-30

FVB Coll. 52: N.C., Camden Co., N.C. 343, South Mills, Mud-packed decaying leaves at edge of roadside stream. Substr. pH 6.0.

•Locality B-31.

FVB Coll. 53: N.C., Camden Co., N.C. 343, 2 mi. N.W. of Camden. Mud from small bog at edge of small, shaded lagoon formed by slow, black water stream. Substr. pH 5.5.

•Locality B-32.

FVB Coll. 54: N.C., Camden Co., 2 1/2 mi. E. of Camden on U.S. 158. Peat-like mud in root system of small shrubs and weeds at edge of ditch overflowing with black, stagnant water. Substr. pH 5.1.

•Locality B-33.

FVB Coll. 55: Va., City of Virginia Beach. Back Bay (no precise location given). Black mud from weedy growth in tidal marsh. Substr. pH 6.0. Site of many *Dasyhelea cincta* gr. specimens, incl. at least one new species nr. *D. maculata*.

FVB Coll. Nos. 56-59: Sites A-E.

•Locality B-7.

Coll. Nos. 60 & 61: 8 May 1969 [same locality as Coll. 5, 61, 66, 67].

FVB Coll. 60: Va., Giles Co., near Goldbond. Black mossy ooze from relictual bog in effluent from small, clear stream flowing into Big Stony Creek. Substr. pH 5.0.

FVB Coll. 61: Locality as Coll. 60, etc. Mossy mud at edge stagnant stream flowing into Big Stony Creek. Substr. pH 5.6.

FVB Coll. 62-65: Sites A-E.

- Locality B-7. Coll. Nos. 66,67: 16 May 1969 [see also 5, 60, 61]
FVB Coll. 66: Va., Giles Co., Goldbond, 12 mi. N. of U.S. 460. Black mossy ooze in bog, exposed to flow of small, clear stream running into Big Stony Creek; exact site as Coll. 60.
FVB Coll. 67: (same locality as Coll. 66) 10 ft. upstream from Coll. 66; black moss-covered mud in bog exposed to periodic flooding from adjacent small stream but beyond normal water level.
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FVB Coll. Nos. 68-79: Sites A-E.

Coll. Nos. 80-98: 6 June 1969.

- Locality B-35: Coll. 80-83.
FVB Coll. 80: Va., Henry Co., U.S. 220, 5 mi. S. of Martinsville, at Narrowbone Creek. Sandy mud at creek's edge, pH 6.3.
FVB Coll. 81-83. Not productive.
- Locality B-36.
FVB Coll. 84: N.C., Rockingham Co., U.S. 158, 9 mi. E. of Reidsville. Decaying leaves and black mud in lowlying, shaded area adjacent to stream. Substr. pH 4.8.
- Locality B-37.
FVB Coll. 85: N.C., Caswell Co., U.S. 58, 5 mi. E. of Yanceyville. Red mud in marshy growth at edge of small pond. Substr. pH 5.6.
- Locality B-38.
FVB Coll. 86: N.C., Caswell Co., U.S. 158, 7 mi. E. of Yanceyville. Black mud at edge of lagoon beneath bridge and adjacent to small stream. Substr. pH 6.5.
- Locality B-39.
FVB Coll. 87: N.C., Caswell Co., U.S. 158, 9 mi. E. of Yanceyville at Hyco Creek. Dark sandy mud alongside stream (Hyco Creek) in heavily shaded, broad gully.
- Locality B-40.
FVB Coll. 88: N.C., Person Co., U.S. 158, 7 mi. W. of Roxboro at South Hyco Creek. Dark, thick mud at creek's edge.
- Locality B-41.
FVB Coll. 89: N.C., Granville Co., U.S. 158, 12 mi. W. of Oxford. Thick mud beneath roots of tree overhanging small stream.
- Locality B-42.
FVB Coll. 90: N.C., Granville Co., U.S. 158, 9 mi. W. Oxford at Berea. Heavily polluted mud from edge of hog pond.

•Locality B-43: 91,92.

FVB Coll. 91: N.C., Warren Co., Va. state line, Smith Creek at U.S. 1. Sandy mud beneath bridge, creek's edge.

FVB Coll. 92: N.C., Warren Co., at Va. state line, Smith Creek off U.S. 1. Black substrate in bog adjacent to stream.

•Locality B-44.

FVB Coll. 93: Va., Mecklenburg Co., Lake Gaston, Steel Bridge Landing. Very thick, Black mud in little bog beneath U.S. 1 bridge.

•Locality B-45.

FVB Coll. 94: Va., Mecklenburg Co., Miles Creek at U.S. 1. Sandy mud on tiny island (mud bar) in stream.

•Locality B-46: 95,96.

FVB Coll. 95: Va., Mecklenburg Co., Va. 47, 4 mi. W. of Chase City. Mud beneath bridge at stream edge (same place as Coll. 96 but taken outside fenced area).

FVB Coll. 96: Locality as Coll. 96. Heavily polluted mud at cattle crossing, exposed to cattle traffic.

•Locality B-47: Coll. 97,98.

FVB Coll. 97: Va., Halifax Co., U.S. 58 at Lawson Creek, South Boston. Yellowish mud and sand near edge of Lawson Creek in shaded area accessible to cattle.

FVB Coll. 98. Not productive.

Coll. Nos. 99-103: 7 July 1969.

•Locality B-48

FVB Coll. 99: Va., Pittsylvania Co., Va. 40, 4 mi. E. of town of Mount Airy. Red mud interspersed with moss in tall, reedy growth at edge of stagnant pond.

•Locality B-49.

FVB Coll. 100: Va., Pittsylvania Co., Va. 40, 3 1/2 mi. E. of Mt. Airy at Allen Creek. Polluted red mud at edge of creek at cattle crossing.

•Locality B-50: 101,102.

FVB Coll. 101: Va., Pittsylvania Co., Va. 40, 1 mi. E. of Mt. Airy, Dry Branch. Manure-polluted sand at edge of Dry Branch inside pasture.

•Locality B-50.

FVB Coll. 102: Va., Pittsylvania Co., 1 mi. E. of Mt. Airy on Va. 40, at Dry Branch. Thick, drying mud beneath bridge, just downstream and outside of pasture mentioned in Coll. #101.

•Locality B-51.

FVB Coll. 103: Va., Pittsylvania Co., 4 mi. E. of Gretna, on Va. 40, Georges Creek. Manure-polluted sand at creek's edge.

Coll. Nos. 104-114: 9 June 1969.

•Locality B-54 : Coll. 104,105.

FVB Coll. 104: W. Va., Monroe Co., Waiteville. Mud among weeds and rocks at edge of swift, clear stream (Pott's Creek) 50 ft. downstream from pasture. Substr. pH 5.3.

•Locality B-55.

FVB Coll. 106: W. Va., Monroe Co., 3 mi. N. of Waiteville. Leaf litter in channel of small mountain stream (Potts Cr.) on slope of mountain. Substr. pH 6.4. Site of *Monohalea macfieii*, *Isohelea* n. sp. 2, *Culicoides piliferus*, *C. travisi*;

NOTE: *Palpomyia walteri* Grogan and Wirth paratype from here.

•Locality B-56.

FVB Coll. 107: W. Va., Monroe Co., 2 mi. S. of Gap Mills. Mud from edge of farm pond. Substr. pH 6.9.

•Locality B-55.

FVB Coll. 108: W. Va., Monroe Co., 5 mi. W. of Gap Mills. Farm pond mud, pH 8.0.

•Locality B-56.

FVB Coll. 110: W. Va., Monroe Co., 1 mi. SE. of Pickaway. Mud from edge of farm pond, pH 7.4.

•Locality B-57.

FVB Coll. 112: W. Va., Monroe Co., 5 mi. W. of Sinks Grove on W. Va. #3. Heavily polluted sandy mud, edge of Broad Run. Substr. pH 8.0.

•Locality B-58.

FVB Coll. 113: W. Va., Greenbrier Co., W. Va. 3; Alderson, at western edge of city limits. Stagnant sandy mud at edge of swift, clear stream in deep wooded ravine.

•Locality B-59.

FVB Coll. 114: W. Va., Summers Co., W. Va. 20, 11 mi. S. of Hinton. Leaf litter and neighboring fine gravel and sand at edge of swift stream in deep wooded ravine. Substr. pH 7.6. Site of *Culicoides spinosus* and *Palpomyia hastata*.

FVB Coll. Nos. 115-117: Sites A, B, C.

•Locality B-60: Coll. Nos. 118-119; 12 June 1969.

FVB Coll. 118: Not productive.

FVB Coll. 119: Va., Montgomery Co., VPI campus. Dark mud at Duck Pond edge. Coll. G. Tanner.

FVB Coll. Nos. 120-127: Sites A, B, C and E.

Coll. Nos. 128-136: 27 June 1969. Alabama (east-central)

•Locality B-61.

FVB Coll. 132: Ala., Talladega Co., McElderry, at junction of Co. Rts. 96 and 105. Thick sandy mud beneath bridge; mud at stream's edge completely shaded by bridge; apparently not subject to periodic flooding from stream. Substr. pH 7.0. Site of Dasyhelea sp. 7 (mutabilis gr.), D. brevicosta (significant range extension).

•Locality B-62: 133, 134.

FVB Coll. 133: Ala., Talladega Co., Road 96, 3 mi. E. of McElderry. Dark, sandy mud at edge of stream in heavily shaded glen. Substr. pH 4.6.
FVB Coll. 134: Ala., Talladega Co., Road 96, 3 mi. E. of McElderry. Decaying muck composed largely of leaves, edge of stream in heavily shaded glen.

FVB Coll. Nos. 135-140: Sites A, B, C, and E.

•Locality B-63: 7 July 1969.

FVB Coll. 141: Va., southwestern Giles Co., 5 mi. E. of Va. Rt. 606 on Forest Serv. Rt. 201 along Dismal Creek. Sandy mud at stream edge in dark wooded glen. Elev. ca. 2500 ft. (760 cm.) between Brushy Mtn. and Flattop Mtn.

FVB Coll. Nos. 142-149: Sites A, B, C, and E.

•Locality B-64: Coll. Nos. 150-155, 17 July 1969.

FVB Coll. 150: Va., Giles Co., Mountain Lake, Univ. of Virginia Biological Station; elev. 3800 ft. (1158 m), 4 mi. N. of Mtn. Lake. Red ooze from bog.

FVB Coll. 151. NP.

FVB Coll. 152: Location as Coll. 150. Black substrate from bog beside stream in heavily wooded area.

FVB Coll. Nos. 153-155. NP.

•Locality B-65: 28 July 1969.

FVB Coll. Nos. 156, 157: New Jersey sites: NP.

FVB Coll. Nos. 158-192: Sites A, B, C. (end)

Appendix G. SUBSTRATE AND AQUATIC CHEMISTRY DATA

G.1 Substrate Chemistry Data for Knausenberger's 1975-78 Collections.

Appendix, Table 51. Substrate chemistry data for collections taken by W.I. Knausenberger from 1975 to 1978.

Includes only those sites which consisted chiefly of soil; plant-material substrates were not tested. Collection numbers with "-1", or "-2" attached represent replicated samples. Organic matter content is represented by O.M.

WIK Coll. No.	pH	CaO	MgO	P2O5	K2O	Sol. Salts	O.M. %	NO3 mg/l
12	7.1	1650.0	199.0	12.0	40.0	397.0	1.7	5.0
17	7.4	1650.0	199.0	3.0	64.0	499.0	1.4	34.5
18A	6.8	193.0	30.0	138.0	21.0	410.0	2.2	11.3
18B	5.8	1238.0	144.0	138.0	54.0	1126.0	9.3	45.0
20	7.4	1650.0	199.0	3.0	89.0	666.0	6.8	9.0
21	4.6	1142.0	138.0	21.0	144.0	922.0	15.0	.
23-1	5.9	1321.0	131.0	28.0	56.0	410.0	5.3	5.0
23-2	5.1	977.0	111.0	21.0	47.0	563.0	6.2	30.0
24	4.5	262.0	48.0	12.0	27.0	248.0	3.3	16.0
26	4.7	1650.0	199.0	102.0	189.0	282.0	15.0	110.0
28	5.6	1650.0	136.0	3.0	81.0	358.0	10.0	8.3
29	5.3	633.0	58.0	21.0	22.0	141.0	2.4	5.0
31-1	4.5	743.0	140.0	55.0	75.0	410.0	15.0	21.0
30-2	3.9	165.0	60.0	12.0	58.0	704.0	1.0	5.0
31	5.4	1650.0	143.0	14.0	95.0	307.0	15.0	7.0
32	4.4	908.0	81.0	12.0	93.0	598.0	15.0	27.5
34	5.6	537.0	90.0	55.0	109.0	141.0	5.9	9.8
36	5.5	1114.0	106.0	37.0	140.0	397.0	13.3	30.0
37	5.9	1362.0	199.0	37.0	54.0	717.0	15.0	5.8
38	4.9	867.0	90.0	37.0	40.0	294.0	13.3	5.0
39	5.7	650.0	109.0	5.0	34.0	576.0	3.5	42.5
41A	7.9	1650.0	199.0	12.0	15.0	179.0	0.6	17.0
42	5.9	1004.0	199.0	12.0	106.0	896.0	6.5	5.0
43	7.2	1650.0	199.0	14.0	34.0	358.0	1.5	16.0
44	5.5	344.0	131.0	28.0	40.0	614.0	3.4	9.0
45-1	6.9	468.0	111.0	8.0	22.0	729.0	0.4	14.0
45-2	7.4	358.0	96.0	21.0	24.0	154.0	0.3	5.0
47	6.4	1650.0	199.0	76.0	189.0	1856.0	15.0	22.0
48-1	7.3	1650.0	199.0	17.0	123.0	896.0	4.0	250.0
48-2	6.8	1059.0	199.0	8.0	47.0	192.0	1.4	8.0
49	5.5	1650.0	153.0	5.0	54.0	486.0	8.5	5.3
50	7.1	1650.0	199.0	8.0	32.0	192.0	1.8	7.0
51	5.6	1650.0	111.0	21.0	62.0	384.0	6.8	13.5
52	5.1	275.0	60.0	12.0	65.0	102.0	3.6	5.0
53	7.8	1444.0	199.0	21.0	24.0	410.0	1.0	44.5
54	4.4	674.0	118.0	21.0	64.0	256.0	15.0	5.0

Appendix, Table 51. (continued)

WIK Coll. No.	pH	CaO	MgO	P2O5	K2O	Sol. Salts	O.M. %	NO3 mg/l

		mg/l						
55	5.5	1650.0	199.0	12.0	56.0	230.0	10.1	31.3
56	5.4	1555.0	153.0	5.0	139.0	487.0	7.4	.
57A-1	7.2	1650.0	138.0	37.0	73.0	218.0	13.3	19.5
57B-2	7.0	1650.0	138.0	44.0	36.0	128.0	3.2	9.8
59	7.2	1114.0	52.0	12.0	82.0	179.0	0.5	5.8
60	4.8	977.0	95.0	59.0	105.0	538.0	15.0	37.5
61	6.5	1650.0	138.0	17.0	52.0	286.0	4.6	23.0
63-1	6.9	1650.0	68.0	28.0	28.0	346.0	2.0	22.5
63-2	7.4	1650.0	199.0	5.0	48.0	307.0	3.0	7.5
64	7.2	1650.0	181.0	12.0	30.0	294.0	3.5	5.0
65B	7.1	1650.0	199.0	12.0	7.0	1856.0	10.1	82.5
67	7.2	1650.0	144.0	11.0	106.0	870.0	2.0	85.0
68	7.2	1650.0	105.0	8.0	30.0	819.0	4.0	15.5
69A	7.8	1650.0	199.0	4.0	99.0	3072.0	4.2	24.0
69B	7.0	1650.0	199.0	24.0	97.0	1152.0	5.9	65.0
69C	7.9	1650.0	199.0	59.0	93.0	1203.0	6.5	50.0
70	7.5	1650.0	199.0	1.0	64.0	858.0	3.0	6.0
71	7.4	1650.0	199.0	44.0	52.0	384.0	1.6	5.0
73	7.3	1650.0	199.0	5.0	58.0	474.0	3.4	5.0
74	7.4	1142.0	199.0	3.0	47.0	243.0	0.8	5.0
76-1	7.2	1650.0	199.0	3.0	36.0	4736.0	6.8	160.0
76-2	7.4	1650.0	199.0	18.0	61.0	5440.0	7.1	221.0
77	7.3	1650.0	199.0	3.0	24.0	858.0	3.2	14.5
78	6.9	1650.0	199.0	8.0	30.0	12800.0	12.5	32.5
79	7.3	1650.0	169.0	5.0	32.0	12800.0	4.8	90.0
81-1	5.4	1389.0	199.0	8.0	133.0	243.0	11.7	14.5
81-2	5.0	784.0	143.0	37.0	92.0	474.0	11.7	50.0
82	4.2	647.0	121.0	24.0	70.0	410.0	15.0	5.0
83	7.0	1650.0	199.0	24.0	79.0	512.0	4.8	42.0
84	7.2	1650.0	199.0	40.0	93.0	704.0	4.6	36.3
85	6.1	96.0	12.0	8.0	15.0	10.0	0.8	5.0
86	7.2	1650.0	125.0	5.0	51.0	640.0	3.0	14.0
87A	6.2	1486.0	199.0	28.0	112.0	358.0	5.0	48.8
87B	7.3	1650.0	136.0	5.0	47.0	1050.0	5.0	55.0
88	7.6	1651.0	135.0	30.0	38.0	614.0	3.1	23.0
89	5.9	1679.0	79.0	41.0	41.0	397.0	.	22.0
90B-1	4.7	908.0	154.0	21.0	32.0	320.0	14.1	7.8
90B-2	4.7	413.0	52.0	47.0	56.0	358.0	4.8	.
91	7.3	1650.0	199.0	5.0	105.0	1664.0	5.9	60.0
92A	5.3	1527.0	199.0	21.0	15.0	1536.0	11.7	.
92B	5.8	1650.0	199.0	30.0	48.0	1984.0	11.7	62.5
93	5.6	1650.0	199.0	28.0	147.0	947.0	7.4	27.5

Appendix, Table 51. (continued)

WIK Coll. No.	pH	CaO	MgO	P2O5	K2O	Sol. Salts	O.M. %	NO3 mg/l
		----- mg/l						
94B	5.9	1650.0	199.0	81.0	166.0	602.0	10.9	47.5
94D	7.9	1650.0	199.0	137.0	188.0	2368.0	14.5	18.0
94E	6.4	1650.0	199.0	102.0	177.0	807.0	10.1	6.0
95-1	7.5	1650.0	32.0	62.0	38.0	128.0	0.9	17.5
95-2	7.5	1650.0	199.0	1.0	70.0	1011.0	1.8	52.5
96-1	5.7	1650.0	199.0	102.0	99.0	819.0	8.5	67.5
96-2	7.5	1650.0	199.0	3.0	93.0	525.0	1.3	23.0
97	7.0	1650.0	199.0	3.0	40.0	1318.0	12.5	5.0
99	7.1	1650.0	199.0	14.0	34.0	1114.0	1.5	17.5
100A	7.3	1650.0	199.0	55.0	44.0	832.0	1.8	16.0
100B	7.1	1650.0	199.0	12.0	38.0	371.0	1.7	13.0
101	7.0	1650.0	199.0	12.0	95.0	896.0	2.9	18.5
102	6.2	1650.0	199.0	28.0	189.0	640.0	15.0	.
103	7.2	1650.0	199.0	138.0	189.0	1216.0	4.8	93.8
104	6.7	1650.0	199.0	76.0	189.0	1280.0	15.0	22.0
105	7.0	1650.0	199.0	55.0	56.0	1075.0	13.3	27.0
106	6.6	1650.0	199.0	62.0	157.0	.	15.0	22.0
107	8.0	1650.0	186.0	102.0	189.0	3200.0	15.0	.
108	8.6	1403.0	142.0	62.0	64.0	666.0	2.9	5.0
109	4.2	426.0	192.0	24.0	108.0	2816.0	13.3	16.8
110	4.4	399.0	88.0	24.0	102.0	806.0	13.3	16.8
113A	6.6	1650.0	199.0	24.0	109.0	960.0	5.6	5.3
113B	7.1	1650.0	199.0	8.0	61.0	550.0	2.5	5.0
114	5.4	1637.0	199.0	24.0	44.0	3968.0	7.8	17.3
115	4.8	1403.0	199.0	36.0	11.0	5622.0	5.9	36.3
116	5.2	1650.0	199.0	58.0	31.0	6080.0	6.5	7.5
117	6.6	1650.0	199.0	43.0	129.0	1344.0	7.8	8.0
119	4.5	1059.0	174.0	33.0	66.0	806.0	13.3	13.8
120	5.5	522.0	147.5	127.0	58.0	371.0	1.7	5.0
123	4.9	536.0	69.5	11.0	33.0	333.0	15.0	5.0
124	4.8	1306.0	161.0	20.0	82.0	768.0	7.4	6.0
125	3.8	729.0	117.5	27.0	120.0	768.0	15.0	5.3
126	5.2	1650.0	199.0	137.5	177.0	1152.0	9.3	165.0
127	6.9	1650.0	79.0	86.0	52.0	563.0	2.4	14.5
128	4.1	137.0	28.0	11.0	37.0	256.0	0.2	5.0
130	4.1	1279.0	199.0	43.0	117.0	3712.0	8.5	8.5
132	5.5	41.0	13.0	11.0	27.0	102.0	0.1	5.0
133	5.2	55.0	13.0	17.0	33.0	179.0	0.1	5.0
134	4.9	921.0	199.0	36.0	36.0	46080.0	12.5	57.5
135	6.6	206.0	199.0	55.0	124.0	5760.0	0.1	33.3
137	5.2	660.0	199.0	33.0	26.0	9600.0	3.4	22.8
138	5.2	632.0	199.0	24.0	58.0	5440.0	7.8	13.3
140	6.1	1650.0	199.0	11.0	44.0	384.0	6.5	5.0
141	5.4	894.0	131.0	71.0	95.0	704.0	2.7	5.0

Appendix, Table 51. (continued)

WIK Coll. No.	pH	CaO	MgO	P2O5	K2O	Sol. Salts	O.M. %	NO3 mg/l

						mg/l		
142	4.6	1155.0	185.0	11.0	82.0	486.0	15.0	11.5
144	6.8	1650.0	199.0	20.0	126.0	1792.0	2.1	22.0
145A	4.8	1059.0	109.0	14.0	37.0	640.0	7.4	5.0
146	4.6	990.0	117.0	4.0	170.0	640.0	15.0	5.0
147	4.9	701.0	69.0	11.0	30.0	256.0	4.6	5.0
148	3.9	550.0	91.0	8.0	58.0	346.0	15.0	8.0
149	5.4	1650.0	199.0	14.0	88.0	486.0	15.0	65.0
152	5.7	1650.0	152.0	17.0	54.0	563.0	14.1	7.5
153	5.4	1650.0	195.0	17.0	76.0	742.0	14.1	30.8
154	5.1	729.0	116.0	3.6	48.0	358.0	6.8	5.0
156	4.3	729.0	114.0	8.0	66.0	499.0	13.3	5.0
158	6.6	1650.0	199.0	2.5	41.0	678.0	1.3	5.3
159	6.7	1650.0	199.0	4.5	33.0	1472.0	13.3	.
160-1	6.4	1650.0	199.0	138.0	189.0	1216.0	4.8	93.8
160-2	6.7	1650.0	199.0	137.0	188.0	1600.0	4.9	19.5
161A	7.2	1650.0	199.0	55.0	65.0	1024.0	4.4	18.0
161B	7.7	1650.0	199.0	8.0	78.0	6400.0	6.2	48.0
161C	7.2	1650.0	199.0	59.0	32.0	896.0	5.0	4.0
162	7.1	1650.0	199.0	8.0	54.0	2176.0	3.3	11.8
163	5.7	1650.0	188.0	11.0	8.0	1190.0	2.3	5.0
164	7.2	1650.0	199.0	4.0	31.0	870.0	2.1	92.5
165	7.1	1650.0	199.0	11.0	188.0	2368.0	3.4	232.5
166A	5.9	1650.0	199.0	62.0	188.0	1280.0	7.4	43.8
166B	5.8	1650.0	199.0	86.0	124.0	486.0	10.9	80.0
167L	6.4	1650.0	199.0	27.0	15.0	1152.0	5.6	80.0
167U	7.1	1650.0	164.0	4.5	41.0	870.0	1.4	6.8
168L	7.2	1650.0	199.0	2.0	50.0	1344.0	3.1	92.5
169	5.9	1403.0	169.0	20.0	33.0	320.0	4.0	24.5
171	3.9	632.0	199.0	11.0	47.0	7360.0	15.0	.
174	5.2	990.0	199.0	43.0	84.0	8000.0	3.4	37.5
175A	5.6	110.0	18.0	20.0	12.0	209.0	0.2	6.8
175B	4.6	1004.0	154.0	40.0	74.0	1638.0	5.3	6.8
176	4.9	1155.0	116.0	27.0	76.0	730.0	11.7	6.0
177A	4.8	1141.0	161.0	17.0	91.0	1242.0	5.0	11.0
177B	5.0	1114.0	199.0	24.0	82.0	730.0	11.7	6.0
177C	4.9	1637.0	179.0	27.0	82.0	922.0	10.1	.
178	4.2	866.0	129.0	27.0	91.0	1920.0	12.5	.
179	4.3	866.0	124.0	27.0	172.0	1395.0	13.3	.
180	4.3	646.0	76.0	17.0	58.0	461.0	14.1	37.5
181	4.0	399.0	53.0	20.0	43.0	525.0	10.1	40.0
182	4.8	192.0	26.0	11.0	21.0	154.0	0.8	9.8
183-1	4.1	179.0	66.0	14.0	47.0	678.0	1.4	38.8
183-2	4.0	179.0	53.0	17.0	36.0	666.0	1.5	36.3

Appendix, Table 51. (continued)

WIK Coll. No.	pH	CaO	MgO	P2O5	K2O	Sol. Salts	O.M. %	NO3 mg/l

mg/l								
186	4.4	1650.0	174.0	24.0	54.0	896.0	15.0	6.8
187	4.0	619.0	69.5	17.0	40.0	896.0	10.1	72.5
188	4.1	1637.0	146.0	8.0	52.0	1216.0	15.0	107.5
190	4.8	275.0	199.0	24.0	115.0	1664.0	1.8	45.0
191	4.8	137.0	51.0	11.0	30.0	461.0	0.3	14.8
192	4.2	44.0	199.0	40.0	68.0	2048.0	5.6	43.8
194	7.2	1650.0	156.0	5.0	93.0	806.0	3.2	7.5
195	4.9	1159.0	169.0	33.5	78.0	1242.0	14.1	.
196	5.1	275.0	103.0	58.5	30.0	282.0	1.5	30.8
200	6.2	206.0	46.5	17.0	72.0	333.0	0.7	29.5
201A-1	6.2	1650.0	199.0	12.0	64.0	819.0	14.5	97.5
201A-2	5.2	1650.0	199.0	33.0	58.0	1510.0	15.0	.
20C	5.1	1609.0	199.0	17.0	123.0	870.0	4.9	107.5
203	6.8	578.0	144.0	97.0	22.0	307.0	4.2	5.0
204	6.2	894.0	199.0	96.0	65.0	5120.0	7.1	180.0
206-1	6.5	881.0	98.0	14.0	22.0	807.0	0.3	26.3
206-2	5.9	963.0	199.0	40.0	96.0	1638.0	1.5	66.3
207A	5.9	756.0	199.0	27.0	172.0	2944.0	3.8	155.0
207C	5.2	1650.0	199.0	24.0	106.0	6400.0	.	.
208	4.7	96.0	11.0	17.0	20.0	282.0	0.3	48.8
210	6.0	296.0	198.0	17.0	127.0	7855.0	1.8	56.1
211	5.0	756.0	136.0	24.0	120.0	934.0	13.3	48.8
214B	5.9	646.0	131.0	50.0	55.0	166.0	3.4	5.0
216	6.4	101.0	6.0	15.0	9.0	.	0.2	5.0
222A	4.8	319.0	36.0	28.0	15.0	128.0	5.0	5.0
222B	4.9	470.0	59.0	30.0	35.0	179.0	6.5	5.0
224	4.3	268.0	34.0	11.0	28.0	397.0	1.9	52.5
230	4.0	587.0	107.0	93.0	50.0	499.0	15.0	5.8
231	5.6	1527.0	87.0	17.0	84.0	230.0	15.0	5.0
234	5.9	403.0	50.0	34.0	133.0	141.0	3.6	.
236	10.9	5.0
237	6.2	487.0	77.0	74.0	176.0	307.0	13.3	16.3
238	7.6	1679.0	199.0	25.0	65.0	462.0	5.6	13.5
239	7.8	1679.0	199.0	4.0	33.0	602.0	2.6	5.0
240B	7.3	1679.0	199.0	10.0	117.0	2112.0	14.1	140.0
241A	8.3	1679.0	191.0	5.5	18.0	209.0	0.9	5.0
243	7.5	1393.0	199.0	14.0	35.0	691.0	1.5	5.0
245	7.7	1645.0	199.0	12.0	60.0	576.0	2.0	10.0
253	8.0	1259.0	193.0	15.0	26.0	243.0	1.3	9.3
254	6.7	1007.0	187.0	17.0	58.0	448.0	.	.
257B	7.5	1679.0	87.0	71.0	41.0	102.0	1.5	5.3
257C	7.8	1679.0	107.0	23.0	79.0	192.0	.	5.3

Appendix, Table 51. (continued)

WIK Coll. No.	pH	CaO	MgO	P2O5	K2O	Sol. Salts	O.M. %	NO3 mg/l
		----- mg/l						
261C	6.8	638.0	105.0	7.0	31.0	209.0	2.4	5.0
262	6.6	671.5	65.0	30.0	84.0	333.0	5.0	5.5
263C	7.5	1679.0	63.0	21.0	30.0	462.0	2.2	47.5
268C	7.0	738.0	99.0	14.0	123.0	141.0	5.9	8.0
272B	5.1	806.0	55.0	12.0	30.0	320.0	5.0	37.5
282	7.7	201.0	32.0	3.0	11.0	141.0	0.3	5.0
285A	6.5	822.0	73.0	25.0	77.0	307.0	5.6	5.0
285B	6.7	1679.0	137.0	49.0	60.0	410.0	6.8	15.0
292	4.8	1142.0	183.0	57.0	176.0	1638.0	6.5	6.5
294	4.7	1645.0	187.0	37.0	90.0	1242.0	14.1	115.0
297	7.8	1645.0	199.0	54.0	188.0	10240.0	1.6	120.0
298	7.7	1679.0	199.0	41.0	188.0	10240.0	1.3	140.0
301	6.9	302.0	199.0	40.0	180.0	17920.0	2.7	155.0
302	6.2	1679.0	199.0	57.0	45.0	1984.0	13.3	.
306	5.5	806.0	199.0	46.0	188.0	17920.0	.	.
307	6.6	1595.0	174.0	125.0	188.0	10240.0	.	.
309	6.3	806.0	139.0	32.0	73.0	1114.0	14.1	.
310	6.5	722.0	199.0	36.0	188.0	11520.0	13.3	.
312A	6.0	1376.0	91.0	25.0	135.0	2150.0	.	.
313A	6.3	856.0	79.0	14.0	58.0	858.0	13.3	.
314A	7.7	503.0	129.0	16.0	24.0	333.0	1.3	5.5
315	6.9	688.0	199.0	13.0	30.0	499.0	4.2	6.5
316E	6.3	621.0	63.0	33.0	67.0	422.0	3.5	18.5
319A	8.0	1679.0	199.0	2.0	82.0	704.0	2.6	33.8
319E	7.0	990.0	199.0	8.5	79.0	1472.0	.	.
320B	6.4	520.0	111.0	4.5	58.0	742.0	7.1	.
322A	7.7	1679.0	199.0	2.0	52.0	435.0	5.6	47.5
325A	5.3	822.0	71.5	5.5	67.0	462.0	10.1	23.5
325B	5.5	1192.0	93.5	10.0	50.0	512.0	5.9	37.5
327B	5.4	1292.0	111.0	15.0	37.0	499.0	6.8	80.0
329A	5.4	1611.0	115.0	20.0	77.0	870.0	7.1	55.0
329B	5.7	1679.0	103.0	13.0	45.0	870.0	7.4	52.5
330B	7.3	1679.0	199.0	29.0	139.0	1088.0	13.3	.
331A	6.2	268.0	50.0	3.5	35.0	397.0	1.1	8.8
332A	4.8	856.0	199.0	16.0	143.0	653.0	2.7	23.5
332B	7.3	302.0	75.5	35.0	18.0	128.0	0.2	6.3
333A	6.9	1326.0	199.0	8.0	67.0	934.0	2.3	40.0
333B	5.4	1595.0	127.0	7.0	71.0	1408.0	8.5	82.5
345	7.8	1679.0	199.0	10.0	178.0	730.0	4.0	18.5
347	5.5	906.0	199.0	23.0	119.0	6080.0	14.1	9.5
351	7.1	1645.0	199.0	13.0	106.0	934.0	4.4	150.0

Appendix, Table 51. (continued)

WIK Coll. No.	pH	CaO	MgO	P2O5	K2O	Sol. Salts	O.M. %	N03 mg/l
		----- mg/l						
353	4.0	1511.0	199.0	25.0	188.0	7680.0	7.8	67.5
354	5.7	655.0	199.0	13.0	7.5	6080.0	10.1	5.3
360A	6.2	1041.0	65.0	5.0	30.0	435.0	3.4	20.0
361A	5.9	1679.0	191.0	14.0	50.0	806.0	5.9	75.0
361B	5.8	1679.0	199.0	5.0	48.0	1152.0	10.1	225.0
362	7.2	1679.0	199.0	3.0	188.0	1472.0	9.3	165.0
363	7.2	1679.0	199.0	8.0	113.0	1536.0	2.9	225.0
364	7.4	1679.0	199.0	2.0	65.0	1510.0	8.5	92.5
369	6.2	1041.0	199.0	7.0	60.0	371.0	3.4	31.3
402	4.7	755.5	127.5	12.0	46.0	422.0	15.0	5.8

G.2 Substrate Chemistry Data for F. V. Battle's Collections

Appendix, Table 52. Substrate Chemistry Data for samples taken by F. V. Battle in Virginia, North Carolina, and West Virginia for a *Culicoides* survey conducted during 1969. I evaluated the Ceratopogonidae from those samples for this study, and compiled the substrate data to permit analysis and for presentation here.

FVB Coll. No.	pH	CaO	MgO	P2O5	K2O	O.M. %
		----- mg/l				
1	7.9	1525.5	181.5	34.5	128.5	4.8
2	8.1	1680.0	199.0	53.0	83.0	3.1
3	7.5	1680.0	199.0	5.0	118.0	5.6
4	6.1	1680.0	199.0	28.0	41.0	4.2
6	8.0	1680.0	199.0	2.0	87.0	3.6
7	7.9	1680.0	199.0	7.0	117.0	3.3
8	7.8	1680.0	199.0	1.0	101.0	4.9
9	5.6	1680.0	199.0	9.0	76.0	2.5
10	7.8	1680.0	199.0	5.0	183.0	4.2
11	7.8	1680.0	199.0	5.0	45.0	3.6
12	7.9	1680.0	199.0	5.0	120.0	4.8
13	5.9	840.0	163.5	11.0	38.0	3.6
14	7.6	1680.0	199.0	0.5	52.0	2.9
15	7.5	1680.0	199.0	5.0	36.0	3.2
16	7.5	1680.0	199.0	0.5	99.0	5.0
17	6.0	891.0	199.0	17.0	38.0	2.5
18	7.5	1680.0	199.0	1.0	66.0	3.0
19	7.3	1680.0	199.0	200.0	101.0	5.6
20	7.5	1680.0	199.0	2.0	117.0	4.9
21	7.0	1680.0	199.0	2.0	55.0	7.8
22	7.0	1680.0	191.5	52.0	68.0	4.2
23	7.6	1680.0	147.5	47.0	48.0	1.5
24	7.2	1680.0	179.5	20.0	54.0	14.5
25	4.0	319.0	169.5	75.0	176.0	9.3
26	4.6	201.0	42.0	20.0	31.0	1.5
27	6.3	1680.0	79.5	66.0	40.0	3.2
28	7.1	1680.0	199.0	17.5	71.0	0.2
29	5.6	1075.0	199.0	300.0	264.0	12.5
30	5.2	504.0	199.0	46.0	135.0	3.2
32	5.3	588.0	199.0	34.0	90.0	3.2
33	4.9	218.0	75.5	11.0	29.0	1.4
34	5.1	672.0	199.0	14.5	47.0	4.4
35	5.7	906.0	199.0	9.0	271.0	7.4
36	4.8	537.0	199.0	12.5	64.0	4.8

Table 52(cont'd.)

FVB Coll. No.	pH	CaO	MgO	P2O5	K2O	O.M. %
		----- mg/l				
37	5.5	957.0	191.0	26.5	54.0	1.8
38	5.6	537.0	199.0	28.0	155.0	3.1
39	5.8	672.0	175.0	49.0	141.0	2.9
40	7.1	1680.0	155.0	20.0	117.0	1.9
41	7.9	1680.0	199.0	4.0	81.0	2.0
42	7.8	1680.0	199.0	4.0	31.0	2.4
43	7.6	1680.0	199.0	4.0	130.0	4.8
44	7.5	1680.0	199.0	11.0	83.0	4.8
45	7.5	1680.0	199.0	5.0	134.0	7.4
46	5.0	891.0	171.5	14.5	66.0	6.5
47	7.8	1680.0	199.0	0.5	145.0	5.3
48	7.5	1680.0	199.0	16.5	57.5	6.5
49	7.6	1680.0	199.0	4.0	126.0	7.1
50	6.0	1041.0	199.0	5.0	57.5	3.2
51	5.2	1545.0	199.0	32.5	40.0	14.1
52	6.0	857.0	113.0	37.0	29.5	3.6
53	5.5	1125.0	199.0	14.5	36.5	9.3
54	5.1	957.0	199.0	9.0	43.5	9.3
55	6.0	1092.0	199.0	23.5	45.0	3.3
56	7.8	1680.0	199.0	1.0	85.0	3.6
57	7.8	1680.0	199.0	1.0	43.5	2.9
58	7.4	1680.0	199.0	1.0	137.0	5.3
59	5.8	1092.0	175.5	4.0	66.0	3.1
60	5.0	420.0	75.5	1.0	40.0	4.2
61	5.6	571.0	83.5	7.0	36.0	3.3
62	7.7	1680.0	199.0	11.0	62.5	3.4
63	7.7	1680.0	199.0	7.0	70.0	2.2
64	7.6	1680.0	199.0	4.0	104.0	4.2
65	5.8	1159.0	199.0	9.0	52.0	2.5
66	5.0	353.0	69.0	10.0	52.0	3.6
67	5.3	319.0	75.5	7.0	26.0	2.9
68	7.7	1680.0	199.0	6.0	126.0	4.2
69	7.7	1680.0	199.0	4.0	50.5	2.3
70	7.3	1680.0	199.0	6.0	118.0	4.9
71	7.4	1680.0	199.0	14.5	43.5	6.5
72	7.8	1680.0	199.0	6.0	120.0	3.0
73	7.7	1680.0	199.0	4.0	43.5	3.6
74	7.6	1680.0	179.5	7.0	107.5	4.2
75	6.0	873.0	125.5	4.0	36.5	2.1
76	7.8	1680.0	199.0	1.0	66.0	2.3
77	7.6	1680.0	199.0	1.0	31.5	4.8
78	7.5	1680.0	199.0	10.0	40.0	4.2

Table 52(cont'd.)

FVB Coll. No.	pH	CaO	MgO	P2O5	K2O	O.M. %
		----- mg/l				
79	7.6	1680.0	199.0	1.0	106.0	5.3
80	6.3	554.5	83.5	7.0	28.0	0.2
84	4.8	655.0	111.5	7.0	66.0	4.2
85	5.6	521.0	199.0	1.0	28.0	1.3
86	6.5	991.0	199.0	7.0	29.0	0.9
87	6.0	873.0	199.0	8.0	38.0	0.7
88	5.5	672.0	147.5	1.0	29.0	2.2
89	5.5	588.0	123.5	7.0	31.0	1.4
90	5.4	773.0	179.5	8.0	111.0	2.0
91	5.6	302.0	44.0	1.0	22.0	1.5
92	5.2	369.0	38.0	7.0	29.0	1.4
93	6.0	1613.0	199.0	1.0	48.0	1.5
94	5.4	168.0	38.0	1.0	21.0	0.2
95	6.1	974.5	199.0	7.0	21.0	1.2
96	6.0	151.0	199.0	1.0	29.0	2.9
97	6.5	369.5	101.5	1.0	26.0	0.1
98	5.7	487.0	99.5	1.0	26.0	0.2
99	5.4	302.5	50.0	1.0	54.0	0.1
100	5.5	773.0	101.5	4.0	54.0	1.8
101	5.8	420.0	105.5	7.0	80.0	0.6
102	5.2	806.5	143.5	3.0	50.0	1.5
103	6.3	437.0	105.5	47.5	71.0	1.2
104	5.3	336.0	44.0	1.0	22.0	0.7
105	5.4	605.0	69.5	1.0	36.0	4.9
107	6.9	1680.0	199.0	50.5	536.0	4.9
108	8.0	1680.0	199.0	94.5	994.0	5.0
109	6.7	1680.0	143.5	10.0	278.0	2.5
110	7.3	1680.0	137.5	1.0	162.0	2.0
111	7.8	1680.0	199.0	1.0	43.0	2.3
112	8.0	1680.0	155.5	1.0	145.0	1.4
113	7.6	1680.0	199.0	1.0	26.0	1.4
114	7.6	1680.0	199.0	1.0	40.0	1.8
115	7.7	1680.0	199.0	1.0	373.0	2.0
116	7.4	1680.0	199.0	1.0	47.0	4.8
117	7.5	1680.0	199.0	1.0	97.0	4.0
118	7.8	1680.0	199.0	1.5	38.0	3.2
119	7.5	1680.0	199.0	1.5	54.0	7.1
120	7.9	1680.0	199.0	1.0	66.0	2.3

Table 52(cont'd.)

FVB Coll. No.	pH	CaO	MgO	P2O5	K2O	O.M. %
		----- mg/l				
121	7.6	1680.0	199.0	1.0	40.0	4.4
122	7.4	1680.0	199.0	1.0	43.5	4.4
123	7.4	1680.0	199.0	1.0	93.5	4.8
124	7.7	1680.0	199.0	1.0	248.0	3.1
125	7.5	1680.0	199.0	1.0	47.0	4.2
126	7.4	1680.0	199.0	1.0	45.0	3.6
127	7.7	1680.0	169.5	1.0	93.5	4.9
128	5.7	554.5	91.5	1.5	26.0	2.2
129	6.0	269.0	79.5	1.5	19.0	0.9
130	5.0	353.0	66.0	1.5	19.0	3.4
131	5.9	773.0	137.5	1.5	33.0	2.2
132	7.0	1680.0	199.0	1.5	132.0	2.9
133	4.6	319.0	60.0	1.5	50.0	3.1
134	4.8	605.0	95.0	1.5	36.0	4.2
135	6.6	1092.0	199.0	3.0	45.0	2.9
136	7.0	1680.0	199.0	29.5	40.0	4.9
137	7.7	1680.0	199.0	1.0	80.0	3.4
138	7.5	1680.0	199.0	1.0	43.5	2.5
139	7.6	1680.0	199.0	1.0	97.0	4.9
140	5.7	1008.0	141.5	1.0	57.5	2.2
141	5.3	134.0	30.0	1.0	22.5	2.0
142	7.8	1680.0	199.0	1.0	111.5	2.7
143	7.2	1680.0	199.0	1.0	71.5	5.6
144	7.3	1680.0	199.0	1.0	38.0	2.9
145	7.2	1680.0	199.0	1.0	115.0	4.9
146	7.7	1680.0	199.0	1.0	76.5	3.5
147	7.5	1680.0	199.0	1.0	81.5	4.2
148	7.5	1680.0	199.0	1.0	106.0	4.8
149	5.6	1109.0	171.5	1.0	50.0	2.4
150	4.9	470.5	83.5	1.0	47.0	6.5
151	4.8	67.0	14.0	1.5	14.0	0.6
153	7.3	1680.0	199.0	1.0	149.0	5.3

Table 52(cont'd.)

Coll. No.	pH	CaO	MgO	P2O5	K2O	O.M. %
		----- mg/l				
154	7.8	1680.0	199.0	1.0	14.0	0.6
155	5.1	420.0	48.0	1.0	8.0	1.5
152	5.8	1680.0	199.0	7.0	36.0	10.1
156	4.8	521.0	103.5	92.0	40.0	1.5
157	4.5	101.0	44.0	72.5	40.0	2.4
158	7.8	1680.0	199.0	1.0	73.0	2.5
159	7.6	1680.0	199.0	1.0	64.5	3.3
160	7.5	1680.0	199.0	1.0	95.5	3.6
161	7.7	1680.0	199.0	1.0	153.5	2.9
162	7.7	1680.0	199.0	7.0	62.5	3.3
163	7.5	1680.0	199.0	1.0	168.0	4.9
164	7.8	1680.0	199.0	1.0	132.5	3.5
165	7.7	1680.0	199.0	5.0	81.5	2.9
166	7.7	1680.0	199.0	1.0	172.0	4.8
167	7.8	1680.0	199.0	1.0	94.0	2.5
168	7.7	1680.0	199.0	1.0	72.5	4.2
169	7.5	1680.0	199.0	1.0	172.0	4.9
170	8.0	1680.0	199.0	1.0	188.0	4.9
171	7.7	1680.0	199.0	25.0	115.5	4.8
172	7.9	1680.0	199.0	15.5	164.0	4.8
173	7.8	1680.0	199.0	1.0	188.0	2.9
174	7.4	1680.0	199.0	1.0	84.5	6.5
175	7.5	1680.0	199.0	1.0	102.0	6.5
176	7.5	1680.0	199.0	1.0	90.0	2.4
177	7.4	1680.0	199.0	8.0	71.0	4.2
178	7.2	1680.0	187.5	4.0	136.5	3.6
179	7.7	1680.0	199.0	3.0	178.0	4.8
180	7.4	1680.0	199.0	4.0	84.5	4.9
181	7.3	1680.0	199.0	3.0	100.0	5.6
182	7.5	1680.0	199.0	1.0	89.0	2.9
183	7.4	1680.0	199.0	1.0	72.5	3.6
184	7.6	1680.0	199.0	1.0	168.0	4.9
185	7.5	1680.0	199.0	7.0	146.0	3.2
186	7.5	1680.0	199.0	7.0	104.0	5.0
187	7.4	1680.0	199.0	7.0	178.0	5.0
188	7.8	1680.0	199.0	3.0	126.0	2.9
189	7.7	1680.0	199.0	4.0	84.5	3.5
190	7.4	1680.0	199.0	5.0	188.0	4.8
191	7.4	1680.0	199.0	9.0	75.0	5.6
192	7.2	1680.0	198.0	14.5	248.0	7.1

Table 53. Available temperature and water chemistry data for samples which include free water in collections taken by the author.

WIK Coll.	Temperature			pH	Salinity ppt	Cond. mhos /cm
	Air °C	Water °C	Subst. °C			
20	29.4			6.9		
21				6.3		
76	31.6	32.2		7.6	2.5	4,100
77	32	29.4	22.2	7.1	0.2	510
78				7.9	1.9	3,710
79	31	34.9	33.3	7.4	8.0	10,700
80	28.8	27.2	26			
81	25.5	23.9	21			
83	26.7	26	24.4			
84	27.8	23.9	25.5	7.5		
85	23.3		17.8			
86	29		27.2			
87	30		31.7			
88	28.3		28.8			
89	30		24.4			
90A,B	23.3	18.3	20.5	5.0		
114	28.3		29	7.0	1.1	1,950
115	20.3		24.4	6.9	1.5	2,320
116	32.2		29	7.1	2.2	3,510
118				6.9	2.8	5,020
127				6.2		115
158	20.5	18.3				
159	28.3	21				
160	29.4	21.1	24	7.6		
161A	32.2		28	7.9		
161B	32.2		26	8.0		
162	32.2		24.4			
163	34	28.9	27.4			
164	31.1	24.4	24.4			
165	29.4	21				
166A	30.5	25	22.2			
166B		24	29			
167U	30.3	21.3	24			
167L	30	21.7	27.2			
168U	30	35	31.1			
168L						
169	30.3	23.3	26			
170	23.3		22.2			
174	30	28	25			

Table 53. Cont'd.

WIK Coll.	Temperature			pH	Salinity ppt	Cond. mhos /cm
	Air °C	Water °C	Subst. °C			
175A	27	23	25			
175B	27	23	25			
176	29	28	25			
177A	26	26	25			
178	29	24	24			
179A	29	23	23			
180	30		33Sun 27Sh			
181	30		24			
182	29	29	25			
183	32	32	33			
184	29	32	31			
186	24	24	24			
187	30	N/A	76			
188	29.5		74			
189	29	N/A	24			
190	32.7		81			
191	32.7	81	81			
195	27.2	34	29	6.3	0	215
200	20	19.5-21	70	8.4		
201A	20	19.5		7.3	0	82
202	21	24		8.6	8.9	14,800
204	25	24.2		7.15	5.4	9,000
205	29	23.8		7.2	0.3	660
206	28.5	25		7.1	1.0	1,600
207A	28	26		8.9	1.2	2,520
207C	27	23.5	25	6.8	1.0	1,830
208	26.2	25		7.3	0	59
209	29	24.5		6.8	18	29,000
210	29	27	27	6.6	16.7	28,100
211	28	22.3	24	6.2	<0.1	189
212	29.8	24.3		6.2	<0.1	173
214A	14	15	15	7.0	0	110
214B						
215	15	15.5	11			
216		13.8		7.3	0	47
217		15		7.3	1.2	2,200
218A	18	16		7.0	0	100
218B	18	16				
219	18	15	14	5.8	0	81
220	18	13		4.6	0	43
221	18	14.5		5.5	0	68

Table 53. Cont'd.

WIK Coll.	Temperature			pH	Salinity ppt	Cond. mhos /cm
	Air °C	Water °C	Subst. °C			
222A		14		5.0	0	55
222B				5.0		
224	18	13	15	5.3	0	48
225	20.5	17				
226	20	12		3.8	0	145
227A,B						
228	21	12.5		3.6	0	135
229A	21	15		3.4	0.2	375
231				5.9	0	65
232A	20	17		7.8	0.2	450
232B		17		7.8	0.2	450
233	20	14.3		7.0	0	130
234	18	13.8		3.8	0	89
235		13		4.0		80
236				7.8		
240A	21					
240B						
241A				7.5		
242				8.0		
243	13	11		7.0		
245	13	11				
246	13	17		7.1		325
247	20	N/A		7.4		
248	21	11		7.5		
249	16	12		7.5		
251						
252	20	17	15	7.8		
253	20	20				
254						
257A	16	12		7.8		
257B	16	12				
257C						
258	25			7.5		
260	21	15.5				
261C	21	17.5	19	7.0		
262	23.5	22	18	6.4		
263A	23.5	22.5	23	6.9		
263B	23.5	22.5	23	6.8		
263C	23.5	22.5	23	7.0		
265	28.5	24		6.6		
266A	21	10		6.8		
268A	25	27	27	6.4		

Table 53. Cont'd.

WIK Coll.	Temperature			pH	Salinity ppt	Cond. mhos /cm
	Air °C	Water °C	Subst. °C			
268B	25	27	27	6.2		
268C	25	27	27	5.7		
269A	21	15	15	6.1		
269B	20		15	6.0		
269C	20	15		6.2		
270A	20	18		4.9		
270B	20	18		4.8		
270C	20	18		4.9		
270D	20	18		4.6		
270E	20	18		4.7		
272B	20	13	14.5	5.4		
273A	22	17.5		6.6		
273B	22	17.5		6.6		
274	20.5			5.0		
275	20.5	14		6.3		
277				6.4		
279	22	17	18	6.6		82
280	25	20		6.4		
281	25	24		6.6		83
282	25	17		6.8		123
283A		11		6.9		13
283B				6.7		
283C	18.5	13.2		6.0		9
284	24	23.5	25.5	6.4		19
285A	23	29	24.5	6.9		70
285B		19	15	7		98
285C		24		6.9		
285D	23	25		5.3		166
286A	23	19	20	6.5		35
286B				6.6		40
287A				6.1		
287B						
288A	31.5	26.6	78	4.2		160
288B	31.1		75			
289	31.0	20Sh 26Sun		5.8		130
290A	30	25		4.5		
290B	30	24				
291A	32	27	28.5	6.6		
291B	32	27.5	28	6.6		115
292	34	34	34	6.7		163

Table 53. Cont'd.

WIK Coll.	Temperature			pH	Salinity ppt	Cond. mhos /cm	D.O. mg/l
	Air °C	Water °C	Subst. °C				
295	29.4	28		7.7		311	
296		28Sh 36Sun		6.7		95	
297	32.2	36	31	7.5	12.5	25,000	
298	29.4	32	30.5	7.8	19.0	34,500	
299	27	26.5		7.2	0.3	620	
300	30.5	27		7.8	24.0	38,000	
301	31.1	32		7.8	14.5	27,000	
302	26	22.5		7.4	0.1	280	
303A		30		7.8	29	50,000	
303B		30					
304							
305		30			3	5,000	
306							
307	28.9	29		7.2	11.0	20,000	
308	28.2	29		6.8	9	11,000	
309		26		6.1	0	190	
310	18.3	23.5		6.7	7.5	13,000	1.7
311		28		7.2	15	24,000	2.9
312A		25.5		7.2	0	250	2.4
312B		24		6.4		900	1.7
313A	24	23		6.8		120	2.2
313B		24		6.4		900	1.7
313C							
314A		23		8.0		80	6.9
315	21	20.5		7.6		65	6.9
316A		25		7.6		49	3.9
316B	21	21.5		7.4		40	7.1
316C	21			7.5		48	
316D	21			7.5		59	
316E	21			7.4		42	
318A							
319A	21	22.5		7.2		80	
321		22.5		7.2		80	
322A	21	14				25	
322B		14		6.8			
323A	25	21.5		6.8		30	
324							
325A				5.5			
325B		17	16	7.2		73	
330A		16		7.7		223	

Table 53. Cont'd.

WIK Coll.	Temperature			pH	Salinity ppt	Cond. mhos /cm	D.O. mg/l
	Air °C	Water °C	Subst. °C				
330B		19		7.4		310	
331A	24	15		7.2		87	
331B							
332A	27						
332B							
333A	25	26	25Sh 27Sun	8.8		130	
333B				6.5			
333C				6.5			
346	16	13.5		8.3		270	
347	9	19		6.2	0.7	990	
					0.8	1,080	
348				7.8	3.2	4,270	
349				7.0	11.4	16,000	
350				6.8	0.2	345	
351	6	12				280	
352							
353	12	9	14	0.9		1,100	
354	15	14	16	6.4	1.2	1,580	
356	16	20-14			0.2	470	
357	14	8		6.5	0.2	500	
358							
359	9	6		6.8	0	50	
				7.0			
360	10	7		6.7	0	75	
361A	15	13		6.6			
361B							
362	12	11		7.6	0	175	10.1
363				7.0		580	
364				7.4		458	
365		17		8.3		240	
366							
367A		16		7.6		124	
368A				7.4		95	
368C				7.1		101	
369				6.4		120	
370A	17	20.5					
370B							
370C							
371B	15	12		6.0	0	100	
372							
373A	15	15		6.4		40	
374A				6.2	0	54	

Table 53. Cont'd.

WIK Coll. No.	Temperature			pH	Salinity ppt	Cond. mhos /cm	D.O. mg/l
	Air °C	Water °C	Subst. °C				
374B							
374C							
375A	6	10.5		6.4	0	36	
375B						59	
375C				6.2			
375D				6.6			
376				5.9			
377	8	15		5.7	0	43	
378B							
378A						75	
379	25	23					
380							
381	25	27		6.6	0	75	
382	25	19		7.1	0	220	
283		16		6.7		790	
386							
387				7.5			
387B							
387C				6.8			
388	21.5	9		5.6			
389				6.2		800	
390				7.6		550	
391						140	
392				6.6		50	
393						115	
394	25	18		6.8		18	
395				6.1		102	
396A							
396B						407	
397A	25	23					
398A							
400B						85	
401A		15		8.0		350	
403		32	30	8.2	7.7	5,900	1.0
407A	30			7.8		1,850	
407B	31	36	35				7.2
407C	30	27	30	8.6	0.4	410-	8.05
						550	
407D				8.3	7.9		7.25
407E	30	29	32	7.8	22.1	36,800	6.7
407F				7.7	7.0	5,550	

Appendix H. STREAM POLLUTION STUDY SITES

Table 54 . Location and physical characteristics of sites on Cedar Run, Montgomery Co., Va.

Site km from STP	Location	Elev. (m) (ft.)	Stream order ^{3/}	Mean current velocity ^{4/} (ft/sec)	Mean flow ^{4/} (m ³ /sec) (cfs)	Mean width ^{4/} (m)	Littoral Substrate		Vegetation ^{6/}
							Description	m _d ^{5/} (mm) Ø	
B-1A -0.15	On right headwater branch of Cedar Run, 150 m up-stream of sewage lagoon/STP outlet	650 1980	1	25 0.83	0.0025 0.09	0.4	Pebbles in silt-clay matrix	0.12 +3.0	Restricted (< 10%) Herbs and grasses; marshy growth
B-1B -0.20	On left headwater branch of Cedar Run, 200 m up-stream of sewage lagoon/STP outlet	650 1980	1	30	0.003 0.11	0.5	Stones in sand matrix	2.00 -1.0	Restricted Herbs and over-hanging grasses
STP ^{1/}	On Va. Route 603, 0.7 mi. (1.1 km) from junction of Va. 603 and U. S. 460, SE of Blacksburg								
B-2A 0.015	At base of rip-rap embankment, 15 m downstream of STP outlet pipe	646 1970	1	20 0.67	0.011 0.38	0.8	Fine sand, small gravel	0.10 +3.1	Negligible Herbs and grasses
B-2B 0.060	On right edge of sewage lagoon, 5 m upstream of spillway	645 1968	Lagoon	N/A	-	30 x 20	Mud-silt	0.05 +3.7	Moderate (10-50%) Herbs, some grasses
F-M out-let ^{2/}	At lower lip of sewage lagoon spillway, ca. 70 m from STP outlet								
B-3 0.10	On left bank, 30 m down-stream of F-M outlet	639 1950	2	25 0.83	0.025 0.88	1.0	Very fine sand	0.06 +3.8	Restricted Herbs, grasses, marsh growth
B-4 0.47	On right bank, 400 m downstream of F-M outlet, 50 m upstream of culvert passing under Va. 603	633 1930	2	35 1.16	0.025 0.88	1.2	Medium sand; rock out-croppings	0.25 +2.0	Negligible; periphyton on rocks Grasses, herbs, some brush
B-5 3.27	On right bank, 20 m down-stream of Va. 723 bridge over Cedar Run, 3.2 km. downstream of sewage lagoon	489 1490	2	30 1.00	0.034 1.20	2.3	Coarse sand and gravel	0.50 +1.0	Negligible; periphyton on rocks Grasses and herbs, some trees

1/ Sewage treatment plant of Blacksburg-VPI Sanitation Authority
 2/ Federal-Mogul Corp. discharge pipe
 3/ Horton's classification as modified by Strahler (1957)
 4/ Measured during 10 lowest months (sensu Pennak, 1971)
 5/ Median particle-size diameter (Cummins, 1962)
 6/ After schema of Pennak (1971)

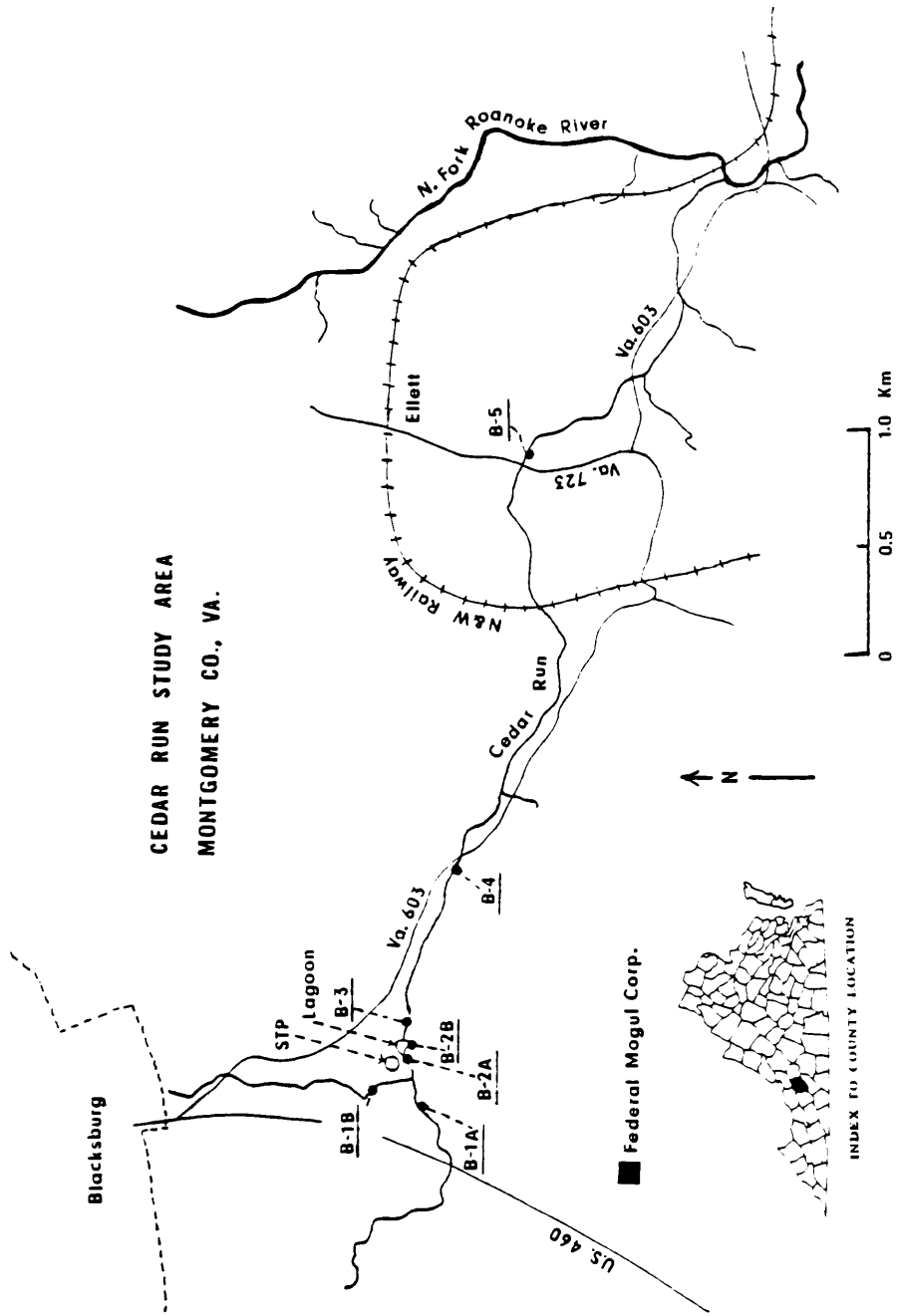


Figure 22. Stream pollution study sites on Cedar Run, Montgomery Co., Virginia. The Ceratopogonidae and Chironomidae were sampled to evaluate their possible response to a combination of domestic sewage treatment plant and industrial electroplating wastes.

Table 55 . Location and physical characteristics of the sites on the South Fork of the Roanoke River, near Green Hill meat packing plant.

Site	Location	Elev. (m) (ft.)	Stream order ^{1/}	Mean current velocity cm/sec	Mean flow ^{2/} m ³ /sec (cfs)	Mean width ^{2/} (m)	Littoral Substrate		Vegetation ^{4/}		
							Description	m ³ /d (mm)	Max. rooted aquatic cover	Shoreline growth (dominant)	
											ø
BSM	Right bank, 50 m upstream of first U. S. 11/460 bridge N of Elliston, 2100 m above Green Hill, Inc. outlet. Lat. 37°12'30" N; Long. 80°13'38" W.	407 1240	3	20	0.34 (12.0)	11	Sand on gravel; leaf deposits	3.00	-1.3	Restricted (< 10%) aquatic cover	Trees and some bushes, with herbaceous ground-cover
GH-1	Right bank, 100 m below outlet 20 m downstream of U. S. 11/460 bridge, 1150 m upstream of confluence with North Fork of Roanoke River. Lat. 37°13'20" N; Long. 80°12'35" W	394 1200	3	15	0.37 (13.5)	15	Muddy sand, with some gravel; leaf banks	0.25	+2.0	Restricted	Bushes and herbaceous undergrowth
GH-2	Right bank, 20 m downstream of U. S. 11/460 northbound bridge adjacent to Montgomery-Roanoke Co. line, 2080 m below confluence with North Fork. Lat. 37°14'15" N; Long. 80°11'40" W.	384 1170	4	15	0.76 (26.7)	18	Gravel in sand-mud matrix; interspersed with roots	2.00	-1.0	Restricted	Overhanging trees and bushes; little herbaceous growth

1/ Horton's (1945) classification as modified by Strahler (1957) (Kuehne, 1962).

2/ Measured during 10 lowest months in study period.

3/ Median particle-size diameter (Cummins, 1962).

4/ After schema of Pennak (1971).

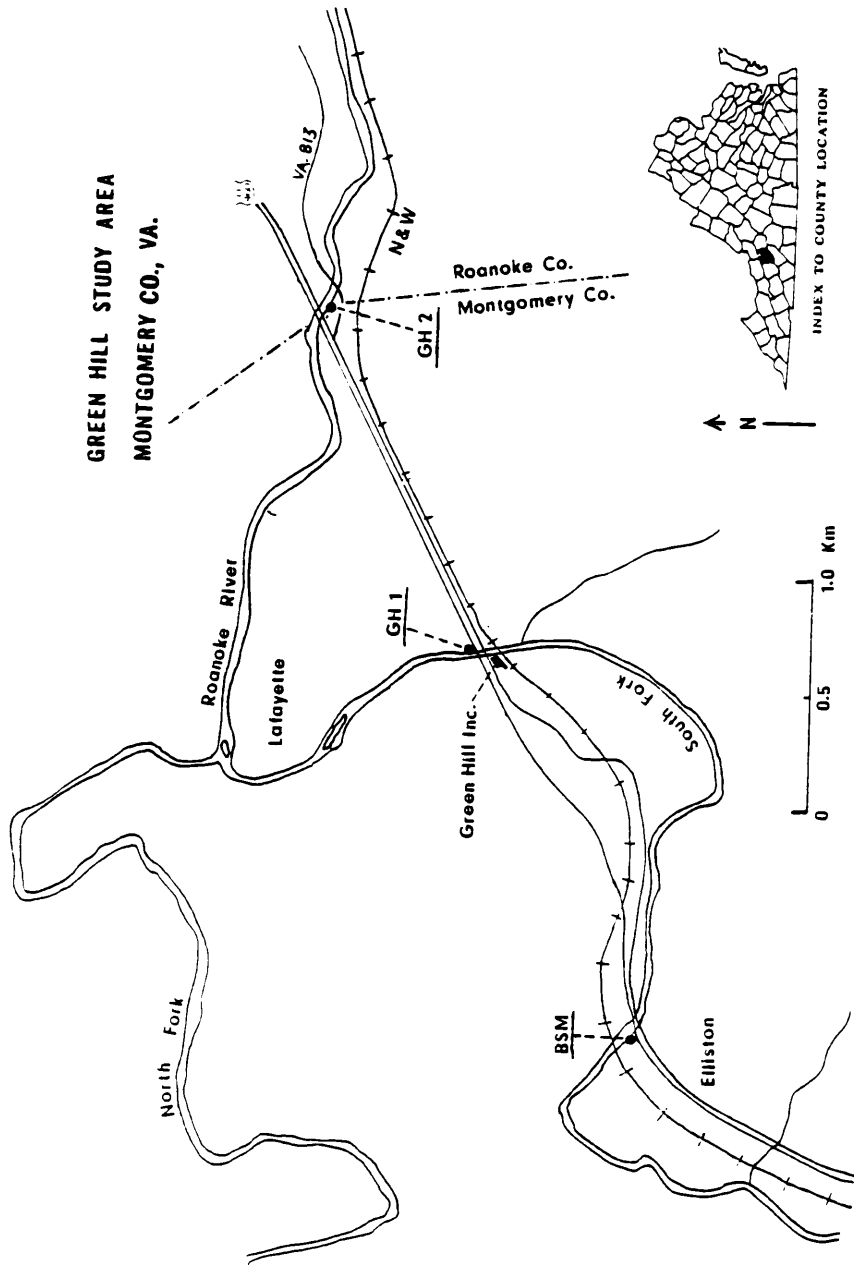


Figure 23. Stream pollution study sites at the South Fork of the Roanoke River, Montgomery Co., Virginia, where the ceratopogonid and chironomid faunae were evaluated for response to organic waste effluents from a meat-packing plant.

Table 56 . Location and physical characteristics of the New River sites near Glen Lyn, Giles Co., Virginia

Site	Location	Elev. (ft.)	Stream order ^{3/}	Mean current velocity ^{4/} (cm/sec)	Mean flow ^{4/} m ³ /sec	Mean width ^{5/} (m)	Littoral Substrate		Vegetation ^{7/}		
							Description	m ^{6/} d (mm)	Max. rooted aquatic cover	Shoreline growth (dominant)	
GL-1	On right bank, 2.1 km up-river from East River, 190 m NW from railroad bridge over Va. 649. Lat. 37°22'30" N; Long. 80°50'49" W.	1495	6-7	18	-	230	Sandy mud, organic fragments	0.07	+3.4	Restricted; periphyton on logs	Large overhanging trees, some shrubs, few herbaceous plants
APCO ^{1/}	On right bank, adjacent to U. S. 460 bridge, at Glen Lyn, Giles Co., Va.										
USCS ^{2/}	On right bank at upstream side of northbound bridge on U. S. Highway 460, 680 m upstream from East River	1490.24	6-7	-	138 ^{5/}	220					
GL-2	On right bank, along rock rip-rap embankment of the bottom ash pond, 240 m upriver of East River, 110 m downriver from southbound lane of U. S. 460 bridge	1489	6-7	21	-	170	Fine sand and clay; tiny coal particles	0.08	+3.3	Absent	Large overhanging trees, some shrubs, few herbaceous plants
GL-3	On right bank, 50 m upriver of new fly-ash pond outlet, 1630 m downriver from East River. Lat. 37°23'03" N; Long. 80°52'48" W.	1485	6-7	20	-	200	Fine sand and silt; tiny coal particles	0.09	+3.2	Absent	Large overhanging trees, some shrubs, few herbaceous plants
GL-4	On right bank, 2.5 km downriver from East River, 100 m from unsurfaced road paralleling New River	1480	6-7	21	-	230	Very fine sand and mud; tiny coal particles	0.07	+3.4	Restricted; periphyton on rocks	Large overhanging trees, some shrubs, few herbaceous plants
GL-5	On right bank, 5.3 km down-river from East River, adjacent to New River Park, 550 m downstream of Cooper Branch	1470	6-7	24	-	190	Medium sand and mud; coal particles	0.10	+3.1	Restricted; periphyton on rocks	Large overhanging trees, some shrubs, few herbaceous plants

^{1/} Appalachian Power Company.

^{2/} United States Geological Survey Gauging Station.

^{3/} Using Horton's classification as modified by Strahler (1957).

^{4/} Near shore, non-flood conditions.

^{5/} Measured by USGS.

^{6/} Median particle-size diameter (Cummins, 1962).

^{7/} After schema of Pennak (1971).

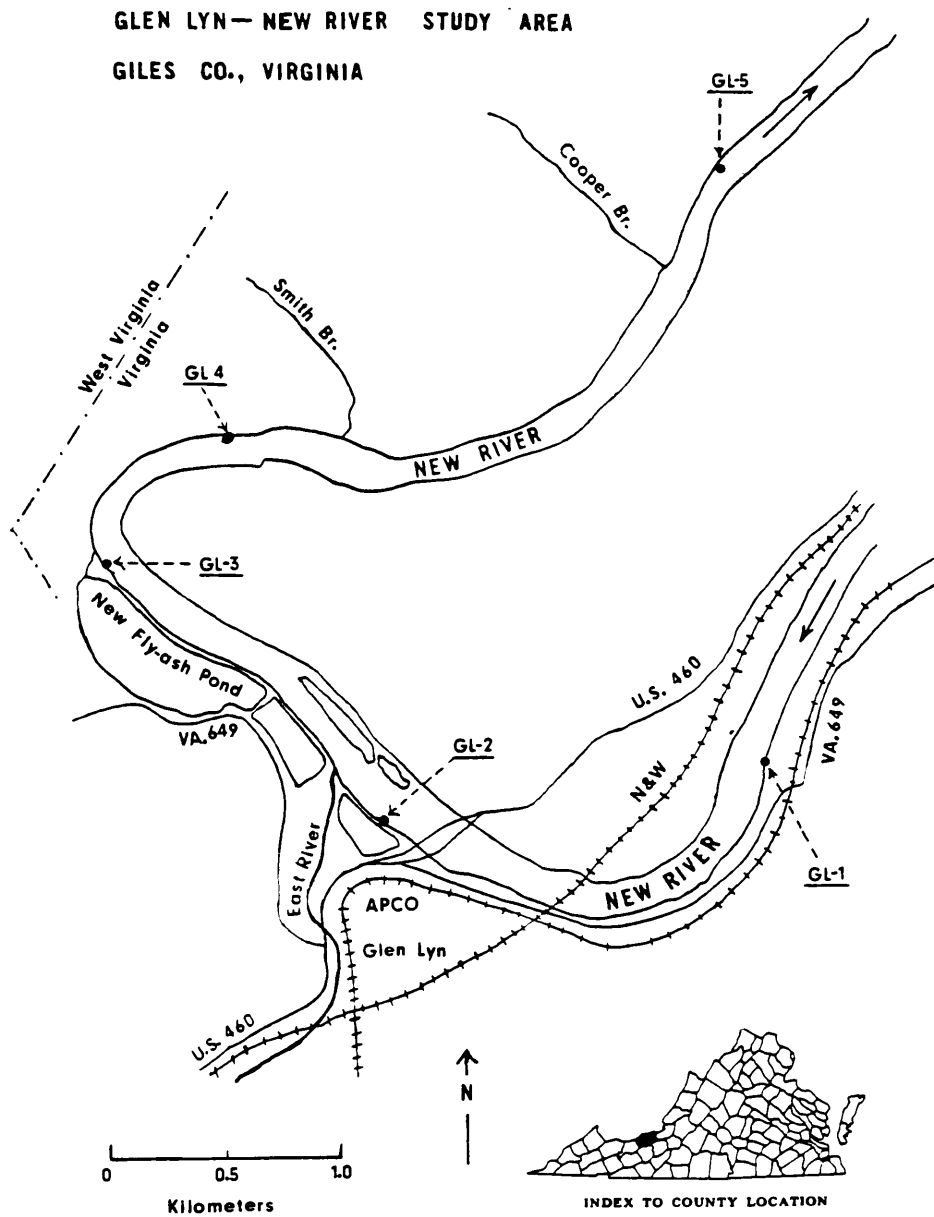


Figure 24. Stream pollution study site at Glen Lyn on the New River, Giles Co., Virginia, to evaluate the impact of thermal effluent from the Appalachian steam generation power plant upon littoral midges.

Table 57. Location and physical description of Reed Creek sites in the Wytheville area, Wythe County, Virginia

Site	Location	Elev. (m) (ft.)	Stream order ^{2/}	Mean current velocity ^{3/} (cm/sec)	Mean flow ^{3/} (m ³ /sec) (cfs)	Mean width ^{3/} (m)	Littoral Substrate		Vegetation ^{5/}		
							Description	m _d ^{4/} (mm) ϕ	Max. rooted aquatic cover	Streamside growth (dominant)	
W-A	On Adkin's Mill Branch (AMB), 75 m above STP ^{1/} outlet; left bank	2085	2	31	0.019 (0.67)	1.85	Gravel and fine sand; stream artificially re-channelled	2.50	-1.2	Negligible, but exposed roots and algal growth	Herbaceous, some brush
W-B	On left bank of AMB, 150 m below STP outlet, 20 m above confluence with Reed Creek	2080	2	38	0.041 (1.16)	1.70	Medium sand, with clay hardpan, except gravel deposits	0.20	+1.7	Absent	Overhanging trees and herbs; marsh plants
W-C	On Reed Creek, 50 m above confluence with AMB, 80 m above Va. 649 bridge; left bank	2080	4	15	3.82 (135)	20.2	Rich mud, muck, and detritus	0.081	+3.3	Restricted	Densely shaded by overhanging trees; some herbs
W-D	On left bank of Reed Creek, after first bend, 200 m below AMB	2075	4	20	3.88 (137)	16.9	Fine-sand and muck, few leaves	0.086	+3.2	Absent	Sparsely shaded; some herb growth
W-E	150 m downstream of Wytheville Sanitarium sewage disposal lagoon, 3.6 stream km below AMB; right bank	2035	4	12	4.25 (150)	25.4	Rich mud with detritus and leaf deposits	0.060	+3.6	Restricted; some root invasion by adjacent trees	Open shade from trees; dense brush and herb growth
W-F	50 m upstream of Va. 704, 50 m downstream from Spiller Branch, 5.6 km below AMB; right bank	2020	4	4	4.98 (176)	26.8	Rich mud, with leaf and root detritus	0.056	+3.6	Negligible; profuse root invasion by adjacent trees	Densely shaded by trees, limited grass and herb development

^{1/} Sewage treatment plant, Wytheville Sanitation Authority, 150 m N of Va. Route 649 bridge over Reed Creek, 900 air meters SE of American Screw Co. Lat. 36°56'21" N; Long. 81°4'01" W.

^{2/} After Horton (1945), Strahler (1957 in Kuelke (1962)).

^{3/} As measured during 10 lowest months in study period.

^{4/} Median particle-size diameter (Cummins, 1962).

^{5/} After schema of Pennak (1971).

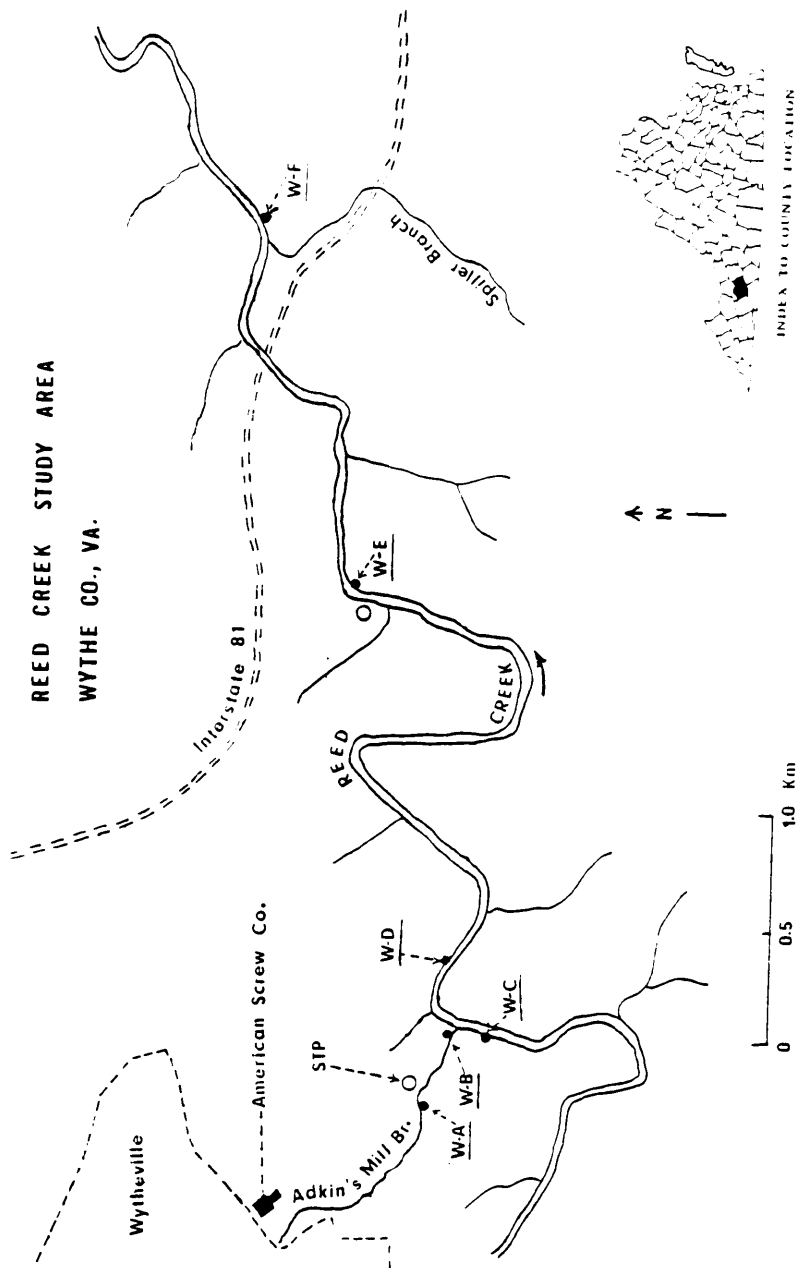


Figure 25. Stream pollution study sites at Reed Creek, Wythe Co., Virginia, where the impact of industrial heavy metal discharges upon the ceratopogonid and chironomid faunae were evaluated.

Appendix I. Published Sources for Locality Records

Table 58. Published literature sources for state and locality records for species of the 29 genera of Ceratopogonidae found in the Middle Atlantic U.S., as listed in the Geographic Checklist (Table 45). Sources including records for several genera are given at the end of this table.

Genera (alphabetical)	State and Locality Record Literature
<u>Alluaudomyia</u>	Glick and Mullen 1982; Grogan and Bystrak 1976; Grogan and Messersmith 1976; Williams 1956; Snow, Pickard and Moore 1957; Wirth 1952a; Wirth and Grogan 1981
<u>Atrichopogon</u>	Boesel 1973; Bowen 1983; Ewen and Saunders 1958; Snow et al. 1957; Wirth 1952b, 1980
<u>Bezzia</u>	Bowen 1983; Carlson 1981; Dow and Turner 1976; Snow et al. 1957; Wirth 1983a,b,c; Wirth and Grogan 1983; Wirth, Forster and Palchick 1984
<u>Brachypogon</u>	Downes 1976; Wirth and Blanton 1970
<u>Ceratoculicoides</u>	Wirth and Ratanaworabhan 1971b
<u>Ceratopogon</u>	Wirth 1965b
<u>Clinohelea</u>	Grogan and Wirth 1975; Snow et al. 1957; Wirth and Grogan 1979
<u>Culicoides</u>	See end of Tables 41 and 42
<u>Dasyhelea</u>	Bowen 1983; Kline (in Ezell 1978); Snow et al. 1957; Waugh and Wirth 1976; Wilkening et al. 1985; Wirth 1965b; Borkent and Forster 1986
<u>Echinohelea</u>	Grogan 1975 (Mosq. News 35(2):231); Wirth 1951b, 1965b
<u>Forcipomyia</u>	Bowen 1983; Bystrak and Wirth 1978 (USDA Tech. Bull. 1591); Dow and Wirth 1972 (Ann. Ent. Soc. Amer. 65:177-201); Grogan and Wirth 1975 (Proc. Ent. Soc. Wash. 77(4):466-71); Snow et al. 1957; Utmar and Wirth 1976 (Fla. Ent. 59(2):109-33); Wirth and Dow 1971 (Fla. Ent. 54(4):289-95); Wirth and Grogan 1978 (Proc. Ent. Soc. Wash. 80:94-102); Wirth and Messersmith 1971 (Ann. Ent. Soc. Amer. 64:15-26); Wirth and Ratanaworabhan 1978 (Proc. Ent. Soc. Wash. 80(4):493-507)
<u>Heteromyia</u>	Brimley 1938, Wirth and Grogan 1977, 1979

Table 58. Cont'd.

Genera (alphabetical)	State and Locality Record Literature
<u>Isohelea</u>	Wirth 1965b
<u>Jenkinshelea</u>	Grogan and Wirth 1977a; Wirth and Grogan 1979; Wirth 1962a
<u>Johannsenomyia</u>	Bowen 1983; Snow et al. 1957; Wilkening et al. 1985; Wirth and Grogan 1979; Wirth 1962b
<u>Leptoconops</u>	Boesel 1948 (Ohio J. Sci. 48(2):69-72); Wirth and Atchley 1973; Clastrier and Wirth 1978
<u>Macropeza</u>	Knausenberger and Wirth 1980; Wirth and Ratanaworabhan 1972b
<u>Mallochohelea</u>	Wilkening et al. 1985; Snow et al. 1957b, Wirth 1962b, Wirth and Grogan 1979
<u>Monohelea</u>	Snow and Pickard 1958; Snow et al. 1957; Wilkening et al. 1985, Wirth 1953a; Wirth and Grogan 1981; Wirth and Williams 1964
<u>Neurohelea</u>	Wirth and Grogan 1979
<u>Nilobezzia</u>	Wirth 1962b
<u>Palpomyia</u>	Grogan and Wirth 1979b; Snow et al. 1957
<u>Parabezzia</u>	Bowen 1983; Grogan and Wirth 1977b; Wirth and Grogan 1981; Wirth 1965b
<u>Phaenobezzia</u>	Bowen 1983, Dow and Turner 1976, Snow et al. 1957; Wirth and Grogan 1982
<u>Probezzia</u>	Bowen 1983; Snow et al. 1957; Wirth and Grogan 1979; Wirth 1951a, 1971
<u>Serromyia</u>	Wirth 1965b
<u>Sphaeromyias</u>	Snow and Pickard 1958; Wirth 1962b; Wirth and Grogan 1979
<u>Stenoxenus</u>	Wirth and Ratanaworabhan 1972a
<u>Stilobezzia</u>	Snow and Pickard 1958; Snow et al. 1957; Wilkening et al. 1985; Wirth 1953b; Wirth and Grogan 1981

Table 58. Cont'd

Genera (alphabetical)	State and Locality Record Literature
Several Genera	Bowen 1983; Brimley 1938, 1942; Snow and Pickard 1958, Snow, Pickard & Moore 1957; Wilkening, Kline and Wirth 1985; Wirth 1965b; Wirth and Grogan 1979, 1981; Wray 1967

VITA

Walter Ingolf H. J. Knausenberger was born in Centre County, Pennsylvania on September 2, 1948, fourth son of seven children of Dr. and Mrs. Georg E. and Anna-Maria Knausenberger. From 1959 - 1968 he lived with his family near Munich, West Germany, and graduated from Munich American High School in 1966. After two years' study at the European Division of the University of Maryland, and work-study in France and Spain, he enrolled at Pennsylvania State University, where he graduated in 1971 with a B.S. in Biophysics. After ROTC Summer Camp, he enrolled, by September 1971, in the graduate program in the Entomology Department at Virginia Polytechnic Institute and State University, with a concentration in aquatic entomology and medical/veterinary entomology. In 1974, he spent a few months traveling abroad. He received the M.S. degree in February 1975. He then was accepted into the Ph.D. program in entomology at VPI&SU.

Before fully analyzing and writing up the voluminous results of three years' field collecting and laboratory work, the author was obliged to seek employment. In January, 1979, he was offered a position as Extension Entomologist with the Virgin Islands Cooperative Extension Service, College of the Virgin Islands, where he also held a joint appointment with the V. I. Agricultural Experiment Station. He has advanced there to the positions of Pest Management Specialist, and more recently, Program Leader for Natural Resources. In 1985 and again in 1986, he was able to obtain leaves of absence to complete his dissertation.

Throughout his academic and subsequent career, the author has been active in extracurricular, community and church affairs, and he holds membership in many professional, civic, and honorary organizations. In December 1975 he married fellow entomologist Janice Gayle Burt in Blacksburg, Virginia. Their first son, Erich, came into the world there in December 1978. Three more sons were born in the U. S. Virgin Islands: Cephas(April 1980); Ari(October 1982); and Anson(December 1984).

Walter Ingolf Krausenberger