

STRUCTURE AND COMPOSITION OF THE AQUATIC INVERTEBRATE COMMUNITY
INHABITING EPIPHYTIC BROMELIADS IN SOUTH FLORIDA AND
THE DISCOVERY OF AN INSECTIVOROUS BROMELIAD

By

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Abstract of Dissertation Presented to the Graduate Council
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A survey of the aquatic invertebrates inhabiting the water-filled leaf axils of 6 species of epiphytic tank bromeliads occurring in south Florida revealed 13 species of dipterous insects, 2 species of ostracods, a mite, a turbellarian, and an oligochaet worm. The list represents 2 new families and 8 new species of bromeliad inhabiting insects, including 7 undescribed new species. Most of these species are widely distributed and abundant, and seem to be restricted to the bromeliad habitat during their aquatic stages. A review of the literature on aquatic fauna inhabiting bromeliads in the Neotropics indicates that the Florida bromeliad fauna is of Neotropical origin but is depauperate as compared to the faunal lists for Costa Rican and Jamaican bromeliads.

A cluster analysis of community structure indicates that species composition and abundance are characteristic of the ecosystem supporting the bromeliad flora with the bromeliad species containing the aquatic community having the least influence upon structure. Differences in amounts and rates of throughfall and leaf litter accumulation among ecosystems supporting bromeliads are suggested to be important factors

in determining community structure since most species of aquatic invertebrates inhabiting bromeliads in south Florida seem to be detritus feeders. Seasonal variation in community structure was greatest in cypress and mangrove ecosystems and least in a tropical hardwood hammock.

The epiphytic bromeliad Catopsis berteroniana (Shult) Mez was found to be insectivorous. This species captures flying insects within erect tube-like leaves which are lubricated with a fine white powder that prevents escape. The white powder also reflects UV light which is believed to attract the insects. The first report of insectivory in the Bromeliaceae represents a new method of nutrient procurement for the family.

INTRODUCTION

Water-holding epiphytic bromeliads are characteristic features of many ecosystems in the American tropics and subtropics, and their abundance in certain areas of south Florida constitutes a major feature of the total landscape. The existence of these plants poses two important questions to the biologist: 1) How do they maintain themselves in the total absence of soil? and 2) What is the nature of the communities of aquatic organisms that inhabit them? Both of these questions are addressed in this dissertation.

The first chapter describes an epiphytic bromeliad that was found to be insectivorous. This discovery represents the first report of insectivory in the Bromeliaceae and provides a new explanation for nutrient procurement in this family in addition to those currently proposed.

The results of a survey of aquatic invertebrates inhabiting the bromeliads of south Florida are reported in the second chapter. This survey indicates that the aquatic fauna is not evenly distributed within all species of water-holding bromeliads or throughout the total ranges of these species. An investigation into the causes of differences in species composition and abundance of the aquatic communities is reported in the third chapter.

These chapters are written in manuscript form and are intended to be submitted with only minor changes in style and form for publication in major scientific journals.

CHAPTER I
INSECTIVORY IN CATOPSIS BERTERONIANA: A NEW METHOD
OF NUTRIENT PROCUREMENT IN THE BROMELIACEAE

The plant family Bromeliaceae contains over 2,000 described species and constitutes a major portion of the epiphytic flora in the Neotropics. In general, growth and maintenance of these plant communities is not easily explained in the absence of a soil substrate, and nutrient procurement by epiphytic bromeliads has been the subject of many recent investigations (Benzing 1970a, 1970b, 1973, Benzing and Burt 1970, Benzing and Renfrow 1974). In adapting to a habitat of extreme scarcity of nutrient salts, several strategies have evolved within this family. The fundamental adaptations have been decreased dependence upon root absorption of nutrients and an increased dependence upon foliar procurement and foliar absorption of nutrients.

At least 3 methods of foliar procurement of nutrients have been identified in the Bromeliaceae (Benzing 1973). 1) Tank bromeliads have tightly overlapping leaf axils which are inflated to impound varying amounts of rain water intercepted by channeled leaves in a tight rosette configuration. They usually occur within or below the forest canopy and intercept nutrients leached by rain from living leaves in the canopy (Tukey 1970a, Benzing and Renfrow 1974). Falling leaf litter also contributes to the nutrient pool which is ultimately broken down by a variety of aquatic invertebrates and microorganisms

living in the leaf-axil water (Picado 1913, Laessle 1961, see also Chapter 2). 2) Atmospheric bromeliads such as spanish moss (Tillandsia usneoides), also absorb nutrients from canopy leachates but are unable to impound water. These plants have a high surface/volume ratio and possess large numbers of epidermal trichomes that act as one-way valves for the absorption of dilute nutrient salts during brief but heavy rains (Benzing and Dahle 1971). 3) Myrmecophytic bromeliads such as T. butzii and T. caput-medusae have moderately inflated leaf axils and an overall bulbous shape. The leaf axils are unable to impound water but instead provide a habitat for colonies of various species of ants. The foraging ants return nutrients to the plant for brood rearing which, in addition to excretory products, provide a nutrient pool for the plant (Benzing 1970a).

A fourth method of foliar procurement, that of insectivory, is here described for the first time in the Bromeliaceae.

The epiphytic bromeliad Catopsis berteroniana ranging from extreme south Florida to southern Brazil, has all of the physical attributes of a tank bromeliad. However, at least in south Florida, it rarely occurs beneath the forest canopy, but instead it is found attached to small branches in the very tops of canopy trees or on dead trees and shrubs in open areas. The water-filled leaf axils rarely contain leaf litter but are instead filled with the chitinous remains of insects. This species is characterized by erect leaves and a conspicuous white chalky powder covering the leaf bases on both sides (Fig. 1A). Both of these features are important components of its insectivorous nature.

The overlapping leaves form a series of tubes having steep sides, and each contains about 10 ml of rain water. Insects are unable to escape from these tubes because of the fine white chalk which effectively lubricates the walls. (When the powder is removed with a brush the insects easily escape.) This unique arrangement constitutes a passive pitfall type trap for securing insect prey which ultimately drown in the water. The pitfall type traps of C. berteroiana are functionally similar to those of insectivorous pitcher plants (Nepenthaceae and Sarraceniaceae), although in pitcher plants, the trap is formed by a single leaf and escape is prevented by numerous downward pointing trichomes on the internal leaf surface (Lloyd 1942, Fish and Carlysle in preparation) instead of a lubricating powder.

The existence of proteolytic enzymes in the leaf axils of tank bromeliads has been suspected for some time (Picado 1913) but has not been investigated by modern biochemical techniques. However, bacterial exoenzymes, introduced with insect prey, are an important component of the digestive fluid of insectivorous pitcher plants (Sarraceniaceae) (Plummer and Jackson 1963), and probably also occur in the leaf axils of C. berteroiana.

Foliar absorption of nutrients in C. berteroiana has previously been demonstrated by Benzing and Burt (1970) who also used P^{32} labelled insects to demonstrate decomposition and subsequent foliar absorption in the leaf axils of the epiphytic tank bromeliad Aechmea nudicaulis (Benzing 1970b). Apparently most, if not all, tank bromeliads have the capacity to break down and absorb both animal and plant matter that accumulates within their leaf axils.

The white powder of the leaf bases might also be involved in the recruitment of insect prey. Photographs of the same sunlit

plant taken with visible light (Fig. 1A) and with a Wratten 18-A UV filter which absorbs visible light (400 nm.) allowing only UV light to be recorded on the film, (Figs. 1B, 1C), shows that the white powder strongly reflects UV light while the uncoated portion of the leaves absorb UV light. In nature, UV light is an indication of open space since natural objects absorb UV light and its only sources are the sun and sky to which insects are believed to orient (Mazokhin-Porshnyakov 1969). With the basal portion of the entire plant acting as a mirror in the UV end of the spectrum, flying insects sensitive to UV may not be able to distinguish this part of the plant from the normal UV radiation in the atmosphere, may collide with the plant, and fall into the water-filled leaf axils. Since C. berteroiana normally occurs only in exposed situations where they would be easily encountered by flying insects, and since nectar secretions or other attractive substances were not evident, it is unlikely that it actively attracts insect prey.

A passive method of capture is further suggested by the wide diversity of insects captured by C. berteroiana in the field. Four plants were transported from their natural habitat in Everglades National Park to Gainesville, Florida, where they were affixed to fence posts 1.5 m above the ground to facilitate observation. Freshly captured insects were removed from the leaf-axils of the plants for 8 consecutive days. The catch totalled 136 specimens representing 8 insect orders in addition to spiders (Table 1). Hymenoptera, Diptera, Coleoptera, and Lepidoptera constituted 87% of the prey. A high incidence of parasites, predators, and phytophagous insects indicates that they were not attracted by a common food source.

Noninsectivorous tank bromeliads typically do not have erect leaves, white powder, or UV reflecting surfaces (Fig. 1D). Consequently they do not recruit or have the capacity to retain insect prey. Also most tank bromeliads usually harbor numerous living terrestrial arthropods such as cockroaches, beetles, ants, scorpions, etc., within the older leaf axils (Picado 1913, Laessle 1961, Fish, unpublished data) a feature never observed in C. berteroiana.

The evolution of insectivory among epiphytic Bromeliaceae is most likely the result of competition among the many species within this family that have adapted to the nutrient poor epiphytic environment from terrestrial ancestors (Pittendriq 1948). Catopsis berteroiana avoids direct competition with other tank bromeliads by being completely independent of nutrients from the forest canopy in addition to being independent from a soil root substrate. Such independence has been achieved in at least two other families (Lentibulariaceae and Nepenthaceae) by giving rise to insectivorous epiphytic species Utricularia montana (Taylor 1967), Nepenthes vetchii, and N. reinwardtiana (Smythies 1965) directly from insectivorous ancestors adapted to nutrient poor terrestrial environments.

CHAPTER II
A SURVEY OF THE AQUATIC FAUNA INHABITING THE LEAF AXILS OF
EPIPHYTIC TANK BROMELIADS IN SOUTH FLORIDA

Introduction

Many species in the plant family Bromeliaceae impound rain water within tightly overlapping leaf axils and are referred to as tank bromeliads. Most are true epiphytes which attach themselves to the trunks and limbs of larger plants with strong fibrous roots. Their channeled leaves and rosette configuration provide for efficient interception of rain water which is funneled directly into the leaf-axil chambers (Benzing et al. 1972). The impounded water can range from a few milliliters to several liters depending upon the size of the plant and degree of leaf base inflation.

Water in the leaf axils contains varying amounts of nutrients obtained from decomposition of allochthonous leaf litter and rain water that has leached minerals and organic matter from living leaves in the above forest canopy (Tukey 1970a, Benzing and Renfrow 1974). Epiphytic tank bromeliads are totally dependent upon the contents of their leaf axils for nutritional requirements in the absence of a root soil substrate (Pittendrigh 1948, Benzing 1973, Benzing and Renfrow 1974) and absorb nutrients directly through the leaf surface (Benzing 1970b, Benzing and Burt 1970).

Foliar impoundment of nutrient laden water by epiphytic tank bromeliads provides a unique arboreal habitat for a variety of aquatic

animal life ranging from protozoa to anuran tadpoles. The communities of aquatic organisms associated with epiphytic tank bromeliads have been studied by Picado (1913) in Costa Rica, Laessle (1961) in Jamaica, and Maguire (1970) in Puerto Rico. These and other studies reviewed by Maguire (1971) have shown that bromeliad communities are useful in investigations of interspecific interactions, community structure, colonization, dispersal, and other aspects of community ecology because they are small, relatively simple, and conveniently sampled.

In addition to their ecological significance, bromeliad communities are important as breeding sites for many species of blood-sucking insects of potential public health importance. Larvae of at least 6 genera of mosquitoes (Culicidae) are known to occur in bromeliads (Horsfall 1972) in addition to horseflies (Tabanidae) (Goodwin and Murdoch 1974) and biting midges (Ceratopogonidae) (Wirth 1974). Very little is known of the ecology of these important groups of bromeliad-breeding insects, or how they are distributed among the bromeliad flora.

Of the more than 2,000 described species of bromeliads in the Neotropics, 17 have become established in subtropical Florida (Craighead 1963). Several of these same species support communities of aquatic invertebrates in the tropics but very little is known of the aquatic bromeliad fauna in Florida. Only mosquitoes (3 spp.) (King et al. 1960), chironomids (3 spp.) (Beck and Beck 1966), and an ostracod (Tressler 1956) have been reported from Florida tank bromeliads and, except for the mosquitoes, these reports are from single collections.

In view of the significance of bromeliad communities in ecological studies and the public health significance of some of the fauna, it

is surprising that so little is known of the species composition of these communities in general, and especially in south Florida where the aquatic invertebrate fauna is relatively well known. The present study represents the first attempt to compile a complete census of aquatic metazoan invertebrates inhabiting the tank bromeliads of south Florida, and to compare these findings with the results of similar studies conducted in other areas of the Neotropics as reported in the literature.

Materials and Methods

Only 7 of the 17 species of bromeliads occurring in south Florida are considered true tank bromeliads; these are Tillandsia utriculata L., T. fasciculata Sw., T. valenzuelana A. Rich., Catopsis berteroiana (Schult) Mez, C. floribunda (Brongh.) Smith, C. nutans (Sw) Griseb., and Guzmania monostachia (L.) Rusby. Several other species of Florida bromeliads are considered ephemeral tank bromeliads. These have very small leaf axils that contain free water only briefly after heavy rain and were not found to support aquatic organisms.

Over 360 bromeliads were sampled from 17 locations in south Florida, (Fig. 2) between January 1974 and December 1975. A variety of major plant communities supporting bromeliad populations were included to insure a representative collection of the bromeliad fauna (Table 2). More detailed floristic descriptions of the collecting sites are provided by Davis (1943) and Craighead (1971).

The frequency that each bromeliad species was sampled is biased toward the most abundant (Table 3). Tillandsia utriculata and T. fasciculata are by far the most abundant of the Florida tank bromeliads

and were consequently sampled heavily in comparison to the other 4 species. Tillandsia utriculata was sampled most frequently as it is more widespread and occurred in most of the sampling sites. Catopsis berteroniana and T. valenzuelana are not widespread but are locally abundant in extreme south Florida, and were sampled on several occasions. Catopsis floribunda and G. monostachia were sampled least frequently since they were found at only one site. Catopsis nutans was not sampled during this study because of its scarcity.

Truly random sampling was not feasible since it would require the numbering of all plants in each location and subsequently collecting them in random sequence. Although the sampling was admittedly biased in favor of accessibility, special efforts were made to collect evenly throughout the habitats, and trees were frequently climbed to obtain specimens high in the canopy. Medium to large plants were purposely selected because they were most likely to contain fauna and were easier to identify.

Bromeliads were identified with a descriptive key by Craighead (1963) and by comparison with herbarium specimens at the University of Florida.

The maximum water holding capacity of each bromeliad species was determined to assess its potential to support aquatic fauna. Depending upon the species, 5 to 20 of the same plants selected for faunal sampling were filled to capacity with tap water and then emptied into a volumetric cylinder. The average water holding capacity of the sample was calculated by dividing the total plant volume by the

average number of leaves on the plants in the sample. The 3 measures -- total plant volume, number of leaves, and volume per leaf axil -- were found to be useful in describing the physical characteristics of the different bromeliad species. However, these measures are not intended to be estimates of the actual water volumes present in the leaf axils in nature since the sampled plants were rarely filled to capacity.

Individual plants were carefully removed from their attachment sites to avoid spilling the leaf-axil water and immediately processed in the field. Processing of the plants involved a modification of the method devised by Frank et al. (1976) for removing the immature stages of bromeliad mosquitoes. Each plant was inverted in a large bucket containing sufficient water to cover the leaves. The leaf axils were washed by a rapid up and down movement with the plant held by its roots. After 30 sec of washing, the plant was removed and the wash water strained through a fine mesh screen to remove the debris and fauna. The collected material was rinsed from the screen into an enamel pan and then rinsed into labelled plastic bags, each containing the contents of one bromeliad. The bags were transported in an insulated box containing ice to the laboratory in Gainesville where they were stored at 8°C until examination.

The efficiency of the sampling method was frequently checked by carefully dismantling bromeliads leaf by leaf. The results indicated that all faunal species were removed by the washing method except Aschelminthes. Rotifers and nematodes were only occasionally retained by the screen and consequently could not be included in the study.

Each sample was examined with a dissecting microscope at 7-30X magnification after removing and rinsing the leaf litter and large debris. Aquatic organisms were collected with a pipet and either preserved in 70% ethanol or set aside for rearing. Rearing proved to be a difficult task because of the number of species involved and the absence of knowledge regarding their feeding habits or pupation requirements. Few specimens would pupate under laboratory conditions. To obtain adequate numbers of adult specimens for identification, dark plastic bags were placed over unemptied bromeliads in the field. Small plastic vials fitted with filter paper cones were placed in an opening at the tops of the bags. Emerging adults trapped in the vials were used to supplement the laboratory reared material.

Since it is difficult or impossible to view these organisms directly in the leaf axils, observations on the behavior and feeding habits of some species were conducted in the laboratory under a variety of experimental conditions. In general, predatory species were provided with other bromeliad organisms for prey, and particulate and filter-feeding organisms were provided with naturally occurring leaf litter, detritus, and bromeliad water.

Preserved specimens of both larval and adult forms were submitted to appropriate systematic specialists for identification or description. Representative collections from this study have been deposited in the Florida State Collection of Arthropods and at the Archbold Biological Station.

Results and Discussion

The measurements of total volume, number of leaves, and volume per leaf axil varied considerably between the samples of different bromeliad species (Table 2).

Tillandsia utriculata is the largest tank bromeliad in Florida with an average total plant volume of 300 cc with exceptionally large specimens holding over 700 cc. The leaf axils of this species are moderately inflated with an average volume of 8.1 cc (Fig. 3). In T. fasciculata the leaf axils are much less inflated and have an average volume of only 1.5 cc, but its large number of leaves provides an average total plant volume of 60 cc. Both T. utriculata and T. fasciculata maintained free water in their leaf axils throughout the year at all sites.

The smallest species sampled was T. valenzuelana having a total plant volume of only 35 cc. It is unable to maintain free water within its leaf axils during much of the dry season (December to April), but frequent rains during the wet season (May to November) provide sufficient water for small populations of a few species of aquatic organisms.

Some specimens of C. berteroiana also become dry but this species seems to retain water much longer than T. valenzuelana during dry weather possibly because of a relatively large leaf-axil volume of 10 cc.

Catopsis floribunda and G. monostachia were sampled only during the wet season and it is not known if they maintain aquatic invertebrate populations throughout the year.

The distribution of bromeliad fauna among the 6 bromeliad species (Table 3) indicates that the number of faunal species found in each

species of bromeliad is related to the frequency that each bromeliad species was sampled. However, the less frequently sampled species are relatively rare and restricted to certain plant communities, whereas T. utriculata and T. fasciculata are widespread throughout south Florida and occur in a variety of plant communities. The numbers of invertebrate species recorded for C. floribunda (7) and G. monostachia (6), which were sampled from just one site, approximate the average 7.6 species occurring per sample site for all sampling locations. The faunal lists of these rarer bromeliad species probably would not be increased significantly by increasing the sample size since the additional samples would be from the same or very similar sites. Catopsis floribunda and G. monostachia have average total plant volumes and leaf-axil volumes larger than T. fasciculata in which 12 invertebrate species were found, indicating that the relatively small numbers of faunal species recorded for these species are a result of their restricted distribution and not their size. Catopsis berteroniana supported more invertebrate species (9) since it is more widely distributed and was sampled from 3 different plant communities (Table 2). However, plant size as well as a restricted distribution may be important factors in limiting the number of invertebrate species inhabiting T. valenzuelana. This smallest bromeliad was abundant in only 2 locations. The most important point learned from sampling the rarer bromeliad species is that they did not support faunal species different from those found in the more common tank bromeliads.

Over 39,000 specimens representing 18 species of aquatic invertebrates were collected from bromeliad leaf axils during the study. The list includes the immature stages of 12 species of insects

representing 7 families of Diptera, an oligochaet worm, a turbellarian, a mite, and 2 species of ostracods. Most species were either abundant in one or more sampling sites or widely distributed among several sites. The rarest species was represented by 29 specimens occurring in 6 samples. Single specimens of 3 different unidentified dipterous larvae, each found in only one sample appeared to be accidental, and were excluded from the study.

The following list of Florida bromeliad inhabitants includes data on collection sites, estimates of relative abundance, and observations on the biology of each species. A brief review of the literature relevant to the species or related forms is also presented in an attempt to clarify its status as a regular bromeliad inhabitant and to provide some indication of its possible origin.

CULICIDAE:

Wyeomyia mitchelli (Theobald) -- Sites 1-12 and 17

Wyeomyia mitchelli is the most abundant and most widely distributed mosquito in Florida bromeliads. The average number of larvae from all of the bromeliad samples was 12.2; however, one large specimen of I. utriculata contained 339 larvae. Larval densities varied among sites but few sites were completely free of larvae, and populations persisted throughout the year reaching their maximum abundance in midsummer.

Wyeomyia mitchelli larvae are free-swimming filter feeders and consume particulate matter and microorganisms suspended in the leaf-axil water. They have a development time of 2-4 weeks (21°C) and pupation lasts 4-5 days.

Bruijning (1959) has proposed synonymy of mitchelli and other similar species with medioalbipes Lutz from Brazil, which has been retained by Stone (1969). However, Belkin et al. (1970) considers mitchelli a distinct species and reports its distribution as Jamaica, eastern Mexico, Cuba, Hispaniola, and south Florida. Obviously, mitchelli is part of a large complex of Neotropical species morphologically similar to medioalbipes.

In Jamaica, W. mitchelli larvae occur in bromeliads and also in the leaf axils of terrestrial Araceae and in the flower bracts of Heliconia spp. (Musaceae) (Belkin et al. 1970). However, in Florida, this species has been collected only from bromeliads including exotic terrestrial species such as Bilbergia sp., a common garden ornamental (Fish, unpublished data).

Wyeomyia vanduzeei D.&K. -- Sites 1-3, 6-8, 12-14 and 17

Wyeomyia vanduzeei, a more distinct species, occurs in south Florida, Cuba, Grand Cayman, and Jamaica (Belkin et al. 1970). The larvae have been collected only from bromeliads throughout its range. The feeding habits of W. vanduzeei are similar to those of W. mitchelli. Although both species cohabit the same bromeliads and are frequently found together in the same leaf axils, there is no evidence of competitive displacement between these 2 species. Wyeomyia mitchelli outnumbers W. vanduzeei by 3 to 2 in the total from all samples, but in the mangrove sites W. vanduzeei was more abundant and in other sites the more abundant species varied seasonally.

Wyeomyia is a large genus of plant-axil-breeding mosquitoes comprised of at least 85 species (Lane 1953). Although 2 species, W. smithii and W. hanei, have adapted to pitcher plants in temperate and

boreal North America, the genus is otherwise restricted to the American tropics.

In Florida, Wyeomyia mosquitoes are not known to transmit disease, but they are avid daytime biters of man and are a problem in some areas when adult populations are high.

Toxorhynchites rutilus rutilus (Coq.) -- Sites 1, 2 and 17

The larvae of T. r. rutilus are predatory upon other mosquito larvae but were rare inhabitants of bromeliads. The few specimens found were restricted to the largest bromeliad T. utriculata possibly because plants having smaller leaf-axil volumes do not contain enough Wyeomyia larvae to support their development. They are not known to have the ability to leave the water of one leaf axil in search of another containing prey. Seabrook and Duffey (1946) reported, finding numerous T. r. rutilus larvae in T. utriculata in several locations along the east coast of Florida. This species is not restricted to bromeliads and is also found in tree holes and artificial containers (Basham et al. 1947). Toxorhynchites r. rutilus occurs throughout Florida and ranges northward into South Carolina and Georgia where it is replaced by T. r. septenioralis which is distributed throughout the Eastern United States (Carpenter and LaCasse 1955).

At least 6 other species of Toxorhynchites have been collected from bromeliads in Central and South America (Horsfall 1972). Picado (1913) found T. superbus (D.&K) to be very abundant in Costa Rican bromeliads, but Laessle (1961) did not find this genus in Jamaican bromeliads. The specificity of Neotropical Toxorhynchites for the bromeliad habitat remains to be determined.

Toxorhynchites r. rutilus is not considered to be an important predator of Wyeomyia mosquitoes since it is not widely distributed in Florida bromeliads.

Other mosquito genera occur in bromeliads with varying degrees of specificity. Notable among those are Anopheles mosquitoes in the subgenus Kerteszia which are obligatory bromeliad inhabitants and are known vectors of human malaria in many areas of South America (Forattini 1962). Picado (1913) reported 65 mosquito species in 5 genera occurring in bromeliads in Costa Rica, and Laessle (1961) found 7 species of 3 genera in Jamaican bromeliads. Miller (1971) found mosquitoes to be the most abundant insects in the bromeliads of St. John, Virgin Island, but did not provide identifications. Mosquitoes are probably the most important bromeliad inhabitants throughout the Neotropics because of their diversity and abundance, as well as their public health significance. They are the second most abundant insect family inhabiting Florida tank bromeliads.

CHIRONOMIDAE:

Metriocnemus abdominoflavatus Picado -- Sites 1, 2, 4-10, 12-15 and 17

Metriocnemus is the most abundant bromeliad inhabitant and is found in all species of Florida tank bromeliads. The overall density was 18 larvae per plant for all plants sampled with a maximum of 183 in one large specimen of T. utriculata. The larvae of this species do not build cases, as do many fresh-water chironomids, but instead crawl freely about the settled detritus particles upon which they presumably feed. The larvae are usually most numerous in bromeliads inhabiting dry exposed sites and least abundant in those inhabiting shaded hammocks.

Picado (1913) found M. abdominoflavatus to be the most abundant chironomid in Tillandsia spp. in the central highlands of Costa Rica, but rare in Bilbergia and Catopsis. Miller (1971) reported Metriocnemus "possibly abdominoflavatus" to be more abundant in I. utriculata in the drier areas of St. John than in Aechmea ligulata of the wet mountainous areas. Picado (1913) also reported that these larvae can resist desiccation for several days which suggests that this species may be adapted to bromeliads inhabiting relatively dry environments.

Monopelopia tillandsia Beck & Beck -- Sites 2, 8 and 17

Monopelopia tillandsia was found only in east-central Florida and only during late winter and spring. The large orange colored larvae are free swimming and predatory upon the larvae of an unidentified Tanytarsini (Chironomidae). They move rapidly with a wild undulating motion when disturbed. The pupae are motile but remain in the water. Under laboratory conditions these larvae were unable to capture each other or any organisms larger than themselves.

Monopelopia tillandsia was originally found by Beck and Beck (1966) in I. utriculata in Florida. Both Laessle (1961) and Miller (1971) reported unidentified predatory larvae in the closely related genus Pentanura occurring in bromeliads. Laessle (1961) found them in all major collecting areas in Jamaica, but Miller found them to be most abundant in the wet mountains on St. John. Picado (1913) described the orange colored larva of Isoplastus (=Ablabesmyia) costarricensis Picado a Pentaneurini from Costa Rican bromeliads, but its relationship to M. tillandsia cannot be ascertained because of the limited description (Beck and Beck 1966).

Tanytarsini (unidentified) -- Sites 2, 8 and 17

This third chironomid species could not be precisely identified because of the systematic disorder of this tribe. It occurs only in T. utriculata and almost always in association with its predator, M. tillandsia. It is much more numerous than M. tillandsia. More than 1,000 larvae were found in one sample with most samples containing over 100.

The smaller bright red larvae of Tanytarsini strongly adhere to leaf litter and other large particles in the leaf-axil water and appear to graze upon growths of microorganisms. They construct cases out of fecal material and detritus particles that provide protection from their aggressive predator. Under laboratory conditions, Tanytarsini removed from their cases were immediately consumed by M. tillandsia without fail.

Miller (1971) reported an unidentified Tanytarsus sp. (Tanytarsini) as being the most abundant chironomid on St. John, inhabiting both T. utriculata and A. lingulata. Picado (1913) also found an unidentified case-bearing chironomid in Aechmea spp. in Costa Rica.

When Tanytarsini and M. tillandsia are numerous in bromeliads other fauna are much reduced or even absent. The red pigmentation of these chironomids indicates a hemoglobin-oxygen transport system which enables the larvae to survive at low dissolved oxygen levels (Walshe 1950). They are usually found in plants that contain large amounts of leaf litter and other organic debris in their leaf axils, which may increase the associated microbial populations and subsequent oxygen demand to the exclusion of much of the normal aquatic fauna intolerant to low oxygen levels.

Chironomids seem to be major components of bromeliad communities. Miller (1971) found them to be third in abundance in bromeliads on St. John, and Smart (1938) lists chironomids as second in abundance in the large terrestrial tank bromeliad, Brocchinia micrantha, in Guyana. Both Laessle (1961) and Picado (1913) report chironomids to be abundant and widespread in their studies of bromeliad fauna. In Florida, this family comprises one-fourth of the total fauna and is the overall most abundant group found in the bromeliad habitat.

PSYCHODIDAE:

Neurosystasis n. sp. -- Sites 1-12 and 17

This new species of psychodid fly is very common and usually quite abundant in Florida tank bromeliads, averaging 16 larvae per plant from all samples. The larvae are found adhering to the submerged leaf litter on which they presumably feed. They are rather slow moving and frequently rest with their posterior siphons exposed to the surface. The pupae are motile and remain in the water.

This species is closely related to N. amplipenna (Knab) reared from unspecified bromeliads in Cuba by Knab (1913a) who also reported another psychodid Philosepedon fumata (Knab) from unspecified bromeliads in Mexico. Other investigators have found unidentified and probably undescribed psychodids from bromeliads. Laessle (1961) found them in Vriesea sintenisci, Guzmania monostachia, and Hohenbergia sp. in Jamaica. Miller (1971) reported them from T. utriculata and A. lingulata on St. John where they represented only 1% of the total bromeliad fauna. Psychodid larvae also occur in Aechmea nudicaulis in the Atlantic lowlands

in Costa Rica (Fish, unpublished data), as well as in unspecified bromeliads in the central highlands (Picado 1913).

CERATOPOGONIDAE:

Forcipomyia seminole Wirth -- Sites 2, 3-8, 10, 12 and 17

The larvae of F. seminole are widely distributed among Florida tank bromeliads, but never abundant. The average density from all plants sampled was 0.2 larvae per plant, with the greatest density of 7 per plant occurring in 2 samples of T. utriculata.

The spiny larvae resemble small caterpillars in appearance and are usually found adhering to bromeliad leaves in a thin film just above the leaf-axil water. When disturbed they quickly crawl into the water and remain submerged indefinitely. Specimens reared to maturity in the laboratory pupated on the sides of containers within 2 cm above the water.

Forcipomyia seminole has only recently been described from light trap collections near Vero Beach (site 17) and this report represents the only records of its larval habitat. It is closely related to F. pictoni, a widely distributed Neotropical species which breeds in rotting cocoa pods in Costa Rica (Wirth 1976).

Forcipomyia (Warmkeia) n. sp. -- Sites 1-7, 9-11, 15 and 17

This species of Forcipomyia is more common than F. seminole averaging 1.2 larvae per plant in all samples, with a maximum abundance of 16 larvae per plant. The small white larvae resemble chironomids in appearance but are behaviorally different in that they do not freely swim in the water but prefer to adhere to the sides of the containers as do F. seminole.

Forcipomyia is a very large genus of biting midges including both temperate and tropical forms. The larvae are usually terrestrial or semiaquatic and are found associated with decaying plant material such as rotting logs, leaf litter, fruits, etc., but several species have been reported from bromeliads and other water-holding plants (Wirth and Stone 1971, Wirth 1974, 1975).

Other ceratopogonid genera have also been reported from bromeliads. Wirth and Blanton (1968, 1970) reported several species of Culicoides from Guzmania sp. and unspecified bromeliads from Trinidad and Mexico, and Laessle reported predatory Bezzia sp. from Hohenbergia sp. in Jamaica. Picado (1913) reported unidentified ceratopogonid larvae from unspecified Costa Rican bromeliads and Smart (1938) reported them from Brocchinia sp in Guyana. Miller (1971) found ceratopogonids to be abundant in T. utriculata and A. lingulata on St. John, where they comprised over 32% of the total fauna.

SYRPHIDAE:

Meromacrus n. sp. -- Sites 2, 7 and 17

The larvae of Meromacrus n. sp. are relatively uncommon and found only in large specimens of T. utriculata. Although they usually occur singly in a plant, one sample yielded 19 first-instar larvae. Mature larvae are the largest of the bromeliad inhabitants, measuring over 80 cm in length with their breathing tubes fully extended, which may explain their absence from bromeliad species with small leaf-axil volumes. They remain completely submerged in the leaf-axil water, feeding upon settled organic matter with only their long breathing tubes reaching the surface until just before pupation when they leave in search of a dry substrate.

This syrphid has previously been identified as M. ruficrus (Weidemann), but is being described as new by Thompson (personal communication).

Although this is the first report of the larval habitat of Meromacrus n. sp., its distribution records coincide perfectly with the range of T. utriculata in Florida indicating that it may be restricted to this habitat. With the exception of one temperate species, Meromacrus is a Neotropical genus of primarily tree-hole breeding species.

From museum records, Thompson (personal communication) found that 6 syrphid genera have been reported from bromeliads, including Quichuana and Leptomyia which appear to be restricted to this habitat, and another species of Meromacrus from Brazil.

Picado (1913) reported Q. picadoi Knab as uncommon in Costa Rican bromeliads. Various unidentified syrphid larvae represent a small fraction of the total bromeliad fauna in the Virgin Islands (Miller 1971) and Guyana (Smart 1938). In the present study, 38 specimens of Meromacrus n. sp. comprise less than 1% of the total bromeliad fauna in south Florida.

AULACIGASTRIDAE:

Stenomicra n. sp. -- Sites 1-12, 15 and 17

This new species of Stenomicra represents a new family of bromeliad-breeding insects. The small dorso-ventrally flattened larvae with forked tails are predatory upon mosquitoes and possibly also chironomids. They actively crawl upon the submerged leaf surfaces and among the accumulated leaf litter in search of prey. Many specimens were reared to maturity in the laboratory on Wyeomyia mosquito larvae. Development is slow and the pupal stage lasts 19 days (range 18-20, N=5) at 21°C.

Stenomicra n. sp. is never abundant, usually 1-5 per plant, but they are widely distributed and occur in all species of tank bromeliads in Florida.

Stenomicra is a pantropical genus with at least 12 species (Sabrosky 1975) and the larval habits are poorly known. In Hawaii, Swezey (1938) reports S. orientalis (Malloch) larvae as predatory and occurring in the water-filled leaf axils of Job's tear Coix lacrymajobi. This species has subsequently been found in other water holding plants on the island including screw pine (Pandanus sp.), sugar cane, and pineapple (Bromeliaceae) (Williams 1939). Malloch (1927) also reported S. australis Mallock from banana plants in Fiji and Sabrosky (1965) listed S. fascipennis Mallock as being collected from screw pine in Guam. Unidentified Stenomicra larvae have been found in both bromeliad leaf-axils (Vriesea insignis and G. monostachia) and those of elephant ear (Colocasia sp.) in Costa Rica (Fish, unpublished data).

Although other published records indicate that Stenomicra is not restricted to plant-held aquatic habitats, the larvae of these unusual insects may not have been identified by previous workers because of the difficulties involved in rearing, and may be widespread in bromeliads and other similar habitats.

MUSCIDAE:

Neodexiopsis n. sp. -- Sites 1-3, 6-8, 11 and 17

The maggot-like larvae of Neodexiopsis n. sp. usually occur singly within an entire plant sample. They are predatory with piercing mouthparts and were reared to maturity on Wyeomyia mosquito larvae. The pupal stage is long, averaging 18 days at 21°C (range 16-19, N=5). Spiracles

on their blunt posterior ends enable these larvae to leave the water of one leaf axil to search in others for prey. Such behavior was noted in the laboratory when several larvae escaped from their containers after consuming their prey.

Neodexiopsis is a large Neotropical genus containing 65 species (Huckett, personal communication), however, little is known of the biology of the immature stages. Picado (1913) reported an unidentified predatory muscoid larva from bromeliads (Aechmea sp.) in Costa Rica which he placed in the genus Coenosia, a genus from which Neodexiopsis has been recently split (Snyder 1958). Synder (1958) observed that collecting in habitats with moist soil often yields teneral adults of Neodexiopsis spp. which indicates that the immature stages of other species are also aquatic but that the genus is not restricted to bromeliads of other plant-axil breeding sites.

Because they are relatively uncommon and rather difficult to rear Neodexiopsis larvae may not have been identified by previous investigators and may be more widely distributed in bromeliads than the literature indicates.

SCIARIDAE:

Corynoptera n. sp. -- Sites 2-5, 12 and 17

The occurrence of Corynoptera n. sp. in Florida tank bromeliads represents a second new family of bromeliad-inhabiting insects. The larvae of this fungus gnat are only moderately distributed and are never very abundant. The average density in all plants sampled was 0.4 larvae per plant with a maximum of 13 found in a single sample. They are easily mistaken for F. (Harmkeia) n. sp. (Ceratopogonidae) as the larval forms are very similar in size and color.

Corynoptera n. sp. presumably feeds upon fungi growing on the decaying leaf litter accumulated in the bromeliad leaf axils as do the larval forms of most other sciarid flies (Borror and DeLong 1971).

ACARI:

Anoetus n. sp. -- Sites 1, 2, 4-12 and 17

This new species of aquatic mite occurred sporadically among the sites investigated, but when present, it appeared in most or all of the plants sampled with an average density of 9 per plant. These small white mites are found in various stages and are difficult to detect when few in number. They attach to small particles of organic matter and tend to hide in hollow twigs and folds of leaves.

Picado (1913) reports an unidentified aquatic mite in the genus Tyroglyphus found on only one occasion in an unspecified bromeliad species in Costa Rica. Many species formerly in this genus are now placed in the family Anoetidae. It is quite possible that what Picado actually found in Costa Rica was Anoetus. However, he provided no description or illustration to support this assumption.

Anoetidae is a large family of mostly aquatic and semiaquatic mites commonly found associated with dead organic matter (Krantz, 1970). Two species of Anoetus occur in temperate pitcher plants; Anoetus gibsoni (Nesbitt) in Sarracenia purpurea L. and A. hughsi Hunter and Hunter in S. flava L. A terrestrial species of Anoetus has been shown to feed on bacteria (Noble and Poe 1972) and Hunter and Hunter (1964) suggest that A. gibsoni feeds on bacteria associated with decomposing insects in the pitcher plant. Anoetus n. sp. probably has similar feeding habits in bromeliads.

Anoetid mites have a resistant hypopal stage and are transported between favorable habitats by attaching themselves to insects (Hughs and Jackson 1958). Hunter and Hunter (1964) suggest that the pitcher plant mosquito Wyeomyia smithii transports A. gibsoni among the leaves of pitcher plants. Several insects could serve this function in bromeliads in addition to Wyeomyia mosquitoes.

OSTROCODA:

Metacypris maracaoensis (Tressler) -- Sites 3, 5 and 13

This ostracod is abundant in T. fasciculata in the tropical hardwood hammocks of Everglades National Park, averaging over 100 per plant. It is less common in C. floribunda and G. monostachia and rarely found in T. utriculata.

This species was originally described from an unidentified bromeliad in the Big Cypress Swamp of south Florida and had since been reported from unspecified bromeliads in Puerto Rico (Tressler 1956, Maguire 1970). Laessle (1961) found 3 species of ostracods to be abundant in Jamaican bromeliads; M. laesslei (Tressler), M. bromeliarum (Muller), and Candonopsis anisitsi (Daday). Other ostracods reported from bromeliads are C. kingsleii in Puerto Rico (Tressler 1941) and 2 undescribed species from Costa Rica (Picado 1913).

Although distribution data for all of these species are fragmentary, M. bromelarium, M. maracaoensis, and M. laesslei are presently known only from bromeliads. Their method of transport among these relatively isolated aquatic habitats is unknown.

Podocopa (unidentified sp.) -- Sites 3, 9 and 13

An unidentified ostracod frequently occurs with M. maracaensis in the bromeliads of the tropical hardwood hammocks. Since only juvenile forms were found, identification was impossible.

OLIGOCHAETA:

Naididae (unidentified) -- Sites 1-5, 6-10, 12 and 17

Unidentified oligochaet worms are widely distributed among Florida tank bromeliads with an average density of 10 per plant for all samples. They are most numerous in the oak hammocks and cypress swamps where their densities average nearly 50 per plant in T. utriculata, but are rare or absent in tropical hardwood hammocks.

These worms do not form tubes, as do many fresh water forms, and are found buried in the water-saturated detritus of the older leaf axils. Like the chironomids M. tillandsia and Tanytarsini, these oligochaet worms are red, suggesting a hemoglobin-oxygen transport system which would enable them to survive under near-anaerobic conditions.

Picado (1913) reports Aulophorus superterrenus Michlsn. (Naididae) as being very abundant in Vriesea sp. in Costa Rica, and Laessle (1961) reports similar forms in unspecified Jamaican bromeliads.

Very little is known of the ecology or systematics of bromeliad-inhabiting oligochaet worms, and it cannot be determined from the literature if certain groups or species are specific for this habitat.

TURBELLARIA:

(Unidentified)

An unidentified rhabdocoel flatworm is the rarest inhabitant of tank bromeliads in south Florida. One to 5 specimens were consistently

found in samples of 10 T. utriculata from the mangrove swamp in Everglades National Park throughout the year, but were only occasionally found at other sites.

Picado (1913) found Geoplana picadoi Beauchamp, Rhynchodemus bromelicola Beauchamp, R. costarricensis Beauchamp and Geocentrophora metamerooides (Beauchamp) in Costa Rican bromeliads and Laessle (1961) found G. metamerooides (Beauchamp) and G. applanata (Kennel) in Jamaican bromeliads. Although flatworms seem to be common bromeliad inhabitants in the Neotropics, very little is known of their systematics or ecology.

Many turbellarians feed on small aquatic organisms which they trap in mucus secretions (Pennak 1953) and some have been observed to be predatory upon the eggs and larvae of mosquitoes (Jenkins 1964, Medved and Legner 1974). Because of the small size of the species occurring in Florida tank bromeliads, it would probably prey only upon the egg stages of other bromeliad fauna.

It is difficult to compare the species composition of the aquatic fauna inhabiting tank bromeliads in south Florida with what has been reported from bromeliads in the Neotropics. Only the studies of Picado (1913) in Costa Rica and Laessle (1961) in Jamaica attempt to list all of the organisms that were found inhabiting bromeliads; but Picado (1913) also lists terrestrial species which frequently leads to confusion in comparing only the aquatic fauna. Interpretation of his results is further complicated by the name changes that have occurred at various taxonomic levels within the past 60 years which cause serious problems in updating his list with valid species names. Also, many important species are not identified in Picado's study and several insect families are mentioned only by name.

Laessle's (1961) study provides more recent data, but unfortunately, only half of the organisms are identified to species. Maquire (1970) identified only the ostracods in his study of Puerto Rican bromeliads. Miller (1971) identified only the chironomid genera that inhabit the bromeliads of St. Johns. Many other scattered reports on aquatic bromeliad fauna include identification of no more than a few species of special interest to the investigators with only passing mention of the other fauna present.

Precise identifications to the species level are sometimes difficult to obtain since most of the organisms are in immature stages and must be reared to adult usually without any prior knowledge of their feeding habits or pupation requirements. Also the systematics of many major groups, including mosquitoes, are badly in need of revision and willing capable specialists for some of the minor groups are difficult to locate.

However, precise species determination of all inhabiting organisms is essential in studying the origin, evolution, and biogeography of bromeliad-inhabiting invertebrate communities, and in assessing the specificity of the fauna for the bromeliad habitat.

Conclusion

The aquatic invertebrate fauna inhabiting the leaf axils of Florida tank bromeliads is composed of 18 species, most of which are abundant and widely distributed in several bromeliad species. Fourteen invertebrate species have been positively identified, including 7 new species, and 4 species remain unidentified pending the actions of systematic specialists and in some cases the acquisition of additional specimens.

Large invertebrate species such as the predatory mosquito I. r. rutilus and the syrphid fly Meromacrus n. sp. seem to be restricted to the largest bromeliad species T. utriculata, but the size and shape of the bromeliad species seems to be less important than its distribution in determining the species composition of the aquatic inhabitants. Tillandsia utriculata and T. fasciculata are widely distributed throughout south Florida and, although quite different in structure and total plant volume, support the largest numbers of invertebrate species. Other bromeliad species are more restricted to certain plant communities and support fewer inhabitant species.

While direct comparison between the Florida bromeliad fauna and the bromeliad fauna reported from other areas cannot be made to any great extent at the species level, certain conclusions can be drawn from the systematic information that is presently available in the literature.

It is apparent from comparing the results of the present study with those of Picado (1913) and Laessle (1961) that the invertebrate fauna inhabiting tank bromeliads in south Florida is relatively depauperate. Aquatic insects are represented by the single order Diptera in Florida bromeliads while Picado (1913) lists the insect orders Odonata, Hemiptera, Coleoptera, and Plecoptera as well as Diptera from Costa Rican bromeliads. In the Diptera he also lists the families Stratiomyidae, Tabanidae, Tipulidae, Anisopidae, and Borboridae which are not present in Florida bromeliads. Picado's total list of aquatic insects include well over 100 species as compared to 13 in Florida bromeliads.

Laessle (1961), in studying the island bromeliad fauna of Jamaica, reports 3 insect orders and 2 families of Diptera not found in Florida

bromeliads with a total of 33 species of aquatic insects. Both Picado (1913) and Laessle (1961) also report additional species of oligochaet worms, ostracods, turbellarians, and water mites not present in Florida bromeliads.

Many theories could be proposed to account for the depauperate nature of the Florida bromeliad fauna including those reviewed by Pianka (1966) and Baker (1970) relating to increased species diversity in the tropics. Also, in view of the insular nature of subtropical south Florida, theories on island biogeography outlined by MacArthur and Wilson (1967) might also be considered. However, at present too little is known of the ecological roles of the various bromeliad inhabitants or of the evolutionary relationship between the bromeliad fauna of different areas to advance or discredit any of these theories.

There is considerable evidence suggesting that epiphytic tank bromeliads in south Florida support an aquatic fauna derived for the most part from Neotropical ancestors specifically adapted to the bromeliad habitat. Much of the aquatic fauna inhabiting Florida tank bromeliads is systematically related to Neotropical bromeliad fauna reported in the literature. The taxonomic levels of relatedness include 4 species at the species level, 6 species at the generic level, and 13 species at the family level. It is very probable that a closer systematic relationship would become apparent if more species determinations were available for the Neotropical fauna.

The aquatic stages of the Neotropical bromeliad fauna are reported to be exclusively restricted to the bromeliad habitat by Calvert (1911), Knab and Malloch (1912), Champion (1913), Knab (1913b), and Picado

(1913). Specialized morphological adaptations are recognized in bromeliad-inhabiting dragonflies (Calvert and Calvert 1917), crane flies (Alexander 1912), and syrphid flies (Knab 1913c). Although gross morphological adaptations were not observed in any of the Florida bromeliad fauna, it is evident from the existing distribution records that most species exhibit a degree of habitat specificity that is characteristic of Neotropical bromeliad fauna.

Only one identified species, T. r. rutilus, is known to occupy other habitats because of its high incidence in tree holes as reported by Basham et al. (1947) and its low incidence in bromeliads as reported in the present study, this predatory mosquito may be considered an opportunistic colonizer of bromeliads in south Florida. Aquatic stages of the remaining 13 identified species have been found only in bromeliads, including 8 species which have been found only during the course of this study. Since most of these species are widely distributed and frequently abundant in bromeliads, it seems unlikely that they would also occupy alternative aquatic habitats to any great extent and totally escape notice. With the exception of T. r. rutilus, there is no evidence from this study that subtropical or temperate species from other aquatic habitats have adapted to bromeliads in south Florida.

The presence of a diverse aquatic fauna restricted to the widespread but discrete habitat of epiphytic bromeliads provides a unique opportunity to study basic concepts of community ecology such as interspecific interactions, energy flow, and species of diversity as well as the evolution of communities. On a large scale these aquatic communities might be useful in experimental studies of island biogeography in areas

such as the Caribbean Islands and in investigations into the causes of latitudinal gradients in species diversity in continental areas.

Hopefully this study will generate renewed interest in the aquatic communities inhabiting epiphytic bromeliads and foster increased cooperation between field workers and systematicists in establishing a sound systematic basis for future investigations concerning the many evolutionary and ecological aspects of these unusual aquatic communities.

CHAPTER III
FACTORS INFLUENCING THE STRUCTURE OF AQUATIC COMMUNITIES
INHABITING EPIPHYTIC BROMELIADS IN SOUTH FLORIDA

Introduction

Communities of aquatic organisms that inhabit the leaf axils of water-holding tank bromeliads are important components of Neotropical ecosystems. The many epiphytic bromeliad species provide a unique aquatic habitat, elevated and discontinuous from surface waters, and increase the overall spacial heterogeneity of available aquatic habitats for a given land area.

The total water volume contained in these arboreal habitats can be considerable. Hazen (1966) reported densities of 4 bromeliads per meter length of tree branch for water-holding Guzmania sp. at a site in Costa Rica. Mature specimens of G. monostachia hold an average of 180 ml of free water (Fish, unpublished data), and considering a conservative 15% of the total bromeliad population as being mature, the total epiphytic free water for this site is estimated to be over 100 ml per meter length of tree branch. Many larger epiphytic bromeliad species hold vast amounts of water with capacities ranging from 2 liters (Laessle 1961) to over 20 liters (Picado 1913). It would not take many of these large bromeliads to approximate the water volume of a small terrestrial pond.

Picado (1913) first recognized the magnitude of the total aquatic habitat provided by epiphytic bromeliads by equating

them as a whole to a large fractionated swamp extending throughout tropical America.

The aquatic fauna inhabiting epiphytic tank bromeliads is extensive. Nearly all of the major groups of fresh water invertebrates have been reported from this habitat including 6 orders of aquatic insects, snails (*Gastropoda*), crabs (*Decapoda*) as well as tadpoles (*Anuara*) (Calvert 1911, Picado 1913, Laessle 1961). Complete faunal lists are rare but Picado (1913) reported over 130 species of aquatic invertebrates from Costa Rican bromeliads, and Laessle (1961) reported over 60 species from Jamaican bromeliads.

Early investigators of the bromeliad fauna noted that nearly all aquatic species are restricted to this habitat and are distinct from allied forms found in other fresh water environments (Calvert 1911, Champion 1913, Picado 1913). These observations have been subsequently supported by more recent studies, (Laessle 1961, see also Chapter II) although the exact degree of habitat specificity for all bromeliad inhabiting organisms remains to be determined.

The arboreal aquatic habitat provided by epiphytic tank bromeliads and its occupation by a diverse and unique aquatic fauna results in overall increased animal species diversity per unit of land area for many areas in the Neotropics. Previous investigations of the aquatic community inhabiting bromeliads have been primarily descriptive and little is known of its structure and dynamics or of factors that influence species composition. However, Laessle (1961) investigated some of the physical and chemical properties of bromeliad water in Jamaica and found that bromeliads growing in full sunlight supported an algae-based

food chain whereas those growing in shaded situations supported a detritus-based food chain.

The results of a survey of the aquatic fauna associated with epiphytic tank bromeliads in south Florida are presented in Chapter II. This study reports 18 species of aquatic invertebrates inhabiting 6 species of tank bromeliads sampled from 17 site locations. However, all 18 species were never found in a single site, and the average number of species found per site was only 7.6. Samples were taken from different species of bromeliads, at different times of the year, and from a variety of major ecosystems occurring in south Florida. Any or all of these factors may influence the structure and composition of the aquatic community inhabiting the bromeliads. Therefore a special sampling program was initiated to determine the effects upon the community structure (in terms of species composition and abundance) of 1) the bromeliad species providing the aquatic habitat, 2) seasonal changes, and 3) the ecosystem supporting the bromeliad flora.

The subtropical climate of south Florida represents the northern limits for 6 species of epiphytic tank bromeliads which are also widely distributed throughout the Caribbean Islands and Central and South America. Most of the aquatic invertebrate fauna inhabiting these bromeliads are also of tropical origin, including several species that are endemic to south Florida (see Chapter II). However, ecosystems occurring in south Florida are of both temperate (cypress swamps) and tropical origin (mangrove swamps and tropical hardwood hammocks). Despite this mixture of temperate and tropical ecosystems, most forested areas in south Florida support populations of epiphytic tank bromeliads and the

factors influencing the structure of aquatic communities inhabiting bromeliads in subtropical south Florida may be operative throughout the Neotropics as well.

Collecting Sites

Epiphytic tank bromeliads occur in a variety of Florida ecosystems and the species composition of epiphyte communities varies among them. Two species of tank bromeliads, Tillandsia utriculata and T. fasciculata, are particularly abundant and widespread in south Florida and exhibit the least site preference of any of the tank bromeliads. Both species have been shown to support a large and diverse aquatic fauna inhabiting their leaf axils (see Chapter II). The presence of one or both of these species in separate and distinct ecosystems were the major criteria for site selection.

Three study sites were established that met these criteria: 1) a cypress swamp supporting both T. utriculata and T. fasciculata, 2) a mangrove swamp supporting T. utriculata, and 3) a tropical hard wood hammock supporting T. fasciculata. In this manner the effects of the bromeliad species upon the aquatic community structure could be determined at the cypress site, and the effects of the ecosystem could be determined by comparing the community structure of each bromeliad species at the cypress site with either the mangrove site or the tropical hardwoods site.

Cypress Swamp Site

This site is located in the Fisheating Creek Wildlife Management Area, Glades County, which contains a large stand of bald cypress Taxodium distichum extending over 40 km along the Fisheating Creek flood plain. Sampling was restricted to a 1/2-ha area adjacent to

the stream bed about 2 km west of the main campground. This area was chosen because of its large population of both T. utriculata and T. fasciculata. Estimates of their densities ranged from 2 to 12 specimens per tree (average 6.5) with T. fasciculata outnumbering T. utriculata by approximately 4 to 1. Other bromeliads are also abundant at this site, especially T. balbisiana and T. usneoides which do not hold water.

Mangrove Swamp Site

This site is located adjacent to the Flamingo road near Snake Bight Trail in Everglades National Park. White mangrove Laguncularia racemosa and buttonwood Conocarpus erecta occur in a nearly continuous strand along the embankment of the road in this area as well as in small clumps distributed throughout the surrounding batis marsh. Tillandsia utriculata is abundant along several km on both sides of the road and in the many tree clumps in the batis marsh. However, sampling was restricted to an approximate 100 m length of the roadside strand where epiphyte densities are the highest, and T. utriculata occurs at an average density of 1.5 plants per tree. Other epiphytes are common and include T. fasciculata, T. flexuosa, T. pruinosa, and orchids (Epidendrum spp.).

Tropical Hardwood Hammock Site

Clapp's Hammock is located 1.5 km north of the Missile Base road in Everglades National Park. It is typical of the 125 or more tropical hardwood hammocks in the pinelands area of the Park that develop on slightly higher elevations of limestone rock (Craighead 1971). Clapp's Hammock is relatively small (1/2 ha) but supports a large

population of T. fasciculata at densities of approximately 3 plants per tree and is less than 200 m from a much larger hammock supporting an equivalent epiphytic flora.

Tropical hardwood hammocks of this region support a mixture of tropical and temperate trees such as live oak Quercus virginiana, gumbo limbo Bursera simaruba, poisonwood Metopium toxiferum, mahogany Swietenia mahogani, and dove plum Coccoloba diversifolia. Other epiphytes are abundant and include T. valenzuelana, T. setacea, and Epidendrum spp.

Sampling Program

Epiphytic tank bromeliads provide natural sampling units and a series of plants provide replicate samples of the aquatic community inhabiting the bromeliads in a particular site. Each collection consisted of 10 specimens each of T. utricularia and 10 of T. fasciculata from the cypress site and 10 of T. utricularia from the mangrove site. Only 5 T. fasciculata were sampled on each occasion from the tropical hardwoods site because of the possible adverse effects that plant removal might have upon the total bromeliad fauna occurring in this relatively small area.

All 3 sites were visited within 2 weeks at 3-month intervals from September 1974 to June 1975, so seasonal changes in community structure could be determined throughout one complete year.

Sampling procedures and the processing of invertebrate fauna are described in detail in Chapter II and will only be summarized here. Bromeliads could not be sampled in a truly random fashion but were collected evenly throughout each site using tree-climbing spurs when necessary to obtain specimens above reach from the ground. The plants

were removed from their attachment sites and the aquatic fauna contained in each was washed from the leaf axils. Each sample was kept in a separate labelled plastic bag during storage and transportation. In the laboratory all aquatic organisms found in each bromeliad sample were identified and the numbers of individuals in each species counted to determine the community structure represented in each sample. Protozoa and Aschelminthes (rotifers and nematodes) were not efficiently sampled by the methods employed and were consequently eliminated from the study. The replicate samples from each bromeliad species and each site were averaged to represent a total community structure for each collecting occasion.

Analytical Methods

Satisfactory and readily available methods of comparing the structure of biological communities have recently been developed as a result of applying ecological data to numerical analytical techniques introduced by Sokal and Sneath (1963). Numerical methods are frequently employed in comparative studies of plant communities (Whittaker 1962, 1973; McIntosh 1967), but their application in the analysis of animal communities has been less common (Clifford and Stephenson 1975).

Numerical methods are particularly useful in defining assemblages of organisms and relating these assemblages to environmental or biotic factors. Stephenson et al. (1970, 1974) successfully used numerical methods in relating recurring groups of marine benthic fauna to differences in physical characteristics of bottom sediments in Moreton Bay, Australia, and Fager and McGowam (1963) were able to associate groups of zooplankton with differences in water mass types in the North Pacific. Using similar methods, Kikkawa (1968) was able to demonstrate

that bird communities of similar species composition in Eastern Australia were associated with structurally similar plant formations. Because of their proven usefulness in determining species groups which can be related to other factors, numerical methods were employed to analyze the collection data from the bromeliad samples.

Numerical analysis of ecological communities involves 2 procedures. The first procedure is to measure similarities (or dissimilarities) among collections of organisms, and the second is to organize or classify the collections on the basis of their similarities (or dissimilarities).

Methods of comparing the structures of biological communities have only been recently adopted in ecological studies. Previously species composition in terms of presence and absence data was the only criteria used in measuring similarity between communities, and measures such as Jaccard's Co-efficient (Jaccard 1908) and Sorenson's Index (Sorenson 1948) were used to quantify comparisons (Odum 1950, Kikkawa 1968, Roback et al. 1969). While these measures are still successfully used in plant ecology (Williams et al. 1970, Goodall 1973), these measures are frequently unsatisfactory in studies of animals because they ignore the relative abundance of each species present among the communities to be compared.

Some animals, and especially insects, are extremely motile and the presence of one individual in a community is not always ecologically meaningful, but would carry the equivalent weight of hundreds or thousands of individuals in terms of presence or absence data. Furthermore, measures based on presence and absence data from communities of very

similar species composition but drastically different in abundance would provide little information as to their true likeness.

To gain the most information from the sampling efforts, both species composition and abundance were used in the analysis of bromeliad communities. Euclidean distance was adopted as a dissimilarity measure using species abundances as attributes (Clifford and Stephenson 1975). Distances were calculated by the equation:

$$D = \left[\sum_{j=1}^n (x_{ij} - x_{ik})^2 \right]^{1/2}$$

where x_{ij} = the number of individuals in species i of communities j and k .

The community structure data was standardized as a percent of the total for each collection and reduced to exclude species that comprised less than 0.5% of the total fauna for all collections. Justification and details on data reduction and standardization can be found in Clifford and Stephenson (1975). The collection data were arranged on a 9×16 matrix (Table V) and euclidean distances were calculated among the 16 collections in terms of the abundances of 9 species.

In the second procedure the community collections were arranged in a hierachial classification based on euclidean distances. This procedure is available in the preprogrammed Statistical Analysis System (SAS) (Barr et al. 1976) which was employed in the analysis. The cluster procedure performs a hierachial cluster analysis based on an algorithm outlined by Johnson (1967). Clusters are formed using the furthest-neighbor technique (Sneath and Sokal 1973). This SAS program is particularly convenient because it also computes euclidean distances for the cluster analysis. The resulting dendrogram (Figure 4)

shows the relationship between entities (communities) based upon attributes (species and abundance) in terms of dissimilarity.

Results and Discussion

Five of the 18 species of aquatic invertebrates known to occur in Florida tank bromeliads did not occur in any of the 3 sampling sites. An additional 4 species were rare, each representing less than 0.5% of the total fauna collected and were excluded from the analysis in the data reduction process. A total of 9 species of aquatic organisms were used in the final analysis (Table IV). The data matrix (Table V) of the mean abundance for each species in each of the 16 collections represents a total of over 13,000 organisms.

The cluster analysis of euclidean distance dissimilarity measures among the 16 collections (Figure 4) shows that the greatest differences in community structure occurred among the 3 sites. The sites did not cluster until a fusion level of 1.27 was reached, almost twice the distance of the highest seasonal clustering at 0.70. Seasonal differences were greater in mangrove and cypress sites at fusion levels of 0.69 and 0.71, respectively, than in the tropical hardwood site at fusion level 0.22. The community structures contained in T. utriculata and T. fasciculata show the least difference among the 3 factors considered. Tillandsia utriculata fused with T. fasciculata in the spring, summer, and fall at the 0.20 level before fusing with T. fasciculata in the winter at 0.38.

It is evident from this analysis that the ecosystem supporting the bromeliad flora has a greater effect upon the structure of the

aquatic community inhabiting the bromeliads than does either season or bromeliad species. Although microclimate may have some effect upon the aquatic community, the major factor to be considered is the nutrient input to water contained in the bromeliads.

Epiphytic bromeliads intercept dissolved nutrients leached by rain from the above forest canopy as well as allochthonous leaf litter, which are impounded within the inflated leaf axils (Tukey 1970b, Benzing and Renfrow 1974). This pool of dilute nutrients and decomposing leaf litter is ultimately utilized by the plant through foliar absorption (Benzing 1970b, Benzing and Burt 1970), but these substances also serve as nutrient sources for the inhabiting aquatic fauna. Nutrients leached from forest canopies vary both quantitatively and qualitatively among both temperate and tropical ecosystems (Tukey 1970a, b, Bernhard-Reversat 1975) and impoundments of these nutrients within bromeliad leaf axils will certainly reflect these differences. Likewise, both the quantity and quality of leaf litter entering tank bromeliads will affect the chemical and nutrient composition of the leaf-axil water. The amount and rate of leaf litter accumulation will vary among different ecosystems depending upon tree species composition and especially between deciduous and evergreen forests. Also, the material leached from the decomposing leaf litter will vary among ecosystems depending upon tree species composition (Nykvist 1962).

Although canopy leachates (throughfall) and leaf litter were not measured during this study, it can be assumed that significant differences in both the quantity and quality of these materials exist among the 3 different ecosystems studied.

Differences in structure of the aquatic community inhabiting bromeliads are likely the result of differences in nutrient input. All of the aquatic fauna inhabiting tank bromeliads in south Florida seem to be detritus feeders (see Chapter II). Dissolved nutrients from both throughfall and leaf litter decomposition provide a substrate for the growth of bacteria and protozoa (Parsons and Seki 1970, and Slater 1954), which are in turn food sources for mosquito larvae and ostracods (Yonge 1928 and Clements 1969). Particulate leaf litter also serves as a substrate for microbial growths which are in turn grazed by other aquatic organisms (Kaushik and Hynes 1968), although many aquatic insects feed directly upon particulate leaf litter (Cummins 1973).

The chemical and nutrient composition of streams in both temperate and tropical ecosystems are also influenced by throughfall and leaf litter from surrounding forests (McCall 1970, Reichle 1975, Soli 1975) which directly affect the structures of inhabiting invertebrate communities (Nelson and Scott 1962, Minshall 1967). In this respect aquatic communities of bromeliads and those of streams are quite similar in trophic structure and energy flow because both communities are trophically dependent upon an outside source of detritus. However, the aquatic communities inhabiting bromeliads are likely to be much more sensitive to changes in ecosystems than stream communities because of their closer proximity to the nutrient source.

The cluster analysis also shows differences in the structure of the aquatic community inhabiting bromeliads at different seasons in both the mangrove and cypress sites. These seasonal changes may be due to seasonal changes in nutrient input. Cypress trees are deciduous

and provide a massive input of leaf litter in the fall months (Carter et al. 1973) and thereafter throughfall nutrients would be unavailable to the bromeliads until the spring growth provides new leaves. Mangrove ecosystems have a period of maximum leaf litter production but also maintain leaves throughout the year. Tropical hardwood hammocks are predominately evergreen and produce relatively constant inputs of both throughfall and leaf litter which may explain the greater seasonal similarities among the community structure of bromeliads inhabiting the ecosystem.

It is difficult to separate the climatic factors from the biological characteristics of each ecosystem in explaining the seasonal variation in community structure. Rainfall and temperature obviously have some effect upon the aquatic organisms because of the pronounced cool dry season (November to April) and the warm wet season (May to October) in south Florida. Seasonal variation in rainfall would influence the rates of throughfall input as well as the total water volumes available to the aquatic organisms. Water volumes were not measured at the time of collection, but water was observed to be permanently maintained in the bromeliad leaf axils at all sites throughout the year.

Seasonal variation in temperature may also affect the aquatic fauna directly. Low temperatures will prolong the development times of the aquatic stages, and light frosts may kill a certain proportion of the adult insect populations resulting in a temporary population decline. Marked seasonal variation in the number of adult bromeliad-bred *Wyeomyia* mosquitoes was observed at the cypress site with maximum

adult populations appearing in midsummer. Adults were rare in the winter months although larval populations were still high, and the area had been subjected to a series of frosts during this time. However, mosquito larval populations completely disappeared from bromeliads at the mangrove site during the winter with no frost having occurred in the area during the entire winter.

Tropical hardwood hammocks tend to buffer temperature extremes and are warmer in the winter and cooler in the summer than the surrounding area (Craighead 1971) which may also have contributed to the increased stability observed in the aquatic community inhabiting the bromeliads in this site.

The species of bromeliads supporting the aquatic community seems to have less influence upon community structure than either seasons or ecosystems. This is indicated by fusion of the *T. utriculata* community with that of *T. fasciculata* at a lower level than that at which the seasonal fusions occurred. The 2 bromeliad species differ markedly in both size and structure. *Tillandsia utriculata* holds an average maximum water volume of 300 ml with each leaf axil holding an average of 3.1 ml, whereas *T. fasciculata* holds a maximum average of 60 ml with an average leaf axil volume of only 1.5 ml (see Chapter II). But despite these size differences both bromeliad species contain aquatic communities which are structurally very similar.

Leaf-axil size may actually be more important in determining the community structure than this analysis indicates. The two largest insect species inhabiting Florida tank bromeliads seem to be restricted

to I. utricularia in other areas (see Chapter II) but these are rare and did not occur in any of the study sites. Leaf-axil size is a significant factor in the distribution of Odonata and large Coleoptera among Costa Rican bromeliads (Fisa, unpublished data) and may have a greater influence upon community structure in the Neotropics where there is more diversity in the size and shape of bromeliads than in south Florida.

Conclusion

The numerical analysis of the composition and abundance of the aquatic invertebrate species inhabiting the epiphytic tank bromeliads in south Florida indicates that community structure is more characteristic of the ecosystem supporting the bromeliad flora than the species of bromeliad that supports the community. This implies that the relationship between the aquatic fauna and the bromeliad host plant is not as specific as phytophagous arthropod-plant relationships. Although the fauna inhabiting bromeliad leaf axils seem to be specific for bromeliads there is little evidence that this specificity occurs at the level of bromeliad species. It appears that the aquatic fauna has adapted to a unique epiphytic habitat provided by the Bromeliaceae and occupy all suitable water-holding forms regardless of the bromeliad species.

The significance of throughfall and leaf litter accumulation in determining the structure of the aquatic communities inhabiting bromeliads may have further implications in understanding the structures of other heterotrophic aquatic communities such as those that inhabit rot holes in trees, artificial containers, and small ground pools.

Conceivably these communities would be similarly affected by differences in quantity and quality of nutrient input. It is apparent that a more thorough understanding of ecosystem nutrient cycles is essential in understanding the ecology of the many small but important aquatic communities that populate both temperate and tropical forests.

Table 1. Insect prey recovered from *C. berteroiana* leaf-axils over 8 days (29 June to 2 July) at Gainesville, Florida.

Insect Order	Plant Number				Total
	1	2	3	4	
Hymenoptera	6	5	4	13	28
Diptera	6	12	4	4	26
Lepidoptera	4	8	4	3	19
Coleoptera	9	2	2	5	18
Homoptera	2	3	1	2	8
Neuroptera	0	0	2	0	2
Arachnida	1	0	1	0	2
Hemiptera	0	0	1	0	1
Orthoptera	1	0	0	0	1
Total	29	30	19	27	105

Table II. Summary of site descriptions and collecting data of bromeliad samples from south Florida

Site No.	Location	Description	Species	Date(s)
1	Fishheating Creek Wildlife Management Area, 1.5 km west of campgrounds	Cypress Swamp	<i>I. utriculata</i> (40)*	7 Sep 74, 14 Dec 74, 22 Mar 75, 21 Jun 75
			<i>I. fasciculata</i> (40)	7 Sep 74, 14 Dec 74, 22 Mar 75, 21 Jun 75
2	Schewy's Hammock, 10 km west of Vero Beach ^t	Palm-Maple Hammock	<i>I. utriculata</i> (30)	6 Feb 74, 31 Aug 74, 30 Nov 74
			<i>I. fasciculata</i> (10)	30 Nov 75
3	Everglades National Park 1.5 km northeast of Myrarez Pond	Buttonwood-Mangrove Swamp	<i>I. utriculata</i> (40)	14 Sep 74, 2 Jan 75 22 Apr 75, 21 Jul 75
4	Everglades National Park, Clapp's Hammock	Tropical Hardwood Hammock	<i>I. fasciculata</i> (?)	15 Sep 74, 2 Jan 75, 22 Apr 75, 22 Jul 75
5	Homestead, Fuchs Hammock Sanctuary	Tropical Hardwood Hammock	<i>C. berteroiana</i> (5)	10 Aug 74
			<i>C. floribunda</i> (5)	10 Aug 74
6	8 km west of North Port Charlotte east of US 41	Oak Hammock	<i>G. monostachya</i> (5)	10 Aug 74
			<i>I. utriculata</i> (10)	21 Jul 74
7	Highlands County, 5 km north of SR 70; on south side SR 29	Bay Swamp	<i>I. utriculata</i> (10)	1 Sep 74
8	Christmas, south side US 50	Bay Swamp	<i>I. utriculata</i> (10)	25 Jun 74
9	9 km, S.W. Homestead, south side SR 27	Tropical Hardwood Hammock	<i>I. utriculata</i> (10)	29 Jun 74
			<i>I. fasciculata</i> (10)	29 Jun 74
10	Collier-Seminole State Park south side US 41	Oak Hammock	<i>I. utriculata</i> (10)	9 Aug 74
			<i>I. fasciculata</i> (10)	9 Aug 74
11	Ponce Inlet, 13 km, south of Daytona Beach	Oak Hammock	<i>I. utriculata</i> (10)	17 Oct 74
12	US 441, 16 km, southwest of West Palm Beach	Cypress Swamp	<i>I. fasciculata</i> (10)	22 Sep 75
13	Everglades National Park 1.5 km north of site Base Rd.	Scrub Buttonwood	<i>C. berteroiana</i> (10)	2 Jan 75, 26 Oct 75
14	Everglades National Park 13 km north of Mahogany Hammock	Scrub Mangrove	<i>C. berteroiana</i> (5)	23 Apr 75
15	Collier County, Jct. US 41 and SR 94	Custard Apple Swamp	<i>I. valenzuelana</i> (10)	23 Mar 75
16	Collier County, south bend on SR 94 (Loop Rd.)	Custard Apple Swamp	<i>I. valenzuelana</i> (10)	4 Jan 75
17	Vero Beach, Fla. Medical Entomology Lab.	Oak hammock	<i>I. utriculata</i> (50+)	8 Feb 74, 24 Mar 75

^{*} Total samples indicated by numbers in ().^t Destroyed by fire February 1975

Table III. Distribution of aquatic invertebrates within 6 species of Florida tank bromeliads

Bromeliad species	Tillandsia utriculata	T. fasciculata	Catopsis berteroiana	C. floribunda	Guzmania monostachia	T. valenzuelana
Ave. total volume (cc)	300	60	129	64	180	35
Ave. no. leaves	37	40	13	25	43	22
Ave. vol. per leaf axil (cc)	8.1	1.5	10	2.5	4.2	1.6
No. specimens sampled	220+	90	20	5	5	20
<u>Wyeomyia mitchelli</u>	X	X		X		
<u>W. vanduzei</u>	X	X	X			
<u>Toxorhynchites r. rutilus</u>	X					
<u>Metriocnemus abdominalis</u>	X	X	X	X	X	X
<u>Monopelopia tillandsia</u>	X					
Tanytarsini (unidentified)	X					
<u>Neurosystasis</u> n. sp.	X	X	X	X	X	
<u>Forcipomyia seminole</u>	X	X				
<u>F. (Warmkeia)</u> n. sp.	X	X	X	X	X	X
<u>Meromacrus</u> n. sp.	X					
<u>Stenomicra</u> n. sp.	X	X	X	X	X	X
<u>Neodexiopsis</u> n. sp.	X	X				
<u>Corynoptera</u> n. sp.	X	X			X	
<u>Anoetus</u> n. sp.	X	X	X			
<u>Metacypris maracaoensis</u>	X	X	X		X	
Podocopa (unidentified)	X		X	X		
Naididae (unidentified)	X	X	X	X		
Turbellaria (unidentified)	X					
Total species	18	12	9	7	6	3

Table IV. List of aquatic invertebrate species included in the analysis.

Species Number	Species
1	Culicidae: <u>Wyeomyia mitchelli</u> (Theob.)
2	Culicidae: <u>W. vanduzeei</u> (D.&K.)
3	Aulacigastridae. <u>Stenomicra</u> n. sp.
4	Psychodidae: <u>Nuerosystasis</u> n. sp.
5	Chironomidae: <u>Metriocnemus abdominalisflavatus</u> Picado
6	Ceratopogonidae: <u>Forcipomyia (Warmkeia)</u> n. sp.
7	Anoetidae: <u>Anoetus</u> n. sp.
8	Oligochaeta: Naididae (unidentified)
9	Ostracoda: <u>Metacypris maracaensis</u> Tressler

Table V. Two-way coincidence table showing abundances of aquatic invertebrate species (with species numbers) within bromeliad species at 3 sites and 4 seasons.

Tropical

* 1 = spring; 2 = summer; 3 = fall; 4 = winter.

[†] Species abundances represent means for 10 samples in cypress and mangrove sites and 5 samples in the tropical hardwoods site.

Species names corresponding to species numbers appear in Table IV.

Figure 1. Visible and UV light photographs of bromeliads illuminated by natural sunlight.

- A. Visible light photograph of insectivorous C. berteroiana.
- B. UV light photograph of same specimen showing strong reflectance by white powder on the leaf bases.
- C. UV reflecting powder also provides a lubricated leaf surface which prevents insects from escaping the leaf axils.
- D. UV light photograph of T. utriculata, a typical noninsectivorous tank bromeliad showing no UV reflecting leaf surface.

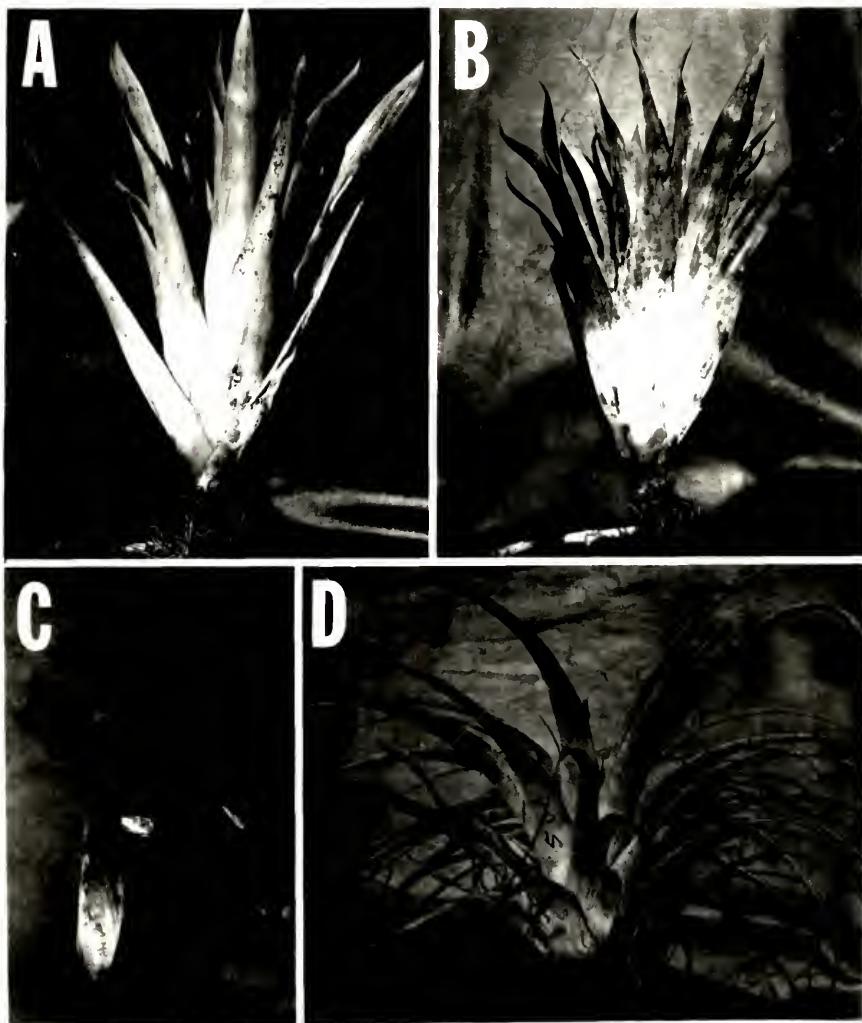


Figure 2 Locations of bromeliad collection sites in Florida

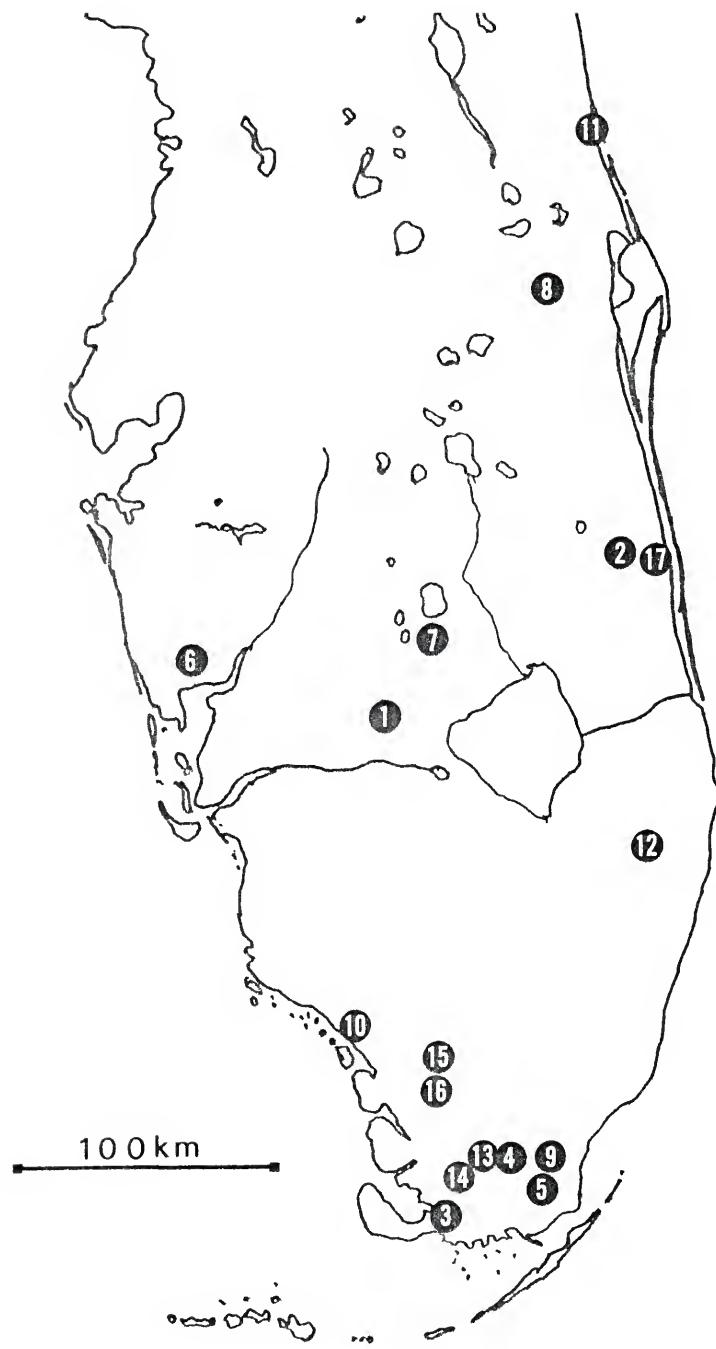
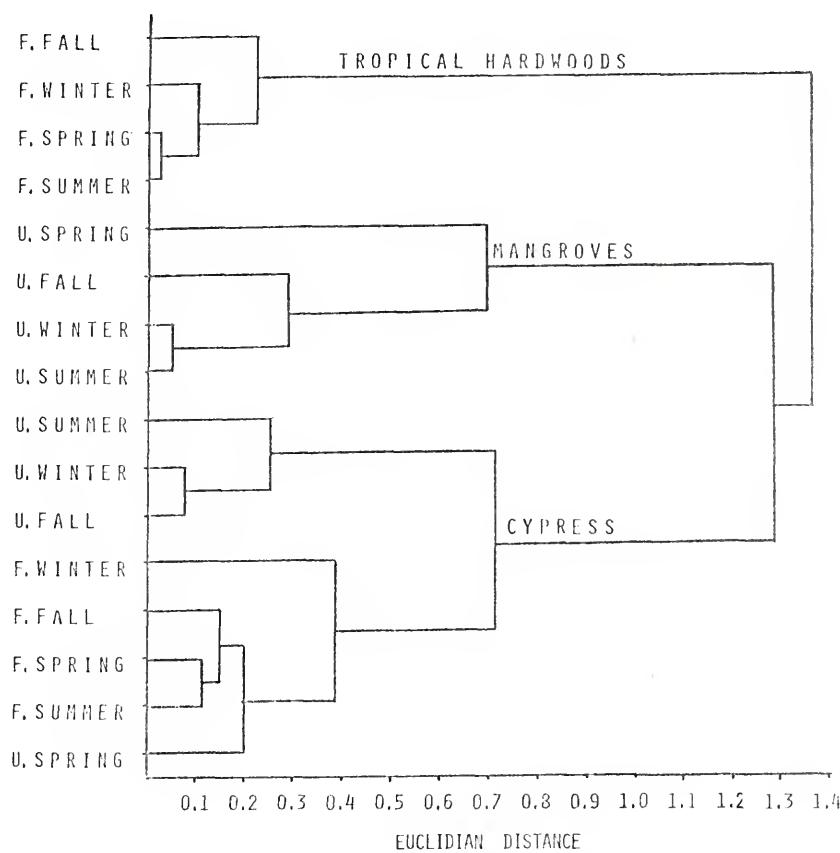


Figure 3. Sagittal (A) and cross-sections (B) of T. utriculata showing inflated leaf axis that form water-holding chambers.



Figure 4. Cluster analysis of euclidian distances among structures of the aquatic community inhabiting 2 bromeliad species ($U = T. utriculata$, $F = T. fasciculata$) at different times of the year and in 3 major south Florida ecosystems.



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APPENDIX
COLLECTION DATA USED IN THE CLUSTER ANALYSIS IN CHAPTER III

	<u>Wyeomyia mitchelli</u>							
	<u>W. vanduzeei</u>							
	<u>Toxorynchites r. rutilus</u>							
	<u>Metriocnemus abdominalisflavatus</u>							
	<u>Forcipomyia seminole</u>							
	<u>F. (Warmkeia) n. sp.</u>							
	<u>Neurosyntaxis n. sp.</u>							
	<u>Corynpotera n. sp.</u>							
	<u>Stenmicra n. sp.</u>							
	<u>Neodexiopsis n. sp.</u>							
	<u>Anoetus n. sp.</u>							
	<u>Metacypris maracaensis</u>							
	<u>Naididae</u>							
	<u>Turbellaria</u>							
<hr/>								
Fisheating Creek								
<u>T. utriculata</u>								
7 SEP 74								
Plant no.	141	4	2	64	4			
	142	11	27	19				
	143	25	70	3				
	144			148				
	145	2	9	47				
	146	7	16	40				
	147	7	13	40				
	148	21	47	36				
	149	1	16	48				
	150	34	89	60				
<hr/>								
14 DEC 74								
Plant no.	221	106	101	34				
	222	15	9	46				
	223	7	5	34				
	224	21	30	58				
	225			44				
	225	4	4	133				
	227	6	2	19				
	228	33	104	161				
	229	22	10	15				
	230	4	12	64				
				37				

APPENDIX CONTINUED

APPENDIX CONTINUED

		<u>Wyeomyia mitchelli</u>	<u>W. vanduzeei</u>	<u>Toxorhynchites r. rutilus</u>	<u>Metriocnemus abdominalisflavatus</u>	<u>Forcipomyia seminole</u>	<u>F. (Wamkea) n. sp.</u>	<u>Neurosympsis n. sp.</u>	<u>Coryncptera n. sp.</u>	<u>Sternomicro n. sp.</u>	<u>Neodexiopsis n. sp.</u>	<u>Anoetus n. sp.</u>	<u>Metacypris maraccensis</u>	<u>Naididae</u>	<u>Trubellaria</u>
ENP Mangrove Site															
T. utriculata															
14 SEP 74															
Plant no.		165	5	125			112			1		76			
		166		41			50								
		167	4	28		3	28		2	1		12			
		168		24			23								
		169	6	72		4	37		2						
		170	17	141		3	70	1		3					
		171	3	49			36			5					
		172	7	52		2	44			1	1	96			
		173	3	26		3	32		1						
		174		16		3	22		2						
2 JAN 75															4
Plant no.		251					18					12			
		252	4	1			92					4			
		253	3	168		1	149			1	36				
		254		35		5	109				28				
		255		13			77			1					
		256		3			38		1			4			
		257	3	74		3	84			1	1				
		258		38		4	101		1			4			
		259		1		1	29								
		260					4								
22 MAR 75															
Plant no.		331					37								
		332					25								
		333					12								
		334				1	15								
		335					38								
		336				7	6					2			
		337				1	163								
		338				8	6					8			
		339					25					1			
		340					52					8			

APPENDIX CONTINUED

	<u>Wyeomyia mitchelli</u>	<u>W. vardouzei</u>	<u>Toxorhynchites r. rutilus</u>	<u>Metricnemus abdominalis</u>	<u>Metricnemus flavatus</u>	<u>Forcipomyia seminole</u>	<u>F. (Warnecka) n. sp.</u>	<u>Neurolystasis n. sp.</u>	<u>Corynoptera n. sp.</u>	<u>Stenomicra n. sp.</u>	<u>Neodexiopsis n. sp.</u>	<u>Anoetus n. sp.</u>	<u>Metacypris maracaensis</u>	
21 JUL 75														
Plant no.	411	2	44					62	26		1	4		
	412		10			2	1	36						
	413		1	13				24				12		
	414		1	19			1	62	7					
	415		3	12				80		4				
	416			27				70	4					
	417		1	14				8	14			32		
	418			19				25	2					
	419		1	6				15	3	1				
	420		12	53				88	1		1			
Tropical Hardwoods														
15 SEP 74														
Plant no.	175	7												
	176	1					1					64		
	177	6				4	11					8		
	178	9					1					40		
	179	3								1		80		4
2 JAN 74														
Plant no.	261				39							248		
	262				11				4			132		
	263				4							188		
	264											84		
	265		1					8		4		40		
22 MAR 75														
Plant no.	341											20		
	342											648		
	343											52		
	344											8		
	345							4				12		
21 JUL 75										1				
Plant no.	421							1			1		164	
	422		5						5				260	
	423		4						7				56	
	424		4							1			56	
	425		1						4				192	

Naididae

Turbellaria

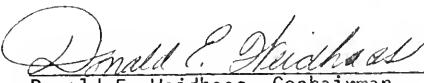
BIOGRAPHIC SKETCH

The author was born on November 23, 1944, in Berwick, Pennsylvania and graduated with a B.S. Degree in Biology with a Chemistry minor from Albright College, Reading, Pennsylvania in 1966. From 1966 to 1970 he was employed by the Pennsylvania Department of Environmental Resources where he served for one year as County Health Officer and three years as Regional Vector Control Coordinator. He received an M.S. Degree in Entomology from the University of Massachusetts, Amherst in 1973.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality as a dissertation for the degree of Doctor of Philosophy.


Dale H. Habeck
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Professor Entomology

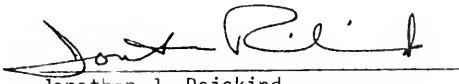
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality as a dissertation for the degree of Doctor of Philosophy.


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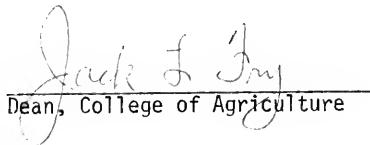
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