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INVERTEBRATE ANIMALS EXTRACTED FROM NATIVE *TILLANDSIA* (BROMELIALES: BROMELIACEAE) IN SARASOTA COUNTY, FLORIDA

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ABSTRACT

Twenty four epiphytic bromeliads belonging to four species (*Tillandsia fasciculata* Swartz, *T. recurvata* (L.), *T. setacea* Swartz, and *T. utriculata* L.) were collected in Sarasota County, Florida, in October-November 1997. Macroscopic invertebrate animals were extracted from each by washing in water, filtering, and preserving in 75% ethanol. Plant sizes were measured in several ways, and their substrate was identified. Invertebrates were sorted, counted, and identified as far as possible to the species level. Two species (*T. fasciculata*, *T. utriculata*) that impound water in their leaf axils housed aquatic dipteran larvae and pupae (Psychodidae, Culicidae, Ceratopogonidae, Chironomidae, Muscidae, and Aulacigastridae) representing 7 species in 6 genera. Only *T. utriculata* had a clear relationship between plant size and number of invertebrates, which was steeper when only aquatic insect larvae were counted. Plants of all four species housed terrestrial invertebrates, representing minimally an additional 82 species in 75 genera and 63 families, very few of which are known to have an obligate relationship with bromeliads, but showing that these plants support a diverse invertebrate fauna. The presence of ant nests in some bromeliads complicated analysis. Such a list of terrestrial invertebrates, identified to the species level, has not before been compiled for bromeliads in Florida. Some collaborating taxonomists obtained specimens of species that they could not identify, including probably undescribed species.

Key Words: Bromeliads, phytotelmata, insects, *Tillandsia utriculata*, bromeliad inhabitants

RESUMEN

Se colectaron 24 bromeliáceas epífitas que pertenecen a cuatro especies (*Tillandsia fasciculata* Swartz, *T. recurvata* (L.), *T. setacea* Swartz, y *T. utriculata* L.) en el Condado de Sarasota, Florida, durante octubre-noviembre de 1997. Se extrayeron los animales invertebrados macroscópicos de cada planta lavándola en agua y filtrando, seguido por preservación de los especímenes en etanol de 75%. Se midieron los tamaños de las plantas por varios parámetros, y se identificó su sustrato. Los invertebrados se ordenaron, contaron e identificaron tanto posible al nivel de especie. Las dos especies (*T. fasciculata*, *T. utriculata*) que embalsan agua entre sus axilas de hojas alojaron larvas y pupas acuáticas de moscas (Psychodidae, Culicidae, Ceratopogonidae, Chironomidae, Muscidae y Aulacigastridae) representando 7 especies en 6 géneros. Solo *T. utriculata* tuvo una relación clara entre tamaño de planta y cantidad de invertebrados, la cual fue más fuerte cuando se contaron solamente las larvas de insectos acuáticos. Plantas de las cuatro especies alojaron invertebrados terrestres, representando un mínimo de 82 especies adicionales en 75 géneros y 63 familias, muy pocas de las cuales se conocen tener una relación obligada con bromeliáceas, pero demuestran que estas plantas sostienen una diversa fauna de invertebrados. La presencia de nidos de hormigas en algunas bromeliáceas complicó el análisis. Tal lista de invertebrados terrestres, identificados al nivel de especie, no ha sido recopilado anteriormente para bro-

meliáceas en Florida. En este proyecto, varios taxónomos obtuvieron especímenes no-identificados, incluyendo especies probablemente no-descritas.

Translation provided by the authors.

Bromeliads (Bromeliaceae) are a family of at least 2500 species of monocotyledonous plants, almost restricted to the Neotropical region, but including all of Mexico and southernmost USA. The complex architecture of some species traps water in leaf axils (forming phytotelmata) and harbors many species of invertebrate animals. There are thus three types of associations of invertebrates with these plants: (a) those that feed on the plants, (b) organisms aquatic at least in their immature stages, and (c) those terrestrial organisms for which bromeliads provide concealment, humidity, or prey (Frank 1983). Within all three groups are specialists, associated only with bromeliads, as well as generalists that occupy similar (non-bromeliad) habitats.

Four approaches have been followed in attempts to unravel the mysteries of bromeliad fauna. They may be termed (i) brief reports of new discoveries, (ii) in-depth studies (behavioral or ecological or taxonomic) of selected taxa, (iii) whole-fauna inventories, and (iv) broad-scale hypothesis tests. Major difficulties with the last two approaches are the need to involve teams of specialist taxonomists, and of distinguishing transient species from those that have some kind of obligate or at least usual relationship with bromeliads.

In Florida, an inventory of the macroscopic aquatic invertebrate fauna in bromeliad tanks (phytotelmata) is contained in an unpublished Ph.D. dissertation (Fish 1976). A little of the content of that work was reviewed in Frank (1983). An introduction to, and a bibliography of, studies of the fauna and microflora of bromeliad phytotelmata, in Florida and abroad, are WWW-published (Frank 1996 a, b). A complete illustrated key to all developmental stages of all aquatic invertebrates in bromeliad phytotelmata in Florida cannot now be prepared because some species are yet undescribed (unknown to science). In contrast, there are only 16 native species of bromeliads in Florida, identifiable by color photographs online as part of Frank & Thomas (1996) or (for the more botanically adept) by a key in Wunderlin (1998).

In Florida, there has been one inventory of the entire invertebrate fauna in the bromeliad *Tillandsia utriculata* L. (Sidoti 2000), but most of its identifications reached only the level of order. There are works on some insects that feed on and harm bromeliads. Detection of a moth, whose larvae destroy pods of the bromeliad *Tillandsia fasciculata* Swartz, led to a publication about larvae of several moths that occasionally are collected from native bromeliads in Florida (Heppner & Frank 1998). Detection of a Mexican weevil, *Metamasius callizona* (Chevrolat), in Florida led

to several publications about bromeliad-eating weevils, reviewed and augmented by Frank (1999) and expanded in two webpages (Larson & Frank 2000; Larson et al. 2001) and two websites (Frank & Thomas 1996; Larson 2000). Notable studies in other countries are by Picado (1913) in Costa Rica, and Beutelspacher (1971a, b) and Palacios-Vargas (1981, 1982) in Mexico.

The Marie Selby Botanical Gardens (MSBG), Sarasota, Florida, have an "Intern Program." Under this program, students interested in plant ecology and other aspects of botany are brought from elsewhere to conduct a short-term (few months) research project in one of these subjects. Margaret Lowman (Research Director, MSBG) and Sheeba Sreenivasan (an intern from Trinidad and Tobago) in 1997 designed a project that was to be a quantitative examination of the invertebrate fauna associated with native bromeliads in Sarasota County. One of us (JHF) was asked to visit MSBG to explain to Sheeba how to extract invertebrates from bromeliads and preserve them for examination, and also to receive her in his laboratory and provide her with literature that would help her to make preliminary identifications of the invertebrate specimens. These were limited to insects, arachnids, myriapods, molluscs, annelids, and the larger crustaceans. Further development depended upon specialist taxonomists to take the preliminary identifications as far as possible to the species level.

In November 1997, Sheeba visited JHF's laboratory at the University of Florida, and used a leaf-area-area meter for about 3 days to measure the leaf-areas of the bromeliads she had collected. To help complete the project, he sorted Sheeba's specimens, some to family, but others only to the level of order. He provided genus- or species-level identification of the immature mosquitoes and a few other dipteran larvae with which he was familiar and, much later, drafted a manuscript for review by the other contributors. All the remaining specimens had to be sent to specialist taxonomists for reliable identification, and the contacts were made and specimens shipped before the end of 1997. Fortunately, taxonomists of the Florida State Collection of Arthropods (FSCA) were receptive to providing help. Here is an account of these invertebrates. This account recognizes the essentiality of the contributions of several taxonomists, who were offered co-authorship (some declined).

MATERIALS AND METHODS

Twenty four bromeliads were collected from sites in Sarasota County, principally from old-

growth hammocks in the Myakka River State Park, and secondarily two sites in Sarasota. They were removed from various substrates including living trees, dead trees (snags), and a gate (Table 1). While it was being collected, each plant was kept as upright as possible to prevent spillage. The plant was then placed into a polyethylene bag and briefly sprayed with insect repellent before fastening the bag.

Invertebrates were extracted from bromeliads by a variant of the method of Frank et al. (1976). Each plant was cleaned with a jet of water from a hose, with the washings directed into a bucket. The plant was repeatedly submerged and shaken in the bucket before being returned to its bag. The water in the bucket was then filtered with a tea-strainer (mesh size 500 μm) and the residue examined for invertebrates with a dissection microscope. Collected invertebrates were preserved in vials containing 75% ethanol for subsequent identification.

The collected bromeliads included whole specimens of the epiphytic species *Tillandsia utriculata*, *T. fasciculata*, *T. setacea*, and *T. recurvata*. These include all the most widespread of Florida's 16 native species except *T. usneoides* (L.). Only the first two of these impound water in leaf axils, and they do this only when they have reached a certain minimal size (exceeded by the specimens). The volumetric capacity of the water-impounding leaf axils of *T. utriculata* has been related to length of longest leaf and to age (in one habitat) by Frank & Curtis (1981), so length of longest leaf was one of the measurements made (Volumetric capacity in ml = $0.003251 \times \text{leaf length in cm}^{2.7799}$). Other measurements were made by dismantling each plant, leaf by leaf, starting from the outermost and working inward. This was done on a white background to facilitate detection of any remaining invertebrates. A component part was considered to be either a leaf or an infructescence (the fruiting phase of an inflorescence). Each element was further designated as live or dead. Each bromeliad's live and dead leaves were counted. All components were refrigerated until leaf and infructescence areas were measured with an area meter (LI-COR Portable Area Meter, model LI 3000, LI-COR Inc., Lincoln, NE, USA). They were then oven-dried for 48 hr before weighing. Table 1, which lists the measurements, is thus a habitat description rather than results.

RESULTS

Table 2 lists the invertebrates collected to the level of family (with number of specimens) for each of the 24 bromeliads sampled. Identification of the invertebrates to the species level, where possible, is given below. Comments are made where deemed appropriate. Three vials containing Mollusca and four with Thysanoptera were

misplaced somewhere in the Florida State Collection of Arthropods; details of their contents would not substantially change the conclusions.

Mollusca

None was identified. The three missing vials (6 specimens) may be located in FSCA. No mollusc has a known, obligate relationship to bromeliads. However, H. E. Luther (pers. comm.) has observed snails eating bromeliad trichome caps in the field and greenhouse. Assume minimally one family, one genus, and one species.

Isopoda (identified by G. B. Edwards)

Oniscidae: genus and species unidentified (17 specimens).

Rhyscotidae: genus and species unidentified (9 specimens).

Diplopoda (identified by G. B. Edwards)

Chilognatha: family and genus unidentified, species 1 (12 specimens), species 2 (1 specimen).

Pselaphognatha: Polyxenidae: *Polyxenus fasciculatus* (Say) (5 specimens).

These were collected from all three *Tillandsia* species in MRSP. They have no known relationship to bromeliads. All of the Chilognatha were immature, so could not be identified reliably.

Chilopoda (identified by G. B. Edwards)

Lithobiidae: *?Neolithobius* sp. (1).

This immature specimen was collected from *T. utriculata* in MRSP. It has no known relationship to bromeliads.

Araneae (identified by G. B. Edwards)

Segestriidae: *Ariadna bicolor* (Hentz) (2).

Theridiidae: *Phoroncidia americana* (Emerton) (1 immature), ?genus (1 immature).

Mysmenidae: *Mysmenopsis cymbia* Levi (10).

Linyphiidae: *Ceraticelus ?phylax* Ivie & Barrows (1 female).

Tetragnathidae: *Dolichognatha pentagona* (Hentz) (1), *?D. pentagona* (1 immature, damaged), *?Tetragnatha* sp. (2 immatures).

Lycosidae: ?genus (2 immatures).

Pisauridae: *?Dolomedes* sp. (1 immature).

Agelenidae: *?Agelenopsis* sp. (1 immature).

Hahniidae: *Hahnina okefinokensis* Chamberlin & Ivie (1).

Dictynidae: *Emblyna capens* Chamberlin (1), *Emblyna* sp. (2 immature), *Lathys delicatula* Gertsch & Mulaik (2).

Anyphaenidae: *Lupettiana mordax* (O.P. Chamberidge) (1).

Liocranidae: *Scotinella pintura* (Ivie & Barrows) (3), *Scotinella* sp. (1 immature).

TABLE 1. BROMELIAD MEASUREMENTS (NUMBER OF LIVE LEAVES, DEAD LEAVES, LONGEST LEAF, AREAS OF LIVING AND DEAD LEAVES, OF LIVING AND DEAD INFRACTESCENCES, AND DRY WEIGHTS) MATCHED TO SAMPLE NUMBER (CODE), SUBSTRATE ON WHICH IT GREW, AND IDENTIFICATION.

Code	Substrate	No. live leaves	No. dead leaves	Longest leaf (cm)	Live leaf area (cm ²)	Dead leaf area (cm ²)	Live infr. area (cm ²)	Dead infr. area (cm ²)	Dry wt (g)
<i>Tillandsia fasciculata</i>									
8	<i>Cephalanthus</i>	64	4	58.4	2621.99	60.18	0	0	57.5
9	<i>Cephalanthus</i>	65	20	62.0	2794.81	316.20	0	0	71.5
10	<i>Cephalanthus</i>	51	11	46.4	898.86	66.24	0	0	21.5
15	snag	55	13	44.5	2002.08	199.07	0	0	33.0
17	<i>Ulmus</i>	33	3	44.5	881.81	44.55	0	0	10.5
18	fallen branch	55	2	22.8	350.46	37.23	0	0	6.5
19	rooted in soil	58	10	29.2	475.15	27.79	0	0	11.5
20	<i>Quercus</i>	76	13	55.4	5006.87	371.90	0	0	189.5
<i>Tillandsia utriculata</i>									
1	snag	41	6	32.0	531.62	38.44	0	0	8.0
2	snag	56	29	46.5	1793.91	237.25	0	0	32.0
3	snag	55	22	33.0	824.92	63.65	0	0	11.5
4	snag	62	11	17.9	164.69	14.34	0	0	2.5
16	<i>Quercus</i>	60	12	91.1	9285.81	909.66	0	0	147.0
24	<i>Quercus</i>	59	11	93.3	7350.48	0	0	0	152.5
<i>Tillandsia recurvata</i>									
21	<i>Sabal</i>	1140	71	10.1	672.1	48.60	0	0	10.5
22	wooden gate	80	1	9.3	51.69	2.37	6.02	0	1.0
23	<i>Quercus</i>	537	58	13.5	305.72	82.25	34.36	23.00	5.0
<i>Tillandsia setacea</i>									
5	snag	196	82	19.0	151.37	62.86	0	0	3.5
6	snag	349	24	18.6	236.57	17.15	0	0	3.0
7	snag	158	22	27.2	210.06	27.90	28.20	5.58	8.0
11	<i>Cephalanthus</i>	419	63	32.1	556.39	60.18	67.68	7.97	16.5
12	<i>Cephalanthus</i>	338	29	28.9	437.23	62.32	18.87	16.13	9.5
13	<i>Cephalanthus</i>	81	34	23.5	185.37	36.46	26.92	0	3.0
14	<i>Quercus</i>	379	32	29.8	298.02	18.81	4.93	5.33	8.5

Clubionidae: *Clubiona pygmaea* Banks (3), *Clubiona* sp. (1 immature), *Elaver excepta* (L. Koch) (10).

Gnaphosidae: *Litopyllus cubanus* Bryant (1), *Sergiolus* sp. (1 immature).

Sparassidae: *Pseudosparianthis cubana* Banks (1 immature).

Thomisidae: *Bassaniana floridana* (Banks) (1), *Bassaniana* sp. (4 immatures).

Salticidae: *Anasaitis canosa* (Walckenaue) (2).

The spiders seem to represent 21 species, in 21 genera and 17 families. For only one spider (*Pelegrina tillandsia* [Kaston]) is a bromeliad (*Tillandsia usneoides*) in the southern USA known to be the preferred habitat. In the Neotropical region, however, other spiders typically inhabit bromeliads and even are semi-aquatic in bromeliad leaf axils.

Pseudoscorpiones (identified by G. B. Edwards)

Chthoniidae: genus and species unidentified (2 immatures).

One specimen was from *T. fasciculata* and the other from *T. setacea*. They were unidentifiable because immature. Pseudoscorpions have no known obligate relationship to bromeliads.

Acari (identified by W. C. Welbourn)

Liodidae: *Liodes* sp. 1 (16), *Liodes* sp. 2 (13), *Liodes* sp. 3 (3).

Ascidae: *Lasioseius* sp. (2).

Haplozetidae: genus and species unidentified (1).

Oripodidae: genus and species unidentified (1).

Uropodidae: *Uropoda* sp. (2).

Oppliidae: genus and species unidentified (1).

Orbataloid: genus and species unidentified (1).

Histiostomatidae: *Hormosianoetus* sp. (37).

None of these 10 species in 8 genera and 8 families is known to have any obligate relationship with bromeliads. There is a pressing need for more basic taxonomic work on Floridian Acari other than those of economic importance; only then will specimens be identifiable to the species level.

TABLE 2. ORIGIN (CODE/PLACE) OF *TILLANDSIA* SPECIMENS AND NUMBERS OF ARTHROPODS EXTRACTED, TO FAMILY LEVEL. ALL WERE COLLECTED IN MID-OCTOBER TO MID-NOVEMBER 1997 IN SARASOTA COUNTY, FL.

CD/PL	Fauna to level of family, and number of specimens	Sum
<i>Tillandsia fasciculata</i>		
08/ M	CRUSTACEA: Isopoda: Rhyscotidae (2), ARACHNIDA: Araneae: Theridiidae (1), Mysmenidae (10), Hahniidae (1), Liocranidae (1), INSECTA: Homoptera: Aphididae (1), Lepidoptera: Tineidae (larvae, 1), Diptera: ?Muscidae (larva 1), Hymenoptera: Formicidae (1)	19
09/ M	ARACHNIDA: Araneae: Tetragnathidae (1), Dictynidae (1), Liocranidae (1), Clubionidae (2), Salticidae (1), INSECTA: Isoptera: Kalotermitidae (4), Blattodea: Blattellidae (2), Psocoptera: Lepidopsocidae (nymphs 2), family indet. (nymphs 2), Diptera: ?Muscidae (larva 1), Hymenoptera: Formicidae (1)	18
10/ M	CRUSTACEA: Isopoda: Rhyscotidae (6), ARACHNIDA: Araneae: Linyphiidae (1), Age-lenidae (1), Clubionidae (2), Acari: Uropodidae (1), INSECTA: Orthoptera: Gryllidae (3), Psocoptera: Lepidopsocidae (1), Archipsocidae (1), Peripsocidae (2), family indet. (1), Coleoptera: Tenebrionidae (1), Hymenoptera: Formicidae (1)	21
15/ M	DIPLOPODA: Pselaphognatha: Polyxenidae (1), ARACHNIDA: Araneae: Segestriidae (1), Pisauridae (1), Acari: Histiostomatidae (19), INSECTA: Thysanoptera (1), Psocoptera: Lepidopsocidae (1), Orthoptera: Gryllidae (2), Coleoptera (larvae 3, of 3 families), Diptera: Psychodidae (larvae 32), Culicidae (larva 1), Ceratopogonidae (larvae 3)	65
17/ M	CRUSTACEA: Isopoda: Rhyscotidae (1), DIPLOPODA: Chilognatha: family indet. (1), ARACHNIDA: Araneae: Clubionidae (2), Pseudoscorpionida: Chthoniidae (1), INSECTA: Blattodea: Blattellidae (4, and one egg case), Lepidoptera: family indet. (larvae 5), Coleoptera: Carabidae (larva 1), Diptera: Ceratopogonidae (larva 1)	17
18/ M	ARACHNIDA: Araneae: Anyphaenidae (1), Thomisidae (1), Salticidae (1), Acari (?1), INSECTA: Orthoptera: Gryllidae (1), Coleoptera: Scirtidae (1), Hymenoptera: Formicidae (1)	7
19/ M	CRUSTACEA: Isopoda: Oniscidae (3), DIPLOPODA: Pselaphognatha: Polyxenidae (3), Pselaphognatha: family indet. (3), ARACHNIDA: Araneae: Lycosidae (2), INSECTA: Blattodea (egg case 1), Homoptera: Ortheziiidae (1), Coleoptera: Brentidae (1), Hymenoptera: Formicidae (128 plus brood), Ichneumonidae (2)	144
20/ M	MOLLUSCA (3), CRUSTACEA: Isopoda: Oniscidae (10), ARACHNIDA: Araneae: Dictynidae (1), Sparassidae (1), INSECTA: Blattodea: Blattidae (1), Orthoptera: Gryllidae (1), Lepidoptera: family indet. (larva 1), Diptera: Psychodidae (larvae 2), Ceratopogonidae (larvae 8, pupae 2) Chironomidae (larvae 4), Aulacigastridae: (larva 1, pupa 1)	36
<i>Tillandsia utriculata</i>		
01/ M	ARACHNIDA: Araneae: Dictynidae (1), Acari: Liodidae (1)	2
02/ M	CRUSTACEA: Isopoda: Oniscidae (2), DIPLOPODA: Chilognatha: family indet. (5), ARACHNIDA: Araneae: Tetragnathidae (1), Liocranidae (2), Clubionidae (1), Acari: Ascidae (2), INSECTA: Blattodea: Blattellidae (1), Psocoptera: Pseudocaeciliidae (1), Liposcelidae (1), family indet. (nymph 1), Diptera: Ceratopogonidae (larva 1), Psychodidae (larvae 16), Hymenoptera: Formicidae (5)	39
03/ M	DIPLOPODA: Pselaphognatha: Polyxenidae (1), ARACHNIDA: Araneae: Clubionidae (1), Thomisidae (1), INSECTA: Psocoptera: Caeciliusidae (1), Archipsocidae (1), Liposcelidae (1), Lepidopsocidae (nymph 1), family indet. (nymph 1), Blattodea: Blattidae (2), Homoptera: Coccidae (1), Coleoptera: Curculionidae (3), Diptera, Ceratopogonidae (larvae 2)	16
04/ M	DIPLOPODA: Chilognatha: family indet. (2), ARACHNIDA: Araneae: Clubionidae (1), Thomisidae (2), Acari: Liodidae (1), INSECTA: Blattodea: Blattellidae (2), Coleoptera: Curculionidae (1), Diptera: Chironomidae (1)	10
16/ M	CHILOPODA: Lithobiidae (1), DIPLOPODA: Chilognatha: family indet. (1), ARACHNIDA: Acari: Histiostomatidae (18), INSECTA: Blattodea: Blattidae (1), Psocoptera: family indet. (1 nymph), Thysanoptera (2), Lepidoptera: family indet. (larva 1), Diptera: Psychodidae: (larvae 108, pupa 1), Culicidae: (larvae 28), Ceratopogonidae (larvae 47), Chironomidae (larvae 3), Aulacigastridae: (5), Cecidomyiidae (adults 2, pupa 1), Hymenoptera: Formicidae (6)	226
24/ S	ARACHNIDA: Araneae: Dictynidae (1), Gnaphosidae (1), INSECTA: Collembola: Entomobryidae (22), Psocoptera: Trogiidae (2), family indet. (nymph 1), Coleoptera: Coccinellidae (1), Diptera: Psychodidae (larvae 31), Hymenoptera: Formicidae (76, of 2 spp., each with brood)	135
<i>Tillandsia recurvata</i>		
21/ S	INSECTA: Psocoptera: Lepidopsocidae (1), Coleoptera: Elateridae (1), Hymenoptera: Formicidae (2)	4
22/ S	No animals were collected	0

TABLE 2. (CONTINUED) ORIGIN (CODE/PLACE) OF *TILLANDSIA* SPECIMENS AND NUMBERS OF ARTHROPODS EXTRACTED, TO FAMILY LEVEL. ALL WERE COLLECTED IN MID-OCTOBER TO MID-NOVEMBER 1997 IN SARASOTA COUNTY, FL.

23/ S	MOLLUSCA (1), ARACHNIDA: Araneae: Gnaphosidae (1), INSECTA: Hemiptera: Miridae (nymphs 2), Psocoptera: Trogiidae (1), Hymenoptera: Formicidae (1)	6
<i>Tillandsia setacea</i>		
05/ M	Diplopoda: Pselaphognatha: Polyxenidae (1), ARACHNIDA: Acari: Liodidae (4), Haplozetidae (1), Oripodidae (1), INSECTA: Psocoptera: Peripsocidae (1), Archipsocidae (1 nymph), Lepidopsocidae (1 nymph), Orthoptera: Gryllidae (1)	11
06/ M	ARACHNIDA: Araneae: Clubionidae (2), Thomisidae (1), Acari: Liodidae (9), INSECTA: Psocoptera: Peripsocidae (2), Homoptera: Aphididae (4), Hymenoptera: Aphelinidae (1)	19
07/ M	MOLLUSCA (2), ARACHNIDA: Araneae: Segestriidae (2), INSECTA: Blattodea: Blatellidae (2), Lepidoptera: family indet. (larvae 2), Hymenoptera: Formicidae (52)	60
11/ M	ARACHNIDA: Araneae: Dictynidae (1), Clubionidae (1), Acari: Liodidae (2), INSECTA: Thysanoptera (1), Coleoptera: Scirtidae (1)	6
12/ M	ARACHNIDA: Araneae: Theridiidae (1), Tetragnathidae (2), Thomisidae (1), Acari: Liodidae (2), Oppiidae (1), 'orbataloid' (1), Pseudoscorpionida: Chthoniidae (1), INSECTA: Collembola: Hypogastruridae (5), Thysanoptera (2), Psocoptera: Peripsocidae (nymph 1), Hymenoptera: Formicidae (1)	18
13/ M	CRUSTACEA: Isopoda: Oniscidae (2), ARACHNIDA: Araneae: Clubionidae (1), Acari: Liodidae (13), INSECTA: Psocoptera: Liposcelidae (1), Diptera: Cecidomyiidae (1)	18
14/ M	ARACHNIDA: Araneae: Clubionidae (1), Acari: Uropodidae (1), INSECTA: Lepidoptera: Gelechiidae (larva in flower) (1), Hymenoptera: Formicidae (1)	4

Notes: CD = code number (collection no.)/PL = place (M = Myakka River State Park, S = Sarasota). SUM = total number of invertebrate animals of the groups sampled. Presence of immature stages suggests that development was taking place in the bromeliad unless the individuals fell from the tree above.

Collembola (identified by R. J. Snider)

Entomobryidae: *Seira steinmetzi* Wray (22).
Hypogastruridae: *Xenylla* sp. (5).
The specimens of *Xenylla* represent an undescribed species and were retained by R. J. Snider.

Orthoptera (identified by T. J. Walker)

Gryllidae: *Cycloptilum trigonipalpus* (Rehn & Hebard).
All 8 specimens of Orthoptera were identified as of this species or were unidentifiable because immature, but probably belong to this species. Seven of them were collected from *T. fasciculata* and one from *T. setacea*, all within MRSP.

Blattodea (identified by M. C. Thomas)

Blattellidae: *Cariblatta* sp. prob. *lutea* (Sausure & Zehnter) (12).
Blattidae: *Eurycotis floridana* (Walker) (4).
Neither species has any known obligate relationship with bromeliads.

Isoptera (identified by R. H. Scheffrahn)

Kalotermitidae: *Cryptotermes ?cavifrons* Banks (4).
No termite is known to have an obligate relationship with bromeliads. Most likely these had fallen from a dead tree limb.

Psocoptera (identified by E. L. Mockford)

Trogiidae: *Cerobasis guestfalica* (Kolbe) (4).
Lepidopsocidae: *Echmepteryx* (*Thylacopsis*) *madagascariensis* (Kolbe) (3), *Echmepteryx* sp. (1), *Nepticulomima* sp. (1), unidentified nymphs (4).
Liposcelidae: *Liposcelis ornata* Mockford (1), *Liposcelis* sp. (2).
Archipsocidae: *Archipsocus* sp. (2), unidentified nymphs (1).
Peripsocidae: *Peripsocus* sp. (5).
Caeciliusidae: *Valenzuela indicator* (Mockford) (= *Caecilius indicator* Mockford) (1).
Pseudocaeciliidae: *Pseudocaecilius citricola* (Ashmead) (1).
Epipsocidae: *Mesepipsocus niger* (New) (3), unidentified nymphs (4).
None of these 12 species in 9 genera and 8 families is known to have an obligate relationship to bromeliads. As in so many other groups, it is difficult to identify nymphs reliably to the species level. The surprise among these specimens was the finding of specimens of *C. guestfalica* from two *Tillandsia* specimens (*T. recurvata*, *T. utriculata*) from the city of Sarasota; it is an adventive species.

Thysanoptera

None was identified. The four missing vials (6 specimens) may be located in FSCA. Assume minimally one family, one genus, and one species.

Hemiptera/Homoptera (identified by S. E. Halbert)
(Ortheziidae by A. B. Hamon)

Miridae: unidentified nymphs.

Aphididae: *Myzocallis* sp. (4), unidentified genus (1 cast skin).

Ortheziidae: *Orthezia* sp. (1 nymph).

Coccidae: genus and species unidentified (1 adult male).

The *Myzocallis* aphids are known to feed on oak; one of the specimens was parasitized by *Aphelinus* sp. (Hymenoptera: Aphelinidae) (det. G. A. Evans, FSCA). The only species of *Orthezia* reported from *Tillandsia* in Florida is *O. tillandsiae* Morrison, but the specimen obtained (from *T. fasciculata* in MRSP) is immature and could not be identified with certainty. The Miridae were unidentifiable because they were immature.

Coleoptera (identified by M. C. Thomas)

Scirtidae: *Ora* sp. (1), *Cyphon* sp. (1).

Elateridae: *Conoderus amplicollis* (Gyllenhal) (1).

Tenebrionidae: *Glyptotus cribratus* LeConte (1).

Brentidae: *Apion* sp. (1).

Curculionidae: *Acalles clavatus* Say (3); *Conotrachelus maritimus* Blatchley (2).

Larvae of Scirtidae are aquatic. It is possible that the two adults of Scirtidae are associated with bromeliad phytotelmata, but both specimens were found in *T. setacea*, which does not form phytotelmata. Alternatively, their larvae may develop in treeholes. Specimens mislaid include one adult of Coccinellidae and several beetle larvae, of which one is of Carabidae.

Lepidoptera (identified by D. H. Habeck)

Tineidae: genus and species unidentified (1 larva).

Gelechiidae: genus and species unidentified (1 larva).

Family uncertain: (8 larvae).

Lepidoptera were represented only by larvae of "primitive" families. Their identification was uncertain. It is not clear whether these larvae were feeding on bromeliads, on debris in the bromeliads, or on the tree canopy (or epiphytes) above. The gelechiid larva was found clinging to a flower (which was not a bromeliad flower) in the bromeliad, but there is no evidence it was feeding on that flower. There is a clear need to rear lepidopteran larvae encountered in bromeliads, to allow identification of adults and associate larvae with adults.

Diptera (identified by J. H. Frank)

(Cecidomyiidae by R. J. Gagné, Ceratopogonidae by G. J. Steck)

Cecidomyiidae: *Campylomyza* sp. (1 adult), *Lestodiplosis laticaulis* Gagné (2 adults and 1 pupa).

Psychodidae: *Alepiea* sp. (190 larvae and pupae).

Culicidae: *Wyeomyia mitchellii* (Theobald) (25 larvae), *W. vanduzeei* Dyar & Knab (3 larvae).

Ceratopogonidae: *Forcipomyia* sp. or spp. (62 larvae, 2 pupae)

Chironomidae: *Monopelopia tillandsia* Beck & Beck (53 larvae), (1 damaged unidentified adult).

Aulacigastridae: *Stenomicroa* (7 larvae).

?Muscidae: genus and species unidentified (2 larvae) (perhaps this is the *Neodexiopsis* sp. of Fish [1976]).

Specimens of Cecidomyiidae were shipped in vials of alcohol to R. A. Gagné; he found both species interesting and retained one specimen of each. He reports that *L. laticaulis* is known as a predator of *Diaspis echinocacti* (Bouché) (Homoptera: Diaspididae) a scale insect on *Opuntia* cacti—so its presence in *T. utriculata* is unexpected. Larvae of Psychodidae, Culicidae, many Ceratopogonidae, Chironomidae, and Aulacigastridae are aquatic and, expectedly, were found only in *T. fasciculata* and *T. utriculata*. Identification of these larvae was made by J. H. Frank (who makes no claim to be an expert on larvae of Diptera), either by prior experience (larvae of *Wyeomyia* mosquitoes), by use of keys to larvae of Chironomidae (Epler 2001), or (for the other families) according to the brief descriptions by Fish (1976). Although 27 years have passed since Fish (1976) reported his collections, the "*Neurosystasis*" (Psychodidae) and "*Stenomicroa*" (Aulacigastridae) occurring in Florida bromeliads have not yet been formally described. G. J. Steck (FSCA) questioned the name *Neurosystasis* (he identified them as belonging to *Telmatoscopus*) and suggested contacting Larry W. Quate (Poway, California), a specialist in the family. Quate requested adult specimens reared from field-collected larvae in order to make a precise identification and, if necessary, prepare a formal description. Thereupon, JHF (with help from M. M. Cutwa and G. F. O'Meara, Florida Medical Entomology Laboratory, Vero Beach) obtained larvae from bromeliads in southeastern Florida and provided them to G. J. Steck who from them reared a few adults and shipped them to Quate in 1999-2000. Quate reported that they represent the first Nearctic record for a member of the genus *Alepiea*, and he was pleased to see the associated larvae. Tragically, Larry Quate died in January 2002. It should be fairly easy to obtain more larval specimens and rear more adults to replace those unreturned by his estate.

Hymenoptera (ants identified by M. A. Deyrup)

Formicidae: *Camponotus floridanus* (Buckley) (2), *Camponotus planatus* Roger (26), *Crematogaster ashmeadi* Mayr (64), *Paratrechina longicornis* (Latreille) (50), *Pheidole megacephala* (Fabricius) (5), *Pheidole moerens* Wheeler (129).

Ichneumonidae: genus and species unidentified (2) (det. L. A. Stange, FSCA).

Aphelinidae: *Aphelinus* sp. (1) (see under Hemiptera and Homoptera).

Ant nests with brood were detected in *T. utriculata* (*C. planatus* and *P. longicornis*), *T. fasciculata* (*P. moerens*), and *T. setacea* (*C. ashmeadi*). The other ant specimens doubtless were foraging from nests elsewhere. It has long been known that ants will nest in the dry, outer leaf axils of bromeliads such as *T. fasciculata* and *T. utriculata* that hold water in their inner axils. One plant of *T. utriculata* in Sarasota provided space for nests of two species: *C. planatus* and *P. longicornis*. *Paratrechina longicornis*, *P. megacephala*, *P. moerens*, and *C. planatus* are adventive species.

Ants were identified from *Tillandsia* spp. in various Neotropical countries and Florida by Wheeler (1942). However, the *Tillandsia* were not identified to species level, nor were the localities in Florida nor dates of collection specified.

Table 2 arranges the collection data by sample number, with invertebrates identified to the level of family. This arrangement was designed to allow extraction of numerical data for statistical analysis. However, the Table suggested few patterns that would yield useful analysis. To further complicate the table by including species names would have been unwieldy.

A simple analysis was made by contrasting the content of the three smallest with three largest plants within each species (Tables 1 and 2), a valid statistical method. For *T. fasciculata* the smallest plants were nos. 17, 18, and 19 (with 17, 7, and 144 invertebrates). The three largest were 8, 9, and 20 (with 19, 18, and 36 invertebrates). The presence of an ant nest in plant 19, with 128 adult ants was the cause of the high count in a small plant. Even if all data for ants were omitted, the evidence for relationship of plant size to number of invertebrates would have been negligible.

For *T. utriculata*, the three smallest plants were 1, 3, and 4 (with 2, 16, and 10 invertebrates), and the three largest were 2, 16, and 24 (with 39, 226, and 135 invertebrates). In plant 24, ants accounted for 76 of the invertebrates. Whether or not we exclude data for ants, the largest plants clearly have more invertebrates, and these were mainly aquatic dipteran larvae (Ceratopogonidae, Culicidae, and Psychodidae; except in plant 24). If we exclude ants and aquatic insect larvae, the three smallest plants had 1, 14, and 9 invertebrates whereas the three largest had 17, 28, and 28; again there is a relationship between plant size and number of invertebrates, but it is shallower than when including the aquatics. If we include only the aquatic invertebrates, then the 3 smallest plants had 0, 2, and 1 invertebrates, whereas the three largest had 17, 191, and 31; the larger plants clearly had many more, but variance is huge. We might expect that the number of

aquatic dipteran larvae would best be associated with volumetric capacity of bromeliad axils (calculated from length of longest leaf). But intraplant variance in numbers of contained invertebrates warns us that the fitting of regressions will suffer from high sums-of-squares errors. The presence of ant nests adds greatly to variance.

For the three *T. recurvata* plants sampled, the number of invertebrates was not related to plant size. For *T. setacea*, the three smallest plants were 5, 6, and 13 (with 11, 19, and 18 invertebrates) and three largest were 11, 12, and 14 (with 6, 18, and 4 invertebrates); there was no relationship of plant size to number of invertebrates.

DISCUSSION AND CONCLUSION

The total number of invertebrates in leaf axils of *T. utriculata* was related to plant size, but the number of aquatic insect larvae increased more strongly with plant size. The numbers of invertebrates were not or not clearly related to plant size in the other three bromeliad species, although such a relationship is something that would be expected given a very large number of samples (because larger plants provide more habitat). Data in Tables 1 and 2 could be the materials for hundreds of regression analyses, should anyone wish to do these.

This study scratches the surface of Florida's bromeliad fauna. It reaffirms that larvae of several aquatic Diptera (Psychodidae, Culicidae, Ceratopogonidae, Chironomidae, Muscidae, and Aulacigastridae), perhaps one species of scale insect (Ortheziidae), and perhaps one or more species of Lepidoptera (Tineidae and/or Gelechiidae) have an obligate relationship with bromeliads. The null hypothesis for all the remaining species is that they "just happened to be there" and may additionally be found in tree canopies or in leaf litter on the ground. This null hypothesis cannot now be tested for lack of studies of the canopy fauna or the leaf litter fauna in Myakka River State Park.

This in no way discounts the importance of bromeliads as habitat for large numbers of invertebrate species: how many other small plants have such a diversity of invertebrates? At least 70 families with 82 genera and 90 species are represented in the few (24) samples. Further sampling should yield very many more species (and genera and families) at least in Coleoptera, and perhaps some other orders, including species that just happen to be represented in the bromeliads at the time of sampling.

If sampling is to be repeated, this should be (a) with very many more samples to allow more replication and thus a more useful comparison between the faunas of the four bromeliad species, (b) with prior agreement (probably involving funded written subcontracts for expenditure of

time) from numerous specialist taxonomists to devote time to the project, (c) with the collector charged with rearing representatives of all the immature arthropods to the adult stage. The advantage of having more samples will be the availability of a series of adult specimens of every species represented, except perhaps a few of the transients. The advantage of rearing the immature arthropods will be that adult specimens will be available for identification, and identifiers will then have immature specimens reliably associated with the adults; thereafter, the specialists may be able to provide identification keys to the immature stages. The collector should be proficient in invertebrate classification, and should have the time to rear immature arthropods to the adult stage.

Raw data used to compile Table 2, on invertebrates associated with the 24 plants, will be offered to the "Bromeliad tank dwellers database" on the website of the Florida Council of Bromeliad Societies (<http://www.fcbs.org>). It records any animal species detected in or on a bromeliad, not just tank dwellers (the aquatic species in tanks). This could lead to detection of other animals frequently associated with bromeliads, even if it takes tens of thousands of records. It was not easy to obtain identifications to the species level of invertebrates collected from bromeliads in Florida, and we were only partially successful, and only for some groups. We warn investigators who would like to conduct similar studies in the Neotropics that they will encounter severe taxonomic problems. The effort to collect the specimens is small compared with the effort required to identify the specimens reliably to the species level. Identification not made to the species level is worth rather little. Taxonomists need to be convinced that the project is worth their support. In this project, some taxonomists obtained useful and interesting specimens, at least of *Xenylla* (an undescribed species), *Cerobasis guestfalica*, *Camptomyza* sp., *Alepia* (the first Nearctic record), and various mites of uncertain identity.

The sampling method did not collect microscopic aquatic organisms. For these, it would be better to use a siphon or large syringe (such as an "oven baster") to extract the water from leaf axils of *T. fasciculata* and *T. utriculata*, and to decant this water directly into Petri dishes for microscopic examination. Such a method should collect bacteria, Fungi Imperfecti, algae, rotifers, nematodes, platyhelminthes, annelids, ostracods and copepods. But identification of these would have been beyond the skills of the taxonomists involved in the present study.

Future projects of this nature in Florida with all four of these plant species are unlikely in the near future. This is because the weevil *Metamasius callizona* was detected in Myakka River State Park in September 1999 and, since then,

has been relentlessly destroying the park's populations of *T. utriculata* and *T. fasciculata* (T. M. Cooper in Larson 2000). Similar destruction has been detected in almost all southern Florida counties. These two bromeliad species are rightfully listed in the Florida Administrative Code as endangered species. Recovery of their populations is unlikely unless the weevil can be brought under biological control.

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REFERENCES CITED

- BEUTELSPACHER B., C. R. 1971a. Una bromeliácea como ecosistema. *Biología (Mexico)* 2(7): 82-87.
- BEUTELSPACHER B., C. R. 1971b. Fauna de *Tillandsia caput-medusae* E. Morren 1880 (Bromeliaceae). *Anales Inst. Biol., Univ. Nac. Autón., Mexico (Ser. Zool.)* 43: 25-30.
- EPLER, J. H. 2001. Identification manual for the larval Chironomidae (Diptera) of North and South Carolina. A guide to the taxonomy of the midges of the southeastern United States, including Florida. Spec. Publ. SJ 2001-SP 13. North Carolina Dept. Envir. Nat. Resources, Raleigh, NC and St. Johns Water Management District, FL, 526 pp.
- FISH, D. 1976. Structure and composition of the aquatic invertebrate community inhabiting epiphytic bromeliads in south Florida and the discovery of an insectivorous bromeliad. Ph.D. dissertation, Univ. Florida, Gainesville, ix + 78 pp.
- FRANK, J. H. 1983. Bromeliad phytotelmata and their biota, especially mosquitoes, pp. 101-128. In J. H. Frank and L. P. Lounibos. *Phytotelmata: Terrestrial plants as hosts for aquatic insect communities*. Plexus; Medford, NJ, vii + 293 pp.
- FRANK, J. H. 1996a. Bromeliad biota. (<http://Bromeliad-Biota.ifas.ufl.edu/>) (September 2002).

- FRANK, J. H. 1996b. Bibliography of bromeliad phytotelmata in Bromeliad Biota (<http://BromeliadBiota.ifas.ufl.edu/fitbib1.htm>) (September 2002).
- FRANK, J. H. 1999. Bromeliad-eating weevils. *Selbyana* 20: 40-48.
- FRANK, J. H., AND G. A. CURTIS. 1981. Bionomics of the bromeliad-inhabiting mosquito *Wyeomyia vanduzeei* and its nursery plant *Tillandsia utriculata*. *Florida Entomol.* 64: 491-506.
- FRANK, J. H., G. A. CURTIS, AND H. T. EVANS. 1976. On the bionomics of bromeliad-inhabiting mosquitoes. I. Some factors influencing oviposition by *Wyeomyia vanduzeei*. *Mosquito News* 36: 25-30.
- FRANK, J. H., AND M. C. THOMAS. 1996. Weevil pests of bromeliads in Pests of bromeliads in Bromeliad Biota (<http://BromeliadBiota.ifas.ufl.edu/wvwbrom.htm>) (September 2002).
- HEPPNER, J. B., AND J. H. FRANK. 1998. Bromeliad pod borer. Univ. Florida, Entomol. Nematol. Dept., Featured Creatures, EENY-40 (http://Creatures.ifas.ufl.edu/orn/bromeliad_pod_borer.htm) (September 2002).
- LARSON, B. C. 2000. Save Florida's native bromeliads. Published on WWW at (<http://SaveBromeliads.ifas.ufl.edu/>) (September 2002).
- LARSON, B. C., AND J. H. FRANK. 2000. Mexican bromeliad weevil. Univ. Florida, Entomol. Nematol. Dept., Featured Creatures, EENY-161 (http://Creatures.ifas.ufl.edu/orn/m_callizona.htm) (September 2002).
- LARSON, B. C., J. H. FRANK, AND O. R. CREEL. 2001. Florida bromeliad weevil. Univ. Florida, Entomol. Nematol. Dept., Featured Creatures, EENY-209. (http://Creatures.ifas.ufl.edu/orn/m_mosieri.htm) (September 2002).
- PALACIOS-VARGAS, J. G. 1981. Collembola asociados a *Tillandsia* (Bromeliaceae) en el Derrame Lavico del Chichinautzin, Morelos, Mexico. *Southw. Entomol.* 6: 87-98.
- PALACIOS-VARGAS, J. G. 1982. Microartrópodos asociados a bromeliáceas. *Actas VIII Congreso Latino Americano Zool.* 1: 535-545.
- PICADO, C. 1913. Les broméliacées épiphytes considérées comme milieu biologique. *Bull. Sci. France Belgique* 47: 215-360.
- SIDOTI, B. J. 2000. Faunal inhabitants of a Florida bromeliad. *J. Bromeliad Soc.* 50: 227-233.
- WHEELER, W. M. 1942. The epiphytic Bromeliaceae and their fauna, p. 133-143. *In* Studies of Neotropical ant plants and their ants. *Bull. Mus. Comp. Zool. Harvard* 90: 1-262, pl. 1-56.
- WUNDERLIN, R. P. 1998. Bromeliaceae, pp. 192-195. *In* R. P. Wunderlin, Guide to the Vascular Plants of Florida. Univ. Press of Florida, Gainesville, 806 pp.