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Insects and allies associated with bromeliads: a review

J. H. Frank¹ and L. P. Lounibos²

J. H. Frank: jhfrank@ufl.edu

¹ Entomology & Nematology Dept., University of Florida, Gainesville, Florida 32611-0630, USA

² Florida Medical Entomology Laboratory, 2009th St. SE, Vero Beach, Florida 32962, USA

Summary

Bromeliads are a Neotropical plant family (Bromeliaceae) with about 2,900 described species. They vary considerably in architecture. Many impound water in their inner leaf axils to form phytotelmata (plant pools), providing habitat for terrestrial arthropods with aquatic larvae, while their outer axils provide terraria for an assemblage of fully terrestrial arthropods. Many bromeliads are epiphytic.

Dominant terrestrial arthropods with aquatic larvae inhabiting bromeliad phytotelmata are typically larvae of Diptera, of which at least 16 families have been reported, but in some circumstances are Coleoptera, of which only three families have been reported. Other groups include crabs and the insect orders Odonata, Plecoptera, and Trichoptera, plus Hemiptera with adults active on the water surface. The hundreds of arthropod species are detritivores or predators and do not harm their host plants. Many of them are specialists to this habitat.

Terrestrial arthropods with terrestrial larvae inhabiting bromeliad terraria include many more arachnid and insect orders, but relatively few specialists to this habitat. They, too, are detritivores or predators.

Arthropod herbivores, especially Curculionidae (Coleoptera) and Lepidoptera, consume leaves, stems, flowers, pollen, and roots of bromeliads. Some herbivores consume nectar, and some of these and other arthropods provide pollination and even seed-dispersal.

Ants have complex relationships with bromeliads, a few being herbivores, some guarding the plants from herbivory, and some merely nesting in bromeliad terraria. A few serve as food for carnivorous bromeliads, which also consume other terrestrial insects.

Bromeliads are visited by far more species of arthropods than breed in them. This is especially notable during dry seasons, when bromeliads provide moist refugia.

Keywords

Phytotelmata; carnivory; herbivory; predation; pollination; ecology; ethology

Introduction

The end-product of research on arthropods associated with bromeliads depends upon the viewpoint of the reader. For the systematist, it is the synthesis of the evolutionary pathway leading to bromeliad-inhabiting species of a named clade such as those of *Platynus* (Carabidae) in the West Indies (Liebherr, 1988), or *Copelatus* (Dytiscidae) (Balke et al., 2008), or Culicidae in Venezuela (Navarro et al., 2007). Along the way to such an objective should come illustrated species descriptions (e.g. Brailovsky and Cervantes, 2008), species lists (e.g. Palacios-Vargas, 1981), perhaps faunal works for restricted clades and geographical areas (e.g. Liebherr, 1987) including keys to identification that may be used by other biologists. For the ethologist

and autecologist, it is the quantified details of how a single species exists in a habitat limited by physical and biotic factors. For the plant ecologist, it is about how arthropods limit bromeliad populations (Winkler et al., 2005), or pollinate (e.g. Kromer et al., 2008) or disseminate seeds, or how bromeliads sustain arthropod populations (e.g. Benzing, 1970). For the community ecologist, it is about how populations interact in trophic webs (e.g. Frank, 1983). For the population ecologist, it is the quantification of regulation of the arthropod populations (e.g. Lounibos et al., 1987b).

Biologists dedicated to economic interests contributed much new knowledge. For the agronomist, the objectives are availability of identificatory materials and practical control methods for pests of pineapples (e.g. Salas et al., 1993) and a few other bromeliad species, or the same for cultivated ornamental bromeliads, or how to conserve populations of bromeliad-inhabiting cacao-pollinating ceratopogonid midges (Winder, 1977). For the medical entomologist, it is the availability of identificatory materials and practical control methods, when there is need, for Diptera of public health importance whose larvae develop in bromeliad leaf axils (Downs and Pittendrigh, 1946). For the conservationist, it is species lists and an attempt to identify all species of a local community (e.g. Frank and Fish, 2008), providing methods for monitoring populations of those that are rarest, and useful methods for their protection.

This brief review tries to address all of the above issues which, of course, developed slowly through simple surveys and natural history to reach their current standings. All studies, including those aimed at conservation or solving an economic problem, rely on species-level identifications, and most need knowledge of life histories. The issues are poorly balanced because some aspects have received much attention while others have scarcely been broached. This review is not a catalogue. Instead, it attempts to delimit each group of bromeliad-associated arthropods (excluding those that are aquatic in all developmental stages, in keeping with the objectives of Terrestrial Arthropod Reviews). It provides entries to the literature, which is much more copious than is apparent from citations given here and emphasizes ethology (behavior) and ecology.

Bromeliads

Bromeliaceae (bromeliads in English, bromeliáceas in botanical Spanish and Portuguese) are a family of monocotyledonous plants native to the Neotropics, with extension of a few species into the southern USA. They are classified into three subfamilies (Pitcairnioideae, Bromelioideae, and Tillandsioideae), about 60 genera (some of which are *Aechmea*, *Ananas*, *Araeococcus*, *Billbergia*, *Brocchinia*, *Bromelia*, *Canistrum*, *Catopsis*, *Glomeropitcairnia*, *Guzmania*, *Hechtia*, *Hohenbergia*, *Neoglaziovia*, *Neoregelia*, *Nidularium*, *Puya*, *Tillandsia*, *Vriesia*, and *Wittrockia*) and about 2,900 described species (Holst and Luther, 2004). Some species are terrestrial, growing in soil (including marshy soils and in arid habitats), or on rocks, but many are epiphytic. Roots of the terrestrial species may absorb nutrients, but those of the epiphytic species do not penetrate their tree hosts, and serve as holdfasts rather than nutrient-absorbing structures. Instead, the epiphytic species absorb minerals through the leaves. There is no evidence that they are parasitic on their tree hosts (Benzing, 2000).

Ananas comosus L. (pineapple) is a very important crop in tropical countries worldwide, with annual production of \approx 13 million tonnes. A few other species are grown locally in the Neotropics to provide food or drink (e.g. *Bromelia pinguin* L. and *Puya raimondii* Harms) or fiber (e.g. *Aechmea magdalenae* (André) and *Neoglaziovia variegata* (Arruda da Camara)). Bromelain, a proteolytic enzyme extracted from pineapple fruits, has pharmaceutical use as an anti-inflammatory, and is also used as a meat-tenderizer. Hemisphericin is a proteolytic enzyme extracted from *Bromelia hemisphaerica* Lamarck (Gutiérrez et al., 1993). Bromeliad

inflorescences are, lamentably, harvested from the wild on a large scale in Neotropical countries as decoration for churches on religious holidays. Many hundreds of species and thousands of cultivars are grown as ornamental plants especially in Europe and North America. Native epiphytic bromeliads have in the U.S.A. been dubbed 'air plants'; many vernacular names are used in the Neotropics.

An outstanding feature of many bromeliad species in many genera is that they impound water in the leaf axils. Some writers define tank bromeliads as those having a central water-impounding tank, perhaps surrounded by additional water-impounding axils. Other writers include any bromeliads that impound water in their axils, even if there is no central tank. The latter position is adopted here for convenience, not because the concept has greater merit. Large bromeliad specimens may impound substantial volumes (many liters) of water. The impounded water is rainwater, enriched with nutrients leached from tree canopies (throughfall) if the bromeliads grow under tree canopies, or with minimal wind-blown nutrients if growing in the open. These contrasting nutritional modes were called dendrophilous nutrition and anemophilous nutrition by Frank (1983). Plant architecture determines whether each of many axils holds a separate small pool of water, or the central axils combine to form a tank with some outlying axils. These pools of water, called phytotelmata, provide an aqueous medium with nutrients for absorption by the plant (Picado, 1913). Under dendrophilous nutrition, bromeliads contain fallen, decomposing leaves and seeds and twigs of trees. These decomposing materials (added to throughfall) provide nutrients that can be absorbed by the bromeliad after decomposition caused by fungal and bacterial action, and by aquatic invertebrate animals. Under anemophilous nutrition, algae use the wind-blown nutrients and a food chain depends upon consumption of algae (Laessle, 1961; Frank, 1983).

Animals use bromeliads in four ways. First, bromeliad phytotelmata are exploited by some aquatic animals as aquaria. Second, non-water-holding axils of bromeliads (terraria) are occupied permanently or almost so by some small animals. Third, bromeliads are an occasional place of concealment or hunting ground, or the water in phytotelmata is used as a moisture source, by some terrestrial animals, so these animals are visitors. Fourth, the bromeliads are food for some terrestrial animals. Insects exploit bromeliads in all four ways, and among the species using each way are specialists, which have no other means of existence or habitat. Thus, bromeliads are essential to the existence of many insect species. Many other invertebrate animals and a few vertebrates also play a role, as do microorganisms, a few plants that grow in the bromeliads, and the host trees of epiphytic bromeliads. There are at least three ways in which bromeliads exploit arthropods: as dispersers of seed, as pollinators, and as food.

Arthropods using bromeliad phytotelmata as habitat for their aquatic immature stages

Crustacea: Grapsidae

Sesarma angustipes—Dana was described from Brazil (later detected in Trinidad), and *Metopaulias depressus* Rathbun from Jamaica, both in the 19th Century (Abele, 1972). Phylogenetic analysis of Jamaican land crabs suggested that *M. depressus* separated from other lineages about 3 MYA (Schubart et al., 1998). Their immature stages develop only in the habitat provided by bromeliad axils, and *M. depressus* provides maternal care to its brood, including emptying of an *Aechmea paniculigera* (Swartz) Grisebach leaf axil of organic debris to form a nursery, provisioning its young with snails and millipedes as food, and protection of the young from predation by damselfly nymphs [*Diceratobasis macrogaster* (Selys)] and spiders (Diesel, 1989, 1992).

Odonata

Larvae of dragonflies and damselflies are aquatic and predatory. They have well-developed legs and thereby can climb out of the water from one leaf axil and into the water in another. At least 12 species have been reported from bromeliad phytotelmata in Neotropical countries, and some of them appear to be specialists to this habitat. These specialists are all species of damselflies, especially of the genera *Leptagrion* and *Bromeliagrion* (Coenagrionidae), but also of *Mecistogaster* (Pseudostigmatidae) (Corbet, 1983; Melnychuk and Srivastava, 2002; Srivastava et al., 2005; Marmels and Garrison, 2005). Their prey includes mosquito larvae (Lounibos et al., 1987a) and immature crabs where these exist (Diesel, 1992). Predation by *Mecistogaster modesta* Selys on detritivores increases nitrogen cycling by preventing its export from the bromeliad axils by emerging adults of the detritivores, allowing uptake by the plant (Ngai and Srivastava, 2006).

Plecoptera: Perlidae

An unidentified species of *Perla* was reported from an unspecified bromeliad in Costa Rica by Picado (1913) without behavioral information. Lack of subsequent mention of stoneflies from bromeliads raises questions about whether the initial record was due to ovipositional error by a female *Perla*, or whether the species in question is now extinct.

Orthoptera

Semiaquatic Orthoptera are mentioned later, under *Terrestrial arthropods using bromeliad terraria*.

Hemiptera: Veliidae

Aquatic Hemiptera are represented in bromeliads by eight species of seemingly obligate bromeliad-dwellers in the family Veliidae. Four belong to the genus *Paravelia* and four to *Microvelia* (Polhemus and Polhemus, 1991). These genera belong to separate subfamilies, which suggests that adaptation to the bromeliad habitat occurred independently at least twice. Like mosquitoes of the genus *Toxorhynchites*, veliids include species that develop in treeholes but, unlike *Toxorhynchites* larvae, veliids may be found in aggregations in bromeliad axils; although all are predatory, *Toxorhynchites* larvae differ from these veliids by being cannibals under certain conditions.

Lepidoptera

Semiaquatic Lepidoptera are mentioned later under *Herbivory*.

Coleoptera

“Aquatic” larvae of three beetle families have been detected from bromeliads, and the adults, too, have been found. Individuals are all small. The families are, Dytiscidae, Hydrophilidae and Scirtidae. Everything stated below about diet of these species is inferred, correctly or not, from studies on species that occur in other habitats.

Dytiscidae—Dytiscids have predatory larvae and adults. They are represented by the genera *Copelatus* (note that bromeliad-inhabiting species formerly placed in *Aglymbus* are now assigned to *Copelatus*) and *Desmopachria*. Six bromeliad-inhabiting species of *Copelatus* are now recognized and are related to species that inhabit forest-floor water puddles. They do not form a single clade, but diverged at various times from their puddle-inhabiting relatives up to 16.4 MYA, a date similar to that of the first bromeliads to have formed tanks. They are known from *Aechmea*, *Brocchinia*, *Guzmania*, *Hohenbergia*, *Nidularium*, *Tillandsia*, and *Vriesia* (Balke et al., 2008).

Hydrophilidae—Bromeliad-inhabiting species are assumed to be predatory as larvae and perhaps scavengers as adults. They include species placed under the generic names *Coelostoma*, *Lachnodacnum* (and its synonym *Psilodacnum*), and *Phoenonotum*. Adults and larvae of *Omicrus ingens* Hansen and Richardson (1998) were described from *Guzmania* sp. in Puerto Rico and seem to be bromeliad specialists. All belong to the subfamily Sphaeridiinae whose members live in moist terrestrial habitats unlike the aquatic subfamily Hydrophilinae.

Scirtidae—The family names Cyphonidae and Helodidae in the literature refer to Scirtidae. The description of *Scirtes championi* Picado included external and internal structure of the larva and a note that fully grown larvae pupate on a bromeliad leaf surface above the water line, but the author was unable to rear larvae and did not specify the food of either larvae or adults (Picado, 1913). No behavioral information was given with the description of *Cyphon bromelius* Klausnitzer (1980). Scirtids were found to be the most abundant insects in *Tillandsia turneri* Baker in a woodland in the Colombian Andes (Ospina-Bautista et al., 2004). Some recent studies have shown that scirtid larvae inhabiting water-filled treeholes scrape the surfaces of leaf litter and break it down, their feces then are consumed by mosquito larvae; this is likely to be the case in bromeliad leaf axils, too.

Diptera

This order (flies) has the record for the largest number of families (at least 16) and species (hundreds) having aquatic larvae reported from bromeliad phytotelmata. Families listed in the literature are Limoniidae (but formerly attributed to Tipulidae), Psychodidae, Culicidae, Corethrellidae, Thaumaleidae, Ceratopogonidae, Chironomidae, Sciaridae, Anisopodidae, Stratiomyidae, Tabanidae, Phoridae, Syrphidae, Periscleridae (formerly attributed to Aulacigastridae), Muscidae, and Sphaeroceridae (formerly Borboridae). Reports of some of these families may be due to misidentification, and much work remains for correct identification and life histories of the species.

Limoniidae—Picado (1913) collected, reared, and illustrated the first limoniid (at that time called tipulid) larvae and pupae from bromeliad leaf axils in Costa Rica. He provided specimens to C. P. Alexander who wrote the taxonomic description (Alexander, 1912). Three more species were then described from Mexico, and later one from Dominica and Puerto Rico. All five are now assigned to the subgenus *Paramongoma* of *Trentepohlia*, and in order of description are respectively *T. bromelicola* (Alexander), *T. leucoxena* (Alexander), *T. subleucoxena* Alexander, *T. bromeliae* Alexander (from *Aechmea mexicana* Baker), and *T. dominicana* Alexander from Dominica and Puerto Rico. *Paramongoma* includes many more species whose larvae do not develop in bromeliads. Their diet is unknown.

Psychodidae—Psychodid larvae have been observed in abundance in bromeliad phytotelmata in many localities. Where generic names have been given, these have been as *Alepiea*, *Neurosystasis*, *Philosepedon*, and *Telmatoscopus* in the subfamily Psychodinae (sometimes called moth flies), but much taxonomic study is required. The larvae most likely are saprophagous. Larvae of the subfamily Phlebotominae have not been reported from bromeliads.

Culicidae—To the year 1980, there had been reported 962 mosquito species from the Americas south of the USA. The 14th part of “Collection records of the project ‘Mosquitoes of Middle America’” was published (Heinemann et al., 1980). These 14 works, spanning eight years, systematically sampled immature stages of mosquitoes from many documented habitats in many countries, and reared them where necessary for identifications. Analysis of data from all these works allowed a classification of the habitats into bromeliads, other plant leaf axils, bamboo internodes, treeholes, and various other categories, and quantification of the number

of samples by mosquito species (Frank and Curtis, 1981). The analysis revealed that immature stages of 200 mosquito species and 14 corethrellid species had been reported from bromeliads, but that the level of specialization varied, with some species known only from bromeliads, some only from bromeliads and other plant leaf axils, and others rarely in bromeliads. Furthermore, the size of individual adults of the bromeliad-inhabiting species in those genera and subgenera for which published data exist was smaller than that of their congeners (other species found in other habitats). This suggested that small individual size is an advantage to bromeliad-inhabiting species.

Interest in mosquitoes developing in bromeliad leaf axils was given impetus by discovery of the ability of *Anopheles* mosquitoes belonging to subgenus *Kerteszia* to transmit malaria. In Trinidad in the 1940s, the two species incriminated were *Anopheles bellator* Dyar and Knab and *A. homunculus* Komp, whose larvae developed especially in *Aechmea aquilega* Salisbury but also *Vriesia amazonica* (Baker) and other bromeliads which were abundant epiphytes of tall shade trees (*Erythrina* spp.) in cacao plantations. Differences in humidity requirements between adults of the two species allowed those of *A. bellator* to fly at higher levels in the forest and in open areas outside the forest. Humidity levels below the canopy were generally too low for *A. homunculus* but ideal for *A. bellator*. Thus, larger numbers of *A. bellator* larvae in *A. aquilega* and *V. amazonica* were partly attributable to the higher level of these plants in tree canopies and partly to the architecture of the plants. The investigations, however, failed to reveal a better method to control the vector mosquitoes than destruction of the bromeliads that served as habitat for their larvae. This was attempted initially by manual removal from the trees, but later by killing them with herbicidal sprays, of which copper sulphate (copper is especially toxic to bromeliads) was the preferred compound (Downs and Pittendrigh, 1946).

A larger project with the same objective was begun in the Brazilian state of Santa Catarina in 1942 and continued for a decade. The major bromeliads serving as habitat for *Kerteszia* larvae were *Canistrum lindenii* (Regel) Mez, *Vriesea gigantea* Gaudichaud, *V. philippocoburgii* Wawra, *Nidularium innocentii* Lemaire, *Hohenburgia augusta* (Vellozo) E. Morren, and *Vriesea jonzei* (K. Koch) E. Morren in descending order, but this was related to water-holding capacity and not to phylogenetic affinity (Reitz, 1983). The mosquitoes were *Anopheles bellator*, *A. homunculus*, and *A. cruzii* Dyar and Knab, of which *A. cruzii* was seen as the most important. Methods used to destroy bromeliads depended upon locality. In and near the cities/towns of Brusque, Blumenau, Joinville, Florianópolis, Cabeçudas, Tijuquinhas, and Caldas da Imperatriz in 1949–1952, bromeliads were removed physically from an area over 7,419 km², and a deforested band [a cordon sanitaire: Ferreira et al. (1951) showed that few of the mosquitoes crossed a deforested zone of 1 km] 1.0 or 1.5 km wide, covering more than 3,730 km² was created around towns and cities (Reitz, 1983). Partial reforestation was later initiated in some areas, with non-native *Eucalyptus* trees that do not support growth of bromeliads. This destruction of bromeliads in Brazil's Atlantic forest was made to protect humans from malaria (a disease which is believed to have been accidentally imported into the Americas by humans). As bad as all that may seem to the conservationist, it pales in terms of overall destruction of Brazil's Atlantic forest [scarcely more than 7% remains (Leme and Marigo, 1993)], and indeed the forest supporting bromeliads throughout the Americas, in the names of agriculture and development.

Bromeliads cultivated in countries where they are not native have sometimes added to the habitat available for mosquito larvae. Cultivated pineapple plants do not normally provide phytotelmata, but a pineapple variety grown in Uganda provided habitat for larvae of *Aedes simpsoni* (Theobald), a vector of yellow fever (Haddow, 1948). *Alcantarea imperialis* (Carrière) Harms grown as an ornamental plant in the vicinity of Auckland, New Zealand, provided habitat for larvae of the invasive mosquito *Aedes notoscriptus* Skuse, a potential disease vector (Derraik, 2005).

Perhaps the projects in Trinidad and Brazil explain why public health workers seem to have adopted a concept that bromeliads are a major source of mosquitoes transmitting diseases. During periods of epidemic transmission of dengue in Brazil, *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse), known as invasive container mosquitoes and the two most important vectors of this disease, were recovered from bromeliads grown in urban gardens (Cunha et al., 2002, Forattini et al., 1998), which discoveries fomented subsequent, widespread destruction by municipal workers of ornamental bromeliads considered to pose a public health threat. More thorough inventories of bromeliads in urban and suburban São Paulo State and in Rio de Janeiro's botanical garden located in the center of that city indicated subsequently that these two dengue vector species were very rare in bromeliad phytotelmata dominated by native species of Culicidae (Marques et al., 2001; Mocillin et al., unpublished). This conclusion is consistent with results of surveys of mosquitoes occupying *Billbergia pyramidalis* (Sims) Lindley phytotelmata in southern Florida, in which samples resident *A. aegypti* were uncommon (Frank et al., 1988).

Wyeomyia mitchellii (Theobald) was originally described from Jamaica, and is known also from other islands of the Greater Antilles, eastern Mexico, and Florida. *Wyeomyia vanduzeei* Dyar and Knab was originally described from Florida, and is known also from Cuba, the Cayman Islands, and Jamaica. Both species are considered native to Florida. Adults of both species are active during daylight hours. Of the two, *W. mitchellii* is more restricted to shaded habitats. Females of both species use color vision to detect bromeliads in which to oviposit, although their color preferences differ slightly. They hover over leaf axils while ovipositing, and eggs of *W. vanduzeei* are made buoyant by a remarkable sculpted wax-like coating. Their typical nursery plant is *Tillandsia utriculata* L. (Frank and Curtis, 1982), but they also will develop in other native water-impounding *Tillandsia* spp. and in the insectivorous bromeliad *Catopsis berteroniana* (Schultes). Larvae filter-feed and browse on small particles in a nutrient-poor environment which is enriched by throughfall from tree canopies above. They compete intra- and inter-specifically for food, and have evolved a remarkable ability to survive long periods of starvation. Further breakdown of the organic particles and probably digestion of bacteria and fungi in the guts of mosquito larvae make the nitrogenous content more rapidly available for uptake by the bromeliads. Thus, the presence of the mosquito larvae is helpful to the bromeliads, and the bromeliads provide a habitat for the mosquito larvae, so this is a case of mutualism (Frank, 1983).

These *Wyeomyia* larvae will not develop in less time than about two weeks (larvae of many other mosquitoes develop much more rapidly), and attempts to provide them with a rich diet to hasten their development in the laboratory may prove fatal to them. Under laboratory conditions with input into nutrient-containing Petri dishes of newly-hatched *W. vanduzeei* larvae, males developed on average faster than females and starvation ensued with high input, resulting in slow development and much mortality. Further addition of food then allowed some of the larvae to complete development. However, when such newly-hatched larvae were added continuously, once every three days, a cycle with bimodality of 33–37 days was imparted to pupal production, for unexplained reasons (Frank et al., 1985). Both of these *Wyeomyia* mosquitoes have adapted to the habitat provided by imported, ornamental bromeliads that usually are cultivated terrestrially in urban habitats in southern Florida. They are sometimes present in greenhouses and even outdoors in northern Florida where these plants are grown beyond the northern limit of native, water-impounding bromeliads. They create a pest problem in the vicinity of bromeliads because females of both species readily bite humans during daylight hours, but they are not known to transmit diseases to humans in Florida.

The most appropriate long-term, environmentally sound method for reducing *Wyeomyia* populations is biological control by competition. Such biological control would introduce organisms that would compete for nutrients with the mosquito larvae. Such competitors would

probably be Neotropical species of non-biting midges such as Chironomidae. Pathogens (*Pilospora fishi* Hazard and Oldacre, *Coelomomyces* sp. and *Vorticella* sp.) have been detected in *W. vanduzeei* larvae but are uncommon. Use of predators against the mosquito larvae in *T. utriculata* (because of its architecture with many separate axils holding water) would likely provide no solution at all – because survivors of predation would inherit the food resources and thus develop faster and produce larger and thus more fecund adults. Insecticidal sprays used against the adults were ineffective. The ecological question raised here is about diet overlap among various chironomid and mosquito larvae occupying bromeliads in various parts of the Neotropics, and how the bromeliad fauna could be modified by introduction of innocuous species (with non-biting adults) to reduce populations of pests, and especially of disease-transmitting pests. Good answers to such questions should conserve bromeliads while controlling transmission of diseases.

Collections during the 1990s of mosquito immatures from ornamental bromeliads in nine localities in peninsular Florida demonstrated a significant negative correlation between mean abundances of native *Wyeomyia* spp. and the invasive *A. albopictus* (Lounibos et al., 2003). The invasive species was particularly common in bromeliad phytotelmata of northern Florida, beyond the known distributional limits of *W. vanduzeei* and *W. mitchellii*. Experiments in large outdoor cages demonstrated no effect of the presence of *Wyeomyia* spp. larvae on oviposition by *A. albopictus* in *B. pyramidalis*, but the presence of fourth instar larvae of *Wyeomyia* spp. negatively affected the growth and survivorship of *A. albopictus* first instars, probably via interspecific competition (Lounibos et al., 2003). Bromeliad species was also shown to affect the outcome of encounters between immatures of *Wyeomyia* spp. and *A. albopictus*, the invasive species faring better competitively with *Wyeomyia* spp. in the more open tanks of *Neoregelia spectabilis* (T. Moore) L.B. Smith than in the less capacious phytotelmata of *B. pyramidalis* (Raban, 2006).

In experiments designed to assess the effect of predation on aquatic communities in various phytotelmata, first instars of *Toxorhynchites haemorrhoidalis* (Fabricius) were deposited into *Aechmea nudicaulis* (L.) Grisebach and *A. aquilega*, suspended in lowland rainforest in Venezuela (Lounibos et al., 1987b). Survivorship of the predatory mosquito larva was superior and effects of predation more apparent in *A. nudicaulis*, which has a more compact tank than *A. aquilega*. Larvae of *T. haemorrhoidalis* in *A. nudicaulis* significantly reduced the abundance, decreased species richness, and altered size-class distributions of several taxa of dipterous prey compared to control plants without predators. However, this predacious mosquito species suffered reduced survivorship in the presence of, and was negatively associated with, larvae of the damselfly *Leptagrion siquierai* Santos, which was significantly more common in *A. aquilega* than in *A. nudicaulis* (Lounibos et al., 1987a). [Marmels and Garrison (2005) suggest that the damselfly may have been *Leptagrion aculeatum* Santos].

It should be noted that the aforementioned experiments of Lounibos et al. (1987b) were conducted in relatively small specimens of *Aechmea* spp. to facilitate manipulations and recovery of predators. In nature, epiphytic bromeliads may grow old and large, and Srivastava (2006) showed that increases in size and complexity of bromeliads which provide this phytotelm habitat reduced predator and detritivore efficiencies. On a landscape scale, the macrohabitat in which bromeliads occur also influences structure of their phytotelm communities (Yanoviak et al., 2006).

Corethrellidae—This family of frog-biting midges currently includes 97 described species, whose aquatic immature stages inhabit either phytotelmata or ground pools (Borkent, 2008). Of the 36 species whose habitats as immatures are known, four (*Corethrella pallida* Lane, *C. douglasi* Dyar, *C. ananacola* Borkent and *C. squamifemora* Borkent) have been collected multiple times from bromeliad phytotelmata. *Corethrella appendiculata* Grabham, which has

been shown to be a keystone predator in treeholes in Florida, has been occasionally found in bromeliad axils (Borkent, 2008).

Ceratopogonidae—In a cacao-growing area of Bahia, Brazil, 12,000 cacao flowers yielded adults of 16 species of ceratopogonids, some of which were thought to be important in pollination (Winder, 1977). *Vriesia procera* (Martius ex Schultes f.) Wittmack contained on average three *Forcipomyia caribbeana* Saunders larvae within the water-filled leaf-axils. In general, ceratopogonids were third (among other aquatic insects) in abundance in bromeliads. An increase in abundance of such bromeliads within a cacao-growing area may improve pollination (Fish and Soria, 1978). Most reports of ceratopogonids are of various species of *Forcipomyia*, but *Bezzia*, *Culicoides* and *Lasiohelea* also are reported from bromeliads. They are probably scavengers with the capability of crawling out of the water and eating stranded mosquito larvae.

Chironomidae—Descriptions of the larvae of four species (named as *Ablabesmyia costaricensis*, *Metriocnemus abdominoflavatus*, *Chirocladius pedipalpus* and *Chironomus* sp.) from bromeliads from Costa Rica (Picado, 1913) were exemplary for the time, but as pointed out by Epler and Janetzky (1998), their taxonomic placement needs reevaluation. At least five species are now known from Jamaica (Epler and Janetzky, 1998). There are three from *Aechmea lingulata* (L.) Baker and *Tillandsia utriculata* in St. John, US Virgin Islands (Miller, 1971), perhaps four from Puerto Rico (Richardson et al., 2000), and seven from Florida (Frank and Fish, 2008) although one of those is not a specialist so its occurrence in a bromeliad was just by chance. These larvae include case-making feeders on micro-organisms (*Tanytarsus* spp.), free-living detritivores (*Metriocnemus* spp.), algivores (“*Chironomus* sp.” of Laessle, 1961) and predators (*Monopelopia* spp.). Remarkably, larvae of five species were found in axils of a single *Aechmea paniculigera* (Swartz) Grisebach plant in the Cockpit Country of western Jamaica, partitioning the axils between them (Epler and Janetzky, 1998). Chironomid larvae fill various ecological roles and need much more taxonomic and behavioral study.

Sciaridae, Cecidomyiidae, and Anisopodidae—Sciaridae (e.g., *Corynoptera* sp.), Cecidomyiidae, and Anisopodidae (e.g. *Anisopus picturatus* Knab) larvae in bromeliad phytotelmata are likely to be scavengers and saprophages, but their diets have not been studied. *Corynoptera* larvae may feed on fungi.

Tabanidae—Tabanid larvae and pupae have been detected in bromeliad phytotelmata in Panama (e.g. *Stibasoma* spp.), Argentina, and Brazil with evidence that they are aquatic and are restricted to this habitat. A recent report is of larvae of *Fidena rufopilosa* (Ricardo) developing in 8% of terrestrial bromeliads examined belonging to *C. lindenii*, *Nidularium innocentii*, and *Vriesia friburgensis* (Mez) in Santa Catarina, Brazil (Zillikens et al., 2005). Such larvae are predatory, but their diet has not been determined.

Syrphidae—Examples of syrphid genera reported in the literature from bromeliads are *Meromacrus* and *Quichuana*. *Lejops barbiellinii* (Ceresa) larvae were reared from bromeliads in Paraná, Brazil (Morales and Marinoni, 2008). In an effort to expand knowledge of syrphids, Rotheray et al. (2007) reared larvae collected from living and dead bromeliads from 1998 to 2004 in Bolivia, Costa Rica, Ecuador, Mexico, and Trinidad. Of 23 species of *Copestylum* reared, 22 were new to science and were described. These larvae are saprophagous. One species, *T. volcanorum* Hancock and Rotheray, seemed restricted to “*Tillandsia major*” in Bolivia, but most bromeliads encountered were not identified.

Phoridae, Sphaeroceridae, Stratiomyidae, Muscidae, Perisclididae—Phoridae (e.g. *Dohrniphora*) and Sphaeroceridae (e.g *Limosina bromeliarum* Knab and Malloch) larvae

in bromeliad phytotelmata are likely to be scavengers and saprophages, and those of Stratiomyidae (e.g. *Nototelus*) filter-feeders, but their diets have not been studied. Predatory larvae of Muscidae (*Neodexiopsis*) and Periscolidae (*Stenomicro*) have been maintained on a diet of *Wyeomyia* mosquito larvae (Frank and Fish, 2008). Predatory larvae of a species of *Coenosia* reported from Costa Rican bromeliads by Picado (1913) were wrongly stated to be anthomyiids whereas that genus belongs to Muscidae and is related to *Neodexiopsis*.

Trichoptera: Calamoceratidae

Larvae of most *Phylloicus* caddisflies live in freshwater streams. One species, *Phylloicus bromeliarum* Müller, has evolved in southern Brazil to the habitat provided by bromeliad phytotelmata, and its larval cases are formed from pieces of leaf (Müller, 1878). Apart from its subsequent detection in Argentina, and reaffirmation of its distinctness from its congeners, it remains poorly studied.

Terrestrial arthropods using bromeliad terraria as habitat for their immature stages

Terraria are the leaf axils that cannot impound water because they leak. They accumulate moist organic materials which eventually break down to form soil (Paoletti et al., 1991). In many mature bromeliads, inner axils form phytotelmata whereas outer axils form terraria (e.g. Beutelspacher, 1971). The upper parts of the water-impounding axils that are choked with fallen plant debris might also be considered as terraria. Bromeliad terraria provide habitat for many visitors and a few specialist organisms.

Spiders (Araneae) are commonly associated with bromeliads, and most are visitors (e.g. Frank et al., 2004). The surprise was to find a few species that seem to be obligate bromeliad-dwellers. *Pachistopelma rufonigrum* Pocock (Therophosidae) adults and immatures have been found so often in terrestrial water-impounding bromeliads that their association seems to be obligate. It occupies *A. aquilega*, *A. lingulata*, and *Hohenbergia ramageana* Mez in open coastal vegetation types in Rio Grande do Norte and Sergipe in northeastern Brazil as well as higher altitudes farther inland in Sergipe (Santos et al., 2004). A second Brazilian species, *Psecas chapoda* (Peckham and Peckham) (Salticidae), reproduces only on the non-water-impounding *Bromelia balansae* Mez in São Paulo, Brazil (Romero and Vasconcellos-Neto, 2005). In the southern USA, *Pelegrina tillandsia* Kaston (Salticidae) is constantly associated with the atmospheric epiphytic bromeliad *Tillandsia usneoides* (L.) (Kaston, 1973), although the architecture of this plant does not provide terraria.

Mites (Acari) belonging to many families are frequent denizens of bromeliad terraria in Morelos, Mexico (Palacios-Vargas, 1982) and Florida (Frank et al., 2004), although such is the poor state of their taxonomy many of them from Mexico and Florida could not even be identified to the level of genus, let alone species, even by expert acarologists. Evidence that any of them is a specialist in bromeliads must await further taxonomic insight.

Scorpions (Scorpionida) are less abundant in bromeliads than are spiders, and as with spiders it was a surprise that they include any bromeliad-specialists. However, Santos et al. (2006) cited literature records of scorpions detected in bromeliads in the Neotropics and pointed out that *Tityus neglectus* Mello-Leitão (Buthidae) seems to be a specialist. Restricted to semi-arid coastal restinga and tabuleiro woodland in Rio Grande do Norte, northeastern Brazil, it occupies *A. aquilega*, *A. lingulata*, and *Hohenbergia ramageana* and often partitions this habitat with the spider *P. rufonigrum*. Harvestmen (Opiliones) likewise occur in bromeliads, and among them is *Bourguyia hamata* (Roewer) (Gonyleptidae) in *A. nudicaulis* in Brazil,

whose presence correlated positively with plant size and presence of water in leaf axils (Osse et al., 2007).

Pseudoscorpions (Pseudoscorpionida), woodlice (Isopoda), centipedes (Chilopoda), and millipedes (Diplopoda), have all been detected in bromeliad terraria (Picado, 1913; Frank et al., 2004). One pseudoscorpion, *Macrochernes attenuatus* Muchmore (Chernetidae), has been detected as a bromeliad specialist in Puerto Rico (Richardson, 1999).

Springtails (Collembola) from soil and from the “suspended soil” inside axils of *Tillandsia prodigiosa* (Lemaire) Baker, *T. violacea* Baker, *T. roseospicata* Matuda and other *Tillandsia* spp. in Morelos, Mexico, were extracted by Berlese funnel and compared in terms of species composition. Thirty-one species were identified from the soil, of which 58% also were found in the bromeliads, and none of them was found only in the bromeliads (Palacios-Vargas, 1981).

Orthoptera are represented by non-specialist crickets and grasshoppers (e.g. Picado, 1913; Frank et al., 2004). Additionally, they include certain Conocephalidae, unidentified to genus and species, detected abundantly in water-filled leaf axils of unidentified bromeliads in Huánuco, Peru. The nymphs submerge themselves in the water and prey on other insects that approach the water surface from above (such as ovipositing Odonata) or are aquatic (Burmeister, 1985).

Blattodea are often present in bromeliad leaf axils (e.g. Picado, 1913) and a few of the species found there appear to be amphibious, diving into the water when disturbed; examples are *Audreia bromeliadarum* Caudell in Panama and *Dryadoblatta scotti* (Shelf) in *Tillandsia* spp. and *Glomeropitcairnia erectiflora* Mez in Trinidad (Roth and Willis, 1960). Thirty-five cockroach species mentioned in the earlier literature as from bromeliads are listed by Albuquerque and Lopes (1976) who add records and many illustrations of 31 more South American, mostly eastern Brazilian, species (nine of them new to science), mentioning many of the names of host bromeliads but giving no information about behavior nor of whether any of these cockroaches are restricted to bromeliads. Growers of ornamental bromeliads in Florida credit cockroaches with damage to young leaves and flowers, so the presence of some species is not benign.

Dermaptera (earwigs) are represented by numerous non-specialists, with 28 named species in Costa Rica alone (Picado, 1913) and more elsewhere. Psocoptera (barklice, booklice) are likewise thus far represented only by non-specialists (e.g. Frank et al., 2004).

Among the several hundred species of *Platynus* (Coleoptera: Carabidae: Platynini), some have specialized to existence in leaf axils of epiphytic bromeliads, and their adults and immature stages occur nowhere else. Although their food is uninvestigated, they are most likely predatory in concordance with their closest relatives. So bromeliads serve as hunting grounds for their adults and larvae. These bromeliad specialists occur in Mexico, Central America, and the West Indies (Liebherr, 1987, 1988). A study contrasting the ground beetle (Carabidae) fauna at three altitudes in Veracruz, Mexico detected 37 species in bromeliads, of which species of Lebiini (mostly arboreal) and a few non-arboreal species were prevalent at lower altitude, whereas species of Platynini were dominant at altitudes higher than 1,000 m (Montes de Oca et al., 2007).

Rove beetles (Coleoptera: Staphylinidae) likewise have many times been reported from bromeliads, e.g. Picado (1913) for Costa Rica, Lüderwaldt (1915) for Brazil, and Zaragoza, (1974) for Mexico, but nobody has yet determined which of the (probably all) predatory species are obligate bromeliad-dwellers. That task awaits expert taxonomic review of the doubtless

thousands of specimens collected from bromeliads and now scattered among public insect collections.

The larva of a scarab beetle, *Trigonopeltastes delta* Forster (Coleoptera: Scarabaeidae: Cetoniinae), was encountered in a leaf axil of *T. utriculata* in southern Florida and probably was feeding on detritus there (Cave, 2005). In January 2007, another was found under similar circumstances. It is yet unclear whether bromeliad axils are the usual habitat for this species.

Ants (Hymenoptera: Formicidae). See antplants (myrmecophytes).

Terrestrial arthropods using bromeliads as occasional habitat: the visitors

Visitors are here considered to be animals that neither eat bromeliads nor reproduce in them. They may be seeking moisture, or prey, or concealment from enemies, or they may be present just because their wanderings have taken them there. In tropical areas with pronounced wet and dry seasons, more individuals and species of insects may be present in bromeliad leaf axils in the dry season, when bromeliads provide oases of moisture as well as prey for the predators among these insects (Murillo et al., 1983). A survey of the organisms found in native epiphytic *Tillandsia* bromeliads in Florida revealed that most species encountered were most likely just wanderers (Frank et al., 2004) as did a survey of cultivated *Bromelia hemisphaerica* in Morelos, Mexico (Gutiérrez et al., 1993). This viewpoint is supported by studies of the scorpions, Collembola and mites found in bromeliad terraria (above).

Arthropods as dispersers of bromeliad seed

Seeds of the bromeliad subfamily Tillandsioideae are dispersed by wind, and those of Pitcairnioideae by gravity. The seeds of many Bromelioideae, however, have a fleshy pericarp and may attract vertebrate animals; birds, mammals and even insects may disperse them (Holst and Luther, 2004).

Arthropods as pollinators of bromeliads

Feeding by animals at bromeliad nectar may be considered as a special case of phytophagy because this does no harm to the plants, unless perhaps the animals should consume nectar without Thecting pollination (see “hummingbird flower mites” below). Visits to flowers by hummingbirds and bats are doubtless to obtain nectar, with pollination a general consequence. Bees may visit flowers to collect nectar and pollen, taking some proportion of the pollen for their own use, with pollination a usual consequence, but other flower-visiting insects may or may not collect or eat pollen, and may or may not pollinate. Microscopic examination of such insects after they have left the flowers may reveal pollen grains on their exterior surfaces (if they are capable of pollination) or inside their crop (if they consume pollen), or chemical analysis of the crop content may reveal the presence of sugars matching the profile of the sugars produced by nectaries of the flower just visited. In other words, field observation of visits to flowers may be inadequate to reveal the role of these insects. Field observation during night hours (when moths and some other insects may visit flowers) is obviously more difficult than field observation during daylight hours (when butterflies, bees, and another set of insects may visit flowers). Some of the conclusions reported in the literature (below) may need reinterpretation in the light of such observational constraints.

Elevational transects in the Bolivian Andes were the basis for comparing pollination of bromeliads, and it was found that pollination by insects decreased with altitude as contrasted with pollination by hummingbirds (Kromer et al., 2006). Seventy-four forest sites in the Bolivian Andes and adjacent lowlands contained 188 bromeliad species whose pollination modes were judged as 115 by birds, 45 by insects, 14 by bats, eight self-pollinated, and six

mixed; terrestrial forest bromeliads showed mainly insect pollination as did bromeliads at arid sites (Kessler and Kromer, 2008). In eastern Brazil, the butterfly *Heliconius ethilia narcaea* Godart was more aggressive than *H. sara apseudes* (Hübner) (Lepidoptera: Heliconiidae) when both were exploiting nectar and pollen of *Aechmea gracilis* Lindman (Rocha and Duarte, 2001). In eastern Brazil, visits to *Aechmea*, *Billbergia*, *Nidularium*, *Tillandsia*, and *Vriesia* bromeliads, were recorded as 62.5% by butterflies to *Tillandsia* spp., and 72–96% by hummingbirds to species of the other four genera (Varassin and Sazima, 2000). At a higher elevation in eastern Brazil, five bromeliad species of the genera *Nidularium*, *Vriesia*, and *Wittrockia* were found to be pollinated by hummingbirds, two *Vriesia* spp. by bats, and one *Aechmea* sp. by bees (Kaehler et al., 2005). Nectar sugar composition for 111 bromeliad species was analyzed and contrasted on the basis of whether the bromeliads were thought to be pollinated by bats, hummingbirds, or Lepidoptera, which yielded a better match than did the phylogenetic relationships of these plants (Kromer et al., 2008).

Arthropods as food for bromeliads (carnivory)

Catopsis berteroniana in southern Florida was the first bromeliad to be declared carnivorous (Ward and Fish, 1979), followed by the realization that *Wyeomyia* mosquito larvae nevertheless develop in water in its axils (Frank and O'Meara, 1984). It grows epiphytically, typically above tree canopies, so accumulates little or no organic debris from trees. Winged terrestrial insects seem to stumble into it, perhaps confused by an ultraviolet-reflecting plant-produced powder, have difficulty escaping, and drown and are decomposed perhaps by autolysis in water in the axils. Then came detection of *Brocchinia reducta* Baker in southern Venezuela as a carnivorous species (Givnish et al., 1984). It grows terrestrially in a nutrient-poor environment, and perhaps attracts insects to plant-produced odors. Then *B. hechtoides* Mez, living in similar habitats, was found to do the same, and larvae of a chironomid and mosquitoes develop in the axils (Zavortink, 1986; González et al., 1991). The story with *B. reducta* became even more interesting when it was discovered that the supposedly attractive odor is produced only by young plants, and that composition of the prey changes in older plants; although younger plants capture varied prey, ants (*Solenopsis* sp.) nest among the leaves of the older plants and use the 'pitchers' as middens, so these older plants are ant-fed (González et al., 1991).

Antplants (myrmecophytes)

Feeding of *Brocchinia* bromeliads (above) is far from the only effect of ants on bromeliads. Ants of various species often nest in the dry outer axils (terraria) (Wheeler, 1942; Beutelspacher, 1971; Frank et al., 2004). *Aechmea bracteata* (Swartz) Grisebach in Quintana Roo, Mexico, had 96% of its ramets occupied by ants, and ants sheltered in this and other bromeliads were shown to protect host trees against defoliation by an undetermined chrysomelid beetle and the leaf-cutting ant *Atta cephalotes* (L.), while the highest ant diversity (26 species) was observed in *Tillandsia bulbosa* Hooker (Dejean et al., 1995). A question is whether a mutualistic relationship has developed between particular species of ant and bromeliads as has evolved between other species of ants and plants (Wheeler, 1942). Antplants are afforded protection from herbivores while the ants may obtain suitable nesting places and perhaps dietary rewards. A case was made that *Tillandsia butzii* Mez and *T. caput-medusae* E. Morren are myrmecophytes (Benzing, 1970). Some *Tillandsia* bromeliads (e.g. *T. paucifolia* Baker) have inflated leaf bases providing cavities protected from rain, and the cavities thus formed are often occupied by ants; the ants may cut a small hole in a leaf base for ease of access to the cavity. The highest level of ant diversity, with 26 named ant species found, in Quintana Roo, was in *Tillandsia bulbosa* as contrasted with six other *Tillandsia* species (Dejean et al., 1995). Transport of bromeliad seeds by ants to their nests is likely to result in death of the seeds.

Herbivory on bromeliads by arthropods

Leaf loss due to herbivory was low (< 1.5%) in five bromeliad species as contrasted with five fern species (where it was 20%) at \approx 1400 m altitude in Veracruz, Mexico, but conspicuous damage done by insects to reproductive organs and meristematic stem tissue can have a strong effect on fecundity and survival. Herbivory in flowers or inflorescence stalks reduced fecundity by \approx 14–18% (Winkler et al., 2005). Few insects are reported as specialized to eat the leaves of bromeliads by chewing the surfaces or by mining. They include a few leaf beetles (Coleoptera: Chrysomelidae) such as *Acentroptera pulchella* Guérin-Ménéville in southern South America (Mantovani et al., 2005), and *Calliaspis rubra* (Olivier) which was observed to cause 9.8% leaf area loss to *Aechmea nallyi* L.B. Smith in eastern Peru (Burgess et al., 2003). Among Riodinidae (Lepidoptera) the caterpillar of *Napaea eucharilla* Bates was estimated to cause up to 4.4% loss of leaf area on *Werauhia sanguinolenta* (Linden ex Cogniaux and Marchal) J. R. Grant in Panama (Schmidt and Zotz, 2000) and also was found to eat leaves of *A. bracteata* and *A. nudicaulis* in Veracruz, Mexico (Beutelspacher, 1972), while the caterpillar of *Caria ino* Godman and Salvin was observed to eat leaves of *T. caput-medusae* in Guerrero, Mexico (Beutelspacher, 1972). Caterpillars of three South American species of *Dynastor* (Lepidoptera: Nymphalidae) eat bromeliad leaves. Their names are listed with records of their host bromeliads by Penz et al. (1999) with additions by Romero et al. (2005). The caterpillar of *Ziegleria hesperitis* (Butler and Druce) (Lepidoptera: Lycaenidae) was found to eat leaves of *T. caput-medusae* in Guerrero, Mexico (Beutelspacher, 1972). Larvae of a fly, *Melanagromyza rosales* Woodley (Diptera: Agromyzidae), mine the leaves of *B. pinguin* in Costa Rica (Woodley and Janzen, 1995). Generalist insects that chew bromeliad leaves include cockroaches (Blattaria), whose actions are most noticeable in greenhouses, and grasshoppers (Orthoptera: Acrididae). In spring in southern Florida (USA), population explosions of ‘lubber grasshoppers’ (*Romalea guttata* Houttyn (Acrididae)) attack many monocotyledonous plants, including bromeliads; although the damage they cause initially appears locally severe, the plants seem to recover by new growth. This grasshopper has a parasitoid, *Anisia serotina* (Reinhard) (Diptera: Tachinidae), which in 1997 caused an exceptionally high level (82%) of parasitism in the Copeland area of southwestern Florida (Lamb et al., 1999).

Insect larvae that mine stems of bromeliads include various genera and species of Castniidae (Lepidoptera). All were originally mentioned in the literature as being species of *Castnia*. One such is *Castnia boisduvalii* Walker larvae eating *Tillandsia aeranthos* (Loiseleur) L.B. Smith from Rio Grande do Sul, Brazil (Biezanko, 1961). At least eight other species have been reported, most of them because of damage they do to pineapple in Brazil and Venezuela. Subsequent taxonomic research on Castniidae has resulted in name changes at the level of genus, species, and subspecies. Others have been detected occasionally by one of us (JHF) in large epiphytic bromeliads (*Tillandsia*, *Vriesia* and *Werauhia*) in natural areas in Mexico, Honduras, Guatemala, and Panama and doubtless are yet more widely distributed in the tropics. The fully grown pale larvae are large (\approx 5cm), and their mining activities surely result in plant death. Their population sizes may be limited by parasitoids, although such parasitoids have not been reported. Dr. J.Y. Miller is preparing for publication a taxonomic review that will include larval host-plant records.

Larvae of *Acrolophus pallidus* Moschler (Lepidoptera: Acrolophidae) were reported from bromeliads in Costa Rica without details other than they were common (Picado, 1913). Larvae of *Acrolophus vigia* Beutelspacher (1969) were found among organic debris in the water of water-containing leaf axils of *A. mexicana* and *Vriesia chiapensis* Matuda in Veracruz, Mexico. They were noted to produce silk and were reared on a diet of pieces of bromeliad leaf. In 1994, one of us (JHF) stripped the leaves from several large *Werauhia werckleana* (Mez) J. R. Grant on a fallen tree in Chiriquí, Panama, and found several large *Acrolophus* sp. larvae in mines in stems, accompanied by silk; one of these larvae proved to be parasitized by larvae of

Bracon sp. (Hymenoptera: Braconidae). There may be less difference between behaviors of these *Acrolophus* spp. than is apparent from the statements because a larva eating leaves below the water line is surely consuming leaf bases which tightly surround the stem, and likely consuming the stem too; damage to the stem may not be apparent without stripping the leaves off the stem. The most widespread miner of fruits of cultivated pineapple is the larva of a butterfly, *Strymon megarus* (Godart) (Lepidoptera: Lycaenidae), which in much of the literature about pests of pineapples was assigned to the genus *Thecla* and called *T. basilides* (Geyer) (Robbins, 2001). It attacks flowers of various bromeliads, not just *Ananas*, and also plants of the genus *Heliconia* (Heliconiaceae). Larvae of the non-native “banana moth”, *Opogona sacchari* (Bojer) (Lepidoptera: Tineidae), now sometimes attack stems of ornamental bromeliads and cultivated pineapples in southern Florida (Davis and Peña, 1990).

The 23 species of the weevil genera *Cactophagus*, *Metamasius* and *Cholus* weevils whose larvae are known to mine bromeliad stems were considered by Frank (1999). All were classified within the family Curculionidae, but recently the part of that family containing *Cactophagus* and *Metamasius* has been considered by some authors a separate family (Dryophthoridae). Weevil larvae mining in ramets and shoots of *Tillandsia punctulata* Schlechtendal and Chamisso and *T. deppeana* Steudel accounted for an estimated 18% and 31% respectively of death at ≈1400 m in Veracruz, Mexico (Winkler et al., 2005); those authors mentioned only *Metamasius sellatus* Champion, but one of us (JHF) earlier found also *M. callizona* (Chevrolat), *M. flavopictus* (Champion), and *Cactophagus validirostris* (Gyllenhal) mining bromeliads in the same area. Some *Cholus* spp. and *Metamasius* spp. cause substantial damage by mining inflorescence stalks and fruits of cultivated pineapples in southern Mexico, Central America, some West Indian islands, and South America (e.g. Salas et al., 1993). Not all bromeliad-eating *Metamasius* spp. cause substantial damage. For example, in Honduras and Guatemala, larvae of *M. quadrilineatus* Champion seem to attack bromeliads that have fallen from trees, mainly due to breakage of branches, are not positioned vertically but at an angle to the vertical so that they do not retain water in the leaf axils, and are no longer part of the breeding population of bromeliads (Alvarez del Hierro and Cave, 1999). For another example, larvae of *M. mosieri* Barber, supposedly native to southern Florida (and Cuba and Hispaniola), seem to attack only bromeliads of small stature and cause little damage to populations of those plants. The reason why populations of *M. mosieri* are not abundant and damaging to their host plants remains obscure, although no parasitoids have been detected from them (Cave et al., 2006). The weevils *Parisoschoenus ananasi* Moure and *Paradiaphorus crenatus* (Gyllenhal) have long been known to attack cultivated pineapples in Brazil. The life cycle of the baridine weevil *Diastethus bromeliarum* Champion in Central America seems unrecorded, although an unidentified species of *Diastethus* is reported to attack pineapple in Brazil (Petty et al., 2002). Eastern Brazil’s bromeliad-eating baridine weevils include at least nine species of *Diastethus* including *D. bromeliae*, one species of *Melampus* (from *Araeococcus*), one of *Gravatageraeus* (from *Hohenbergia*), and one of *Bromegeeraeus* (from *Aechmea*) (Bondar, 1942). An unidentified baridine weevil attributed to *Baris* is reported to attack pineapple in Venezuela.

It is an invasive species of *Metamasius* that captured the attention of bromeliad-growers and conservationists. *Metamasius callizona* is believed to have arrived in Florida as a contaminant of bromeliads imported commercially to Florida from Veracruz, Mexico (Frank and Thomas, 1984). If its behavior were to mimic that of *M. quadrilineatus* in causing little damage there would be no problem. However, since its detection in 1989, it has spread to 21 counties in southern and central Florida, devastating the breeding populations of native *Tillandsia* bromeliads. Its adults can fly and can potentially live more than a year. Its larvae take about two months to develop and mine the meristematic stem tissue to kill bromeliads (Frank and Cave, 2005). It breeds throughout the year in the field but its phenology on *T. fasciculata* Swartz is not the same as on *T. utriculata* (Cooper, 2008). In attempt to conserve Florida’s native bromeliad flora (12 of 16 species seem to be at risk) and the dependent invertebrate fauna

(Frank and Fish, 2008), a biological control program was initiated. Multiple releases of a tachinid fly, *Lixadmontia franki* Wood and Cave (2006), were made in 2007–2008. This fly was first detected in Honduras (Alvarez del Hierro and Cave, 1999) as a parasitoid of *M. quadrilineatus* (Suazo et al., 2008) but attacks *M. callizona* readily (Suazo et al., 2006).

Larvae of *Epimorius testaceellus* Ragonot (Lepidoptera: Pyralidae) develop within the flower pods of *T. fasciculata* in Florida, producing considerable local damage. A tiny parasitoid (Hymenoptera: Eurytomidae: *Eurytoma*) is reported to attack these larvae (Bugbee, 1975). Curiously, an unidentified species of *Eurytoma* is reported to attack seeds of *Vriesea friburgensis* in southern Brazil (Grohme et al., 2007). A third, *E. werauhia* Gates, is known only from the province of Puntarenas in Costa Rica where its larvae eat the pollen within floral buds of *Werauhia gladioflora* (H. Wendland) J. R. Grant (Gates and Cascante-Marin, 2004). Larvae of *Holcocera bromeliae* (Walsingham) (Lepidoptera: Coleophoridae) are known from bromeliads in Costa Rica (Picado, 1913). Destruction of bromeliad flowers and seeds is achieved not only by larvae of such small moths (Heppner and Frank, 2007), and also by the same weevils and close relatives that attack the meristematic tissue (Pierce and Gottsberger, 2001), and by lygaeid bugs.

Lygaeid bugs (Hemiptera: Lygaeidae) have been described from bromeliads and probably feed on seeds. They include *Ozophora hohenbergia* Slater and Baranowski from *Hohenbergia penduliflora* (A. Richard) Mez, *H. polycephala* (Baker) Mez, and *H. urbaniana* Mez from Jamaica (Slater and Baranowski, 1978) whose immature stages also were detected. They include *Acroleucus bromelicola* Brailovsky from *Tillandsia dasyliiriifolia* Baker, *A. nexus* Brailovsky and Barrera from *Tillandsia oaxacana* L. B. Smith and *T. violacea*, and *A. tensus* Brailovsky and Cervantes from *Hechtia podantha* Mez, all from Mexico (Brailovsky and Cervantes, 2008). *Lygofuscanellus alboannulatus* (Champion) was initially collected on an unidentified bromeliad in Costa Rica.

Adults and nymphs of *Megalocysta gibbifera* (Picado) (Hemiptera: Tingidae) were noted to feed on *Aechmea* leaves at Orosí in Costa Rica, and the nymphs were sometimes parasitized by larvae of small wasps possibly of Braconidae (Picado, 1913). Their discoverer was perplexed that they should often be found stuck firmly in the gelatinous gum exuded by their host plants. We wonder whether the conditions for adhesion of the tingids were created by the method of their capture (forceful dismemberment of bromeliads, perhaps accidentally pressing the insects into the gum); our observations are that such gum is secreted only when bromeliads and members of some related families undergo gross physical damage (for example by breaking a bromeliad flower spike, or tearing the leaves from a stem); thus, under normal circumstances no gum would be exuded, so the tingids would not encounter it. *Canopus dissimilis* (Distant) (Hemiptera: Canopidae), reported from bromeliads in Costa Rica (as *Chlaenocoris dissimilis*) may be a fungal-feeder rather than a genuine bromeliad-dweller.

“Hummingbird flower mites” are transported phoretically by hummingbirds from flower to flower, and there they breed, and feed on nectar and pollen. The mites (Acari: Ascidae) found associated with six *Tillandsia* species at ≈1400 m elevation in Veracruz, Mexico, were *Tropicoseius peregrinator* Baker and Yunker, *T. ornatus* Fain and Hyland, and *Proctolaelaps* sp., and were present in all flowers of all six species with number of mites averaging 4.9–13.5 (variation among the six *Tillandsia* species) (García-Franco et al., 2001).

Bromeliads in greenhouse cultivation seem more often to be attacked by scale insects (Hemiptera: Coccoidea) than by insects of any other group, which may be an artifact due to crowding of plants under unnatural conditions that exclude organisms which could control these pests. In Florida, these scale insects belong to the following six families (numbers of species in parentheses): Asterolecaniidae (2), Coccidae (1), Ortheziidae (1), Pseudococcidae

(6), and Diaspididae (8) (Hamon et al., 2003). Perhaps they may be controlled by opening greenhouse walls to allow ingress of tiny parasitoid wasps (if the greenhouse is in a Neotropical or subtropical area). They could doubtless be controlled by deliberate release of such wasps purchased from biological control supply companies (none of the necessary wasp species seems now to be available commercially, but this could change if there were demand). Growers of ornamental bromeliads tend to use chemical pesticides against scale insects. Growers of pineapples in monocultures also tend to use chemicals against scale insects although various parasitoid Hymenoptera may be effective in natural population regulation but injudicious use of chemicals may destroy these parasitoids in Neotropical countries where the pests and parasitoids are native (Petty et al., 2002). Various viruses are transmitted among cultivated pineapples in several countries by pineapple mealybug, *Dysmicoccus brevipes* (Cockerell) (Hemiptera: Pseudococcidae) (Petty et al., 2002).

The roots of terrestrial bromeliads are not immune to damage by insects. Symphylids of the genus *Hanseniella* can cause severe damage to meristematic root tissue of pineapple (Petty et al., 2002).

Conclusion

The history of studies of bromeliad faunas began with identification and taxonomic description of arthropod species occurring in bromeliads in Amazonian Brazil and then Costa Rica. Natural history of these organisms specialized into works in their ethology and autecology, and the geographic range of studies broadened into many areas of the Neotropics with bromeliad populations. Although steps have been taken in the direction of community ecology, the great incompleteness of the building blocks (taxonomy, ethology, and autecology) is a hindrance.

Most studies were motivated by academic curiosity. A few (*Kerteszia* mosquitoes in Trinidad and Brazil, *Wyeomyia* and *Aedes* mosquitoes in Florida and Brazil) were spawned by public health interests. A few (Ceratopogonidae in Brazil and Costa Rica) were promulgated by the desire to improve pollination of cacao, or (*Cholus* and *Metamasius* weevils in Venezuela, Grenada and Jamaica) to protect pineapples from damage. One (*Metamasius* weevils in Florida) was inspired to protect native bromeliads from damage by an invasive weevil.

In general, the taxonomy of Neotropical arthropods is much less developed than is that of Nearctic arthropods. Even in Florida there are undescribed species of arthropods in bromeliads (Frank and Fish, 2008). The presence of poorly characterized and indeed undescribed species of arthropods in bromeliads makes projects on community ecology difficult to accomplish. However difficult, the documented changes attributed to increased bromeliad size (Srivastava, 2006) and bromeliad context (Yanoviak et al., 2006) argue that community-level studies need to be made. The would-be community ecologist working with bromeliad faunas should develop taxonomic skills and collaborate with specialist taxonomists (including a botanist who can reliably identify to species level the bromeliads encountered even when they are not flowering). Sampling methods that do not destroy the bromeliads, but allow an adequate measurement of their size, are to be preferred. Virtually all Neotropical countries require collection and/or export permits for working with any of the organisms likely to be found in bromeliads, and lack of such foreign permits is a criminal offense under U.S. law when specimens are imported into the USA (Thomas, 1995). Because there is still very much framework to be built from ethology and autecology of described species, those avenues may prove more tractable to anyone who has limited time to study bromeliad faunas.

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