

## HOW MUCH IS KNOWN ABOUT BROMELIACEAE IN 1994?

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If access and utility alone dictated scientific interest, much less would be known about Bromeliaceae today. Fully one half of all its species grow in trees, many in remote rain forests. Another sizable group of terrestrials similarly discourages study by occurring in roadless, bleak, upper montane habitats (e.g., *Navia*, *Puya*, many *Tillandsia* spp.) especially in South America. Commercial promise has not provided much encouragement for researchers either. Beyond the pineapple, some widely marketed ornamentals, and a few minor fiber products, bromeliads simply offer too little potential to merit funding anywhere near that invested to study the more widely useful Poaceae, Fabaceae, Rosaceae and their kind. Nevertheless, bromeliads have attracted more than their share of scholarship beginning with the attentions of an impressive array of nineteenth century, comparative and functional morphologists (e.g., Haberlandt, Mez) and plant geographers (e.g., A. F. W. Schimper). Bromeliaceae continues to attract an ever-widening group of specialists, just a small fraction of whom have authored the contents of this entire volume of *Selbyana*.

Enough information has been compiled on Bromeliaceae to warrant a comprehensive, technical monograph, something not yet available, but coming soon (Benzing in prep). While nothing published in 1994 could even approach a complete synthesis, Bromeliaceae is fast emerging as one of the better known families of flowering plants. Specifically, perspectives on its origin, major radiations, and designs for life under an exceptional variety of often stressful growing conditions are expanding rapidly—faster than progress toward the same goal for most other, comparably large and ecologically diverse clades. However, knowledge of some aspects (e.g., the nature of the many and often important roles these plants play in communities) seems less likely to develop apace due in part to greater impediments to researchers and sometimes simply because interest continues to be too low. Most of the bromeliad literature concerns evolution or systematics and this pattern seems likely to continue.

What follows is a progress report—a brief appraisal of where we stand along the route to eventual synthesis. Coverage is purposely selective;

no exhaustive review of the immense literature is attempted, only highlights of accomplishments, sprinkled here and there with exhortations and a bit of guarded speculation. But first we need some statistics, current and projected, and then some thoughts about the magnitude of the task and the nature of the goals. Areas of inquiry follow, each updated to reflect current status and lastly, a concluding remark.

### SYSTEMATICS, TAXONOMY AND EVOLUTION

Bromeliaceae is the largest, almost exclusively American family (one African *Pitcairnia* sp.) of flowering plants. Likewise, its basic tropical character and relative youth are beyond dispute. However, many additional points, including much of its taxonomy, are more equivocal. Generic alignments continue to shift and the number of described species keeps growing, neither with much likelihood of closure any time soon. Family size has already expanded from the 2110 binomials recognized in Smith and Down's three volume monograph (1974, 1977, 1979) to about 2700 (Luther, pers. comm.). More additions should be expected, many contributed by intrepid amateurs seeking to embellish private collections or horticulturists intent on augmenting commercial stocks. Three thousand is a reasonable projection for the final tally, but the exact number of species will depend also on the judgments of numerous specialists, specifically on how often decisions are made to elevate the status of segregates of the many polymorphic, currently recognized species (e.g., *Tillandsia fasciculata*). Genera will also continue to multiply as so often occurs as complex groups become better known. For example, *Aechmea* (currently 10 recognized subgenera) and *Tillandsia* (7 subgenera) will almost certainly experience this fate. Such movements are afoot already as are others to combine established genera (e.g., *Aechmea* and *Streptocalyx*, Smith and Spencer 1993). Other authorities wisely council patience until changes can be better informed by more comprehensive plant collections and deeper analysis (Brown et al. 1993). Today, we stand on a threshold. Molecular data, which can more unambiguously resolve phylogeny than most other kinds, could

easily undermine hasty decisions that will further clutter the literature and burden users with superfluous nomenclature.

Inquiry on systematics has not been apportioned evenly across Bromeliaceae. Most intensively studied is Tillandsioideae among the three generally recognized subfamilies, with Pitcairnioideae second ahead of Bromelioideae, the greatest challenge of the three. The comparatively greater structural diversity and presumably broader genetic variety of the bromelioids is underscored by inclusion of over half of all the bromeliad genera in this taxon.

Recent progress toward an evolutionary taxonomy of bromeliads has been assisted by three developments: (1) a more thorough evaluation of traditional characters and employment of newer ones from the same organs (e.g., flowers) (2) the emergence of new and more powerful data from previously inaccessible sources (e.g., chloroplast genomes) and (3) the application of phenetic, and particularly cladistic, analyses that, compared to older methodologies, extract more biological information from all kinds of valid data.

Traditional reliance on dried, herbarium materials has been relieved significantly by the establishments of extensive, documented living collections (e.g., at the Marie Selby Botanical Gardens). Supplies of fresh and wet-preserved materials to examine delicate organs (e.g., stigmas) have been further supplemented by more comprehensive field work, aided recently by a network of on-site collectors (e.g., Gilmartin and Brown 1986). Fresh material has also provided a fairly complete picture of the bromeliad karyotype and its evolution (Brown and Gilmartin 1989). Particularly revealing is Brown and Terry's (1992) study of petal scale ontogeny that casts serious doubt on the wisdom of relying so heavily on this appendage to distinguish tillandsioid and probably some other bromeliad genera. These structures may enhance the delivery of nectar, but their apparent, relatively recent evolution, hence marginal utility to circumscribe at least some taxa, seems indisputable.

Pursuit of additional anatomical details, on seeds for example, continues (e.g., Gross 1992, 1993). Data on pollen morphology has been accumulating for several decades as well, but so far without the interpretation necessary to inform systematists and other investigators interested in pollination syndromes and breeding systems. Trichome structure probably also remains under-utilized for taxonomy and considering the amount of information (e.g., Varadarajan and Gilmartin 1987, Benzing and Seemann 1978) certainly offers much untapped potential to explain how the foliar epidermis of the dryer-grow-

ing tillandsioids in particular match growing conditions (humidity, light and temperature) in native habitats.

Especially exciting and central to that eventual, evolutionary synthesis is the progress of molecular systematists, several of whom work with Bromeliaceae. Ranker et al.'s (1990) analysis of restriction site polymorphisms (cpDNA) among species selected to represent all three subfamilies heralded what promises to be the first of a series of penetrating reports on phylogeny. They questioned both the reputed basic position of Pitcairnioideae within the family and the legitimacy of assigning *Glomeropitcairnia* to Tillandsioideae. Coming soon are more complete reconstructions of relationships based on sequence analyses of the gene coding the large subunit (*rbcL*) of rubisco and a second, typically more variable, and less often used plastid gene (*ndhF*) that should allow greater resolution perhaps to genera (Clark et al. in press, Brown and Randall pers. comm.). We can also expect progress shortly on the question of where Bromeliaceae lies within Liliopsida, specifically its relationships to suggested sister taxa (e.g., Rapateaceae, Velloziaceae).

Cladograms not only display relationships among lineages, they can help resolve the origins (often multiple in Bromeliaceae) and modification over time of ecologically important plant characteristics such as CAM, epiphytism and the utilization of ants for dispersal and nutrition (e.g., Chase and Hills 1992). Gilmartin and Brown (1986) recognized this potential in their attempt to determine the status (apomorphic or pleisomorphic) of xerophytism and mesophytism in subgenus *Phytarrhiza* of *Tillandsia*. Both conditions occur in other parts of *Tillandsia* and *Vriesea* and repeatedly elsewhere in the family. Accurate alignments within Bromeliaceae of additional, aberrant genera like *Brocchinia* will increase opportunities for similar sorts of derivative analysis, for example, whether the absorptive capacity of the foliar trichome evolved to promote mineral nutrition, water balance or both phenomena.

#### CARBON AND WATER BALANCE

More data (e.g.,  $H^+_{max}$ ,  $\delta H^+$ ,  $\delta^{13}C$ , patterns of gas exchange) that indicate the mechanisms of carbon and water balance or reveal their ecological consequences have been collected for the bromeliads than for species in any other family. Revelations include the discovery that related species with CAM and C3 photosynthesis sometimes co-occur without substantial differences in water economy (e.g., Griffiths et al. 1986, Griffiths 1988). Shade tolerance deeper than that pre-

modern techniques have become available to plant physiologists. Radiotracers demonstrated substantial uptake of diverse solutes through root systems and the foliage of phytotelm forms (e.g., Nadkarni and Primack 1989). Carnivory is now well documented in *Brocchinia reducta* (e.g., Givnish et al. 1984) and probably operates at a less specialized level in *Catopsis berteroniana*. Owen and Thompson (1988) assessed the fine-structure of the foliar trichome of *Brocchinia reducta* and demonstrated how these appendages probably support carnivory by absorbing the products of degraded prey. Tillandsioid trichomes need to be compared with those of *Brocchinia*. Additional study is also required to establish how the much more common noncarnivorous phytotelm bromeliads process litter rather than prey for nutrition. Diverse shoot forms and varied microflora and microfauna in phytotelmata indicate that different symbiotic biota and methods of processing mediate nutrient flux for these bromeliads (e.g., Bermudes and Benzing 1991).

Two forms of myrmecotrophy occur in Bromeliaceae. Ant-house *Tillandsia* spp and probably additional, similarly accommodating taxa (e.g., *Aechmea bracteata*) are fed by ant colonies residing within inflated leaf bases (Benzing 1991). Nutrient budgets and the importance of the ants to the plants will require deeper inquiry to establish. Another group of bromelioids (e.g., several *Aechmea* and *Streptocalyx* spp.) regularly root in ant cartons, sometimes to the near exclusion of other substrates (e.g., Davidson 1988). Chemical attractants on seeds assure successful dispersal by foraging ants. However, many other aspects of these systems, for example, whether plant nutrition reflects reliance of ant-provided substrates, remain obscure. Atmospheric bromeliads continue to be employed to monitor air quality (Schrimpf 1981, Benzing et al. 1992) because of their normal reliance on the atmosphere and canopy washes for required ions. Extraordinary capacities to accumulate a variety of additional anthropogenic substances underlies their utility for pollution surveillance; these same qualities could prove useful on a broader scale to measure important variables related to global change (Lugo and Scatena 1993).

#### REPRODUCTIVE BIOLOGY

Reproductive biology, like systematics and evolution, has attracted more than its share of the scholarly attention devoted to Bromeliaceae. Numerous reports document modes of pollination of specific species (Sazima et al. 1989). Seed dispersal has received lower priority. Tilland-

sioideae, the best known of the three subfamilies by reproductive mechanisms, attracts a variety of primary pollen vectors including birds, bats, and day- and night-flying insects. Seed dispersal is more uniform (anemochory), but not consistent if air worthiness and tendencies to adhere to specific tested substrates reflect performances in nature (Bennett 1991). Substantially less information has been reported about Pitcairnioideae, but seed size and form indicate considerable variation in mobility, probably more than characterizes the tillandsioids. Least known by floral and dispersal biology, except for those myrmecochorous ant-nest flora, is Bromelioideae. As berry producers, members of this taxon engage in relationships with fauna beyond those arboreal ants and dispersal biology is accordingly complex. Fruits appear to be attractive to birds (e.g., odorless white, blue, many *Aechmea* spp.), bats (e.g., drab, smelling of rotten fruit, some *Billbergia* spp.), and nonvolant mammals (e.g., yellow, orange hidden in foliose inflorescences, many *Nidularium* spp.). Berries of some *Ronnbergia* spp. rupture to eject seeds several meters indicating that mechanical enhancements sometimes supplement or replace animal carriage.

Information on the breeding systems of bromeliads is scattered and the impacts on the genetic structure, and isolation of populations and speciation still poorly known. Some populations routinely fruit autogamously; many more out-cross through a variety of agencies ranging from dioecism and self-incompatibility to various dichogamous and herkogamous arrangements among the self-fertile types. Populations of only three species, predominantly epiphytic *Tillandsia ionantha* and *T. recurvata* and terrestrial *Aechmea magdalenae* have been comprehensively examined (>20 loci) to determine genetic structures (Soltis et al. 1987, Murawski and Hamrick 1990). The latter species relies more heavily on ramets to colonize understory habitats, possibly because soil, relative to arboreal substrates, tends to be more expansive and permanent. Bennett (1991) demonstrated proportionally greater dependence on sexual than asexual reproduction in epiphytes compared to lithophytes among a group of *Tillandsia* spp. chosen to represent both habits.

The bromeliad literature documents how earlier interest (e.g., Downs in Smith and Downs 1974) in the physiology of flowering and fruit development has diminished. Many populations respond to photoperiod and very likely cycling temperatures and rainfall also cue important life history events. Inquiry on seed physiology has moved at about the same slow pace although previous studies indicated differences in viability and dissimilar responses to light and tempera-

viously documented for most CAM plants prevails in certain other bromeliads (e.g., *Aechmea magdalenae*, Pfitsch and Smith 1988). Many additional CAM species grow better in partial shade than full sun (e.g., *Bromelia humilis*) and may be relatively poorly suited for the kinds of terrestrial environments often associated with CAM. On the other hand, some bromelioids are near record holders for  $H^+_{max}$  (474 mol  $H^+$ /m<sup>-3</sup> for *Aechmea nudicaulis*).

*Ananas* spp. are providing insights on how plant performances under different growing conditions have been altered by indigenous agriculture (Medina et al. 1991). Interactions among N and moisture supplies and PFD (photosynthetic photon flux density) that promote different outcomes (e.g., yield, water use efficiency, citric vs. malic acid synthesis) under specific conditions in CAM plants in the field are probably best known in Bromeliaceae. Widely noted, but not yet resolved to causes and biological consequences are the mechanisms responsible for the heavy and variable reliance on respired, compared to atmospheric, CO<sub>2</sub> for nocturnal acidification that so dramatically characterizes many bromeliads (Smith 1989).

Longer-term monitoring in the field and fuller understanding of the subcellular aspects of CAM are needed to determine if and how this syndrome benefits bromeliads under the many different environmental conditions prevailing where these plants grow. What regulatory processes and environmental and internal cues determine the sources, fluxes, and metabolic fates of carbon during CAM? In addition to its capacity to improve water economy, CAM may reduce vulnerability to photodamage or promote N economy under appropriate circumstances. CAM may be most important to some bromeliads for benefits other than water economy or it could affect survival only during uncommonly dry years. Fitness may not be strongly dependent on the type of photosynthetic pathway possessed by phytotelm species native to ever-wet forests and instead may reflect conditions in ancestral more than contemporary habitats. Bromeliaceae do seem to exceed most other families in the variety of plant characters associated with CAM and the kinds of stresses its members encounter on often demanding substrates. Accordingly, more of the full array of benefits CAM imparts to land flora may be expressed in this family compared to most others.

Contrary to the CAM types, little attention has been devoted to the C3 bromeliads, for example to their light relations. Particularly intriguing are the functional correlates of the uneven, but regular distributions of chlorophyll and other pigments in the foliage of certain phytotelm species

(e.g., *Vriesea fosteriana*, Benzing and Friedman 1981). Additional inquiry on the carbon and water balance mechanisms of seedlings and adults of C3 tillandsioids could help test hypotheses concerning the role of heterochrony and the evolutionary status of xerophytism in Tillandsioideae (Adams and Martin 1986). Meanwhile, the controversy over the nature of ancestral environments continues (e.g., Smith 1989), a subject likely to defy resolution until a phylogeny (below the genus) is available to polarize ecologically decisive character states.

Whether or not CAM represents the most efficacious means to fix CO<sub>2</sub> everywhere species so equipped occur, drought limits the productivity of many Bromeliaceae and probably more decisively so than scarcities of any other resource. The importance of drought as a selective force is apparent in those bromeliads that demonstrably achieve some of the most favorable transpiration ratios on record (Smith 1989). Some longstanding questions about water balance remain only partially resolved, for instance, whether or not water vapor can significantly relieve dehydration (e.g., Martin and Schmitt 1989). Low (compared to higher) water vapor pressure deficits in surrounding air allow all land plants to conserve moisture, but claims continue that shoots of some of the heavily trichomed tillandsioids hydrate directly from moist air without prior condensation on absorptive surfaces. The foliar trichome of Tillandsioideae merits closer scrutiny to see how it aids water balance and additionally, to what extent the variously structured and positioned shield matches humidity and other conditions in native habitats.

#### MINERAL NUTRITION AND RELATED PHENOMENA

Occasional reports continue to appear on the mineral nutrition of Bromeliaceae. Several ornamentals have proven amenable to hydroponic culture and success on conventional media indicated no unusual plant requirements (e.g., Schmitt 1982). Methods have been developed for the routine aseptic micropropagation of additional taxa, including some endangered species (e.g., Mercier and Kerbauy 1992). Again, widely-used basal media proved effective. Within the decade transgenic materials that combine desirable horticultural qualities will probably reach the commercial market. Superior shoot form and desired leaf and inflorescence color and texture (historically the highest priorities for hybridizers) will probably remain the major goals.

Bromeliaceae exceed most families in the variety of nutritional modes utilized, all of which have attracted at least passing attention since

originated. Should those species (e.g., *Tillandsia usneoides*, *Bromelia humilis*) with proven value to the study of the widely-occurring aspects of stress physiology continue in that service, insights on how this family has so successfully colonized the canopy and other demanding substrates will become clearer. However, input on a variety of important, but unique features of these plants (e.g., the biology of their foliar trichomes and the workings of phytotelmata) will require the attention of investigators specifically interested in these plants. Finally, elucidation of the many roles Bromeliaceae play in neotropical ecosystems as resources for other biota and as influences on basic ecosystem processes will require more integrated and multi-disciplinary approaches than we have seen so far.

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tures that probably reflect adaptations to specific growing conditions

#### ECOLOGY AND IMPACTS IN ECOSYSTEMS

More is known about the ecology of the epiphytic than terrestrial bromeliads. Co-occurring species in dense forests at a variety of locations segregate within canopies according to exposure and humidity more or less as Pittendrigh (1948) described as the pattern in the mountains of northern Trinidad. Ecophysiologicalists have identified a number of underlying structural and functional characters (as described earlier in the section on carbon and water balance) that dictate plant occurrence at specific locations in the canopy. While host identity, the size of the supporting axis, and other aspects of the substratum (e.g., bare or moss-covered) sometimes influence distributions secondarily, epiphytic bromeliads are generally less fastidious about anchorages than much other arboreal flora, especially the orchids. Many populations of bromeliads with similar if not identical cultural requirements grow interspersed, apparently without clear spacing and may achieve high local diversities in part in response to appropriately scheduled substrate turnover (Benzing 1981). Phytotelm types furnish rooting media for more demanding flora and create high-quality habitat for myriad microflora and fauna, both vertebrates and invertebrates, with pervasive biological consequences.

Bromeliads, more than members of other families, often provide the superstructure for extensive communities, particularly in the canopies of humid montane forests occurring between about 300-3000 m. What so far have been preliminary studies only, provide a glimpse of the impact of this compartment on important processes in supporting ecosystems and early indications suggest substantial significance. Some bromeliads may achieve keystone status as essential resources (mainly housing) for some of the most aggressive and abundant ants in Neotropical forests (Wilson 1987). On a broader scale, the densities and diversities of invertebrates associated with the humus contained in leaf axils may exceed those in adjacent suspended soils and the ground below (e.g., Paoletti et al. 1991). Physical conditions in bromeliad phytotelmata have not yet received enough attention (e.g., Laessle 1967) to fully explain why they support so many and such varied kinds of residents. Insights on the events within phytotelmata that make them high-quality substitutes for nutritive soil will require the co-ordinated efforts of microbiologists and specialists knowledgeable about the workings of various groups of invertebrates.

Viewed from another perspective bromeliads,

through the nutrients they and associated debris sequester, probably deny phorophytes and perhaps other soil-rooted flora adequate nutrition under certain conditions (Benzing and Seemann 1978). At the same time, these and co-occurring epiphytes may increase system-wide capacity to intercept and store key elements for eventual slow release (Nadkarni 1984). Additional benefits accrue to forest residents from the humidity created by evaporation from phytotelmata. Leaf axils may contain the only drinking water and provide the most durable, moist refuges during long dry seasons. No doubt, patterns of aggregate nutrient use and productivity change markedly as forests become heavily colonized with bromeliads and the additional flora their presence encourages. Contributions to overall forest phytodiversity are apparent in the lists of additional epiphytes, many supported by bromeliads, that constitute up to 35% of the total flora of some montane forests (Gentry and Dodson 1987).

Diverse terrestrial, including lithic, substrates support extensive, additional Bromeliaceae, sometimes enough to dominate the associated floras. Land-based communities with substantial and greater bromeliad presences occur on the ground at high elevations (up to 4400 m in the Andes), occupy nearly rainless coastal deserts (Peru), and those inland (*Hechtia*, *Dyckia*), grow virtually unaccompanied by other vascular vegetation on cliff sides, form characteristic assemblages along humid Atlantic coasts (e.g., Brazilian restingas), and form the understories in certain humid forests (e.g., *Aechmea magdalenae*). Some of these species also occur as epiphytes and many more possess similar form and function, in effect, features that blur the distinction between what their obligate relatives suggest are more distinct habits. One of the most interesting of the little researched aspects of bromeliad biology concerns the determinants of habitat choice, which in this ecologically varied family must be extraordinarily diverse and sometimes exceptionally precise.

#### CONCLUDING REMARKS

Research on the evolution, systematics, natural history, structure, and ecophysiology of Bromeliaceae is moving forward at a quickening pace. Soon, probably within the next two decades, bromeliad phylogeny will be sufficiently understood to associate populations into natural genera and these taxa in turn into more natural tribes and subfamilies. This framework in turn will provide opportunity to establish where (in which lineages), how often, and possibly when the characteristics that distinguish the family and account for its considerable ecological novelty

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