

BROMELIACEAE: PROFILE OF AN ADAPTIVE RADIATION

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge, CB2 2RU, UK <http://www.cup.cam.ac.uk>
40 West 20th Street, New York, NY 10011-4211, USA <http://www.cup.org>
10 Stamford Road, Oakleigh, Melbourne 3166, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain

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First published 2000

Printed in the United Kingdom at the University Press, Cambridge

Typeset in 10/13pt Times NR MT in QuarkXPress™ [SE]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Benzing, David H.
Bromeliaceae: profile of an adaptive radiation / David H. Benzing;
with contributions by B. Bennett . . . [et al].

p. cm.

Includes bibliographical references (p.) and indexes.

ISBN 0 521 43031 3 (hardback)

1. Bromeliaceae. I. Title.

QK495.B76B45 2000

584'.85-dc21 99-30141 CIP

ISBN 0 521 43031 3 hardback

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Introduction

Lower and middle Cretaceous Magnoliophyta remain too poorly known to warrant definitive statements about many aspects of early angiosperm radiation (Taylor and Hickey 1992). Discovery of a compressed infructescence purportedly from the Late Jurassic of east central Asia has recently expanded its confirmed record (Sun *et al.* 1998), and raises the specter of more fossils and better resolution ahead. Nevertheless, until this promise is realized, answers to questions as fundamental as the habits (woody vs. herbaceous) of ancestors and the homologies of diagnostic organs (e.g., the gynoecium) will remain speculative. One point germane to bromeliad history is less equivocal: characteristic pollen and macrofossils indicate that Liliopsida had emerged by the middle Cretaceous. However, evidence from several quarters indicates that Bromeliaceae evolved later, and probably not before the Tertiary.

Phytogeography also accords with youth that denied Bromeliaceae opportunity to range beyond tropical America except for a single, probably recent dispersal to west Africa (Fig. 1.1). Members of the three subfamilies (*sensu* Smith and Downs 1974, 1977, 1979) and many of the larger genera (e.g., *Neoregelia*, *Hechtia*) further suggest either exceptionally low mobility (unlikely) or too little time to cross barriers breached by many other lineages. Nevertheless, most authorities (e.g., Cronquist 1981; Dahlgren *et al.* 1985) consider Bromeliaceae phylogenetically isolated among the extant monocots, and a growing body of information on the organization of several sequences of nucleotides within the chloroplast genome (e.g., Ranker *et al.* 1990; Terry *et al.* 1997*a,b*) supports this conclusion. Uncertainty continues over which of the other Liliopsida are most closely related to the bromeliads, particularly which family constitutes the sister group, i.e., shares a common ancestor with Bromeliaceae.

Certain gymnosperms and the flowering plants considered primitive

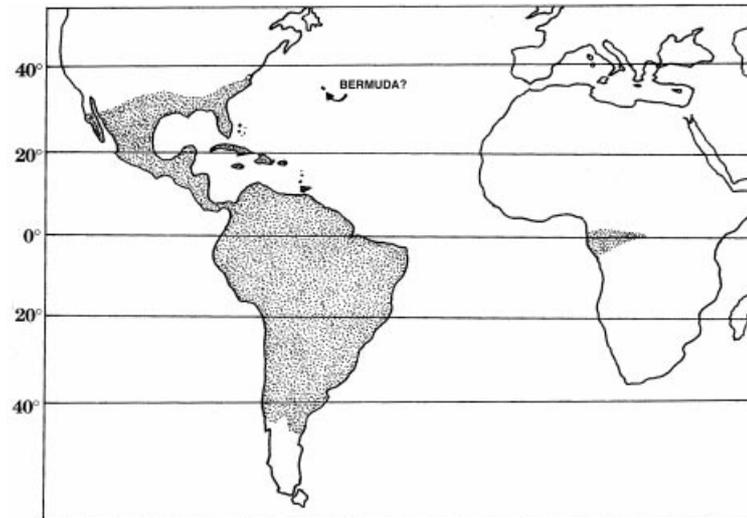


Figure 1.1. Geographic distribution of Bromeliaceae.

according to the paleoherb hypothesis challenge long-standing notions about the nature of antecedents and the characteristics of the Magnoliophyta that favored its ascent to unparalleled size and ecological dominance among land flora. Hypotheses that zoophilous pollination and certain additional aspects of reproduction drove the angiosperm radiation to unparalleled heights must now accommodate discovery that most of these same attributes occur (albeit in less advanced expressions) elsewhere, especially among the gnetophytes (e.g., Friedman 1992; Kato *et al.* 1995). Whether inherited as an older, intact suite of characters or derived piecemeal during the initial Lower Cretaceous expansion, these qualities alone cannot fully explain the unprecedented success of the flowering plants. Novel vegetative form and function were also important, as the bromeliads so clearly demonstrate.

Rather than the woody archaetype (as exemplified by the ranalean magnoliophytes) posited by the euanthial theory, the angiosperm stock is increasingly envisioned as low-growing shrubs to rhizomatous to scrambling herbs of moist, relatively disturbed (r-selecting), perhaps riverine, habitats (e.g., Taylor and Hickey 1992). Rapid maturation made possible by the combined effects of a novel nutritive tissue (endosperm), much abbreviated (fast maturation) male and female gametophytes, and relaxed

Table 1.1. *Plant characteristics presumably responsible for the unprecedented radiation of Magnoliophyta*

Vegetative
(1) Cheap construction (herbaceousness)
(2) Rapid growth, potentially short life cycles
(3) Exceptionally efficient vascular systems
(4) Exceptionally diverse architecture (e.g., vines, herbs, trees)
(5) Exceptionally plastic ecophysiology (carbon fixation pathways, H ₂ O balance mechanisms)
(6) Exceptionally broad capacity to utilize diverse resource bases (e.g., parasitism, carnivory, and other sources of nutrients unavailable to other flora)
(7) Exceptional chemical/mechanical defenses
Reproductive
(1) The flower as a reproductive organ of unmatched capacity for precise and versatile function
(2) Unmatched capacity to manipulate pollinators
(3) Inexpensive, short-lived gametophytes
(4) Endosperm
(5) Devices to routinely screen male gametophytes (pollen tube competition and various pollen recognition systems)
(6) Angiospermy and the associated possibilities for packaging seeds for protection and directed dispersal

needs for costly mechanical tissue probably account in large measure for global dominance by the flowering plants (Table 1.1). These characteristics, complemented by small size and versatile habits, account for the high densities of species in sites like humid tropical forests. Unmatched capacity to manipulate pollinators and seed dispersers in turn probably spurred the speciation necessary to stock the most densely packed modern communities. To what degree additional uniqueness, like angiospermy, which permits the maternal parent to screen haploid genotypes, and greater physiological variety (e.g., C₄, C₃ and CAM photosynthesis) influenced outcomes remains more speculative.

Even though fossils and the geographic distributions of surviving lineages indicate phylogenetic youth, Bromeliaceae exceed many of the pre-Tertiary clades (e.g., Fagaceae, Platanaceae, Juglandaceae) for number of species and especially for adaptive variety (e.g., diverse habits, habitats). Capacity to produce a simple, cheaply constructed, rapid-cycling body varies among the magnoliophytes, and helps explain why some families (e.g., Asteraceae, Poaceae, Orchidaceae) contribute more extensively to angiosperm diversity than predominantly woody groups. Additional plant

Table 1.2. *Plant characteristics that account for the inordinate success of Bromeliaceae in diverse, often demanding, habitats*

Vegetative
(1) Small herbaceous body
(2) Rhizomatous habit
(3) Propensity for heterochrony/heterophylly
(4) Phytotelm shoot
(5) Foliar trichome capable of replacing absorptive roots and providing additional services (e.g., light reflectance)
(6) Propensity for CAM, succulence and other xeromorphic features
Reproductive
(1) Less decisive for family success, although pollination and seed dispersal syndromes are diverse to match opportunities in disparate habitats

characteristics, such as the tight relationships between numerous orchids and their high-fidelity pollinators and propensity to exploit underutilized ecospace (e.g., forest canopy), in turn account in part for the different sizes of the largely herbaceous clades. Although relatively modest by membership, perhaps because of weaker propensity for speciation, Bromeliaceae exceeds these largest taxa for certain other kinds of biological variety, and most certainly for importance to several kinds of fauna (e.g., mosquitoes).

Structure and function itemized in Table 1.1 largely account for the relatively high success of the flowering plants overall, while those traits listed in Table 1.2 represent the finer-scale features that permit Bromeliaceae to surpass most other families on several counts that at least equal species richness as measures of biological importance. This family exhibits an unusually propitious combination of angiospermous qualities and some less pervasive ones conducive to life in widely available, underutilized and often physically demanding ecospace. These more exclusive attributes at once explain how one group of related species can be so ecologically versatile and stress tolerant, and also so often exceed co-occurring flora for impacts in hosting ecosystems. Members tolerate punishing drought as epiphytes and lithophytes; the hardiest terrestrials may not experience rainfall for months and, in the coastal deserts of northern Chile and southern Peru, even for years, surviving solely on more reliable supplies of fog water (e.g., Figs. 1.2, 7.1).

Conversely, certain other bromeliads root in alpine bogs and additional kinds of wetlands, and a few populations spend part of each year submerged in flowing water (Fig. 1.4G). Exposures vary from the UV-B-enriched irradiance that prevails at >4000 m in the central Andes (*Puya*) to

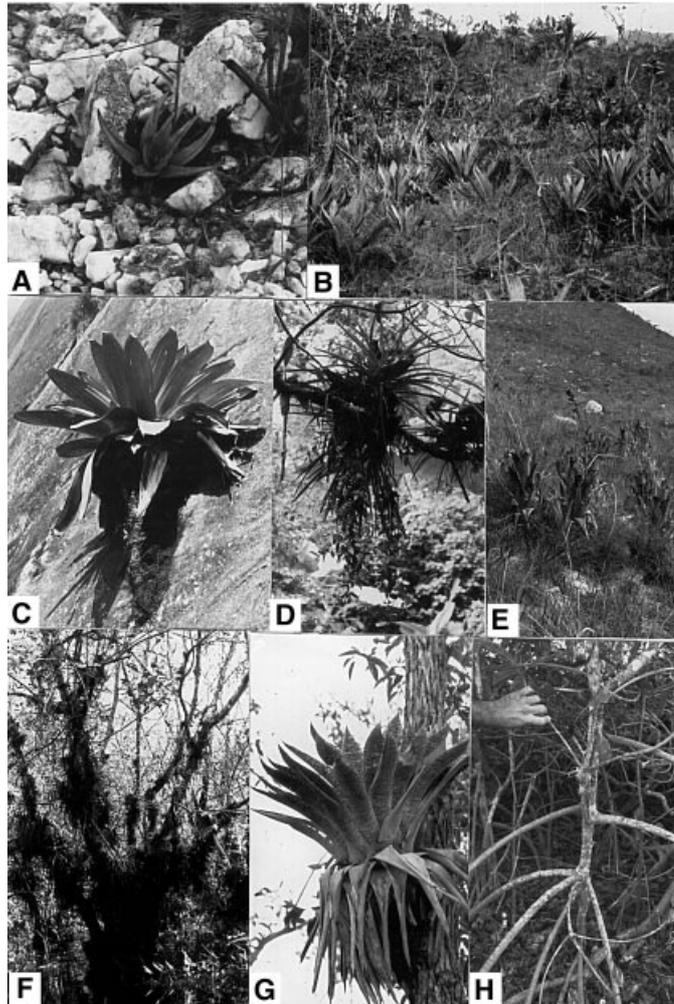


Figure 1.2. Bromeliads *in situ*. (A) *Dyckia* sp. growing in rocky soil of campos rupes-
 tres habitat in Minas Gerais State, Brazil. (B) *Brocchinia tatei* on marshy soil on
 Cerro Neblina, Venezuela. (C) *Alcantarea regina* on granite outcrop in Rio de
 Janeiro State, Brazil. (D) Large *Aechmea angustifolia* plant supporting diverse flora
 in eastern Ecuador. (E) *Hohenbergia* sp. growing as a terrestrial in Bahia State,
 Brazil. (F) *Guzmania monostachia* congregated in the lower crown of *Annona glabra*
 in south Florida swamp forest. (G) *Vriesea gigantea*, a typical phytotelm bromeliad
 in Espirito Santo State, Brazil. (H) Juvenile of *Tillandsia streptophylla* growing on
 the base of *Rhizophora mangle* in Yucatán State, Mexico.

the much attenuated photon flux under the canopies of evergreen forest (e.g., various species of *Cryptanthus*, *Pitcairnia*; Fig. 1.3D). Frost-hardiness adequate for survival at certain temperate latitudes or in tropical alpine habitats characterizes different sets of species. Access to key mineral nutrients runs the gamut from the meager supplies that oblige pronounced oligotrophy (e.g., the *Tillandsia* that clings to a small twig with its nonabsorptive roots; Fig. 1.3C) to relatively plentiful, for example the quantities provided by symbiotic biota that process the litter intercepted by the phytotelm shoots of hundreds of 'tank species' (e.g., Fig. 1.2C,G).

Those qualities that grant Bromeliaceae exceptional tolerance for drought and capacity to grow on nutrient-poor substrates required modifications of certain fundamental angiosperm features, but not of others. Bromeliad flowers probably operate with roughly the same mix of breeding systems and attractants for pollinators expressed across Magnoliophyta. Pollen and seed dispersers, while also diverse, again seem unlikely to set records for promoting speciation, ecological variety or dominance for Bromeliaceae compared with other families. In effect, the bromeliads merit special note among flowering plants for the novelty of the vegetative rather than the reproductive characteristics of the most specialized species.

What poised ancestors for life in epiphytic, lithic and other sparsely vegetated (underutilized) habitats where more than half of the bromeliads reside today was a body plan conducive to rapid cycling despite growing conditions that limit carbon gain and thus diminish vegetative vigor and reproductive power (Table 1.2; Figs. 2.1, 2.3). A remarkably adaptable leaf and shoot assist resource scavenging (for water and nutrients) and promote stress-tolerance (to drought, high and low exposure). Propensities for neoteny and specialized architectures that foster access to unconventional sources of moisture and nutrients and promote economy during the use of these commodities also encouraged radiation into exceptionally stressful habitats.

An ecological taxonomy formulated by German morphologists and biogeographers over a century ago organizes the bromeliads according to often unusual plant features that allow success in widely disparate kinds of habitats (Table 4.2). Most important are aspects of roots, shoot architecture and the foliar trichome, which, depending on the mix of special modifications, favor carbon and water balance and mineral nutrition under relatively conventional to extreme growing conditions. Some suites of characteristics foster epiphytism at relatively humid sites (Types Three and Four), and another (Type Five), use of the same kinds of substrates in drier regions. Five types are recognized in all, and references to specific bromeliads and groups of species hereafter will often employ these designations

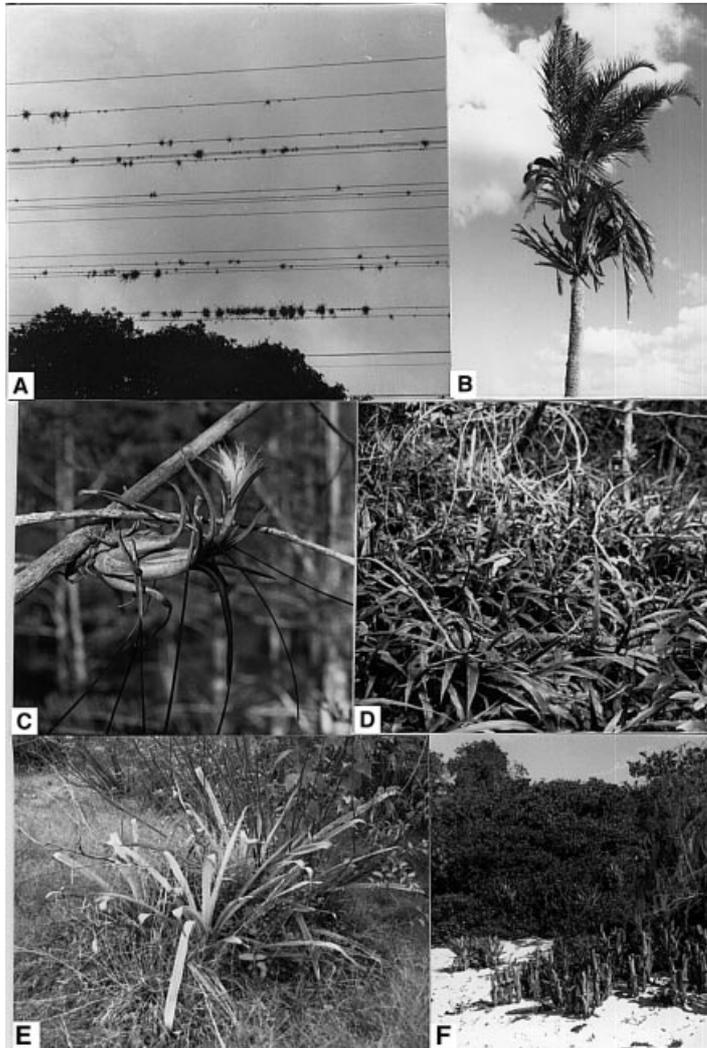


Figure 1.3. Bromeliads *in situ* (continued). (A) *Tillandsia recurvata* growing on telephone wires in southeastern Mexico. (B) *Billbergia porteana* growing on the trunk of a palm in Bahia State, Brazil. (C) *Tillandsia paucifolia* growing on a cypress twig in south Florida. (D) *Cryptanthus bromelioides* growing in the forest understory in Rio de Janeiro State, Brazil. (E) Feral *Ananas comosus* in southern Venezuela. (F) *Aechmea nudicaulis* extending out from a restinga 'island' along the coast of Rio de Janeiro State, Brazil.

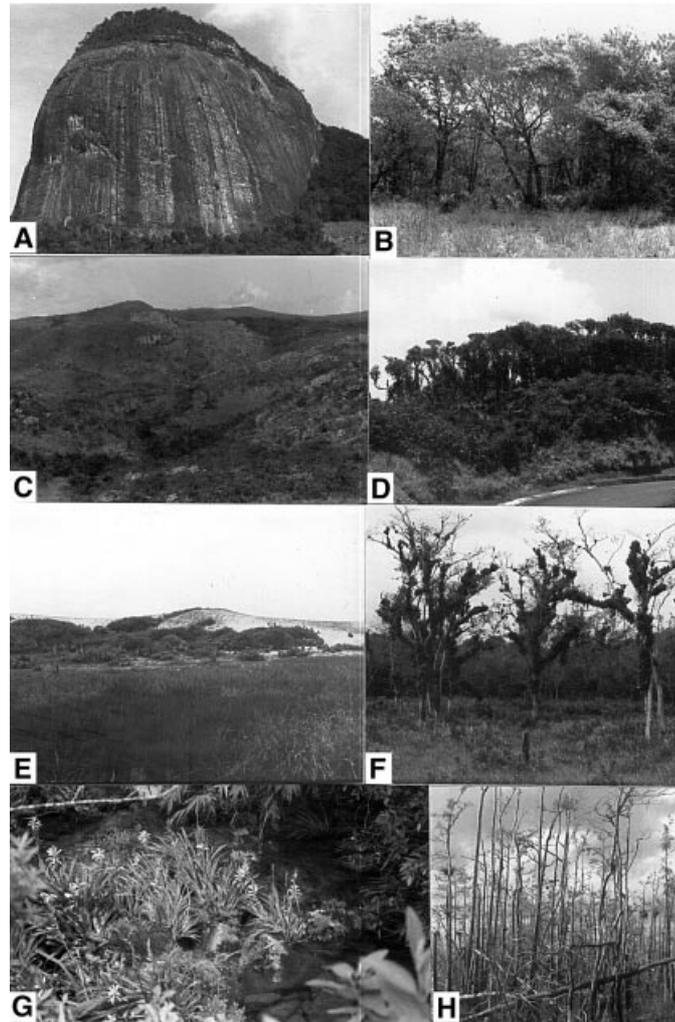


Figure 1.4. Bromeliads *in situ* (continued). (A) Granitic dome (inselberg) covered with lithophytic Bromelioideae in Rio de Janeiro State, Brazil. (B) Caatinga with an understory rich in Bromeliaceae in Bahia State, Brazil. (C) Campos rupestres habitat in Minas Gerais State, Brazil. (D) Elfin forest in eastern Puerto Rico. (E) Restinga in Rio de Janeiro State, Brazil. (F) Remnant Atlantic Forest trees covered with bromeliads in pasture in Rio de Janeiro State, Brazil. (G) A riparian colony of *Pitcairnia flammea* in Rio de Janeiro State, Brazil. (H) Dwarfed cypress forest with bromeliads in south Florida.

(Table 4.2). Familiarity with this scheme is essential to understand bromeliad evolution and functional diversity.

Chapter 2 starts the eight-chapter core with a description of how sympodial branching combined with determinant shoots bearing adventitious roots, or none at all, supports the bromeliads as hemiepiphytic vines, alpine cushion or giant rosette plants, myrmecophytes, carnivores or soil-dependent terrestrials among an even longer list of habits (e.g., Figs. 2.2, 5.3B, 6.12D). Modifications of the shoot, and particularly its epidermis, impart exceptional capacity to endure drought and impoverished substrates. Tolerances for the multiple physical constraints that prevail in the most exceptional habitats occupied by members of this family sometimes foster almost exclusive occurrences there (e.g., Figs. 1.2C, 7.1E). Crassulacean acid metabolism (CAM) promotes the water economy that helps many populations survive seasonal drought and avoid photodamage, while anchored on well-exposed bark and rocks. Similarly endowed relatives utilize wetter habitats with the most vigorous individuals often located in the shadiest microsites. In fact, CAM has been recorded in more members of Bromeliaceae than in any other family (Martin 1994).

The nearly ubiquitous foliar trichome provides diverse services to Bromeliaceae ranging from protection against potentially injurious insolation and insupportable transpiration through secretion to absorption associated with diverse nutritional modes and moisture supplies (Chapters 4 and 5; e.g., Figs. 2.5, 2.8). Bromeliaceae exceed all other families for variety of sources of nutrients and water (Table 5.6). Foliar impoundments that make litter an option for nutrition in turn assure the so-called phytotelm types importance in communities far beyond what plant numbers or total phytomass usually predict (Fig. 2.4). Dense populations of bromeliads in forest canopies can also markedly influence fundamental system-wide processes and phenomena such as mineral cycling and hydrology.

Bromeliad taxonomy remains provisional, and needs substantial improvement ranging from the reordering of species within many genera to the establishment of additional higher taxa to accommodate revelations fostered by accumulating molecular and traditional morphological data. Smith and Downs's three subfamilies include exceptionally isolated lineages (e.g., *Brocchinia*, *Catopsis*, *Glomeropitcairnia*; Tables 1.3, 1.4) in addition to core taxa, and many clades are almost certainly para- or polyphyletic (e.g., *Aechmea*, *Navia*, *Vriesea*). Pitcairnioideae, while closest to the monocot ground plan by many measures, including the status of the trichome, basic plant architecture and reproductive morphology, is not, as often reported, ancestral to either of the other two subfamilies.

Table 1.3. *Bromeliad diversity (number of species) across tropical America*

Location	Bromelioideae	Pitcairnioideae	Tillandsioideae	Total
Colombia	70	125	196	391
Ecuador	56	70	242	368
Peru	59	153	199	411
Rio de Janeiro State, Brazil	170	17	124	311
Costa Rica	27	19	145	191
Florida	0	0	17	17
Venezuela	56	188	120	364

Source: From Fontoura *et al.* (1991) and Holst (1994).

Bromelioideae and Tillandsioideae followed parallel evolutionary trajectories to become heavily epiphytic and dependent on foliar impoundments and CAM. Certain other features diverged at least as much (e.g., fruit types, reliance on foliar trichomes). DNA sequences are beginning to help align and redefine the genera (e.g., *Tillandsia/Vriesea*), and should eventually demonstrate how often, when, and under what conditions important events, like the emergence of the absorbing trichome and CAM, occurred during bromeliad history. Many aspects of vegetative structure and function are homoplasious (e.g., CAM, phytotelm shoot), as are most of the many pollination syndromes recorded for the family.

Specialized Bromeliaceae, and some other flora from comparably demanding habitats, inspired inquiry that helped launch the discipline of physiological ecology during the late 19th century. Early functional morphologists and biogeographers, including A. F. W. Schimper, C. Mez and G. F. J. Haberlandt, firmly established the principle that plant function tracks structure, and that both variables reflect growing conditions *in situ*. Some of the most elegant examples came from experiments performed on advanced Tillandsioideae, specifically those subjects labeled 'atmosphériques' (Type Five; Table 4.2) because they rely on foliar trichomes to absorb airborne water and nutrients instead of the roots most land flora employ to obtain the same resources from soil.

Major contributors since then include C. S. Pittendrigh (1948) who also anticipated some of the discoveries of the current generation of ecophysiologicalists by postulating how plant habit and aspects of leaves and roots account for the distribution of Trinidad's bromeliads. His work also helped validate the ecological classification provided in Table 4.2. Bromeliads occupied a prominent place in Leopoldo Coutinho's efforts in the late 1940s through the mid-1960s (e.g., Coutinho 1963) to demonstrate the

Table 1.4. *The bromeliad genera: selected statistics, ecological type and geographic range*

Genus	Number of species ^a	Ecological type	Geographic range
<i>Acanthostachys</i>	2	I	East central Brazil
<i>Aechmea</i>	220	Mostly III	Tropical America
<i>Alcantarea</i>	15	Mostly IV	Southeastern Brazil
<i>Ananas</i>	7	II	South America
<i>Androlepis</i>	1	III	Central America
<i>Araeococcus</i>	5	I and III	Southeastern Brazil to northern South America
<i>Ayensua</i>	1	I	Guayanan Shield
<i>Billbergia</i>	62	III	Tropical America
<i>Brewcaria</i>	2	I	Guayanan Shield
<i>Brocchinia</i>	17	I and IV	Guayanan Shield
<i>Bromelia</i>	49	I and II	Tropical America
<i>Canistrum</i>	11	III	Southeastern Brazil
<i>Catopsis</i>	21	IV	Predominantly Mesoamerica
<i>Connellia</i>	5	I	Guayanan Shield
<i>Cottendorfia</i>	1	I	Bahia and adjacent states, Brazil
<i>Cryptanthus</i>	42	I	Southeastern Brazil
<i>Deinacanthon</i>	1	II	Argentina and Paraguay
<i>Deuterocohnia</i>	14	I	Mostly Bolivia
<i>Disteganthus</i>	3	I-II	Guianas
<i>Dyckia</i>	120	I	Southeastern South America
<i>Encholirium</i>	30	I	Southeastern Brazil
<i>Fascicularia</i>	5	I	Chile
<i>Fernseea</i>	2	I	Cerro Italia, São Paulo State, Brazil
<i>Fosterella</i>	18	I	Predominantly west central South America
<i>Glomeropitcairnia</i>	2	IV	Lesser Antilles, Trinidad and adjacent Venezuela
<i>Greigia</i>	28	I and II	Predominantly Andean
<i>Guzmania</i>	175	I and IV	Tropical America
<i>Hechtia</i>	51	I	Predominantly Mexican
<i>Hohenbergia</i>	47	III	Mostly Jamaican and southeastern Brazil
<i>Hohenbergiopsis</i>	1	III	Mexico and Central America
<i>Lindmania</i>	36	I	Guayanan Shield
<i>Lymania</i>	6	III	Southeastern Brazil
<i>Mezobromelia</i>	9	IV	Andean
<i>Navia</i>	95	I	Guayanan Shield
<i>Neoglaziovia</i>	3	I	East central Brazil
<i>Neoregelia</i>	95	III	Southeastern Brazil
<i>Nidularium</i>	54	III	Southeastern Brazil
<i>Ochagavia</i>	3	I	Chile (San Fernandez island)
<i>Orthophytum</i>	26	I	Southeastern Brazil
<i>Pepinia</i>	48	I	Predominantly Amazonian

Table 1.4. (cont.)

Genus	Number of species ^a	Ecological type	Geographic range
<i>Pitcairnia</i>	295	I	Tropical America
<i>Portea</i>	9	III	Southeastern Brazil
<i>Pseudaechmea</i>	1	III	Colombia and Bolivia
<i>Pseudananas</i>	1	II	Southeastern Brazil
<i>Puya</i>	194	I	Predominantly Andean
<i>Quesnelia</i>	15	III	Southeastern Brazil
<i>Racinaea</i>	57	IV	Mostly Andean
<i>Ronnbergia</i>	11	III	Panama to Peru, Southeastern Brazil
<i>Steyerbromelia</i>	3	I	Guayanan Shield
<i>Tillandsia</i>	518	I, IV, V	Tropical America
<i>Ursulaea</i>	2	III	Mexico
<i>Vriesea</i>	227	I, IV, V	Tropical America
<i>Werauhia</i>	64	IV	Primarily Mesoamerica
<i>Wittrockia</i>	12	III	Southeastern Brazil

Source: ^aFrom Luther and Sieff (1996).

mechanisms of photosynthesis among Neotropical epiphytes. Bromeliaceae continue to attract investigators seeking more complete answers to questions about carbon, water and nutrient balance, aspects of reproduction, and phylogenetic relationships as detailed in the following eight chapters.

Another set of pioneering biologists (e.g., Picado 1911, 1913) chose to study this family because they recognized the importance of the bromeliad phytotelmata to extensive fauna in many tropical American forests. Foliar impoundments reportedly harbor high diversities and abundances of aquatic and soil-type invertebrates, sometimes at densities above those encountered in equivalent volumes of nearby forest soil (e.g., Paoletti *et al.* 1991; Fig. 8.15). Several more studies provide data on the physical and chemical conditions in these microcosms, and yield insights on why certain bromeliads host so many symbionts. Checklists indicate potentials for litter processing and nutrient release comparable to those that prevail in more conventional rooting media (Table 8.2). Broader perspectives suggest that epiphytic Bromeliaceae, acting with certain other arboreal flora, intercept and release key nutrients in ways that either augment or deprive co-occurring flora depending on conditions at the site (Fig. 7.18).

The eight-chapter core that follows these preparatory remarks also considers reproductive morphology, which, along with profiling the vegetative

body, sets the stage to move on to basic life functions. Evolution is reserved for the final installment. A modest third section contains short chapters authored by specialists who treat several genera and the ethnobotany and conservation of Bromeliaceae. As information continues to accumulate, additional, specialized subjects will be able to be included in future volumes, along with updates of the core chapters on basic structure and function, ecology and family history.