PHYLOGENY, ADAPTIVE RADIATION, AND HISTORICAL BIOGEOGRAPHY OF BROMELIACEAE INFERRED FROM *ndh*F SEQUENCE DATA

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ABSTRACT

Cladistic analysis of *ndh*F sequences identifies eight major bromeliad clades arranged in ladderlike fashion. The traditional subfamilies Tillandsioideae and Bromelioideae are monophyletic, but Pitcairnioideae are paraphyletic, requiring the description of four new subfamilies, recircumscription of Pitcairnioideae and Navioideae, the sinking of *Ayensua,* and description of the new genus **Sequencia.** **Brocchinioideae** are basalmost, followed by **Lindmanioideae**, both restricted to the Guayana Shield. Next is an unresolved trichotomy involving **Hechtioideae** from Central America, Tillandsioideae, and the remaining bromeliads in subfamilies Navioideae, Pitcairnioideae, **Puyoideae**, and Bromelioideae. Bromeliads arose as C_3 terrestrial plants on moist infertile sites in the Guayana Shield roughly 70 Mya, spread centripetally in the New World, and reached tropical West Africa (*Pitcairnia feliciana*) via long-distance dispersal about 10 Mya. Modern lineages began to diverge from each other 19 Mya and invaded drier areas in Central and South America beginning 15 Mya, coincident with a major adaptive radiation involving the repeated evolution of epiphytism, CAM photosynthesis, impounding leaves, several features of leaf/trichome anatomy, and accelerated diversification at the generic level. This "bromeliad revolution" occurred after the uplift of the northern Andes and shift of the Amazon to its present course. Epiphytism may have accelerated speciation by increasing ability to colonize along the length of the Andes, while favoring the occupation of a cloud-forest landscape frequently dissected by drier valleys. Avian pollination (mainly by hummingbirds) evolved at least twice ca. 13 Mya; entomophily was ancestral. *Hechtia, Abromeitiella–Deuterocohnia–Dyckia–Encholirium,* and *Puya* exhibit a remarkable pattern of concerted convergence in six anatomical and physiological leaf traits adapted to drought.

Key words: Brazilian Shield, *Brocchinia,* correlated evolution, phylogeography.

INTRODUCTION

The largely Neotropical family Bromeliaceae (56 genera, 2600 species) has traditionally been divided into three subfamilies: Pitcairnioideae with winged (or rarely naked) seeds, Tillandsioideae with plumose seed appendages, and Bromelioideae with baccate fruits (Smith and Downs 1974, 1977, 1979; Smith and Till 1998). Beginning 15 years ago, several studies attempted to infer relationships among these subfamilies and their constituent genera using morphological and (especially) molecular data (see Gilmartin and Brown 1987; Clark and Clegg 1990; Givnish et al. 1990, 1992; Ranker et al. 1990; Clark et al. 1993). Early progress was limited, partly because bromeliads exhibit substantial homoplasy in morphology (e.g., Varadarajan and Gilmartin 1988), partly because they occupy an isolated taxonomic position with no clear outgroup with which to polarize character-states (Gilmartin and Brown 1987; Terry et al. 1997*a*; Givnish et al. 2000; Pires and Sytsma 2002), and partly because their chloroplast DNA evolves at an exceptionally slow rate (Gaut et al. 1992, 1997; Givnish et al. 2004, 2006).

Seven years ago, Terry et al. (1997*a*) revolutionized bromeliad systematics by obtaining sequences of the rapidly evolving, chloroplast-encoded *ndh*F gene for several genera representing each of the putative subfamilies. They found that *Brocchinia acuminata*—a placeholder for a genus traditionally viewed as pitcairnioid—occupies a position at the base of the family; Tillandsioideae are monophyletic and form the next divergent branch. The remaining pitcairnioids studied are paraphyletic, with single species of *Dyckia, Encholirium, Fosterella, Pitcairnia,* and *Navia* forming one clade, and *Puya* sister to a monophyletic Bromelioideae. This study was a fundamental contribution, but fell short of being a comprehensive basis for analyzing phylogeny, ecological diversification, and historical biogeography across bromeliads, because more than half the pitcairnioid genera were not sampled, including most of the critical genera endemic to the Guayana Shield in northern South America (Givnish et al. 1997), as well as the only bromeliad found outside the New World, *Pitcairnia feliciana* of West Africa (Porembski and Barthlott 1999).

Horres et al. (2000) analyzed nucleotide variation in the *trn*L intron of cpDNA across 62 bromeliad species and 32 genera. They found three major clades in an unresolved trichotomy: (1) single species of *Ayensua* and *Brocchinia*; (2) three species of *Hechtia*; and (3) all other bromeliad genera sampled. The last group itself entailed an unresolved polytomy of five additional clades, including a monophyletic Bromelioideae. Resolution was limited because they detected only 73 informative base substitutions among 62 taxa, compared with 71 substitutions among many fewer taxa in the *ndh*F study by Terry et al. (1997*a*). Several crucial pitcairnioid taxa were again not examined, including almost all of the Guayana Shield endemics. Horres et al. (2000) did, however, sequence *P. feliciana* and showed that it was related to other members of the same genus. Crayn et al. (2000) investigated relationships among 11 of the 16 pit-

cairnioid genera using nucleotide data for roughly half of the cpDNA *mat*K gene, but their results provided little phylogenetic structure beyond individual genera in most cases, recognizing a clade with a nine-way polytomy being sister to *Hechtia*, using tillandsioids as an outgroup. Reinert et al. (2003) used these same *mat*K sequences to analyze relationships among only pitcairnioid genera, and found weak support for *Hechtia* rather than *Brocchinia* being the sister to all pitcairnioids. Crayn et al. (2004) conducted a combined analysis of *mat*K and *rps*16 sequences for 48 bromeliad taxa; while their results were somewhat better resolved than those Crayn et al. (2000) and Reinert et al. (2003), many large-scale relationships remained unresolved. They identified *Brocchinia* as sister to the rest of the family, which they resolved as one major 4-way polytomy, including *Hechtia, Navia phelpsiae* L. B. Sm.–*Cottendorfia*, Tillandsioideae, and a 5-way polytomy, including all of the other taxa sampled (*Pitcairnia* in part, *Fosterella*, *Dyckia–Encholirium–Deuterocohnia*, *Navia igneosicola* L. B. Sm., Steyerm. & H. Rob.–*Pitcairnia* in part, and Bromelioideae).

To reconstruct phylogenetic relationships within Bromeliaceae, we present a molecular phylogeny based on nucleotide variation in *ndh*F, a relatively large (ca. 2200 bp) gene in the chloroplast genome that evolves at a substantially faster rate than *rbc*L (Gaut et al. 1997; Terry et al. 1997*a*; Givnish et al. 2000, 2004; Pires et al. 2006). To clarify overall relationships within the family as a whole, we analyze *ndh*F sequence data for a highly inclusive sample of taxa, including representatives of all three subfamilies and all but two of the pitcairnioid genera, including those endemic to the Guayana Shield. We calibrate the resulting tree against the times of origin of other monocot groups based on an *ndh*F phylogeny across monocots (Givnish et al. 2006) and the inferred divergence of *Acorus* from other monocots 134 million years ago (Mya) (Bremer 2000). We then use this calibrated phylogeny to (1) analyze evolutionary relationships within the family and propose a revised infrafamilial classification, (2) infer the timing of cladogenetic events within the family, (3) relate the latter to datable events in geographic and climatic history, (4) evaluate ancient vicariance vs. recent long-distance dispersal as potential mechanisms accounting for the distribution of *P. feliciana* in West Africa, (5) analyze where the family may have arisen, and (6) correlate the spread of the family outside its area of origin with features related to its extensive adaptive radiation, including the rise of such ecological innovations as epiphytism and CAM photosynthesis.

<center>MATERIALS AND METHODS</center>

Taxon Sampling and Outgroup Analysis

We included 58 *ndh*F sequences in our analysis, including 35 for taxa representing all major groups of Bromeliaceae, and 16 for taxa representing all three subfamilies of Rapateaceae (Table 1). Only two genera of Pitcairnioideae were not sampled: *Connellia* and *Steyerbromelia*. Based on morphology, *Connellia* appears closely related to *Lindmania* and possibly embedded within it, differing mainly in the possession of large, colorful inflorescence bracts; *Steyerbromelia* appears closely related to *Brewcaria* and *Navia*, differing from them in having winged seeds or minute petal append-

ages, respectively (Holst 1997). All genera of Tillandsioideae and Bromelioideae not included in our survey but previously sequenced for *ndh*F (e.g., *Mezobromelia*, *Cryptanthus*) have been shown to belong to these two monophyletic subfamilies (Terry et al. 1997*a, b*).

To maximize the resolution of relationships within the ingroup while minimizing artifacts due to a poor sampling of outgroups (Sytsma and Baum 1996), we used seven outgroup taxa representing Mayacaceae, Typhaceae, Flagellariaceae, Joinvilleaceae, and Poaceae. Based on a cladistic analysis of *ndh*F cpDNA sequences across monocots, Givnish et al. (2006) found that Typhaceae are sister to Bromeliaceae at the base of order Poales (sensu APG II 2003), with Rapateaceae next divergent. Mayacaceae, Eriocaulaceae, and Xyridaceae are sister to Cyperaceae–Thurniaceae; together, these members of the sedge alliance are sister to the remaining families of Poales, including Flagellariaceae, Joinvilleaceae, and Poaceae among others. Based on these inferred relationships, we used species of *Flagellaria, Joinvillea*, and basal grasses as super-outgroups to polarize character-states within Bromeliaceae and their immediate relatives. Appendix 1 gives authorities for all generic names mentioned in the text. Table 1 gives authorities for specific epithets of the taxa sequenced.

DNA Extraction, Amplification, and Sequencing

Total DNAs were isolated from fresh leaves, or material frozen at −80°C or dried in contact with silica gel, using the CTAB (hexadecyltrimethylammonium bromide) technique as modified by Smith et al. (1991). We amplified and cycle-sequenced *ndh*F using standard procedures, and then edited sequences for the forward and reverse strands using standard techniques (Givnish et al. 2000). Sequences were visually aligned following Baum et al. (1994). GenBank accession numbers were acquired for all new sequences obtained; the remaining sequences were downloaded from GenBank (Table 1).

Phylogenetic Analyses

We inferred relationships from *ndh*F sequences using maximum parsimony in PAUP* vers. 4.0b10 (Swofford 2002). Nucleotide positions were considered multistate, unordered characters of equal weight. Unknown nucleotides were treated as uncertainties. Indels were excluded from analysis, because they generally only supported relationships that were already supported by mutations at the level of individual nucleotides. To search for multiple islands of most parsimonious trees (Maddison 1991), we conducted heuristic searches seeded with 500 random addition sequences, using TBR swapping with MULPARS activated. We formed the strict consensus of the shortest trees obtained, and employed bootstrap analysis (Felsenstein 1985) to evaluate the relative support for each node. To produce a tree that could be calibrated against the geological ages of known fossils of other monocot groups, we substituted our selection of bromeliad taxa for the smaller group included in the across-monocot *ndh*F data set of Givnish et al. (2006). Heuristic searches identical to those just described were then conducted, using *Ceratophyllum* as an outgroup.

Molecular Clocks and Historical Biogeography

To test whether *ndh*F evolves in clocklike fashion within Bromeliaceae, we pruned nonfamily members from the maximum-parsimony trees and set the earliest-divergent clade as the outgroup. We then calculated the log likelihoods of these trees with and without enforcing a molecular clock using a six-parameter, fully time-reversible model in PAUP*, employing a gamma distribution of rates fit to quartile means. To test for significant deviations from a molecular clock, we compared twice the difference of these log likelihoods with the X^2 distribution with $n - 2$ degrees of freedom (d.f.), where n is the number of taxa included in the analysis (Felsenstein 1994; Sanderson 1997). We calculated the mean $\pm$ SD of branch lengths from the stem group of each family to all the terminal taxa as alternative measures of regularity in evolutionary rates (Givnish et al. 1999, 2000).

We converted one of the maximum-parsimony trees to ultrametric form—in which the lengths of all branches from the root are identical—using penalized likelihood (PL) in the computer program r8s (Sanderson 2002). PL averages local differences in the rate of DNA evolution on different branches, taking into account the topology of branching. PL differs from nonparametric rate smoothing (NPRS) (Sanderson 1997) in that it assigns a penalty for rate changes among branches which are too rapid or frequent, based on a smoothness parameter. If the smoothness parameter is large, then PL approaches a clocklike model of molecular evolution; if the smoothness parameter is small, then PL approaches NPRS. NPRS behaves well in trees with substantial rate variation, but suffers when rates are clocklike or nearly so (Sanderson 2002, pers. comm.). We employed the cross-verification algorithm in r8s to find the optimal value of the smoothness parameter, minimizing the sum of the squared deviations between observed and expected branch lengths derived through jackknifing each individual branch (Sanderson 2002). The smoothness parameter was varied from 10^0 to 10^3 in steps of 0.25 in the exponent. For comparative purposes, we also used NPRS, Langley-Fitch molecular clocks (Langley and Fitch 1974), and lineage-specific mutation rates (Givnish et al. 1999, 2000) to estimate ages on a pruned monocot tree, consisting solely of Bromeliaceae and its immediate sister group *Typha–Sparganium*. Dates of divergence within the pruned tree were calibrated by setting the age of the stem group of *Typha–Sparganium* equal to 69.5 My, based on the oldest known fossils for the latter group (Herendeen and Crane 1995; Bremer 2000).

We calibrated the cross-verified PL tree against absolute time by equating the time at which Acorales diverged from other monocots to 134 Mya, based on Bremer's (2000) phylogenetic analysis. We constrained the ages of the stem groups of Poaceae–Joinvilleaceae–Flagellariaceae–Restionaceae, Typhaceae, Arales, and Tofieldiaceae to be at least 69.5 Mya, and the corresponding times of origin of Zingiberales and Arecales to be at least 83 and 89.5 Mya, respectively, based on the ages of the oldest documented fossils of each of these groups (Bremer 2000). We had to take this indirect route to calibrating the *ndh*F phylogeny because almost all bromeliads grow in habitats poor for fossil preservation. Indeed, there is only one macrofossil—*Karatophyllum bromelioides* L. D. Goméz, from Costa Rica 36

Mya—clearly assignable to the family (Smith and Downs 1974; Smith and Till 1998); there is also an unpublished report of bromeliaceous pollen from Panama substantially earlier than that from the Eocene (Benzing 2000). We related the timing of inferred cladogenetic events within Bromeliaceae—including the divergence of *P. feliciana* from its nearest Neotropical relative—to the times of uplift and dissection of the tepuis of the Guayana Shield, formation of the Amazon basin, and uplift of the Andes (Ghosh 1985; Briceño and Schubert 1990; Briceño et al. 1990; Sidder and Mendoza 1991; Stallard et al. 1991; Hoorn 1994; Hoorn et al. 1995; Briceño 1995; Edmond et al. 1995; Rasanen et al. 1995; Potter 1997; Doerr 1999).

Historical Biogeography and Adaptive Radiation

To assess historical patterns of biogeographic diversification, we overlaid geographic distributions on the bromeliad phylogeny using MacClade 4.0 (Maddison and Maddison 1992). Geographic ranges of the terminal taxa were divided into recognized biogeographic areas of endemism (Brazilian Shield [including the Atlantic Shield and Phanerozoic deposits near the Rio de la Plata], Guayana Shield, Amazon basin, Andes, Caribbean [including the adjacent littoral of northern South America], Central America, and tropical west Africa). Single species acting as placeholders for large genera (e.g., *Tillandsia, Vriesea*) were coded as polymorphic for all regions occupied by members of those genera. We used accelerated transformation to minimize the number of apparent convergent gains. Spatial shifts in distribution were then related to the chronology obtained from the analysis of ultrametric trees, and to inferred shifts in ecology and associated adaptations.

We overlaid the epiphytic habit and CAM photosynthetic pathway on the bromeliad phylogeny to assess patterns of evolution in two traits thought to be crucial to the ecological abundance and evolutionary success of bromeliads as a whole (Pittendrigh 1948; Tomlinson 1969; Benzing 1980, 2000). We also overlaid ornithophily (avian pollination) on the entire bromeliad phylogeny, and overlaid several leaf traits apparently related to drought tolerance (internal water storage tissue; lack of differentiation within chlorenchyma; hypodermal sclerenchyma; trichomes with extensive wings; and overlapping trichomes arranged in distinct rows and vertical tiers) on that part of the phylogeny corresponding to the traditional Pitcairnioideae. We obtained data on CAM photosynthesis from Martin (1994); on ornithophily and epiphytism, from Smith and Downs (1974), Galetto and Bernardello 1992, Smith and Till (1998), and Benzing et al. (2000b); and on leaf and trichome anatomy of Pitcairnioideae, from Varadarajan and Gilmartin (1988). Our aim was to relate adaptive shifts to the chronology, ecology, and biogeography of bromeliad diversification, and to determine whether individual traits or suites of traits arose once or many times independently.

<div align="center">RESULTS</div>

Phylogeny

For the bromeliad-centered data set, maximum parsimony resulted in 12 shortest trees of length 1617 steps, and a well-

Table 1. Species included in this study. Nomenclatural authorities were obtained from the International Plant Names Index website (IPNI 2004). Herbarium vouchers indicated in italics; initial citations and garden accessions are shown in roman. SEL = Marie Selby Botanical Garden; StL = Missouri Botanical Garden.

Family	Species	GenBank	Voucher/Accession/Citation	Sequence author
Bromeliaceae	*Abrometiella lorentziana* (Mez) A. Cast.	AY438598	SEL ex StL s. n.	K. C. Millam
	Aechmea haltonii H. Luther	L75844	Terry et al. 1997a	R. G. Terry et al.
	Ananas ananassoides (Baker) L. B. Sm.	L75845	Terry et al. 1997a	R. G. Terry et al.
	Ayensua uaipanensis (Maguire) L. B. Sm.	AY438599	*Givnish 4200*, WIS	K. C. Millam
	Brewcaria relexa (L. B. Sm.) B. K. Holst	AY208982	Givnish et al. 1997	K. C. Millam
	Brocchinia acuminata L. B. Sm.	L75859	Terry et al. 1997a	R. G. Terry et al.
	B. paniculata Schult. f.	AY208981	*Fernandez 8236*, PORT	K. C. Millam
	B. prismatica L. B. Sm.	AY438600	Givnish et al. 1997	K. C. Millam
	B. serrata L. B. Sm.	AY438601	*Betancur & Ramírez 1265*, MO	K. C. Millam
	Bromelia L. sp.	L75860	Terry et al. 1997a	R. G. Terry et al.
	Canistrum giganteum (Baker) L. B. Sm.	L75861	Terry et al. 1997a	R. G. Terry et al.
	Catopsis wangerini Mez & Werckle	L75855	Terry et al. 1997a	R. G. Terry et al.
	Cottendorfia florida Schult. f.	AY438602	SEL 96-0695	K. C. Millam
	Deuterocohnia longipetala Mez	AY208984	Hort. Marnier-Lapostelle s. n.	K. C. Millam
	Dyckia L. sp.	L75857	Terry et al. 1997a	R. G. Terry et al.
	Encholirium Mart. ex Schult. sp.	L75862	Terry et al. 1997a	R. G. Terry et al.
	Fosterella penduliflora (C. H. Wright) L. B. Sm.	L75863	Terry et al. 1997a	R. G. Terry et al.
	F. villosula (Harms) L. B. Sm.	AY438603	StL 79-2073	K. C. Millam
	Glomeropitcairnia penduliflora Mez	L75864	Terry et al. 1997a	R. G. Terry et al.
	Guzmania monostachya Rusby	L75865	Terry et al. 1997a	R. G. Terry et al.
	Hechtia guatemalensis Mez	AY438604	SEL 81-1891	K. C. Millam
	H. lundelliorum L. B. Sm.	AY208985	SEL 85-1005	K. C. Millam
	Lindmania longipes (L. B. Sm.) L. B. Sm.	Ay438605	Givnish et al. 1997	K. C. Millam
	Lindmania Mez sp.	AY438606	*Givnish 507*, WIS	K. C. Millam
	Navia saxicola L. B. Sm.	AY208983	Givnish et al. 1997	K. C. Millam
	Neoregelia pineliana (Lemaire) L. B. Sm. var. *pineliana*	L75893	Terry et al. 1997a	R. G. Terry et al.
	Nidularium selloanum (Baker) E. Pereira & Leme	L75894	Terry et al. 1997a	R. G. Terry et al.
	Pitcairnia atrorubens Baker	AY438607	SEL 86-311	K. C. Millam
	P. corallina Linden	AY438608	SEL 86-0574	K. C. Millam
	P. feliciana (A. Cheval.) Harms & Mildbr.	AY438609	SEL 98-0116	K. C. Millam
	P. hirtzii H. Luther	L75901	Terry et al. 1997a	R. G. Terry et al.
	Puya floccosa E. Morr.	AY438610	SEL 90-0612	K. C. Millam
	P. raimondii Harms	AY438611	SEL 91 s. n.	K. C. Millam
	Tillandsia complanata Benth.	L75899	Terry et al. 1997a	R. G. Terry et al.
	Vriesea viridiflora (Regel) J. R. Grant	L75910	Terry et al. 1997a	R. G. Terry et al.
Flagellariaceae	*Flagellaria indica* L.	U22008	Clark et al. 1995	J. F Wendel
Joinvilleaceae	*Joinvillea ascendens* Gaudich.	U21973	Clark et al. 1995	J. F Wendel
Mayacaceae	*Mayaca fluviatilis* Aubl.	BD20001	*Berry 3004*, WIS	J. C. Hall
Poaceae	*Bambusa stenostachya* Hack.	U21967	Clark et al. 1995	J. F Wendel
	Pharus lappulaceus Aubl.	U21994	Clark et al. 1995	J. F Wendel
Rapateaceae	*Amphiphyllum rigidum* Gleason	AF207638	Givnish et al. 2000	T. M. Evans & M. L. Zjhra
	Cephalostemon flavus (Link) Steyerm.	AF207624	Givnish et al. 2000	T. M. Evans
	Epidryos guayanensis Maguire	AF207632	Givnish et al. 2000	T. B. Patterson

Table 1. Continued.

Family	Species	GenBank	Voucher/Accession/Citation	Sequence author
	Guacamaya superba Maguire	AF207636	Givnish et al. 2000	T. M. Evans
	Kunhardtia rhodantha Maguire	AF207635	Givnish et al. 2000	T. M. Evans
	Maschalocephalus dinklagei Gilg & K. Schum.	AF207628	Givnish et al. 2000	T. M. Evans
	Monotrema bracteatum Maguire	AF207625	Givnish et al. 2000	T. M. Evans
	Potarophytum riparium Sandwith	AF207627	Givnish et al. 2000	T. M. Evans
	Rapatea paludosa Aubl.	AF207623	Givnish et al. 2000	T. M. Evans
	Saxofridericia inermis Ducke	AY438612	*Berry 6510*, MO	J. C. Hall
	S. regalis Schomb.	AF207637	Givnish et al. 2000	T. M. Evans & M. L. Zjhra
	Schoenocephalium cucullatum Maguire	AF207634	Givnish et al. 2000	T. M. Evans & M. L. Zjhra
	Spathanthus bicolor Ducke	AY438615	*Givnish 89-125*, WIS	T. M. Evans
	S. unilateralis Desv.	AY438613	*Berry & Bachhuber s. n.* 10 Jul 2000, WIS	J. C. Hall
	Stegolepis hitchcockii Maguire subsp. *morichensis* Maguire	AF207629	Givnish et al. 2000	T. M. Evans
	Windsorina guianensis Gleason	AY438614	*Kelloff 1413*, US, WIS	J. C. Hall
Typhaceae	*Sparganium* L. sp.	AY191213	Givnish, field identification	J. C. Pires
	Typha angustifolia L.	U79230	Graham et al. 2002	S. W. Graham

resolved strict consensus (Fig. 1). For these trees, the consistency index (CI) was 0.66 (0.57 excluding autapomorphies = CI′), while the retention index (RI) was 0.82. Overall, 807 nucleotide sites were variable, of which 510 were phylogenetically informative. Within Bromeliaceae alone, 269 sites were variable and 112 were informative.

Sequence variation in *ndh*F strongly supports the monophyly of Bromeliaceae (100% bootstrap value) and resolves eight major clades, arranged in ladderlike fashion (Fig. 1, 2). Earliest divergent is *Brocchinia,* an extraordinary genus of ca. 20 species restricted to wet, extremely infertile habitats of the tepuis and adjacent sand plains of the ancient Guayana Shield (Givnish et al. 1997). *Brocchinia* has undergone an adaptive radiation in mechanisms of nutrient capture unparalleled at the generic level across the angiosperms, including carnivorous species, ant-fed myrmecophytes, tank epiphytes, impounding treelets, N_2-fixers, and terrestrial forms that absorb nutrients primarily through their roots. *Brocchinia prismatica* is basalmost, consistent with its position based on cpDNA restriction-site data and a more extensive sampling of taxa (Givnish et al. 1997). Monotypic *Ayensua* is embedded within *Brocchinia,* between *B. prismatica* and *B. paniculata* (Fig. 1). The latter is the earliest-divergent member of the Melanacra clade, which is sister to all other *Brocchinia* except *B. prismatica* based on restriction-site data (Givnish et al. 1997). *Ayensua uaipanensis* shares a highly unusual, sharply defined abscission zone at the base of each leaf with *Brocchinia maguirei* L. B. Sm., which restriction-site data place just above *B. paniculata* in the Melanacra clade (Givnish et al. 1997).

The second divergent clade of Bromeliaceae is *Lindmania,* a genus of ca. 20 species limited to the tepuis of the Guayana Shield (Holst 1997). The next two clades—the monophyletic subfamily Tillandsioideae (*Catopsis, Glomeropitcairnia, Guzmania, Tillandsia, Vriesea*) and the xerophytic genus *Hechtia* from Central America and Mexico (Fig. 1)—are part of a hard trichotomy, including the remaining genera of the higher bromeliads. Among this latter group, the fifth major clade of bromeliads includes three taxa restricted to the Guayana Shield—*Brewcaria,* species-rich *Navia,* and the disparate "*Brocchinia*" *serrata*—as well as monotypic *Cottendorfia* from the Brazilian Shield (Fig. 1). Givnish et al. (1997) resolved *Brewcaria reflexa, Navia saxicola,* and "*Brocchinia*" *serrata* as close relatives based on cpDNA restriction-site variation; the last species differs from all others now classified as *Brocchinia* in having a superior ovary and spinescent leaves.

The sixth rung of the bromeliad ladder includes four highly xeromorphic genera (*Abromeitiella, Deuterocohnia, Dyckia, Encholirium*), sister to the slightly more mesomorphic *Fosterella* (native to dry valleys at mid elevations in the northern Andes and Central America [Ibisch et al. 1997]), and ultimately to the large genus *Pitcairnia,* native to the Amazon basin, northern Andes, Guayana Shield, Central America, and the Caribbean, with a single species (*P. feliciana*) in tropical West Africa. Finally, as shown by Terry et al. (1997a), the large genus *Puya* (ca. 120 spp.)—centered in the southern Andes but extending northward into Central America and the Guayana Shield—is closest relative of the monophyletic subfamily Bromelioideae. Together, these two groups form the seventh and eighth major clades of bro-
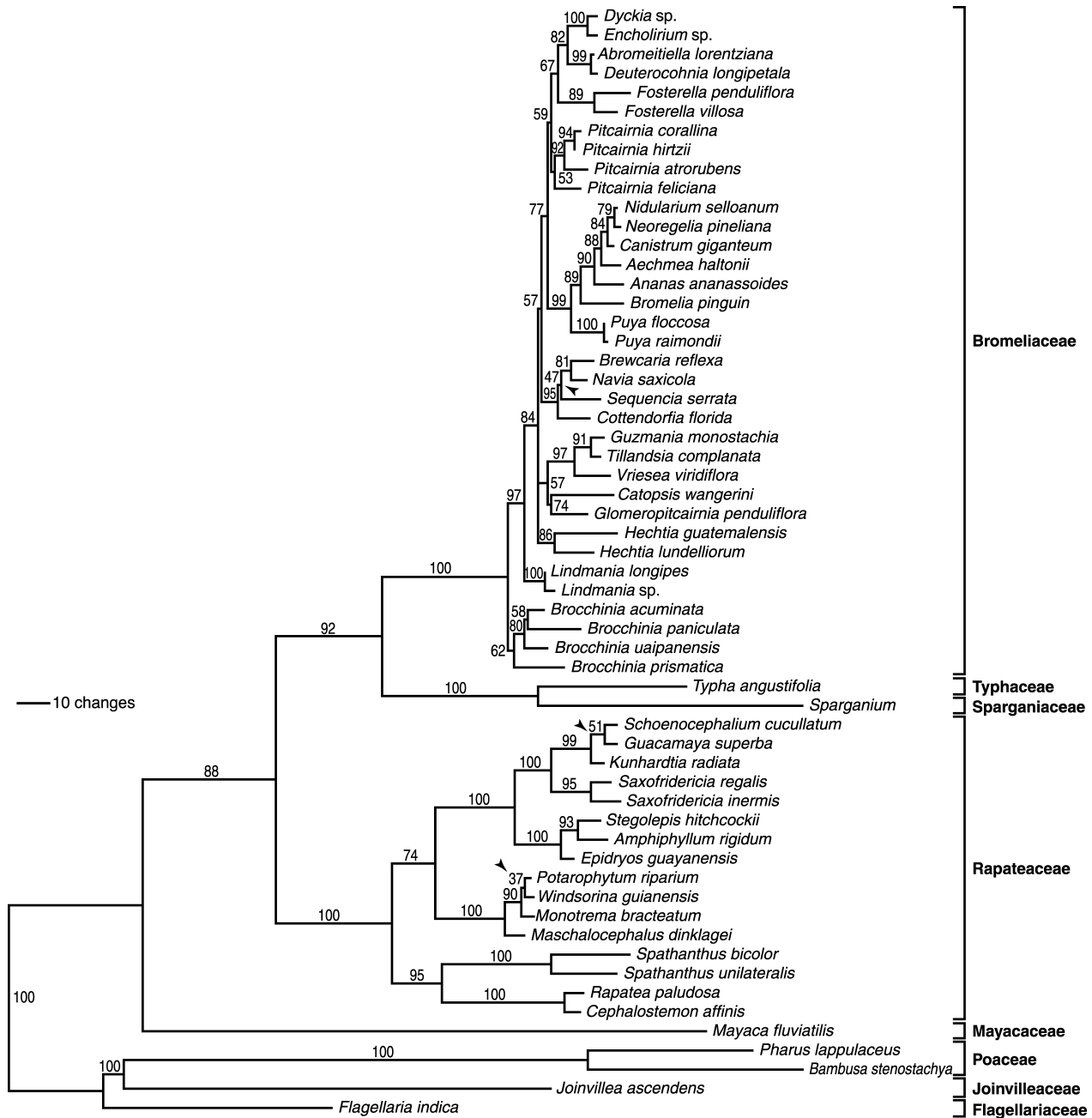
Fig. 1.—Phylogram of one of the 12 most-parsimonious trees based on *ndh*F sequence variation. Numbers above nodes indicate bootstrap support values. Arrows indicate branches that collapse in the strict consensus of the parsimony trees. Note that in all figures, *Brocchinia serrata* is shown as *Sequencia serrata,* and *Ayensua uaipanensis* as *Brocchinia uaipanensis,* reflecting the nomenclatural changes proposed in this paper.

meliads (Fig. 1). The traditional subfamily Pitcairnioideae (highlighted by black bars in Fig. 2) is thus massively paraphyletic, forming the winged-seed matrix from which both plumose-seeded tillandsioids and fleshy-fruited bromelioids emerge, and comprising six of the eight major bromeliad clades.

Reflecting the short branch lengths in the family, bootstrap support values based on *ndh*F for major clades of bromeliads—and for relationships among those clades—are often lower than those in closely related families of Poales (Fig. 1), or across monocots more generally (Givnish et al. 2006).

Brocchinia (including *Ayensua*) is strongly supported as being sister to all other bromeliads (97% bootstrap value), while *Lindmania* has moderate support (84%) as being sister to the rest of the family excluding itself and *Brocchinia–Ayensua* (Fig. 1). *Navia, Brewcaria, Cottendorfia,* and *"Brocchinia" serrata* form a strongly supported clade (95%), as do *Puya* (100%), Bromelioideae (89%), and *Puya–*Bromelioideae (99%), as well as *Dyckia–Encholirium* (100%), *Abromeitiella–Deuterocohnia* (99%) and *Guzmania–Tillandsia–Vriesea* among the tillandsioids (97%). Other relationships within the family have weaker support, includ-
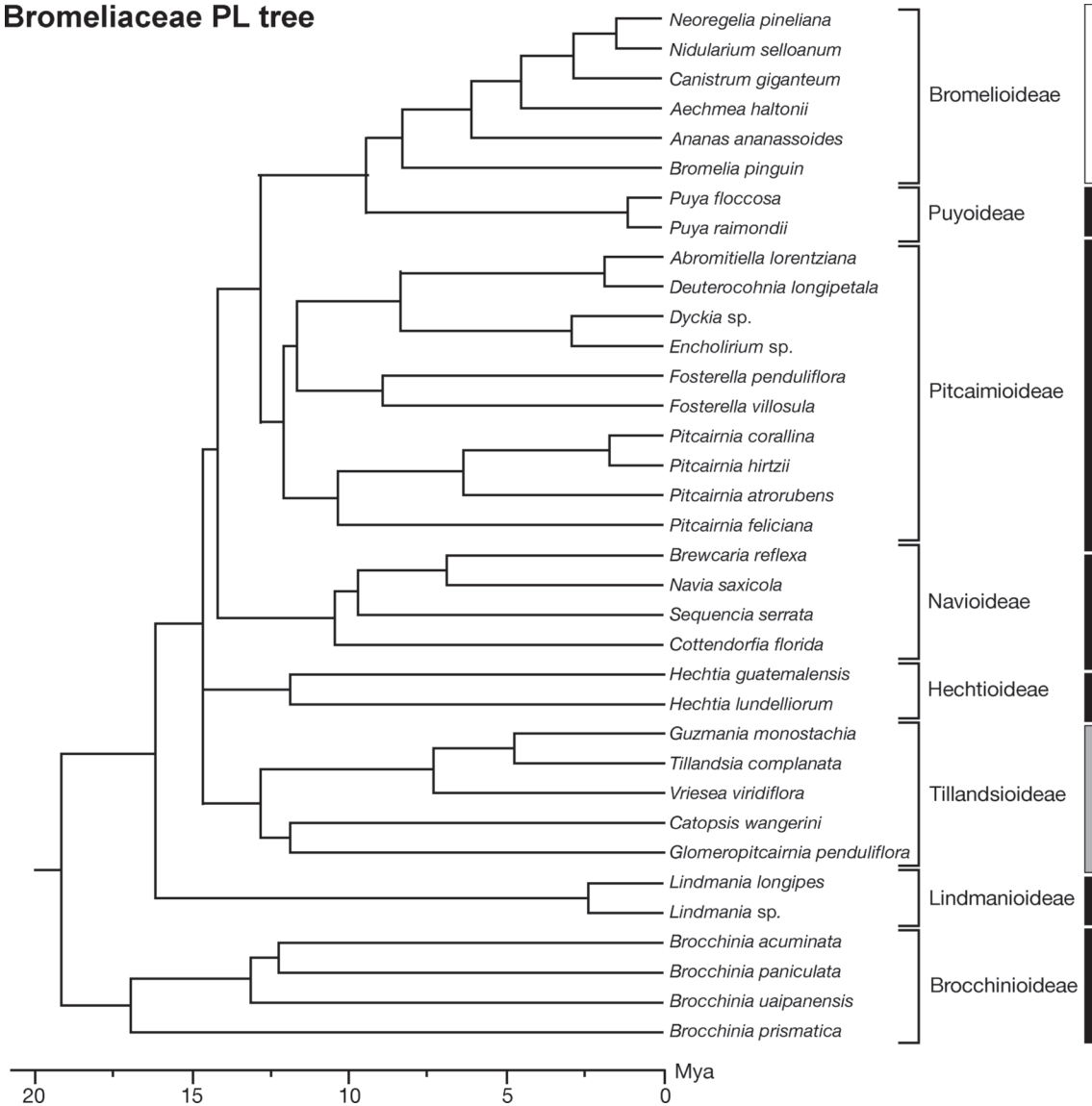
Bromeliaceae PL tree

Fig. 2.—Ultrametric tree for Bromeliaceae based on cross-verified penalized likelihood, showing inferred chronology of cladogenesis over the past 20 My. Major clades (see Discussion for definitions) are highlighted by brackets; membership of these clades in the three traditional subfamilies is indicated by shaded bars. Hollow bar = Bromelioideae; gray bar = Tillandsioideae; solid bars = Pitcairnioideae. Note the manifold paraphyly of Pitcairnioideae, and monophyly of both Bromelioideae and Tillandsioideae.

ing bootstrap values of only 57% for Tillandsioideae and 53% for *Pitcairnia.* Exclusion of non-bromeliads results in two most-parsimonious trees of length 362 steps (CI = 0.81, CI′ = 0.65), and a strict consensus with a topology identical to that obtained from the Poales- and monocots-based data sets.

Molecular Clocks and Historical Biogeography

The *ndh*F gene evolves in a somewhat non-clocklike fashion in Bromeliaceae ($P > 0.053$, X^2 test with 33 d.f.), so simple molecular clocks cannot be used to date cladogenetic events within the family (see also Givnish et al. 2004). Based on a PL analysis across monocots, we infer that Bromeliaceae arose 69.5 Mya—coincident with the rise of *Typha–Sparganium,* one of the events used to calibrate the monocot tree—and that 50 million years (My) elapsed be-

tween the rise of the bromeliad stem group and divergence among the crown group of surviving lineages 19 Mya (Fig. 2). Extant lineages of *Brocchinia–Ayensua* began to diversify roughly 17 Mya (Fig. 2). *Brocchinia* arose at low elevations and then evolved adaptations to nutrient poverty (carnivory, ant-fed myrmecophily, N_2 fixation) that depended on acquiring the tank habit and live absorptive trichomes; evolution of these traits was contingent on occupying rainy, humid, extremely nutrient-poor habitats at high elevations on the tepuis (Givnish et al. 1997). *Brocchinia*'s distribution is coextensive with the Guayana Shield, with almost all species occurring on sand or sandstone on the tepuis or sand plains at low elevations; a few species also occur on granite outcrops at the edge of the Shield, or on low sandstone mesetas in southwestern Colombia (Givnish et al. 1997). *Lindmania* is restricted to the tepuis and arose 16 Mya (Fig. 2).
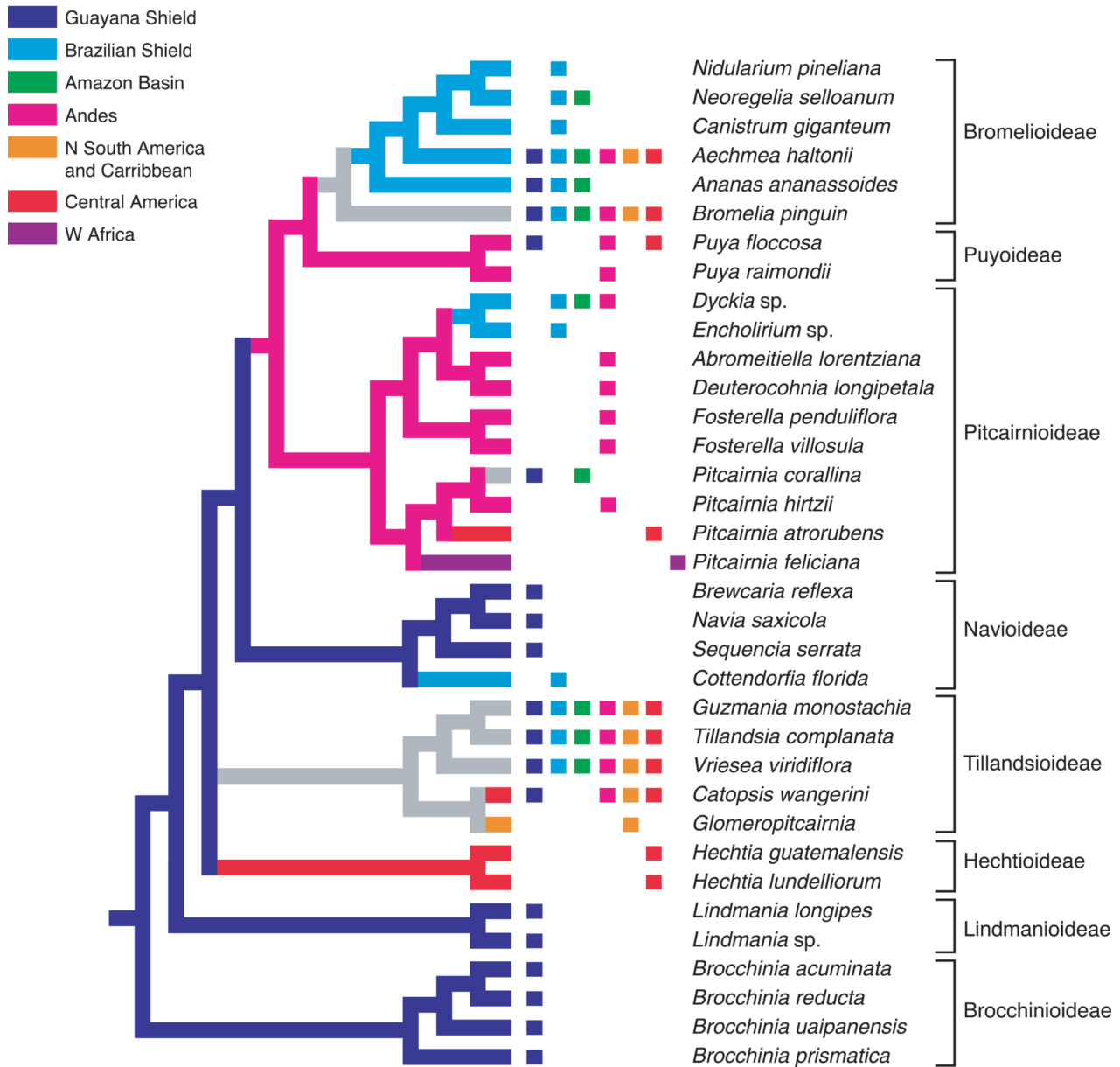
Geographic evolution of Bromeliaceae

Fig. 3.—Phylogenetic reconstruction of geographic diversification in bromeliads, based on the modern distributions of terminal taxa, branching topology, and parsimony. Gray branches indicate uncertainty in the reconstruction of ancestral distributions.

The nesting of two lineages endemic to the Guayana Shield—*Brocchinia–Ayensua* and *Lindmania*—at the base of Bromeliaceae implies that the family arose there. This biogeographic scenario is consistent with the geological age of the terrains involved. The initial uplift of the sandstone and quartzite marine deposits to form the tepuis of the Guayana Shield is widely assumed to have coincided with the rifting of the tropical Atlantic; the dissection of individual tepuis from each other via erosion and chemical dissolution is thus likely to have proceeded for the past 90 My (Givnish et al. 1997).

After the origin of *Brocchinia–Ayensua* and *Lindmania* in the Guayana Shield, and a modest amount of speciation as-

sociated with them, our biogeographic and chronological reconstructions imply that bromeliads began to expand centripetally into other regions of South and Central America about 15 Mya, based on PL (Fig. 2, 3). This period of initial geographic expansion coincided with the origins of strongly xeromorphic lineages, including *Hechtia* (with heavily armed, succulent leaves and CAM photosynthesis) and Tillandsioideae (many epiphytic, with a large number of species in the *Guzmania–Tillandsia–Vriesea* clade having CAM photosynthesis) (Fig. 2–4). *Hechtia* and the tillandsioids represent the first bromeliad invasions of Neotropical regions outside the Guayana Shield (Fig. 3). Both involve northern South America, with *Hechtia* reaching Central America.
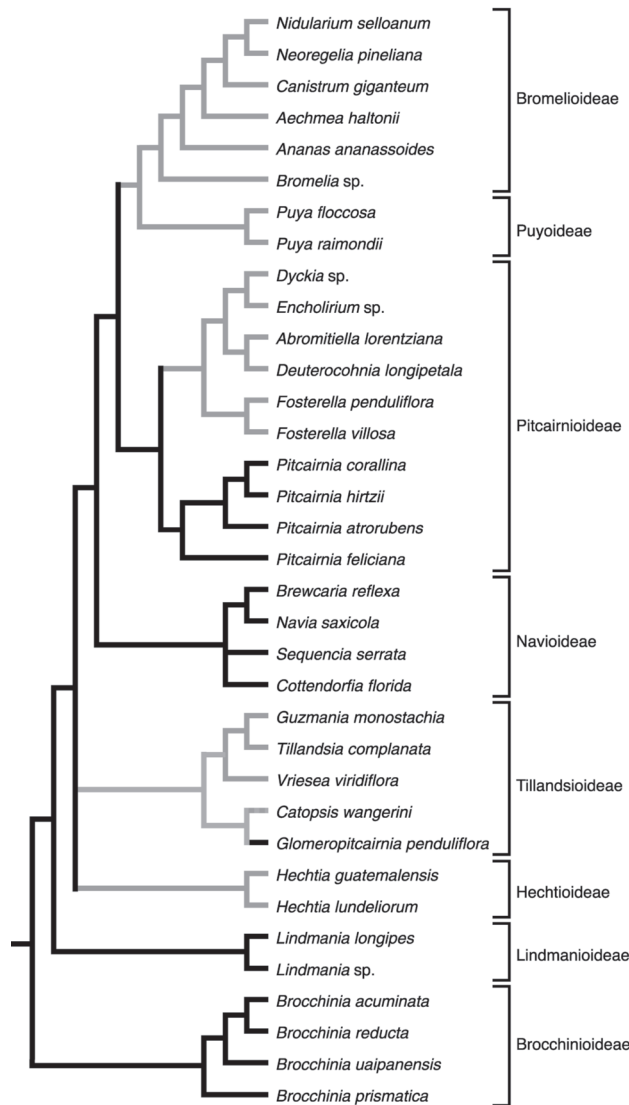
CAM photosynthesis

Fig. 4.—Inferred evolution of CAM photosynthesis (gray) from C₃ ancestors (black) based on parsimony.

Phylogenetic reconstruction suggests that subfamily Tillandsioideae evolved in the Guayana Shield (Fig. 3), but that inference is probably an artifact of the arbitrary choice of species used to represent *Guzmania, Tillandsia,* and *Vriesea.* The latter genera have broad ranges, and are especially diverse in the Andes (Smith and Downs 1977). More important, *Glomeropitcairnia* is endemic to parts of northern Venezuela and Trinidad immediately adjacent to the Guayana Shield, and some *Catopsis* species (e.g., *C. berteroniana* Mez) inhabit the Guayana Shield as part of more extensive ranges (Smith and Downs 1974). Most other tillandsioid genera have ranges overlapping the Guayana Shield, but also occur in other regions and are more diverse outside the Guayana Shield, especially in the Andes. These facts suggest that Tillandsioideae may have originated just beyond the periphery of the Guayana Shield, near the Caribbean littoral. Origin of the species-rich *Guzmania–Tillandsia–Vriesea* clade—including the most highly specialized, "atmospher-

ic" epiphytes in the family, with a center of diversity in the Andes—began 12.7 Mya based on PL (Fig. 2), coincident with the rise of the two major Andean clades of hummingbirds (Bleiweiss 1998). The central and northern Andes were uplifted starting about 20 Mya, corresponding roughly to the time of the initial expansion of bromeliads outside the Guayana Shield, as well as the initial diversification of modern lineages of hummingbirds (see Discussion). The uplift of the northern Andes also coincides with the associated diversion in the Miocene of the Amazon to its present course (Hoorn et al. 1995; Potter 1997).

Brewcaria, Navia, and "*Brocchinia*" *serrata* are restricted to the Guayana Shield, consistent with that area having served as a center of diversification and dispersal for the family up to this level. This group—plus *Cottendorfia* of the Brazilian Shield—originated 14 Mya based on PL (Fig. 2, 3). The shift in the course of the Amazon roughly 20 Mya separated the Guayana and Brazilian Shields with a belt of nutrient-rich sediments derived from the erosion and dissolution of the Andes. We estimate that Brazilian *Cottendorfia* diverged from its closest relative in the Guayana Shield ("*Brocchinia*" *serrata*) ca. 10.2 Mya based on PL (Fig. 2, 3). The date based on PL would require long-distance dispersal to account for *Cottendorfia*'s distribution, while that based on NPRS (20 Mya) would be consistent with an origin of *Cottendorfia* via vicariance.

The clade of genera sister to *Pitcairnia*—which Terry et al. (1997*a*) suggested might be called Pitcairnioideae s.s.—diverged from the ancestor of *Puya* and Bromelioideae 12.7 Mya based on PL (Fig. 2). Phylogenetic reconstruction suggests that the ancestor of these three lineages arose in the Andes (Fig. 3), but we believe that Andean distributions arose much later independently in Pitcairnioideae s.s. and *Puya.* This suspicion is based on (1) the uplift of the northern and central Andes ca. 20 Mya (Hoorn 1994; Hoorn et al. 1995; Rasanen et al. 1995; Potter 1997), (2) the apparent origin of *Puya* much later than this, and (3) the origin of high Andean *Abromeitiella* and *Deuterocohnia* only 8.2 Mya, and (4) the origin of *Fosterella* at mid-elevations in the Andes 11.5 Mya (Fig. 2, 3). Some *Pitcairnia* occur in the northern Andes (Smith and Downs 1974). The Andean species of *Pitcairnia* are of unknown phylogenetic position, but even if the genus arose there, it would have done so no more than 10.2 Mya (Fig. 2), long after the northern and central Andes were uplifted.

The geographic ranges of the genera within Pitcairnioideae s.s. suggest that this clade represents a counterclockwise invasion from the Guayana Shield into the northern Amazon basin and/or northern Andes, then into the central Andes, and finally their southern foothills and drier portions of the Brazilian Shield and Bahia (Fig. 3). Divergence between *Fosterella* and its sister clade may have taken place in southern Bolivia and northern Argentina, where mid-elevation *Fosterella* overlaps with the Andean genera *Abromeitiella* and *Deuterocohnia* (Givnish et al. 2004). The latter genera are closely related and sometimes synonymized (Spencer and Smith 1992). Divergence between the Andean genera and the drought-adapted genera *Dyckia* and *Encholirium*—restricted to lower elevations in the Andean foothills and the Brazilian Shield—appears to have occurred in northern Argentina. Invasion from the southern Andes eastward

to Bahia is suggested by *Dyckia*'s range, which abuts *Deuterocohnia* in the west and *Encholirium* in the east on the horn of Brazil (Givnish et al. 2004). Further research is needed to determine if xeromorphic *Encholirium* is sister to a monophyletic *Dyckia,* or instead derived from within it. Divergence between the species representing each of these genera occurred quite recently, ca. 2.5 Mya; *Abromeitiella* and *Deuterocohnia* appear to have diverged slightly after that, at the beginning of the Pleistocene (Fig. 2).

Based on PL, African *P. feliciana* diverged from its American counterparts 10.1 Mya (Fig. 2). These calculations exclude vicariance via continental drift as a possible explanation for the occurrence of *P. feliciana* in Africa, and point instead to relatively recent long-distance dispersal around 10 Mya.

The lineages that generated *Puya* and subfamily Bromelioideae diverged from each other 9.1 Mya, with *Puya* diversifying mainly along the Andes and the bromelioids arising in one of several places, including northern South America, before invading the Brazilian Shield about 6 Mya (Fig. 2, 3). Some early-divergent bromelioids (including *Bromelia* and the pineapple *Ananas*) occur in a diversity of regions, including seasonal parts of northern South America and Central America, but most of the later-divergent genera are endemic to seasonal parts of the Brazilian Shield (Smith and Downs 1977). Many of the latter, despite their fleshy fruits and potential for long-distance dispersal, have narrow ranges, and they probably represent in situ diversification within the Brazilian Shield. More species of *Puya* (ca. 120 spp.) need to be sequenced to obtain a better estimate of when present-day species began to diverge from each other. We estimate that the small, wide-ranging *P. floccosa* (subgen. *Puyopsis*) and the gigantic *P. raimondii* (subgen. *Puya*) from the central Andes diverged within the past 600,000 years (Fig. 2).

Our estimated dates for the history of Bromeliaceae based on PL are generally consistent with those based on lineage-specific mutation rates or local molecular clocks (data not shown), but much more recent than those based on NPRS (Givnish et al. 2004). The latter produces dates about twice those inferred using cross-verified PL. Important biases in the NPRS approach—especially the amplification of minor differences in branch length in a nearly clocklike tree, and the effects of low rates of molecular evolution in *Pitcairnia* vs. flanking clades—are discussed in detail by Givnish et al. (2004).

Adaptive Radiation

CAM photosynthesis arose at least four times in Bromeliaceae, in *Puya*–Bromelioideae, Pitcairnioideae minus *Pitcairnia* itself, Tillandsioideae, and *Hechtia* (Fig. 4). In each of these clades, CAM is associated with either arid habitats or epiphytic microsites in rain and cloud forests. C_3 photosynthesis is inferred to be the ancestral state. Roughly two-thirds of all bromeliads are estimated to possess CAM (Crayn et al. 2000, 2004) and associated leaf succulence. Together, these traits provide a potent means of reducing transpiration and enduring intense drought, albeit at the cost of reduced photosynthetic capacity (Winter and Smith 1996). Epiphytism also arose at least four times among bromeliads,
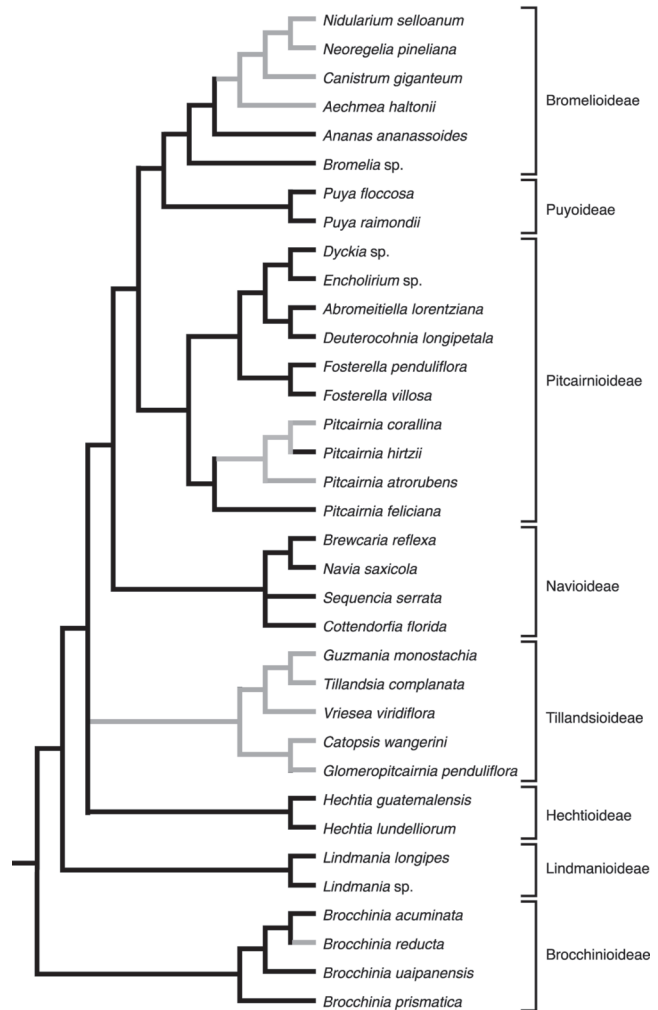
Epiphytism

Fig. 5.—Three inferred origins of epiphytism (gray) from terrestrial ancestors (black) based on parsimony. The terrestrial species *Brocchinia acuminata,* by virtue of its close relationship with the epiphytic *B. tatei* (Givnish et al. 1997), is coded as an epiphyte.

in Bromelioideae, Tillandsioideae, and *Brocchinia* (Fig. 5), as well as *Pitcairnia* (epiphytic taxa not included in our survey). Epiphytes in *Brocchinia* include *B. tatei* L. B. Sm., a tank-forming species that impounds rainwater among its tightly overlapping leaf bases, and is closely related to the carnivorous *B. reducta* Baker and *B. hechtioides* Mez in the Reducta clade (Givnish et al. 1997). Almost surely, *Brocchinia hitchcockii* L. B. Sm. in the Melanacra clade represents an additional origin of epiphytism within the genus (Givnish et al. 1997), and it seems likely that additional origins of epiphytism occur within the three other, much larger clades that possess epiphytic species (Benzing et al. 2000*a*). The ancestral bromeliads apparently evolved at low elevations in the Guayana Shield on moist, infertile substrates of sand or sandstone (Givnish et al. 2004).

Ornithophily arose at least twice: in Tillandsioideae and the common ancestor of Pitcairnioideae–Puyoideae–Bromelioideae (Fig. 6). The occurrence of entomophily in *Catopsis*
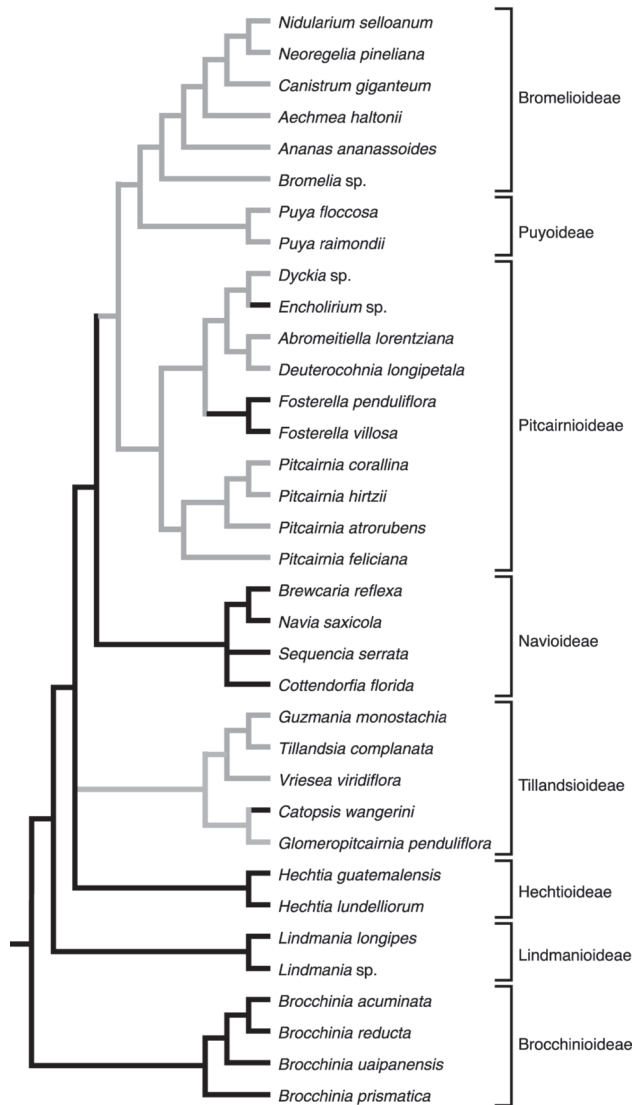
Ornithophily

Fig. 6.—Two inferred origins of avian pollination (gray) from ancestors pollinated primarily by insects. *Encholirium* is bat-pollinated.

may not reflect a reversal from ornithophily in tillandsioids: Terry et al. (1997*b*) place this genus sister to the higher (mostly bird-pollinated) tillandsioids using *ndh*F and a more extensive sampling of tillandsioid genera and species. Hummingbirds (Trochilidae) are the most common avian pollinators (see review by Benzing et al. 2000*b*). Austral blackbirds (Icteridae) also visit some species of *Puya* (Smith and Till 1998; Benzing et al. 2000*b*). Species of *Puya* sect. *Puya* have sterile terminal tips on branches of their inflorescences that serve as perches, as well as relatively shallow flower-tubes; as a result, they attract a variety of both perching and hovering species. By contrast, species of *Puya* sect. *Puyopsis* have deeper-throated flowers held in more densely congested inflorescences, favoring mainly hovering birds (i.e., hummingbirds) (Baker et al. 1998; Benzing et al. 2000*b*). Insect pollination—which characterizes all species of *Brocchinia*

and *Lindmania,* as well as all or most species of *Brewcaria, Catopsis, Cottendorfia, Navia,* and *Fosterella,* based on direct observations or inferences from floral syndrome (Benzing et al. 2000b)—is inferred to be the ancestral state. Most high-elevation groups—even cushion plants of *Abromeitiella* and *Deuterocohnia* in dry microsites of the high Andes (Galetto and Bernardello 1992)!—are pollinated by hummingbirds. *Dyckia,* with yellow to orange flowers and growing in dry microsites at low to mid elevations, also appears to be hummingbird pollinated (Galetto and Bernardello 1992; P. E. Berry and K. J. Sytsma pers. obs.). Reversion to entomophily occurred in *Fosterella,* apparently with retention of ornithophily (or another origin) in hummingbird-pollinated *F. spectabilis* (see Luther 1997). Several lineages in which ornithophily has evolved also possess species pollinated by bees (e.g., *Tillandsia multicaulis* Steud.), moths (*Pitcairnia albiflos* Herb., *Pitcairnia unilateralis* L. B. Sm., *Tillandsia utriculata* L.), and—perhaps most notably—bats (e.g., *Pitcairnia palmoides* Mez & Sodiro, *Puya ferruginea* (Ruíz & Pav.) L. B. Sm., *Guzmania fosteriana* L. B. Sm., *Vriesea* subgen. *Xiphion* E. Morren, *Tillandsia* subgen. *Pseudalcantarea* Mez) (Vogel 1969; Ortiz-Crespo 1973; Gardner 1986; Luther 1993; Sazima et al. 1995; Benzing et al. 2000b; Wendt et al. 2002). More research is needed to determine whether such pollination syndromes have evolved once or many times within individual large genera, or whether certain poorly studied genera (e.g., *Connellia, Lindmania, Navia*) contain ornithophilous species. It is well established that *Encholirium* is bat pollinated (Sazima et al. 1989). Varadarajan and Brown (1988) report that *Ayensua* is also bat pollinated, but this seems quite unlikely, given the minute size of the flowers (comparable to those of entomophilous *Brocchinia*) and the extremely short stature of the plants. *Pitcairnia feliciana* of West Africa bears the hallmarks of avian pollination—orange-red flowers, no fragrance, copious nectar production—and has flowers quite similar to those of many hummingbird-pollinated species of Neotropical *Pitcairnia*; no direct observations of sunbirds pollinating this species have been made as yet, however (Porembski and Barthlott 1999).

Based on the data on leaf and trichome anatomy now available for genera of the traditional Pitcairnioideae (Varadarajan and Gilmartin 1988), several traits associated with life in arid habitats appear to have evolved independently many times, especially in *Hechtia, Puya,* and members of the Xeric clade (*Abromeitiella–Deuterocohnia–Dyckia–Encholirium*; Fig. 7). This clade is restricted to dry habitats in southeastern Brazil, northern Argentina, and high elevations in the central Andes (Givnish et al. 2004). Two traits—foliar trichomes arranged in parallel rows, and overlapping substantially in periclinal tiers—occur in all three of these groups. Two additional traits—internal water storage tissue and a lack of differentiation within the chlorenchyma (no palisade vs. spongy mesophyll)—also occur in all three of these groups, but also extend to *Fosterella,* sister to the Xeric clade. Well-developed wings are present on the foliar trichomes only of *Puya* and the Xeric clade, and are missing from *Hechtia*. Finally, hypodermal sclerenchyma is present in *Hechtia, Puya,* the Xeric clade, *Pitcairnia* sect. *Pepinia* Brongn. ex Andra, *Ayensua,* and certain bromelioids. Thus,

Xeromorphic leaf traits

1. Well-developed wings on foliar trichomes
2. Trichomes in parallel rows
3. Trichomes in periclinal tiers
4. Hypodermal sclerenchyma
5. Internal water-storage tissue
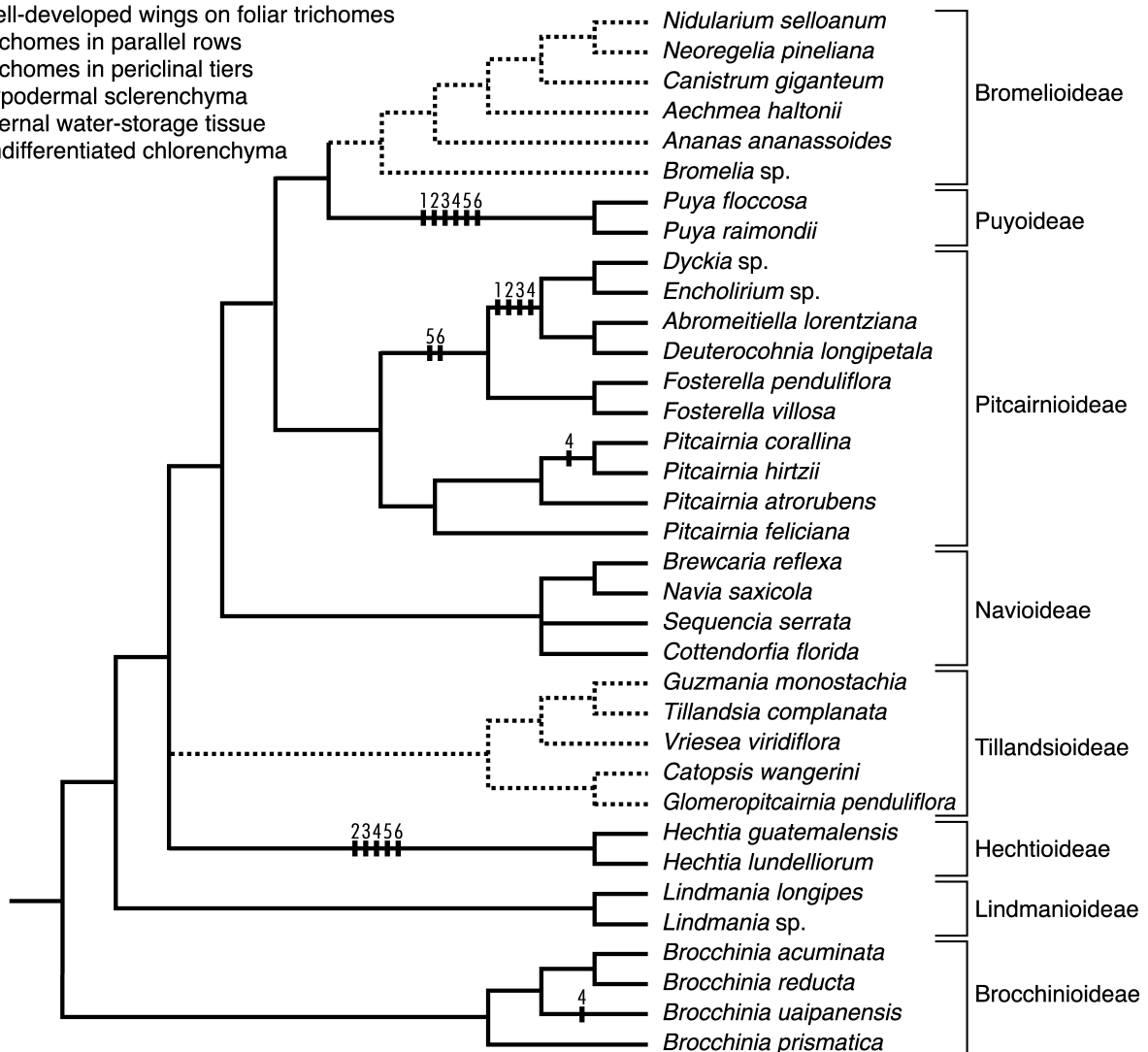6. Undifferentiated chlorenchyma

Fig. 7.—Independent origins of leaf and trichome traits associated with life in arid habitats, based on data for genera placed in Pitcairnioideae s.l. only (tillandsioids and bromelioids, shown with dotted branches, were assigned the apomorphic states). Characters and character states (apomorphic state given in parentheses): 1 = foliar trichomes arranged in parallel rows (vs. irregular pattern); 2 = margins of foliar trichomes overlap extensively in periclinal tiers (vs. little or no overlap); 3 = internal water storage tissue present (vs. only adaxial water storage tissue present); 4 = chlorenchyma undifferentiated (vs. palisade and spongy mesophyll present); 5 = marginal wings of foliar trichomes well-developed (vs. scarcely developed or absent); and 6 = hypodermal sclerenchyma present (vs. absent). Note the apparent pattern of concerted convergence involving independent origins of a suite of drought-adapted characters in *Puya,* the Xeric clade, and *Hechtia.*

these anatomical traits—and especially the first five—have undergone evolutionary convergence, appearing in two to three bromeliad lineages in association with xeric conditions. Furthermore, to the extent that a *suite* of several functionally and developmentally unlinked traits has evolved independently in three lines, it represents a clear case of concerted convergence (Givnish and Sytsma 1997; Patterson and Givnish 2002). This pattern of concerted convergence is so striking that it led Varadarajan and Gilmartin (1988)—based on a cladistic analysis of morphological and anatomical variation—to conclude that *Hechtia* was closely related to members of our Xeric clade, based mainly on the very characters our study shows have undergone concerted convergence.

DISCUSSION

Phylogeny and Systematic Implications

Our findings regarding relationships within Bromeliaceae are largely consistent with the analyses of Terry et al. (1997*a*), Crayn et al. (2000, 2004), Horres et al. (2000), and Reinert et al. (2003), and provide the first comprehensive and well-resolved view of relationships across all major bromeliad lineages. As expected given their joint basis on *ndh*F sequences, our results and those of Terry et al. (1997*a*) coincide for the taxa included in both studies. Our novel results include (1) the embedding of *Ayensua* within *Brocchinia* at the base of the family, (2) the placement of the tepui endem-

ic *Lindmania* as the next-divergent clade, (3) the hard polytomy formed by Tillandsioideae, *Hechtia,* and all remaining bromeliads, (4) a new clade forming the next branch above this polytomy, including *Navia, Brewcaria, Cottendorfia,* and ''*Brocchinia*'' *serrata,* (5) the placement of *Abromeitiella* and *Deuterocohnia* sister to each other, and together sister to *Dyckia* and *Encholirium,* and (6) confirmation of *Fosterella* as the sister group to this clade of four highly xeromorphic genera. The two species of *Pitcairnia* subgen. *Pepinia* (*P. corallina, P. hirtzii*) are sister to each other in our analysis, but monophyly of subgen. *Pepinia*—to say nothing of *Pitcairnia* subgen. *Pitcairnia*—is not supported by a more comprehensive sampling of the genus and *mat*K sequence variation (Reinert et al. 2003). Most important, our *ndh*F phylogeny demonstrates that (7) the traditional subfamily Pitcairnioideae is paraphyletic and that Tillandsioideae and Bromelioideae both evolved from within it. The phylogeny of Horres et al. (2000) is less well resolved than either of the *ndh*F trees, but is consistent with ours in placing single species of *Brocchinia* and *Ayensua* as sister to each other, and in placing this group, *Hechtia,* and all other bromeliads in an unresolved trichotomy. The phylogeny of Crayn et al. (2004), although less well resolved than that of Horres et al. (2000), is also consistent with our findings. Taken together, these results clearly call for two nomenclatural changes involving *Brocchinia* and *Ayensua,* the description of four new subfamilies of Bromeliaceae, and the recircumscription of Pitcairnioideae and Navioideae, as described next.

1. Ayensua.—The position of *Ayensua* within *Brocchinia* is supported not only by our *ndh*F data and the sharing of a highly unusual leaf abscission zone in *Ayensua* and *B. maguirei* (see above), but also by unpublished *rbc*L–*atp*B cpDNA spacer sequences (K. G. Karol, T. J. Givnish, and K. J. Sytsma in prep.). *Ayensua* and *Brocchinia* share a partly to wholly inferior ovary; minute, regular, white or whitish petals; cochlear sepals (the two posterior overlapping margins of the anterior); and stomata with wedge- or bulb-shaped thickenings at apical junctures of the guard cells (Smith and Downs 1974; Robinson and Taylor 1999). Based on the balance of molecular and morphological evidence, we are therefore sinking *Ayensua* into *Brocchinia*:

Brocchinia uaipanensis (Maguire) Givnish, comb. nov.

Basionym: *Barbacenia uaipanensis* Maguire, *Mem. New York Bot. Gard.* **9**: 477 (1957); *Vellozia uaipanensis* (Maguire) L. B. Sm., *Contr. U.S. Natl. Herb.* **35**: 267 (1962); *Ayensua uaipanensis* (Maguire) L. B. Sm., *Mem. New York Bot. Gard.* **18**: 29 (1969).

This species has had a curious history, having been first described as a member of one genus of Velloziaceae by Bassett Maguire, then transferred to another genus in the same family by Lyman Smith, then the expert nonpareil on Bromeliaceae (!), and then finally transferred to Bromeliaceae by Smith (1969) upon the advice of Ayensu (1969). Its leaves are substantially thicker and more awl-like than those of other *Brocchinia* species; it has a sparsely branched habit with persistent, sheathing leaf bases and adventitious roots that run back down the stem under those leaf bases. Overall, its vegetative aspect is indeed similar to some Velloziaceae of order Pandanales. However, *Brocchinia maguirei* also has

persistent leaf bases, and several *Brocchinia* species (e.g., *B. micrantha* Baker) have adventitious roots that interpenetrate the stem cortex. The adaptive significance of *B. uaipanensis'* growth form is unclear. It is restricted to Auyan-tepui and nearby Uaipan-tepui in southeastern Venezuela, and often grows in sparsely covered sites over fractured sandstone, atop windswept brinks and along streams (T. J. Givnish pers. obs.).

Varadarajan and Gilmartin (1988) used a cladistic analysis of morphological data to argue that *Brocchinia* lies at the base of the subfamily Pitcairnioideae, and placed it as the sole genus in a new tribe Brocchinieae. They contended that *Ayensua* should be placed in a new tribe Pitcairnieae with *Fosterella, Pitcairnia, Cottendorfia* (from which *Lindmania* was subsequently segregated), *Connellia,* and *Steyerbromelia.* They also erected tribe Puyeae for the xeromorphic genera *Abromeitiella, Deuterocohnia, Dyckia, Encholirium, Hechtia, Brewcaria,* and *Puya.* None of these proposed entities—adopted by Smith and Till (1998)—is supported by our molecular phylogeny (Fig. 1), so we reject each of these tribal names.

2. New bromeliad subfamilies.—Our *ndh*F phylogeny does indicate that the existing subfamilial classification is outdated; although Tillandsioideae and Bromelioideae are monophyletic and can be maintained, Pitcairnioideae are paraphyletic. Given the ladderlike branching pattern in the *ndh*F bromeliad phylogeny, subfamily Pitcairnioideae must be recircumscribed and at least five new subfamilies erected if all resulting entities are to be monophyletic and the morphologically distinctive Bromelioideae and Tillandsioideae maintained.

We therefore propose the following four new subfamilies of Bromeliaceae, and recircumscribe two others:

Brocchinioideae Givnish, subfam. nov.—TYPE: *Brocchinia* J. H. Schultes.

Fructibus capsularibus, seminibus bicaudato-appendiculatis; petalis minutis, regularibus, liberis; sepalis cochlearibus, duo adaxialis abaxiali superantibus; ovario infero vel partim infero; inflorescentia racemosa paniculata capitatave; foliis integris persaepe chlorenquimate stellato.

Capsular fruits, seeds bicaudate appendaged; petals minute, regular, free; sepals cochlear, with the two adaxial overlapping the abaxial; ovary partly to wholly inferior; inflorescence racemose, paniculate, or capitate; leaves entire, almost always with stellate chlorenchyma.

Included genus: *Brocchinia*

Lindmanioideae Givnish, subfam. nov.—TYPE: *Lindmania* Mez.

Fructibus capsularibus, seminibus bicaudato-appendiculatis; antheris subbasifixis equitantisve, erectis, crassis, filamentis liberis; petalis nudis; sepalis convolutis; stigmatibus erectis, rectis; floribus pedicellatis; foliis integris vel spinosis-dentatis; sine chlorenquimate stellato.

Capsular fruits; seeds bicaudate appendaged; anthers subbasifixed to equitant, straight, stout; filaments free; sepals convolute; petals naked; stigmas erect, straight; flowers ped-

icellate; leaves entire or toothed/spinose; stellate chlorenchyma absent.

Included genera: *Connellia, Lindmania*

Hechtioideae Givnish, subfam. nov.—TYPE: *Hechtia* Klotzsch.

Fructibus capsularibus, seminibus alatis vel fere nudis; floribus dioeciis; foliis succulentis, spinosis raro integris; sine chlorenquimate stellato.

Capsular fruits; seeds winged to almost naked; flowers dioecious; leaves succulent, spinose or rarely entire; stellate chlorenchyma absent.

Included genus: *Hechtia*

Puyoideae Givnish, subfam. nov.—TYPE: *Puya* Molina.

Fructibus capsularibus, seminibus circumferentio-alatis; laminis petalorum arcte torvisis post anthesin; sepalis convolutis.

Capsular fruits; seeds circumferentially winged; petal blades tightly spiralled after anthesis, broad and distinct from claw; sepals convolute.

Included genus: *Puya*

NAVIOIDEAE, descr. emend.

Capsular fruits; seeds winged to naked; petals minute; sepals cochlear, with the two adaxial overlapping the abaxial; stellate chlorenchyma absent; water storage tissue peripheral only, trichomes irregularly arranged with little overlap, epidermis smooth, hypodermal sclerenchyma absent; stellate chlorenchyma absent; leaves entire, serrulate, or spinose, but not succulent; inflorescence paniculate to capitate.

Included genera: *Brewcaria, Cottendorfia, Navia, Sequencia, Steyerbromelia*

PITCAIRNIOIDEAE, descr. emend.

Capsular fruits; seeds winged; petal blades remaining free after anthesis (or, if slightly coiled, then not clawed); petals large and conspicuous or, if minute, then sepals imbricate and anthers basifixed, linear.

Included genera: *Abromeitiella, Deuterocohnia, Dyckia, Encholirium, Fosterella, Pitcairnia*

We offer the following key to identify bromeliads to subfamily:

KEY TO BROMELIAD SUBFAMILIES

1. Fruits indehiscent, baccate . . . . Bromelioideae
– Fruits dehiscent, capsular 2
2. Seeds plumose-appendaged . . . . Tillandsioideae
– Seeds winged or naked 3
3. Flowers dioecious, plants of Central America . . . Hechtioideae
– Flowers perfect, or rarely monoecious or polygamodioecious, or dioecious and plants of the Brazilian Shield 4
4. Petal blades showy, tightly spiralled after anthesis, broad and distinct from claws . . . . Puyoideae
– Petal blades remaining free after anthesis, or if slightly coiled, then not clawed 5
5. Petals large and conspicuous or, if minute, then sepals imbricate and anthers basifixed, linear . . . . Pitcairnioideae
– Petals minute and sepals cochlear, or petals and bracts various and sepals convolute 6
6. Sepals convolute . . . . Lindmanioideae
– Petals minute and sepals cochlear 7
7. Leaves entire, stellate chlorenchyma abundant . . . . Brocchinioideae
– Leaves toothed, stellate chlorenchyma absent . . . . Navioideae

The newly defined Brocchinioideae correspond to *Brocchinia* as recircumscribed in this paper. Varadarajan and Gilmartin (1988) proposed segregating *Brocchinia* into its own tribe within Pitcairnioideae, but failed to recognize its close relationship to *Ayensua.* Smith and Till (1998) adopted the same view and formally recognized Brocchinieae within the pitcairnioids. Terry et al. (1997a) informally suggested that, based on additional data, *Brocchinia* might be best segregated in its own subfamily, and R. Thorne and J. Reveal now use ''Brocchinioideae'' on their websites (*http://www.csdl.tamu.edu/FLORA/newgate/thorcomm.htm* and *http://www.life.umd.edu/emeritus/reveal/pbio/pb450/zing.html*), without citing an authority or formal description. The *trn*L intron data of Horres et al. (2000) support a close relationship between single species of *Brocchinia* and *Ayensua,* consistent with our results—based on a more comprehensive and critical sampling of taxa—which clearly place *Ayensua* within *Brocchinia.*

We have drawn Lindmanioideae so as to permit inclusion of *Connellia.* This genus, restricted to the tepuis of southeastern Venezuela and adjacent Guyana, differs from *Lindmania* mainly in having larger and more brightly colored petals and subbasifixed vs. equitant anthers; both genera appear to be clearly related based on morphology (Holst 1997). The striking difference in the phylogenetic positions of *Lindmania* and *Cottendorfia* supports the decision to segregate taxa that had all been lumped into *Cottendorfia* (Smith 1986; Holst 1997). The position of *Hechtia* just above *Lindmania* and near Tillandsioideae (Fig. 3) is, however, surprising. *Hechtia* shares at least five derived anatomical leaf characteristics with *Abromeitiella, Deuterocohnia, Dyckia,* and *Encholirium* (Varadarajan and Gilmartin 1988), and Robinson and Taylor (1999) placed these genera in a new tribe Dyckieae based on these traits. However, these traits—including adaxial water storage tissue, a lack of differentiation within the chlorenchyma, overlapping trichomes, stomata in sunken pits or rows, grooved epidermis—all appear to be adaptations to extreme drought, and are associated with thick, succulent leaves with CAM photosynthesis that are (at least in the lowland forms) heavily armed. Central American *Hechtia* thus appears to represent an extraordinary case of concerted convergence with *Dyckia* and *Encholirium,* and to a lesser degree with *Abromeitiella* and *Deuterocohnia,* all from central South America. Ranker et al. (1990) found one restriction-site mutation that joined single species representing *Dyckia* and *Hechtia,* but the very small number of characters (19) and bromeliad taxa (10) included in that study, as well as its failure to place *Glomeropitcairnia* in a monophyletic Tillandsioideae, argue against giving it much weight. Crayn et al. (2000) found that *Hechtia* segregated from all other pitcairnioid genera or groups of genera, including (*Abromeitiella*)–*Deuterocohnia*–*Dyckia*–*Encholirium.* Distinction between the latter clade and *Hechtia* had a decay value of at least 7 in the analysis by Crayn et al. (2000), consistent with our finding that these two groups appear at different ends of the bromeliad ladder. Interesting-

ly, however, a second group of *Deuterocohnia* species did not group with those in the clade with *Dyckia* and *Encholirium,* forming part of the large, nine-way polytomy.

Navioideae are recircumscribed here based on *ndh*F sequence variation. The close relationship of *Brewcaria* and *Navia* is suggested by their shared possession of naked seeds; most species of *Brewcaria* were originally placed in *Navia* until Holst (1997) reclassified those with spicate or paniculate inflorescences. *Steyerbromelia* is quite similar to *Brewcaria,* but has winged seeds. A close relationship between *Brewcaria, Navia,* and ''*Brocchinia*'' *serrata* (see below) is strongly supported by a cpDNA restriction-site study that analyzed the same species (and more distantly related *Lindmania longipes*) as part of phylogenetic analysis of *Brocchinia* (Givnish et al. 1997). That study indicated the same pattern of relationships among these three taxa as found in this paper. *Cottendorfia* shares cochlear sepals with *Brewcaria, Navia, Steyerbromelia,* and ''*Brocchinia*'' *serrata,* as well as a few other genera formerly placed in Pitcairnioideae. The association of *Cottendorfia* with *Navia,* among other genera, in Navioideae is supported by the sister relationship of *Cottendorfia florida* with *Navia phelpsiae* based on *mat*K sequence variation (Crayn et al. 2000, 2004; Reinert et al. 2003). However, these studies also place *Navia igneosicola* sister to almost all species of *Pitcairnia* (including subgen. *Pepinia*) in a separate clade, with a decay value of 1. *Navia* is a large and complex genus recently revised by Holst (1997), who found the previous concept of the group overly broad and segregated all of the noncapitate species into *Brewcaria, Steyerbromelia,* and *Brocchinia.* The validity of these shifts has yet to be tested using molecular data, and it may well be that some species remaining within *Navia* remain outside a monophyletic core. If this later proves to be the case, the naming of this broader group will need to be revisited. *Navia igneosicola* differs from several tepui *Navia* in having wider leaves and pigmentation on leaf bases near the inflorescence that shows a more irregular transition to the green of the distal leaf areas. It may simply be an early divergent species of *Pitcairnia* with a condensed, capitate inflorescence. We note that *Pitcairnia leopoldii* (W. Till & S. Till) B. K. Holst—again with a capitate inflorescence—was initially considered a *Navia* due to habit and ovules similar to those of *Navia*; more detailed study showed that it had petal appendages and zygomorphic flowers, so it was described instead as a *Pitcairnia* (Oliva-Esteve 2002). Other *Pitcairnia* may yet lie unrecognized in *Navia.* The genus *Navia* was recognized as a monogeneric subfamily by Harms in 1929, but he promptly sunk it as a monogeneric tribe of Pitcairnioideae (Harms 1930). That subfamily was not accepted by later specialists, and this is the first time a broader Navioideae has been proposed.

Our recircumscription of Pitcairnioideae corresponds roughly to that recommended by Terry et al. (1997*a*), but encompasses genera not included in their study. As recircumscribed, Pitcairnioideae now contain *Abromeitiella, Deuterocohnia, Dyckia, Encholirium, Fosterella,* and *Pitcairnia.* We believe it is better to recognize Puyoideae separate from Bromelioideae, rather than sinking the former into the latter as recommended informally by Terry et al. (1997*a*), given the highly distinctive set of phenotypic synapomorphies distinguishing each of these groups from the other. Our phy-

logeny supports the monophyly of *Pitcairnia* as sampled to date, with *Pitcairnia feliciana* basalmost (Fig. 1). However, our sampling fails to represent a substantial amount of the phenotypic diversity within *Pitcairnia,* including putative Neotropical relatives of *Pitcairnia feliciana.* Such relatives might include *P. fuertesii* Mez from the Caribbean or *P. pungens* Kunth from Ecuador and Peru (Harms and Mildbraed 1938), or certain rock-dwelling species from eastern Brazil, including *P. glaziovii* Baker (Porembski and Barthlott 1999; Benzing 2000); no detailed argument for any of these possibilities has yet been offered. Porembski and Barthlott (1999) assert that *P. feliciana* differs from all other *Pitcairnia* species examined (still very few in this large genus) in several traits: ligula with two toothlike appendages, unlike all other pitcairnioids surveyed; stigma lobes with papillae unlike all other *Pitcairnia* surveyed; seeds with testa cells that have perforated outer periclinal walls (this last trait otherwise known only from certain *Puya*). Resolution of relationships within *Pitcairnia* will require sequencing many more species within the genus. Crayn et al. (2004) found that the eleven species of *Pitcairnia* they sequenced for *mat*K and *rps*16 formed two distinct clades.

It is interesting to note that *Pitcairnia* and *Puya*—each the basalmost genus in two large clades that are sister to each other—share several traits (e.g., zygomorphic flowers associated with avian pollination, and several xeromorphic features of leaf morphology and anatomy) and were once thought to be closely related to each other (e.g., see Smith and Downs 1974). Their similarities thus appear, based on phylogenetic reconstruction based on molecular data, to represent plesiomorphies (i.e., shared ancestral characters) rather than synapomorphies.

We did not sample all genera of Bromeliaceae in this study, but believe there are no ''surprises'' based on excluded taxa that would alter the proposed system of eight subfamilies. The only genera of traditional Pitcairnioideae not sampled—*Connellia* and *Steyerbromelia*—appear, based on morphology, to be very closely related to *Lindmania* and to *Brewcaria* and *Navia,* respectively. All tillandsioid and bromelioid genera not included in our analysis but studied by Terry et al. (1997*a, b*) were also placed in monophyletic subfamilies Tillandsioideae and Bromelioideae, based on *ndh*F sequence variation and a more restricted sampling of traditional Pitcairnioideae.

Although *ndh*F sequences provides a phylogeny that is nearly fully resolved, it must be recognized that only a few synapomorphies support some of the nodes along the ''spine'' of the tree, with relatively low bootstrap support (<60%) for some clades, including Pitcairnioideae exclusive of *Pitcairnia, Pitcairnia* itself, and Navioideae–Pitcairnioideae–Puyoideae–Bromelioideae (Fig. 1). A multigene analysis, drawing on data for several cpDNA segments, is now clearly needed to confirm the results presented here. However, our confidence in the systematic arrangement presented here is bolstered by the fact that analyses based on other single cpDNA segments (Terry et al. 1997*a, b*; Crayn et al. 2000; Horres et al. 2000; Reinert et al. 2003) have already produced results consistent with our phylogeny.

3. Brocchinia serrata.—As noted above, morphology and two lines of molecular evidence place this taxon in Navioi-

deae with *Brewcaria, Cottendorfia,* and *Navia. Brocchinia serrata* differs from other species of *Brocchinia* in having a ⅔ superior ovary (most pitcairnioid genera have a superior ovary) and spinose leaf margins. It clearly does not fit the circumscription of any existing bromeliad genus, and we therefore describe it here as a new genus:

Sequencia Givnish, gen. nov.—TYPE: *Brocchinia serrata* L. B. Sm.

Caule tortuoso-prostrato, lignoso; foliis rosulatis ad 1.8 m longis, laminis linearibus, longe caudato-acuminatis, basi spinis atris curvatis, alibi serrulatis; inflorescentia amplissime paniculata; floribus reflexis, perfectis, ovario ad ⅔ supero; sepalis cucculatis, imbricatis, dense lepidotis; petalis regularis, inappendiculatis; antheris liberis, basifixis, rectis crassisque; filamentis liberis; capsulis septicidalis loculicidalisque; seminibus bicaudatis.

Leaves linear, caudate-acuminate, to roughly 1.8 m long, with dark curved spines near the base and serrulate toward the tip, and arranged in a rosette about a twisted, prostrate stem. Inflorescence amply paniculate; flowers perfect; ovary roughly ⅔ superior; sepals cochleate/imbricate, densely lepidote; petals regular, unappendaged; filaments free; anthers basifixed, stout, straight; capsules septicidal and loculicidal; seeds bicaudate-appendaged.

Sequencia serrata (L. B. Sm.) Givnish, comb. nov.
Basionym: *Brocchinia serrata* L. B. Sm., *Caldasia* **1(4)**: 14, Fig. 2 (1942).

Leaf characteristics and habit differentiate *Sequencia* from several pitcairnioid genera (including *Brocchinia*), but emphasize its similarity to *Brewcaria* and *Cottendorfia*; possession of panicles distinguish it from *Navia*. Perfect flowers separate *Sequencia* from closely related *Cottendorfia*, as well as *Dyckia* and *Hechtia*. An ovary that is two-thirds superior distinguishes it from most pitcairnioid genera. Sepal and petal characteristics separate *Sequencia* from many genera, most importantly *Steyerbromelia*. The dual form of dehiscence is unknown in Bromeliaceae except *Deuterocohnia* (see Smith and Downs 1974).

The generic name *Sequencia* reflects its recognition based on DNA sequence (and restriction-site) characteristics. This monotypic genus is known only from low sandstone mesetas (Cerro de Circasia, Cerro Yapobodá, Cerro de Cañenda) in Vaupés, Colombia. Like many bromeliad genera (see Smith and Downs 1974, 1977, 1979), *Sequencia* cannot be defined by any single character state that it alone possesses, but rather by a suite of character states that individually can be found in other pitcairnioids. Given the apparently slow rate of evolution in bromeliads (Gaut et al. 1992), perhaps reflecting long generation times due to slow growth under short supplies of water and/or nutrients, and the paraphyly of several bromeliad genera defined by single characters (e.g., see Terry et al. 1997*b*; Horres et al. 2000), generic definitions based on character combinations—while not "cladistically correct"—may be necessary, if not indeed expected. Note that subfamilies Navioideae and Pitcairnioideae, as recircumscribed here, lack single unconditional synapomorphies and are also defined based on character combinations. Detailed molecular studies of relationships within Tillandsioideae have shown that some genera as traditionally

defined by one or two characters (e.g., *Tillandsia, Vriesea*) are, in fact, paraphyletic (Terry et al. 1997*b*). Associations among the limited set of traits used to define genera in Bromelioideae are even more combinatorial in nature (Smith and Downs 1979), and molecular phylogenetic investigations on relationships and generic circumscriptions within this recently evolved subfamily are now underway (T. Evans and G. Brown pers. comm.).

Historical Biogeography

Our findings demonstrate that Bromeliaceae arose in the Guayana Shield in northern South America, spread centripetally in the New World from there, and reached tropical West Africa via long-distance dispersal relatively recently—around 10 Mya if we use calculations based on cross-verified PL. Our evolutionary chronology implies that the modern lineages of bromeliads only began to diverge from each other roughly 19 Mya, with invasions of drier peripheral areas in Central America (*Hechtia*) and northern South America (Tillandsioideae) beginning 15 Mya. The northern Andes and Central America most likely were invaded independently by at least three major lineages: the higher tillandsioids (*Guzmania, Tillandsia, Vriesea*) beginning 12.7 Mya; *Fosterella,* beginning about 11.5 Mya, and (throughout the Andes) *Puya,* beginning about 9.1 Mya (Fig. 2; all calculations based on stem groups). Given the low density of taxon sampling at this point, we cannot determine whether any of these lineages invaded the Andes multiple times. Some additional groups (e.g., some *Pitcairnia,* various bromelioid genera) have also colonized the Andes independently, but we do not have adequate taxon sampling to estimate the timing and/or numbers of such events. The Brazilian Shield was colonized at least three times: by *Cottendorfia* from the Guayana Shield, ca. 10.2 Mya; by *Dyckia–Encholirium* from the central Andes, ca. 8.1 Mya; and by the higher Bromelioideae, 5.7 Mya (Fig. 2, 3). Individual species of other diverse groups (e.g., *Guzmania–Tillandsia–Vriesea*) have doubtless invaded this area independently as well. Most of the current diversity of bromeliads involves lineages that have appeared only in the past 15 My, including Tillandsioideae, Bromelioideae, and as well as the remaining large genera *Pitcairnia, Navia, Dyckia, Hechtia,* and (perhaps quite recently, at least for modern lineages) *Puya*. The 50-My period between the rise of Bromeliaceae and the divergence of modern lineages from one another implies that much extinction occurred over the intervening period, and suggests an obvious basis for the morphologically isolated position of the family. The differentiation of most bromeliad genera from each other outside Bromelioideae within a narrow window of about 7 My (see Fig. 2) may help account for the frequent confusion regarding relationships within the family in the past. An alternative analysis of the data presented here, using maximum likelihood and a slightly different set of outgroup taxa, resulted in a chronogram very similar to that presented here (Givnish et al. 2004).

Our phylogeny confirms, in many ways, the traditional view that bromelioids and tillandsioids arose from within the pitcairnioids (Schimper 1888; Mez 1904; Pittendrigh 1948; Tomlinson 1969; Smith and Downs 1974; Benzing et al. 1985; Smith 1989; Benzing 1990). Terry et al. (1997*a*)

reached a similar conclusion, but had a different impression of the proximity of bromelioids and tillandsioids and the seeming isolation of *Brocchinia* as a result of not having sampled two of the eight major clades of Bromeliaceae, and undersampling two others. Terry et al. (1997*a*) also concluded—based on the results of Ranker et al. (1990) and their own belief that *Encholirium* and *Hechtia* were essentially interchangeable—that *Hechtia* was closely allied to *Dyckia, Encholirium, Abromeitiella,* and *Deuterocohnia,* rather than representing a convergent lineage much closer to the base of Bromeliaceae. The phylogenetic treatment of the ''adaptive radiation'' of Bromeliaceae by Benzing et al. (2000*a*) based on the findings of Terry et al. (1997*a*) bring an impressive amount of ecological and physiological data to bear, but in one important sense was premature: too many groups, with crucial biogeographic distributions and physiological and morphological adaptations, were not included. Contrary to previous claims by Varadarajan and Gilmartin (1988) and Benzing et al. (2000*a*), until now there has been no phylogenetic evidence based on relationships *within* Bromeliaceae that the family arose in the Guayana Shield; the distribution there of earliest-divergent *Brocchinia* might have simply been an autapomorphy. Givnish et al. (1999) inferred that bromeliads arose in the Guayana Shield based on an analysis of *rbc*L sequence variation showing an apparent sister relationship between Bromeliaceae and Rapateaceae; the latter clearly originated in the Guayana Shield and remains mostly endemic to that region (Givnish et al. 2000). However, more powerful molecular evidence based on an analysis of *rbc*L, *atp*B, and 18S sequences (Chase et al. 2000), *ndh*F sequence variation (Givnish et al. 2006), a 7-gene analysis (Chase et al. 2006), and a 17-gene analysis (Graham et al. 2006) indicates that Bromeliaceae and Rapateaceae occupy adjacent rungs at the base of order Poales instead of being sister to each other.

The classical hypotheses that bromelioids and tillandsioids emerged from a pitcairnioid ancestor were based not on phylogenetic analysis, but on noting that epiphytes—a highly specialized growth form, involving many adaptations for life without contact with the soil—were far more numerous outside the pitcairnioids. No early writer suggested that *Brocchinia* or *Lindmania* lay at the base of the family, or that pitcairnioids were not a monophyletic, natural group. Smith (1934) suggested that *Puya* represented something close to the ''ur-bromeliad'', but molecular data show that *Puya* arose quite recently: given its sister relationship to Bromelioideae, perhaps *Puya* should now be seen instead as the ''ur-bromelioid''! Smith's (1934) proposal that Rapateaceae evolved from within Bromeliaceae via *Navia* is manifestly wrong (Terry et al. 1997*a*; Givnish et al. 1999, 2000; Givnish et al. 2006).

The conclusion that *Pitcairnia feliciana* represents the outcome of long-distance dispersal from South America to Africa no earlier than 10.1 Mya accords with our earlier finding that *Maschalocephalus dinklagei* of Rapateaceae is also the product of recent (ca. 6 Mya) long-distance dispersal, not ancient vicariance (Givnish et al. 2000, 2004). Recent colonization may help to explain the lack of African speciation in both groups. Historical cycles of aridity (Goldblatt 1993; Querouil et al. 2003) may also have played a role, given that neither Rapateaceae nor *Pitcairnia* are especially drought tolerant. The African endemics of both families occupy nearby ranges: *Mascalocephalus* in savannas and forests on wet sand from Sierra Leone to Côte d'Ivoire; *Pitcairnia feliciana* on sandstone outcrops of the Fouta Djalon massif in Guinea just to the northwest (Porembski and Bartlott 1999; Givnish et al. 2000). The Guinean Mountains retained a wet climate through the Pleistocene and appear to have served as a refugium for wet-climate taxa (Jahns et al. 1998; Dupont et al. 2000). Both Rapateaceae and Bromeliaceae are also likely to be favored by infertile soils, given the origin and continued abundance of both groups in the Guayana Shield. Thus, vicariance of habitat, via rafting of sandstone deposits to either side of the rifting Atlantic, may have played an important role in the disjunct distribution of rapateads and bromeliads, even if the plants themselves colonized Africa much later via long-distance dispersal (Givnish et al. 2004). There are roughly ten other angiosperm families with amphiatlantic distributions (Thorne 1972, 1973); the use of fossil-calibrated molecular clocks also shows that relatively recent, long-distance dispersal probably accounts for this pattern in Melastomataceae (Renner and Meyer 2001) and Vochysiaceae (Sytsma et al. 2004) as well, although the dispersal events also appear to have occurred sometime earlier than in Bromeliaceae.

Adaptive Radiation and Synthesis

Our data show that CAM photosynthesis and associated leaf succulence arose independently from C_3 ancestors in four different lineages, associated with the invasion of arid habitats (deserts, semi-deserts, and high-elevation grasslands and scrub) or epiphytic perches in rain and cloud forests (Fig. 3). CAM and leaf succulence reduce transpiration at the cost of reduced photosynthetic capacity, and are widely considered adaptations to drought (Winter and Smith 1996). Two of the four lineages in which CAM evolved—Tillandsioideae and *Puya*–Bromelioideae—are identical to, or contain, two of the three lineages (*Brocchinia,* Tillandsioideae, higher Bromelioideae) in which epiphytism also evolved. Crayn et al. (2004) largely agree with these inferences, but recognize only three origins of CAM (and only three, somewhat separate origins of epiphytism), based on a somewhat less resolved phylogeny. Givnish et al. (2004) use the phylogeny presented here, together with elevational data on present-day taxa, to infer that the family Bromeliaceae arose at low elevations (<500 m) in the Guayana Shield. With the results presented here, this implies that the ancestral bromeliad had a terrestrial habit and the C_3 photosynthetic pathway, and was adapted to moist lowland conditions on infertile sands or sandstones in the Guayana Shield.

Most tillandsioids and bromelioids have leaf scales (trichomes) that absorb water and nutrients and facilitate life as an epiphyte (McWilliams 1974; Benzing 1980, 2000; Smith 1989). In many tillandsioids, these trichomes have dead cap cells that fill with water after rainstorms, allowing live cells at the base of the trichome to absorb water and nutrients. After the leaf surface dries, the dead cap cells drain and a vapor trap inside them prevents much loss of water from the live, absorptive cells to the open atmosphere. Tillandsioid trichomes thus form an elegant system for the one-way movement of water and nutrients, much like the corky ve-

lamen on the roots of epiphytic orchids; both ensure that epiphytes don't "bleed" water from the very organs that allow them to absorb it in the first place (Benzing 1980, 2000). Some tillandsioids, the so-called "atmospherics" like Spanish moss (*Tillandsia usneoides* L.), are highly specialized and depend almost exclusively on trichomes for their water and nutrient supplies. These trichomes so densely cover the leaves that they reduce light absorption and subsequent transpiration, but can interfere with C_3 photosynthesis when their wet caps are filled with water and cover the leaf surface, as they often are under rain- and cloud-forest conditions. Under these circumstances, CAM photosynthesis can provide a photosynthetic advantage by recycling CO_2 when gas exchange with the external atmosphere is blocked (Pierce et al. 2002). This new physiological insight may help account for the occurrence of bromelioids in many wet (and often shaded) epiphytic microsites, which had previously been thought paradoxical (e.g., see Benzing 2000). Many bromelioids and tillandsioids have an alternative tank habit, in which rainwater is impounded among closely overlapping leaf bases, with water and nutrients being absorbed more slowly.

Absorptive trichomes, and at least two instances of the tank habit, evolved first in *Brocchinia,* sister to all other Bromeliaceae, apparently as adaptations for nutrient absorption in rainy, humid, and extremely mineral-poor environments atop the tepuis (Givnish et al. 1997). However, trichomes in *Brocchinia* retain live cap cells (Givnish et al. 1984, 1997; Owen et al. 1988) and hence do not provide the one-way system for water uptake—and the adaptations for life in drier circumstances, including epiphytism outside the most humid cloud forests—that tillandsioid-style trichomes can provide. Once such trichomes, or the CAM photosynthetic pathway, did evolve, a wide range of dry habitats and epiphytic perches became available, which should have stimulated a great expansion in the diversity of bromeliads and the habitats they were able to occupy. Such a shift appears to have first occurred about 15 Mya, with the accelerated rate of appearance of bromeliad genera with the arrival of *Hechtia* (with CAM photosynthesis), Tillandsioideae (with many species having absorptive trichomes, tank or atmospheric habits, and/or CAM), and the remaining higher bromeliads (with CAM evolving independently later in Pitcairnioideae s.s. and in *Puya*–Bromelioideae, 9.1–11.9 Mya). The appearance of these traits largely coincides with the centripetal movement of bromeliads from the hyperhumid highlands of the Guayana Shield into drier and more seasonal regions nearby, suggesting a strong (and, quite possibly, causal) link between physiological evolution and historical biogeography. The sensitivity of the absorptive trichome of *Brocchinia* may have helped restrict them to the wet, highly humid uplands and highlands of the Guayana Shield. Once the barriers to dispersal posed by aridity were spanned, bromeliads could spread widely, and invade and dominate the epiphytic adaptive zone in the New World. They have also become the dominant (or only!) perennials in some extremely arid communities, including parts of the Atacama Desert (Rundel and Dillon 1998) and sunbaked granitic outcrops of the Brazilian Shield (McWilliams 1974; Kessler 2002*a, b*). The closely related family Rapateaceae has not evolved similar adaptations to drought or epiphytism (except in *Epidryos*

Maguire, which occurs only in humid cloud forests in the Guayana Shield, Panama, and Ecuador) and so have remained much more tightly corralled within the Guayana Shield and Amazon basin (Givnish et al. 2004).

This intimate interplay between bromeliad phylogeny, ecology, physiology, and biogeography on the one hand, and Earth history on the other, could only have been recognized and studied after a calibrated molecular phylogeny for the family was produced. Better calibrated, better supported phylogenies that embrace a wider range of taxa and ecological specializations within and among genera are now needed. An obvious next strategy to pursue would be to sequence a wide range of species chosen by the research community for all of cpDNA regions—*ndh*F, *mat*K, *trn*L–*trn*F region, *rps*16, *rbc*L–*atp*B spacer—upon which individual research groups have focused their energies hitherto. We note that, while cross-verified PL, Langley-Fitch molecular clocks, and lineage-specific rates of molecular evolution all yield quite similar dates for events in the history of Bromeliaceae, NPRS produces dates for all events (except the family's origin) that are roughly twice as old as those produced by the other techniques. Together, both sets of calculations yield estimates of the massive, centripetal movement of the family outside the Guayana Shield—and simultaneous evolution of CAM, epiphytism, and numerous leaf and trichome traits adapted to drought—which straddle the estimated time of uplift of the central and northern Andes, shift of the Amazon to its present course, and ecological separation of the Guayana and Brazilian Shields roughly 20 Mya. As our knowledge of the pattern and tempo of differentiation within monocots continues to grow, it will be important to determine whether the "bromeliad revolution" occurred at the same time as these crucial events, or—as our current calculations indicate—several million years later.

Molecular phylogenies for Bromeliaceae cast light on a classic question regarding the evolution of epiphytism. Schimper (1884, 1888, 1898) asserted that vascular epiphytes arose from lineages adapted to the shaded understories of tropical forests, while Pittendrigh (1948) argued that epiphytic bromelioids and tillandsioids evolved from sun-adapted ancestors native to dry, open habitats. Pittendrigh (1948) described four different ecological types in bromeliads:

Type I—terrestrial species with absorptive roots but lacking absorptive trichomes;
Type II—terrestrial species with absorptive roots and absorptive trichomes on leaf bases;
Type III—terrestrial species or epiphytes with roots that mainly serve as anchors, combined with a tank habit and absorptive trichomes on leaf bases;
Type IV—epiphytes with roots that mainly serve as anchors, no tank, and absorptive trichomes over the entire shoot.

Benzing (2000) subdivided Type III into two categories based on possession of CAM vs. C_3 photosynthesis, and argued that Pittendrigh's Type IV (atmospherics) evolved mainly via neoteny from Type III species (tank epiphytes and terrestrials). The rationale for the latter is simply that the very small size of the "tanks" (impounding leaf axils) in Type III juveniles precludes them from storing much rainwater—or storing it very long—and that such juveniles often

have a much greater coverage of water- and nutrient-absorptive (and light-reflective) trichomes than the tank-forming adults with a more favorable volume/surface area ratio (see Schulz 1930; Tomlinson 1969; Benzing 1980, 2000; Adams and Martin 1986*a, b, c*; Reinert and Meirelles 1993; Benzing et al. 2000*b*).

Phylogenetic reconstruction of ancestral character states at the generic level confirmed the derivation of atmospheric epiphytes from tank species in Tillandsioideae (Benzing et al. 2000*a*). The cpDNA restriction-site phylogeny for *Brocchinia* (Givnish et al. 1997) places Type I in *B. prismatica* and all but one species of the next-divergent Melanacra clade. These taxa occur on thin sands and sandstone, in well-lit microsites that receive abundant rainfall. The earliest tank-formers in two lineages (*B. paniculata, B. micrantha*) are terrestrial arborescent species with large leaves, voluminous leaf axils, and absorptive trichomes and adventitious roots in those axils (Givnish et al. 1997). These species grow in openings in cloud forests at intermediate elevations (ca. 800–1500 m); their highly unusual growth form corresponds to Type II, but again is native to rainy, not arid habitats. Type III taxa—with unusually large and/or dense absorptive trichomes and (in three of four cases) reduced root systems—include two carnivorous species (*B. hechtioides, B. reducta*), one ant-fed myrmecophyte (*B. acuminata*), and one tank epiphyte (*B. tatei*). Molecular data imply epiphytism evolved from carnivory (Givnish et al. 1997); selection for a tank habit and absorptive trichomes to capture nutrients in a moist, wet, nutrient-poor environment represents a pathway consistent with neither the Schimper or Pittendrigh hypotheses (Givnish et al. 1984, 1997; Benzing et al. 1985; Benzing 2000). Reliance on live, desiccation-intolerant trichomes presumably made the atmospheric habit inaccessible to *Brocchinia*. In Tillandsioideae, the basal position of *Catopsis,* then *Glomeropitcairnia* in an extensive set of *ndh*F sequences (Terry et al. 1997*b*) is potentially consistent with the *Brocchinia* scenario, given that *Catopsis berteroniana* is also carnivorous (Fish 1976; Frank and O'Meara 1984). However, data on relationships within *Catopsis* are not yet available. The pathway to tank epiphytism in bromelioids is unclear, given the initial appearance of epiphytism in the large (and potentially poly- or paraphyletic) genus *Aechmea*.

The evolution of the epiphytic habit in Tillandsioideae and Bromelioideae is likely to have accelerated speciation simply through effects on dispersability and range size. In a survey of 172 bromeliad species in Bolivia, Kessler (2002*a*) found that range size is greater (a) in species with fleshy fruits or plumose seed than in those with winged seeds, (b) in epiphytes than in terrestrial species, and (c) in species at lower elevations than at high elevations. The epiphytic habit—and life on ephemeral microsites atop twigs and branches within a given range of diameters—selects for strong dispersal ability (Benzing 1980). Tillandsioids and bromelioids possess plumose seeds and baccate fruits, the most effective means of seed dispersal. The epiphyte *Brocchinia tatei* has a fringed seed appendage approaching the tillandsioid condition compared with the bicaudate wing seen in congeners (Smith and Downs 1974; Givnish et al. 1997). Epiphytism not only opened a new spectrum of ecological resource to partition locally, it allowed bromelioids and tillandsioids to disperse widely and speciate along the length of the Andes

into Central America. Epiphytism is especially favored in cloud forests at middle elevations. Given the greater dissection of habitats at such elevations by drier, lower valleys, it is not surprising that range size decreases with elevation (Kessler 2002*b*), or that closely related species at middle elevations have peripatric ranges that abut near deep Andean valleys (e.g., Berry 1982 [*Fuchsia*]; Molau 1988 [*Calceolaria*]; Norman 2000 [*Buddleja*]). The ability of a lineage to invade a wide geographic area—especially the latitudinally extensive, topographically complex, and climatically intricate Andean cordilleras (Luteyn 2002; Young et al. 2002), coupled with a tendency to speciation at small spatial scales at middle elevations, should lead to high levels of species diversity at continental scales. The much greater diversity of (mainly epiphytic) Ericaceae in the Andes (586 spp.) vs. the Guayana Highlands (71 spp.) (Luteyn 2002) is consistent with this argument. The narrow endemism of high-elevation species in groups like *Deuterocohnia* and *Puya* is consistent with the general patterns documented by Kessler (2002*a*); presumably, the relatively low diversity of such groups (ca. 20–100 spp.) reflects the general drop in plant species richness in exceptionally dry or high habitats.

Avian pollination, primarily by hummingbirds, arose at least twice, and has persisted in association with invasion of mid- to high-elevation communities (*Guzmania–Tillandsia–Vriesea* and many Bromelioideae in cloud forests, *Puya, Abromeitiella,* and *Deuterocohnia* in Andean grasslands, scrub, and puna), low-elevation rain forests (*Pitcairnia*), and mid to low elevation arid and semi-arid habitats (*Dyckia*). Pollination by thermoregulating birds is likely to be favored by wet and/or cool conditions at higher elevations, in which many insect groups are likely to be less active and effective. Ornithophily is indeed the dominant pollination mode at high elevation and in wet regions in bromeliads of the Bolivian Andes (Kessler and Kromer 2000), and shifts to ornithophily in Lobeliaceae on different continents and islands have mainly occurred with the invasion of cloud forests (Givnish 1998). Many epiphytic Ericaceae in the Andes, which inhabit the same cloud forests as many tillandsioids and bromelioids, have also evolved hummingbird pollination (Luteyn 2002). The relationship between bird pollination and habitat, however, is not one-to-one in Bromeliaceae. It is puzzling that ornithophily did not evolve in Brocchinioideae and Lindmanioideae, even though these groups are largely restricted to cool, wet habitats at mid to high elevations, and species in other families in those habitats are pollinated by birds. The short stature of plants in such groups might, however, select against ornithophily, by exposing avian pollinators to terrestrial predators. Bird-pollinated *Abromeitiella* and *Deuterocohnia* are even shorter in stature; however, terrestrial predators may not be a significant threat in their high-elevation tundra environment.

Based on an extensive DNA-DNA hybridization study, Bleiweiss (1998) inferred that the initial divergence among modern lineages of hummingbirds (Trochilidae) occurred in the early Miocene, roughly 18 Mya. Bleiweiss argues that the extraordinary morphological isolation of hummingbirds from swifts, their closest living relatives, is due to the fact that 40 My elapsed between the divergence of Trochilidae from swifts and the diversification of the modern crown group—paralleling the rationale we have given for the sim-

ilar isolation of bromeliads from other monocot groups. Bleiweiss (1998) dated the divergence of the two major Andean clades of hummingbirds to about 12 Mya, which coincides rather precisely with our estimates for the origins of *Guzmania–Tillandsia–Vriesea* and Pitcairnioideae–Puyoideae–Bromelioideae, the two major clades of hummingbird-pollinated bromeliads, with many in this group being Andean in distribution and epiphytic in habit. Berry et al. (2004) have independently dated the origin of the large, mainly hummingbird-pollinated *Fuchsia* sect. *Fuchsia* at 22 Mya, about the time of the initial diversification of the trochilid crown group.

The independent evolution of four to six leaf and trichome anatomical traits in three lineages adapted to dry conditions—*Hechtia, Puya,* and the Xeric clade—is one of the most striking cases of concerted convergence documented to date. Other examples include (1) the retention of inconspicuous flowers, fleshy fruits, broad leaves, net venation, and rhizomes in shade-dwelling members of the core Liliales, and evolution of visually conspicuous flowers, capsular fruits, narrow leaves, parallel venation, and bulbs in relatives inhabiting open microsites (Patterson and Givnish 2002), and (2) the evolution of fleshy fruits and net venation in more than a dozen lineages of monocots, almost always associated with the invasion of shaded forest understories (Givnish et al. 2006). Concerted convergence in the core Liliales confounds phylogenetic analyses based on morphology, and unites species with each suite of characteristics. Concerted convergence in Bromeliaceae may have the same effect, given that a cladistic analysis of relationships within the former Pitcairnioideae based on phenotypic traits identifies two clades characterized by the presence vs. absence of CAM photosynthesis and the drought-adapted states of the leaf and trichome traits evaluated in this paper (see phylogenies presented by Varadarajan and Gilmartin 1988; Reinert et al. 2003).

Finally, the extraordinary radiation in growth form and mode of nutrient capture in *Brocchinia* may reflect not only the adaptive challenges and opportunities produced by life in rainy, humid, extremely nutrient-poor habitats (Givnish et al. 1997), but also an amount of time for differentiation among current-day lineages within *Brocchinia* equal to that (ca. 17 My) for differentiation of almost all the rest of the genera and species in the family as a whole (Fig. 2). *Brocchinia* represents a kind of ''Darwin's finches'' sister to the rest of the family, in which many of the growth forms and mechanisms of nutrient acquisition that arose across a family of ca. 2600 species and 53 genera evolved within a small set of roughly 20 species. It continues to offer an important system for exploring adaptive radiation and geographic diversification. Similar opportunities are offered by the remarkable variation in growth form and pollination syndrome in *Tillandsia* and in the higher tillandsioids more generally in *Pitcairnia,* and in *Puya.* Several of these groups are now being studied intensively using molecular systematics (Terry et al. 1997b; T. Evans and G. Brown pers. comm; M. Barfuss and W. Till pers. comm; P. Fonderie pers. comm.), and should produce several new insights into the ecology, evolution, biogeography, and systematics of Bromeliaceae.

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APPENDIX 1.

Authorities for generic names mentioned in the text.

Bromeliaceae
  Abromeitiella Mez
  Aechmea Ruiz & Pav.
  Ananas Tourn. ex L.
  Ayensua L. B. Sm.
  Brewcaria L. B. Sm., Steyerm. & H. Rob.
  Brocchinia Schult. f.
  Bromelia L.
  Catopsis Griseb.
  Connellia N. E. Br.
  Cottendorfia Schult. f.
  Cryptanthus Otto & Dietr.
  Deuterocohnia Mez
  Dyckia Schult. f.
  Encholirium Mart. ex Schult.
  Fosterella L. B. Sm.
  Glomerapitcairnia Mez
  Guzmania Ruiz & Pav.
  Hechtia Klotzsch
  Lindmania Mez
  Mezobromelia L. B. Sm.
  Navia Schult. f.
  Pitcairnia L'Hér.
  Puya Molina
  Sequencia Givnish
  Steyerbromelia L. B. Sm.
  Tillandsia L.
  Vriesea Lindl.
Acoraceae
  Acorus L.
Buddlejaceae
  Buddleja L.
Ceratophyllaceae
  Ceratophyllum L.
Flagellariaceae
  Flagellaria L.
Joinvilleaceae
  Joinvillea Gaudich.
Onagraceae
  Fuchsia L.
Scrophulariaceae
  Calceolaria L.
Sparganiaceae
  Sparganium L.
Typhaceae
  Typha L.