

ANCIENT VICARIANCE OR RECENT LONG-DISTANCE DISPERSAL? INFERENCES ABOUT PHYLOGENY AND SOUTH AMERICAN–AFRICAN DISJUNCTIONS IN RAPATEACEAE AND BROMELIACEAE BASED ON *ndhF* SEQUENCE DATA

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Rapateaceae and Bromeliaceae each have a center of diversity in South America and a single species native to a sandstone area in west Africa that abutted the Guayana Shield in northern South America before the Atlantic rifted. They thus provide ideal material for examining the potential role of vicariance versus long-distance dispersal in creating amphiatlantic disjunctions. Analyses based on *ndhF* sequence variation indicate that Rapateaceae and Bromeliaceae are each monophyletic and underwent crown radiation around 41 and 23 Ma, respectively. Both exhibit clocklike sequence evolution, with bromeliads evolving roughly one-third more slowly than rapateads. Among rapateads, the divergence of west African *Maschalocephalus dinklagei* from its closest South American relatives implies that *Maschalocephalus* resulted via long-distance dispersal 7 Ma, not ancient continental drift; only its sandstone habitat is vicariant. Rapateads arose first at low elevations in the Guayana Shield; the earliest divergent genera are widespread along riverine corridors there and, to a lesser extent, in Amazonia and the Brazilian Shield. Speciation at small spatial scales accelerated 15 Ma with the invasion of high-elevation, insular habitats atop tepuis. Among bromeliads, *Pitcairnia feliciana* diverges little from its congeners and appears to be the product of long-distance dispersal ca. 12 Ma. *Brocchinia Ayensua* and then *Lindmania* are sister to all other bromeliads, indicating that the Guayana Shield was also the cradle of the bromeliads. Three lineages form an unresolved trichotomy representing all other bromeliads: (1) Tillandsioideae, (2) *Hechtia*, and (3) a large clade including remaining genera of Pitcairnioideae and all Bromelioideae. The last includes a clade of pitcairnioid genera endemic to the Guayana and Brazilian Shields; a xeric group (*Abromeitiella/Deuterocohnia/Dyckia/Encholirium/Fosterella*) from southern South America and the southern Andes, sister to *Pitcairnia*; and Andean *Puya*, sister to Bromelioideae, with many of the latter native to the Brazilian Shield. Both Rapateaceae and Bromeliaceae appear to have arisen at low elevations in the Guayana Shield, experienced accelerated speciation after invading dissected mountainous terrain, and undergone long-distance dispersal to west Africa recently. Bromeliad acquisition of key adaptations to drought (e.g., CAM photosynthesis, tank habit, tillandsioid leaf trichomes) 17 Ma appears to have coincided with and help cause the centripetal invasion of drier, more seasonal regions beyond the Guayana Shield, resulting in a wider familial range and dominance of the epiphytic adaptive zone. Geology, past and present climate, and proximity to South America help account for both families occurring in nearly the same area of Africa. We present a new classification for Rapateaceae, including a new tribe Stegolepideae, a new subfamily Monotremoideae, and revisions to tribe Saxofridericieae and subfamily Rapateoideae.

Keywords: adaptive evolution, historical biogeography, penalized likelihood.

Introduction

Rapateaceae and Bromeliaceae are closely related families of commelinid monocots (Givnish et al. 1999, 2004; Chase et al. 2000; Stevenson et al. 2000; APG 2003), both restricted to the New World with the exception of a single species in each family that occurs in west Africa (fig. 1). The African species—*Maschalocephalus dinklagei* of Rapateaceae and *Pitcairnia feliciana* of Bromeliaceae—occur in a sandstone region that abutted the Guayana Shield of northern South America before continental drift opened the tropical

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Atlantic Ocean 84 to 102 Ma (Briceño and Schubert 1990; Gibbs and Barron 1993; Pitman et al. 1993; Potter 1997). These disjunctions are surprising given the apparently sedentary nature of both groups. Most Rapateaceae have seeds with no apparent means of long-distance dispersal (Maguire 1982; Givnish et al. 2000); *Pitcairnia* and related bromeliads have seeds that are only weakly winged (Smith and Downs 1974) and thus likely to be poorly dispersed (Kessler 2002a, 2002b). Tropical intercontinental disjunctions in the distributions of bromeliads and rapateads and other families across the Atlantic thus pose the question of whether they arose by ancient vicariance via continental drift or by relatively recent long-distance dispersal (Givnish et al. 2000; Sytsma et al. 2004). This question, in turn, raises the broader issues of

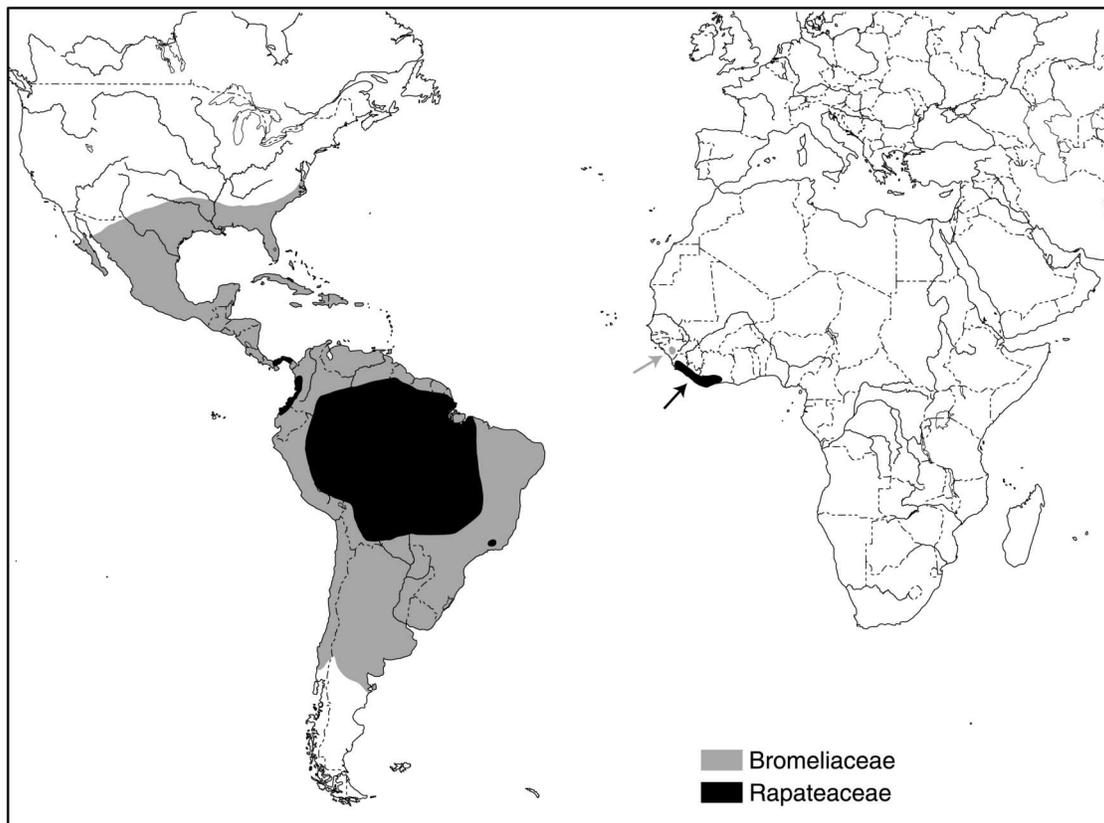


Fig. 1 Amphiatlantic distributions of Bromeliaceae and Rapateaceae. The distribution of rapateads in the New World is completely included within that of bromeliads.

where and when each family evolved and how phylogeny reflects geography and geological history in each lineage, including their relationship to the Guayana Shield and the archipelago of tepuis (sandstone table mountains) that rise 500–3000 m from it above a sea of lowland tropical forests and savannas (fig. 2).

These issues must be addressed indirectly, however. The earliest fossils of Bromeliaceae are only 40 Ma old versus 70–90 Ma for other families of order Poales, and no fossils of Rapateaceae are known (Herendeen and Crane 1995). The scant examples of Bromeliaceae fossils are compounded by the long stem lineage for the family (Bremer 2000; this study) and the difficulty in placing the fossils in any meaningful location in phylogenetic trees. Neither family grows in habitats conducive to fossilization. Thus, inferences as to where and when each evolved must be based on an analysis of their relationships to other families that are better represented in the fossil record, providing dates and phylogenetic branching topologies against which rates of molecular evolution can then be calibrated.

To reconstruct the historical biogeography of Rapateaceae and Bromeliaceae, we present molecular phylogenies for each family based on DNA sequences of *ndhF*, a chloroplast-encoded gene that evolves at a moderately rapid pace (Gaut et al. 1997; Terry et al. 1997a; Givnish et al. 2000). We cali-

brate these trees against the times of origin for both families based on an *ndhF* phylogeny across monocots (Givnish et al. 2004b) using multiple monocot fossils (Bremer 2000) and the inferred divergence of *Acorus* from other monocots 134 Ma (Bremer 2000). We then use these calibrated trees to (1) infer the timing of cladogenetic events within each family, (2) relate them to geologically dated events in Earth history, (3) evaluate ancient vicariance versus recent long-distance dispersal as potential mechanisms underlying the disjunct occurrence of a single species in each family in west Africa, and (4) analyze where each family might have arisen. We use our molecular findings to revise the infrafamilial classification of Rapateaceae, and we consider the factors that might have resulted in similar distributions for both bromeliads and rapateads in tropical west Africa.

Methods

Taxon Sampling and Outgroup Analysis

We included 58 *ndhF* sequences in our phylogenetic analysis, including 35 species representing all known major groups of Bromeliaceae (26 of 59 genera) and 16 species representing all four tribes and both subfamilies of Rapateaceae (14 of 16 genera) (table 1). To maximize the resolution of relationships

Table 1

Species of Order Poales (*sensu* APG 2003) Included in Phylogenetic Analysis of *ndhF* Sequence Divergence

Family and species	Initial citation	GenBank	Voucher	Sequencer
Bromeliaceae:				
<i>Abromeitiella lorentziana</i> (Mez)				
A. Cast.	This article	AY438598	SEL ex StL s.n.	KC Millam
<i>Aechmea haltonii</i> H. Luther	Terry et al. 1997a	L75844	SEL 85-1447	Terry et al.
<i>Ananas ananassoides</i> (Baker)				
L. B. Smith	Terry et al. 1997a	L75845	Brown 3129 RM	Terry et al.
<i>Ayensua uaipanensis</i> (Maguire)				
L. B. Smith	This article	AY438599	Givnish	KC Millam
<i>Brewcaria reflexa</i> (L. B. Sm.)				
B. K. Holst	This article	AY208982	See Givnish et al. 1997	KC Millam
<i>Brocchinia acuminata</i> L. B. Smith	Terry et al. 1997a	L75859	SEL 81-1937	Terry et al.
<i>Brocchinia paniculata</i> Schult. f.	This article	AY208981	Fernandez 8236 PORT	KC Millam
<i>Brocchinia prismatica</i> L. B. Smith	This article	AY438600	See Givnish et al. 1997	KC Millam
<i>Brocchinia serrata</i> L. B. Smith	This article	AY438601	Betancur & Ramírez 1265 MO	KC Millam
<i>Bromelia</i> Adans. sp.	Terry et al. 1997a	L75860	Brown 3128 RM	Terry et al.
<i>Canistrum giganteum</i> (Baker)				
L. B. Smith	Terry et al. 1997a	L75861	Brown 3183 RM	Terry et al.
<i>Catopsis wangerini</i> Mez & Werckle	Terry et al. 1997a	L75855	Palací 1235 RM	Terry et al.
<i>Cottendorfia florida</i> Schult. f.	This article	AY438602	SEL 96-0695	KC Millam
<i>Deuterocohnia longipetala</i> Mez	This article	AY208984	Hort. Marnier-Lapostelle s.n.	KC Millam
<i>Dyckia</i> Schult. f. sp.	Terry et al. 1997a	L75857	Brown 3131 RM	Terry et al.
<i>Encholirium</i> Mart. ex. Schult. sp.	Terry et al. 1997a	L75862	MSBG 1984-0364	Terry et al.
<i>Fosterella penduliflora</i>				
(C. H. Wright) L. B. Smith	Terry et al. 1997a	L75863	SEL 69-1976-12	Terry et al.
<i>Fosterella villosula</i> (Harms)				
L. B. Smith	This article	AY438603	StL 79-2073	KC Millam
<i>Glomeropitcairnia penduliflora</i>				
Mez	Terry et al. 1997a	L75864	Givnish s.n. WIS	Terry et al.
<i>Guzmania monostachya</i> Rusby				
in DC.	Terry et al. 1997a	L75865	SEL 82-225	Terry et al.
<i>Hechtia guatemalensis</i> Mez	This article	AY438604	SEL 81-1891	KC Millam
<i>Hechtia lundelliorum</i> L. B. Smith	This article	AY208985	SEL 85-1005	KC Millam
<i>Lindmania longipes</i> (L. B. Sm.)				
L. B. Smith	This article	AY438605	See Givnish et al. 1997	KC Millam
<i>Lindmania</i> Mez sp.	This article	AY438606	Givnish	KC Millam
<i>Navia saxicola</i> L. B. Smith	This article	AY208983	See Givnish et al. 1997	KC Millam
<i>Neoregelia pineliana</i> var. <i>pineliana</i>				
(Lemaire.) L. B. Smith	Terry et al. 1997a	L75893	SEL 86-261	Terry et al.
<i>Nidularium selloanum</i> (Baker)				
E. Pereira & Leme	Terry et al. 1997a	L75894	Leme 1830 HB	Terry et al.
<i>Pitcairnia atrorubens</i> Baker	This article	AY438607	SEL 86-311	KC Millam
<i>Pitcairnia corallina</i> Linden	This article	AY438608	SEL 86-0574	KC Millam
<i>Pitcairnia feliciana</i> (A. Cheval.)				
Harms & Mildbr.	This article	AY438609	SEL 98-0116	KC Millam
<i>Pitcairnia birtzii</i> H. Luther	Terry et al. 1997a	L75901	SEL 93-294	Terry et al.
<i>Puya floccosa</i> E. Morr.	This article	AY438610	SEL 90-0612	KC Millam
<i>Puya raimondii</i> Harms	This article	AY438611	SEL 91, s.n.	KC Millam
<i>Tillandsia complanata</i> Benth.	Terry et al. 1997a	L75899	SEL 79-0519	Terry et al.
<i>Vriesea viridiflora</i> (Regel)				
J. R. Grant	Terry et al. 1997a	L75910	SEL 78-757	Terry et al.
Flagellariaceae:				
<i>Flagellaria indica</i> L.	Clark et al. 1995	U22008	Clark & Zhang 1305 ISC	JF Wendel
Joinvilleaceae:				
<i>Joinvillea ascendens</i> Gaudich.	Clark et al. 1995	U21973	NTBG* 800379	JF Wendel
Mayacaceae:				
<i>Mayaca fluviatilis</i> Aubl.	This article	BD20001	Berry 3004 WI	JC Hall
Poaceae:				
<i>Bambusa stenostachya</i>	Clark et al. 1995	U21967	Zhang 8400174 ISC	JF Wendel
<i>Pharus lappulaceus</i>	Clark et al. 1995	U21994	L. Clark 1329 ISC	JF Wendel

Table 1
(Continued)

Family and species	Initial citation	GenBank	Voucher	Sequencer
Rapateaceae:				
<i>Amphiphyllum rigidum</i> Gleason	Givnish et al. 2000	AF207638	Fernández, Stergios, Givnish, and Funk 8061 PORT	TM Evans & ML Zjhra
<i>Cephalostemon flavus</i> (Link) Steyerl.	Givnish et al. 2000	AF207624	Smith, Sytsma, Givnish 303 WIS	TM Evans
<i>Epidryos guayanensis</i> Maguire	Givnish et al. 2000	AF207632	Berry and Brako 5539 WIS	TB Patterson
<i>Guacamaya superba</i> Maguire	Givnish et al. 2000	AF207636	Smith, Sytsma, Givnish 301 WIS	TM Evans
<i>Kunhardtia rhodantha</i> Maguire	Givnish et al. 2000	AF207635	Smith, Sytsma, Givnish 300 WIS	TM Evans
<i>Maschalocephalus dinklagei</i> Gilg & K. Schum	Givnish et al. 2000	AF207628	Assí s.n., Côte d'Ivoire 5/95	TM Evans
<i>Monotrema bracteatum</i> Maguire	Givnish et al. 2000	AF207625	Smith, Sytsma, Givnish s.n.	TM Evans
<i>Potaroophytum riparium</i> Sandwith	Givnish et al. 2000	AF207627	Givnish 94-3100 WIS	TM Evans
<i>Rapatea paludosa</i> Aubl.	Givnish et al. 2000	AF207623	Sytsma, Smith, Givnish 5157 WIS	TM Evans
<i>Saxofridericia inermis</i> Ducke	This article	AY438612	Berry 6510, MO	JC Hall
<i>Saxofridericia regalis</i> Schomb.	Givnish et al. 2000	AF207637	Hahn 4675 WIS	TM Evans & ML Zjhra
<i>Schoenocephalum cucullatum</i> Maguire	Givnish et al. 2000	AF207634	Sytsma, Smith, Givnish 5116 WIS	TM Evans & ML Zjhra
<i>Spathanthus bicolor</i> Ducke	This article	AY438615	Givnish 89-125 WIS	TM Evans
<i>Spathanthus unilateralis</i> Desv.	This article	AY438613	Berry & Bachhuber 10 Jul 2000, WIS	JC Hall
<i>Stegolepis hitchcockii</i> subsp. <i>morichensis</i> Maguire	Givnish et al. 2000	AF207629	Smith, Sytsma, Givnish 297 WIS	TM Evans
<i>Windsorina guianensis</i> Gleason	This article	AY438614	Kelloff 1413, US, WIS	JC Hall
Sparganiaceae:				
<i>Sparganium</i> sp. L.	This article	AY191213	T. Givnish, s.n. WIS	JC Pires
Typhaceae:				
<i>Typha angustifolia</i> L.	Graham et al. 2002	U79230	Graham 1040 TRT	SW Graham

Note. Nomenclatural authorities are based on citations at the International Plant Names Index Web site (<http://www.ipni.org/index.html>). SEL indicates accession number at Selby Botanical Garden. StL = Missouri Botanical Garden; the remaining abbreviations in the voucher column are the formal designations for the herbaria in which vouchers are lodged.

visually following the guidelines of Baum et al. (1994). We derived all sequences of Rapateaceae, including four reported here for the first time, obtained a new sequence for *Mayaca fluviatilis*, and obtained 15 *ndbF* sequences for Bromeliaceae. *Typha* was sequenced by J. C. Pires and *Sparganium* by S. W. Graham. The remaining bromeliad sequences, reported by Terry et al. (1997a), were downloaded from GenBank (table 1).

Phylogenetic Analyses

We inferred phylogenetic relationships from *ndbF* sequences using PAUP* 4.0b10 (Swofford 2002). We employed global parsimony (Maddison et al. 1984) to polarize character states and search for the shortest tree(s). Nucleotide positions were considered multistate, unordered characters of equal weight under Fitch parsimony. Unknown nucleotides were treated as uncertainties. Indels were excluded from analysis since we were conducting both maximum parsimony (MP) and maximum likelihood (ML) analyses. To determine whether multiple islands of most parsimonious trees were

present (Maddison 1991), we conducted heuristic searches seeded with 1000 random addition sequences, using tree bisection and reconnection (TBR) with MULPARS on. This approach should facilitate the recovery of all trees within an island (Olmstead et al. 1992, 1993; Conti et al. 1996). We formed the strict consensus of the most parsimonious trees obtained and used bootstrap analysis (Felsenstein 1985, 1988) to evaluate the relative support for each node of that tree.

We also used ML to investigate relationships and obtain better estimates of branch lengths. Models of sequence evolution were analyzed using Modeltest (Posada and Crandall 1998). This program compares 56 models of sequence evolution using a hierarchical framework that calculates the likelihood ratio between models. The starting tree was one of the most parsimonious trees resulting from the parsimony search (see above). A heuristic ML search with TBR branch swapping was then conducted in PAUP* using parameters of DNA substitution determined by the hierarchical likelihood tests.

Molecular Clocks and Historical Biogeography

To test for the operation of *ndhF* molecular clocks in Rapateaceae and Bromeliaceae, we pruned nonfamily members from the ML tree and used the earliest divergent set of species within each family in the global analysis as the outgroup for each intrafamilial analysis. We then calculated the log likelihoods of these shortest trees with and without enforcing a molecular clock using a six-parameter, fully time-reversible model with a gamma distribution of rates fit to quartile means in PAUP*. We compared twice the difference of these log likelihoods with the χ^2 distribution with $n - 2$ degrees of freedom (where n is the number of taxa included in the analysis) to test for significant departures from a molecular clock (Felsenstein 1994; Sanderson 1997). We assessed the average rate of and variation in divergence by calculating the mean \pm SD of branch lengths from the stem group of each family to all the terminal taxa (Givnish et al. 1999, 2000).

We converted the ML tree emerging from Modeltest to an ultrametric tree (in which the lengths of all branches from the root are identical) using penalized likelihood (PL) as implemented in the program r8s (Sanderson 2002). In essence, PL averages local differences in the rate of DNA evolution on different branches, taking into account the topology of branching. It differs from nonparametric rate smoothing (NPRS) (Sanderson 1997) in assigning a penalty for rate changes among branches that are too rapid or frequent on the basis of a smoothness parameter. If the smoothness parameter is large, then PL is reasonably clocklike; 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). We used the cross-verification approach in r8s to determine the optimal value of the smoothness parameter on the basis of minimizing the sum of the squared deviations between observed and expected branch lengths derived through jackknifing each individual branch (Sanderson 2002). We varied the smoothness parameter from 10^0 to 10^3 in steps of 0.25 in the exponent. For comparison, we applied NPRS and Langley-Fitch (1973, 1974) molecular clocks applied to different parts of the phylogeny (bromeliads, rapateads, Typhales, *Mayaca*, *Flagellaria*, and *Joinvillea*, *Bambusa*, and *Pharus*) to obtain alternative ultrametric trees.

We fixed the age of the crown group of Bromeliaceae—that is, its time of origin of extant taxa—at 23 Ma and fixed the corresponding age of Rapateaceae at 41 Ma (table 2). These dates (averages) were obtained by PL analyses of an *ndhF* ML tree based on 277 sequences across all major monocot groups (Givnish et al. 2004b). Following the method of Bremer (2000) on a monocot phylogeny based on *rbcL*, *atpB*, and 18S sequences, we fixed the age of divergence between *Acorus* and the ancestor of all other monocots to 134 Ma and used Cretaceous fossil information to place minimum ages on eight monocot nodes. The resulting calibrated trees produced by r8s were then exported to TreeEdit (Rambaut and Charleston 2002) via PAUP* to produce chronograms with branch lengths proportional to time. To explore the sensitivity of the resulting dates within Rapateaceae and Bromeliaceae to tree topology differences within commelinid monocots and among Poales, we examined four alternative

Table 2

Crown Ages of Rapateaceae and Bromeliaceae Based on PL Analysis of the Across-Monocot *ndhF* Data Set Using Eight Fossil Monocot Dates to Constrain Their Respective Nodes

Tree	Rapateaceae crown age (Ma)	Bromeliaceae crown age (Ma)	Tree topology
1	44.6	24.9	((PO,AR) ((ZI,CO)DA)) I
2	43.9	24.4	(PO ((ZI,CO)(DA,AR))) I
3	44.1	24.7	(AR (PO((ZI,CO)DA))) I
4	36.7	19.1	((PO,DA)AR) (ZI,CO)) I
5	41.3	24.8	((PO,AR) ((ZI,CO)DA)) II
6	40.8	23.4	(PO ((ZI,CO)(DA,AR))) II
7	40.9	24.0	(AR (PO((ZI,CO)DA))) II
8	33.8	18.4	((PO,DA)AR) (ZI,CO)) II
Average	40.8	22.9	

Note. Four different most parsimonious topologies within commelinid monocots were independently assessed with PL. Additionally, two placements of Rapateaceae (I, II) within Poales were evaluated for each of the four commelinid topologies (see text for description of these two placements). PO = Poales, AR = Arecales, ZI = Zingiberales, CO = Commelinales, DA = Dasygogonales.

topologies among commelinid orders seen in the set of MP trees based on the 277 monocot sequences (table 2). In addition, we also examined MP trees in which Rapateaceae are sister to a larger clade including Cyperaceae. Thus, eight monocot-wide trees were used sequentially to obtain a set of crown dates for both Rapateaceae and Bromeliaceae (table 2); these in turn were used in each family-wide PL analysis to obtain a range of possible dates for each node within the trees.

We then related the timing of cladogenetic events within both families to the times of uplift and dissection of the tepuis, 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). We also calculated the times of divergence of *Maschalocephalus dinklagei* and *Pitcairnia feliciana* from their nearest American relatives using lineage-specific rates of evolution (Givnish et al. 2000) as well as ML-estimated rates in PL analysis.

We analyzed spatial patterns of cladogenesis by optimizing both geographical and elevational distributions (Rapateaceae data from Givnish et al. 2000; P. Berry, unpublished data, *Flora of the Venezuelan Guayana* project; Bromeliaceae data from Smith and Downs 1979) of the terminal taxa on the bootstrap majority rule tree using MacClade 4.0 (Maddison and Maddison 2000). This tree is one of the 12 MP trees and is nearly identical to the ML tree (the latter having one zero-length branch). Other MP trees were also examined in order to evaluate how various dichotomizations of the unresolved nodes affected interpretation of geographical and elevation patterns of change. Distributions were atomized into the following biogeographic areas of endemism (unordered): Brazilian Shield (including the Atlantic Shield and Phanerozoic deposits near the Rio de la Plata; fig. 2), Guayana Shield, Amazon basin, Andes, Caribbean (including the adjacent

littoral of northern South America), Central America, and tropical west Africa. Similarly, the terminal taxa of Bromeliaceae were coded for elevational distribution (unordered): low (generally less than 1000 m), high (above 1000 m), or wide-spread (low and high). Elevational data for the more Guayana Shield-restricted Rapateaceae were atomized into lowland (occurring mainly below 500 m), upland (500–1500 m), or highland (mainly >1500 m) (for details of these three types, see Berry et al. 1995; Givnish et al. 2000). To evaluate the effects of using single species as placeholders for large genera (e.g., *Tillandsia*, *Vriesea*, *Stegolepis*), a second analysis was done for each family in which such terminals were coded as polymorphic for all the biogeographic regions and elevation occupied by congeners. Accelerated transformation was used to minimize the number of apparent convergent gains. Spatial shifts in distribution were then related to the chronolo-

gies obtained from the analysis of ultrametric trees, lineage-specific mutation rates, and known ages of geological events.

Results

Phylogeny

Global parsimony resulted in 12 most parsimonious trees of length 1617 steps and a well-resolved strict consensus (fig. 3). The consistency index (CI) for these trees was 0.66 (CI' = 0.57, excluding autapomorphies); the retention index was 0.82. In all, 807 nucleotide sites were variable, of which 510 were phylogenetically informative. Our analysis provides strong bootstrap support for the monophyly of both Rapateaceae (100%) and Bromeliaceae (100%) (fig. 3). The ML

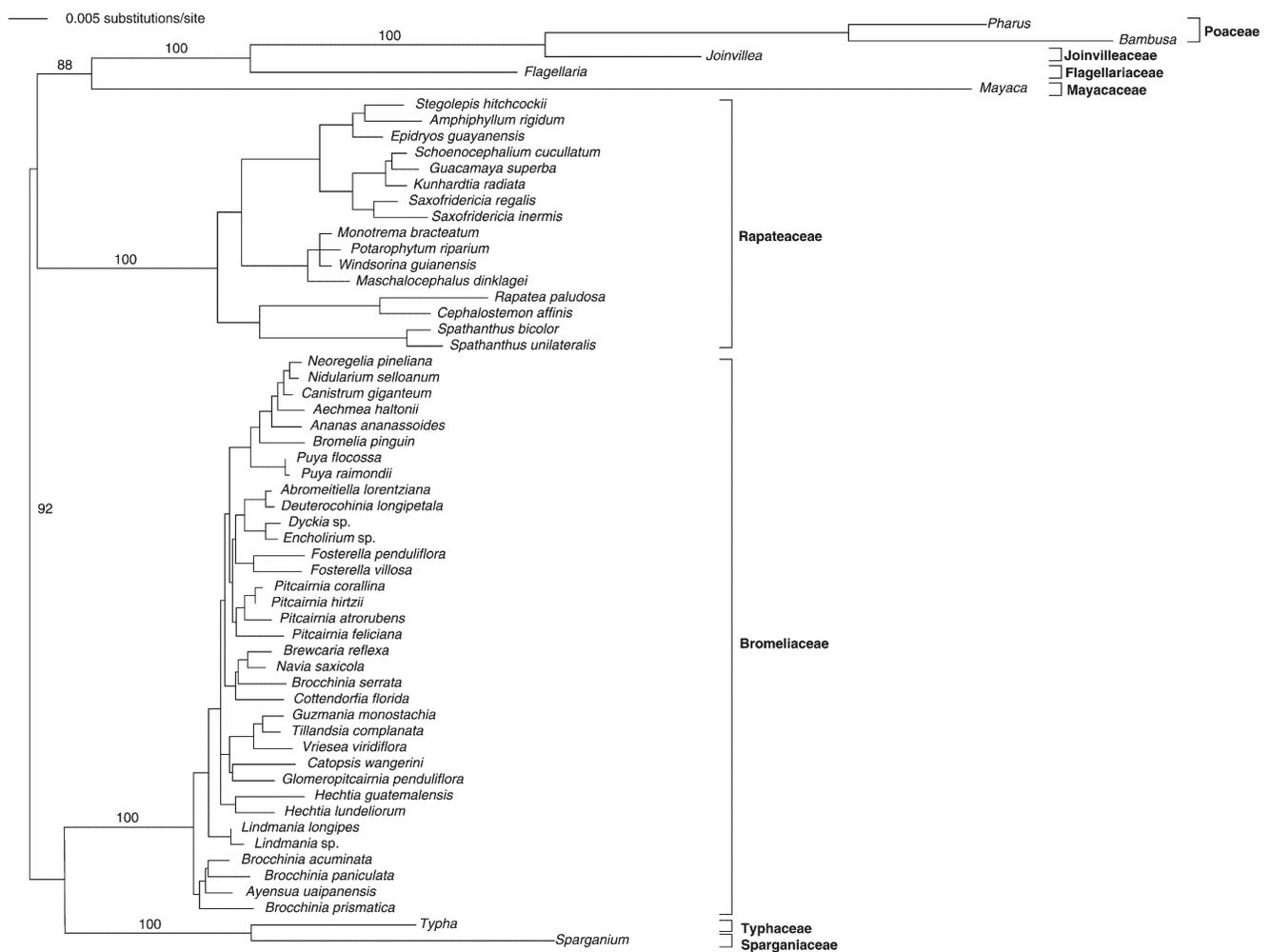


Fig. 3 Maximum likelihood tree of Poales based on *ndhF* sequence variation. The tree is equivalent to one of the 12 most parsimonious trees, except that the trichotomy involving *Monotrema* through *Windsorina* is resolved in the latter. Node below *Brocchinia serrata* collapses in the strict consensus of the maximum parsimony trees. Branch lengths at base of tree were obtained by inclusion of other commelinid lineages from the more global monocot analysis. Bootstrap support values are shown for all nodes outside Bromeliaceae and Rapateaceae; bootstrap support for nodes within these families is given in figs. 4 and 5.

tree is identical in branching topology to one of the MP trees and nearly identical in branch lengths.

Rapateaceae. Subfamily Rapateoideae is paraphyletic, composed of monophyletic tribes Rapateae (*Cephalostemon*, *Rapatea*, *Spathanthus*) and Monotremeae (*Maschalocephalus*, *Monotrema*, *Potarophytum*, *Windsorina*). Rapateae is sister to all other rapateads, and Monotremeae is sister to subfamily Saxofridericioideae (fig. 4). Our resequencing of *Spathanthus bicolor* and inclusion of *Spathanthus unilateralis* makes Rapateae monophyletic under Fitch parsimony as well (fig. 3) and indicates that the position of *S. bicolor* in our previous unweighted analysis reflected noise in the original sequence. Our inclusion of monotypic *Windsorina* confirms its expected membership in tribe Monotremeae. Inclusion of *Saxofridericia inermis* confirms that it falls in the same clade as *Saxofridericia regalis*, sister to tribe Schoenocephalieae (*Guacamaya*, *Kunhardtia*, *Schoenocephalum*), which makes tribe Saxofridericieae (*Amphiphytum*, *Epidryos*, *Marahuacaea*, *Phelpsiella*, *Stegolepis*) paraphyletic as well. Bootstrap support for most major groups is strong: 100% for tribes Monotremeae, Saxofridericieae, and Schoenocephalieae plus *Saxofridericia*; 99% for tribe Schoenocephalieae alone; and 95% for tribe Rapateae (figs. 3, 4). Exclusion of nonrapateads results in six most parsimonious trees of length 324 steps (CI = 0.87, CI' = 0.79) and a strict consensus with the same topology as provided by the global analysis.

Bromeliaceae. Global parsimony resolves eight major clades of bromeliads (figs. 3, 5). Sister to all other bromeliads is *Brocchinia*, a genus of ca. 20 species endemic to the tepuis of the Guayana Shield. Monotypic *Ayensua* is embedded within *Brocchinia*. *Lindmania*, a genus of ca. 20 species (Holst 1997) also endemic to the tepuis of the Guayana Shield, is the second clade and is sister to a hard trichotomy comprising all remaining bromeliads. Two of the three lineages at this polytomy include the monophyletic subfamily

Tillandsioideae (*Catopsis*, *Glomeropitcairnia*, *Guzmania*, *Tillandsia*, *Vriesea*) and the xerophytic genus *Hechtia* from Central America. The Cratonic clade includes three taxa endemic to the Guayana Shield—*Brewcaria*, species-rich *Navia*, and the disparate “*Brocchinia*” *serrata*—as well as monotypic *Cottendorfia* from the Brazilian Shield. The large (ca. 100 spp.) genus *Puya*, native mostly to the Andes, is sister to the monophyletic subfamily Bromelioideae. This larger group is sister to a group consisting of four highly xeromorphic genera (*Abromeitiella*, *Deuterocohnia*, *Dyckia*, *Encholirium*), together with more mesomorphic *Fosterella* of the Andes, and *Pitcairnia* of the Amazon basin, northern Andes, Guayana Shield, Central America, and the Caribbean. The subfamily Pitcairnioideae (highlighted by solid bars in fig. 5) is massively paraphyletic, forming the matrix from which both Tillandsioideae and Bromelioideae emerge.

Reflecting the substantially shorter branch lengths in Bromeliaceae versus Rapateaceae (fig. 3), bootstrap support values for the major bromeliad groups and for relationships among these groups are often lower than those in Rapateaceae. The large clade sister to *Brocchinia*/*Ayensua* is strongly supported (97%), as is the large clade sister to *Lindmania* (84%). The Cratonic clade has strong support (95%), as does the Bromelioideae (99%). Several other relationships within the family, however, have weaker bootstrap support, including 57% for Tillandsioideae (figs. 3, 5). Exclusion of nonbromeliads results in two most parsimonious trees of length 359 steps (CI = 0.82, CI' = 0.66) and a strict consensus with the same topology as that obtained through the global analysis.

Molecular Clocks

The *ndhF* gene shows clocklike evolution in both Rapateaceae ($P > 0.12$, χ^2 test, $df = 14$) and Bromeliaceae ($P > 0.053$, χ^2 test, $df = 33$). On the basis of the average branch length from the stem group to the terminal taxa and

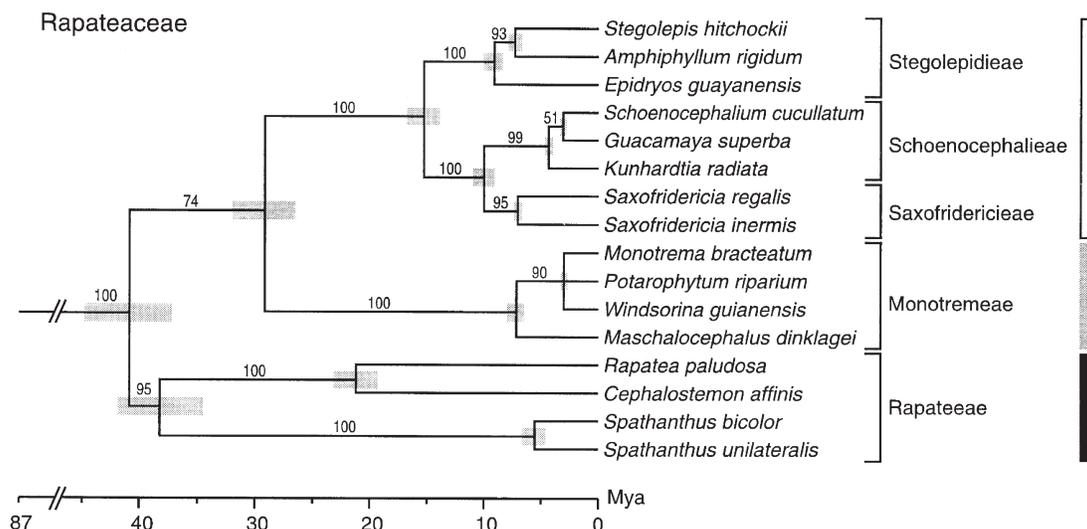


Fig. 4 Chronogram for Rapateaceae based on penalized likelihood, showing inferred timing of cladogenesis in the family. Gray bars at each node indicate \pm SD of inferred date. Tribes and subfamilies under the new infrafamilial classification proposed in this article (see “Discussion”) are highlighted by brackets and bars. *Open bar*, Saxofridericioideae; *gray bar*, Monotremoideae; *solid bar*, Rapateoideae.

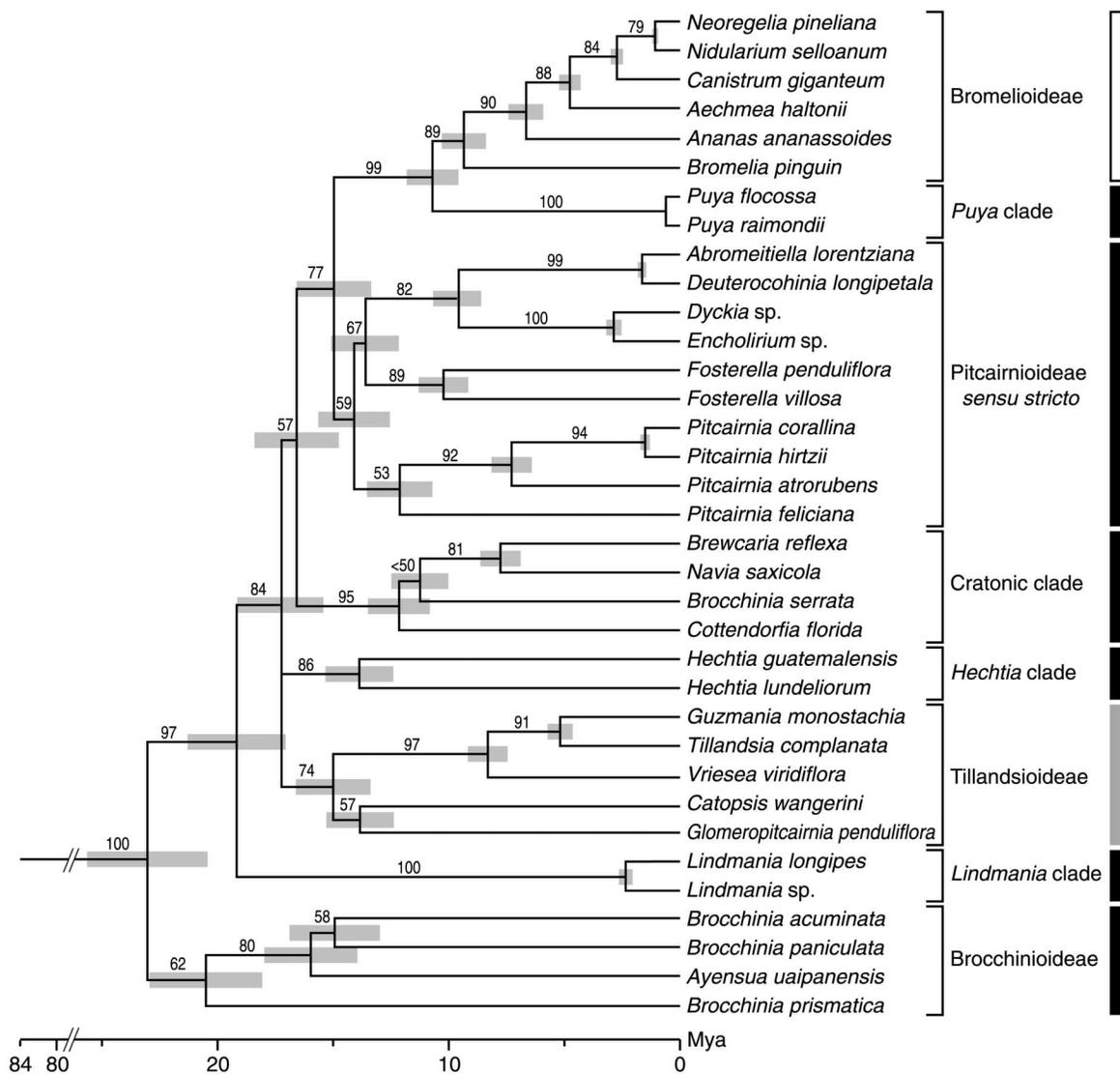


Fig. 5 Ultrametric tree for Bromeliaceae showing inferred chronology of cladogenesis. Gray bars at each node indicate \pm SD of inferred date. Major clades are highlighted by brackets; membership in the three current subfamilies (Smith and Downs 1974, 1977, 1979) is indicated by shaded bars. *Open bar*, Bromelioideae; *gray bar*, Tillandsioideae; *solid bar*, Pitcairnioideae. Note the extreme paraphyly of Pitcairnioideae and monophyly of both Bromelioideae and Tillandsioideae.

on the inferred age of each family, the molecular clock in Rapateaceae appears to tick 53% faster (1.26 ± 0.16 mutations/Ma) than in Bromeliaceae (0.84 ± 0.09 mutations/Ma). This difference is highly significant ($P < 2 \times 10^{-9}$, two-tailed t -test, $df = 39$). For grasses plus *Joinvillea*, *ndbF* evolves nearly twice as fast (2.37 ± 0.64 mutations/Ma) as in rapateads and nearly three times as fast as in bromeliads.

Historical Biogeography

Cross-verification yielded an optimal smoothness parameter of $10^{2.50}$ for the PL algorithm for the monocot-wide analysis of *ndbF*. Dates of crown group radiations for Rapateaceae and Bromeliaceae are based on PL analyses of the eight ML trees from the monocot-wide *ndbF* data set, representing different arrangements of commelinid orders (ta-

ble 2). These average to 41 and 23 Ma for Rapateaceae (fig. 4) and Bromeliaceae (fig. 5), with standard deviations of 3.8 and 2.6 Ma, respectively. The stem lineages of the two families go back 87 and 84 Ma, respectively. Chronograms show times of radiation and subsequent divergence with standard deviations for Rapateaceae and Bromeliaceae (figs. 4, 5). With both Rapateaceae and Bromeliaceae, dates based on PL are generally consistent with those based on lineage-specific mutation rates or local molecular clocks but are much more recent than those based on NPRS. NPRS results are often 50%–70% greater in value than corresponding PL dates.

The shifts in elevation for both families are based on ACCTRANS optimization onto their respective phylogenetic trees (fig. 6). Shown are shifts when the individual species elevations are scored. The elevational shifts are identical in



Fig. 6 Inferred patterns of elevational shifts in Rapateaceae (*left*) and Bromeliaceae (*right*) based on modern distribution of terminal taxa, branching topologies shown in figs. 4 and 5, and parsimony.

Rapateaceae when species-rich genera are coded to accommodate interspecies variation. The pattern in Bromeliaceae becomes less resolved (i.e., more equivocal branches) at the genus level, but the main pattern of shifts from low elevations to higher elevations multiple times is maintained (not shown). Likewise, DELTRANS optimization is identical to that shown for Rapateaceae and only slightly different at the tips for widespread genera for Bromeliaceae.

The crown separation of Rapateaceae into two main lineages (Rapateeeae and remainder of family) occurred at ca. 41 Ma, ca. 46 Ma after the stem lineage of Rapateaceae appears (fig. 4). Within Rapateeeae, separation of *Spathanthus* from the clade of *Rapatea* and *Cephalostemon* quickly followed the initial family radiation, around 38 Ma. This radiation and most of the subsequent divergences of clades within the largely Guayana Shield-restricted Rapateaceae were low-elevation events based on a parsimony reconstruction of ancestral elevations (fig. 6). The separation of largely lowland Monotremeae (except for upland *Potaroiphytum*) from the upland or highland centered clade of three tribes of subfamily Saxofridericioideae occurred around 29 Ma. Within Monotremeae, separation of the African lineage leading to *Maschalocephalus* from the American taxa is quite recent, 7.3 Ma. On the basis of parsimony analysis of elevation, the ancestral elevation for the subfamily Saxofridericioideae is

equivocal (fig. 6). Beginning ca. 10 Ma, several shifts to both uplands and the highlands occur in the subfamily, and one shift (reversal) back to low elevation occurs in the common ancestor of *Schoenocephalum* and *Guacamaya*.

In Bromeliaceae, the stem lineage arose 84 Ma, even deeper in the past than in Rapateaceae and even more removed from the initial diversification of the crown group at 23 Ma. Initial branching gave rise to the clades comprising *Brocchinia* and the embedded *Ayensua* versus all other bromeliads (fig. 5). As with Rapateaceae, initial lineages in the Bromeliaceae apparently inhabited low elevations (fig. 6) within the Guayana Shield (fig. 7). Even within *Brocchinia*, where many species are high-elevation specialists in tepuis, the first split is between low- and high-elevation clades (fig. 6). Diversification within *Brocchinia* appears to have started at 20 Ma and intensified around 15 Ma. Separation of high-elevation, tepui-restricted *Lindmania* from the remainder of the second clade (19 Ma) coincided with this diversification in *Brocchinia*. An important diversification at an unresolved trichotomy around 17 Ma generated three large clades: subfamily Tillandsioideae (unresolved in biogeographic origin), *Hechtia* (Central America), and the remainder of Pitcairnioideae plus all Bromelioideae (origin in the Guayana Shield) (figs. 5, 7). The Tillandsioideae and Bromelioideae crown radiations occurred at 15 and 9.4 Ma, respectively. The Pitcairnioideae

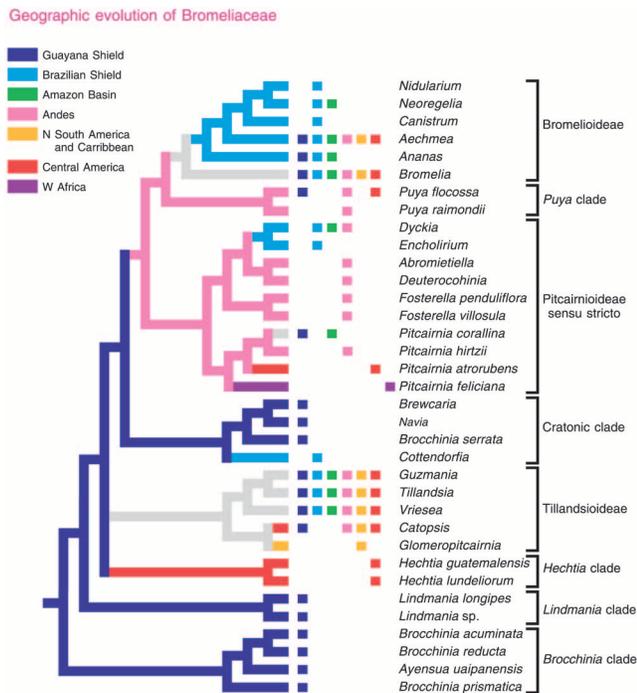


Fig. 7 Inferred pattern of biogeographic diversification in Bromeliaceae based on modern distribution of terminal taxa, branching topology, and parsimony.

s.s. diverged around 14 Ma, possibly in the Andes, with the African *Pitcairnia felciana* separating from American bromeliads slightly thereafter, 12 Ma (figs. 5, 7). The two divergent members sampled for *Puya*, a genus exhibiting a large radiation in the Andes, appear to have diversified only 700,000 yr ago.

Discussion

Phylogeny and Systematic Implications

Rapateaceae. Within Rapateaceae, our findings on the monophyly of and relationships among the four tribes and two subfamilies recognized by Maguire (1958, 1979, 1982, 1984) confirm and extend those derived by Givnish et al. (2000). Inclusion of *Spathanthus unilateralis* shows that *Spathanthus* is sister to *Cephalostemon* and *Rapatea* and that tribe Rapateae is thus monophyletic. Inclusion of lowland *Saxofridericia inermis*—in a portion of the genus other than that occupied by previously studied *Saxofridericia regalis*—demonstrates that *Saxofridericia* is monophyletic and that, with the addition of another species, it continues to occupy its surprising position sister to tribe Schoenocephalieae, making tribe Saxofridericieae as defined by Maguire (1979) paraphyletic. Finally, inclusion of the Potaro River endemic *Windsorina* confirmed that it belongs, as expected, to tribe Monotremeae, that tribe Monotremeae remains sister to subfamily Saxofridericioideae, and that subfamily Rapateoideae as defined by Maguire (1979) is paraphyletic.

The simplest way to eliminate the paraphyly of Rapateoideae and Saxofridericieae is to restrict the former to tribe Ra-

pateae, erect a new subfamily Monotremoideae to contain the highly distinctive tribe Monotremeae, restrict tribe Saxofridericieae to *Saxofridericia* alone, and erect a new tribe Stegolepideae to contain *Amphiphyllum*, *Epidryos*, *Marahuacaea*, *Phelpsiella*, and *Stegolepis*. We make these changes formally below in a revised infrafamilial classification of Rapateaceae.

Subfamily Rapateoideae Maguire. Mem. New York Bot. Gard. 10: 21. 1958.—Carpels uniovulate; involuclral bracts much exceeding the fertile part of the inflorescence, either single or paired and valvate; seeds ovoid-oblongoid and either striate or else smooth with a papillate apical appendage.

Tribe Rapateae Endlicher. Gen. Pl. 1: 131. 1836. (*Rapatea*, *Spathanthus*, *Cephalostemon*, *Duckea*) Tribe Cephalostemoneae Maguire, Acta Amaz. 9:267, 1979; Tribe Spathantheae Maguire, Acta Amaz. 9:267, 1979.

Subfamily Monotremoideae Givnish & P. E. Berry, Subfam. Nov. *Carpellis uniovulatis; bracteis involuclralibus numerosis, imbricatis, vel solitariis subter omni flore; seminibus albo-granulatis, appendicibus apicalibus applanatis.*—Carpels uniovulate; involuclral bracts several and imbricate or else each spikelet subtended by its own bract, mostly shorter than the fertile part of the inflorescence; seeds ovoid-oblongoid, white-granulate, with flattened apical appendage.

Tribe Monotremeae Maguire. Mem. New York Bot. Gard. 10: 21. 1958. (*Monotrema*, *Potarophyllum*, *Windsorina*, *Maschalocephalus*.)

Subfamily Saxofridericioideae Maguire. Mem. New York Bot. Gard. 10:21, 1958.—Carpels multiovulate; seeds not uniformly ovoid or oblongoid, rather prismatic, pyramidal, lenticular, or crescent shaped.

Tribe Saxofridericieae Maguire. Mem. New York Bot. Gard. 10:21, 1958. (*Saxofridericia*)—Scapes one per leaf axil; involuclral bracts two, connate-saccate and pierced by the emerging flowers; petals obcordate, yellow, with spreading blades.

Tribe Schoenocephalieae Maguire. Mem. New York Bot. Gard. 10:21, 1958. (*Schoenocephalum*, *Kunhardtia*, *Guacamaya*)—Scapes one per leaf axil; involuclral bracts two, valvate to connate-saccate; petals lanceolate and remaining tightly imbricate, red, white, or yellow; flowers nectar-producing.

Tribe Stegolepideae Givnish & P. E. Berry, trib. nov. *Scapis vulgo multiplicibus; bracteis involuclralibus nullis vel imbricatis raro valvatis; petalis unguiculatis, flavis raro niveis.*—Scapes generally several per leaf axil; involuclral bracts lacking, imbricate, or rarely valvate; petals with basal claw and usually spreading, yellow or whitish, rounded blade. (*Stegolepis*, *Amphiphyllum*, *Epidryos*, *Marahuacaea*, *Phelpsiella*.)

Saxofridericia occupies a noteworthy position in this revised classification. It shares several characters (e.g., partial lignification of the stelar parenchyma; Carlquist 1966) with tribe Stegolepideae and yet is sister to tribe Schoenocephalieae, making it difficult to define Stegolepideae based on any single morphological character (only multiple inflorescences per leaf axil appear to serve as a synapomorphy). The new Saxofridericieae might have been distinguished from Stegolepideae and Schoenocephalieae simply by saccate bracts that the opening flowers pierce, except that some populations

of *Kunhartia* share this trait as well. Several of the traits defining Schoenocephalieae appear to be directly related to hummingbird pollination (Givnish et al. 2000). In essence, Schoenocephalieae emerged recently from within a morphologically cohesive but paraphyletic group (Stegolepideae plus *Saxofridericia*). Paraphyly of the latter became evident only with molecular data, much as Sytsma and Gottlieb (1986) discerned the emergence of *Heterogaura* from within paraphyletic but morphologically cohesive *Clarkia*. If *Saxofridericia* had become extinct and saccate populations of *Kunhardtia* had disappeared, it would have been easy to describe several single-character synapomorphies for Stegolepideae (as well as the synapomorphies already discernible for Schoenocephalieae). Alternatively, if evolution had proceeded further in Saxofridericieae and Stegolepideae, single-character synapomorphies might have appeared. However, even though we can clearly recognize Stegolepideae, Saxofridericieae, and Schoenocephalieae as monophyletic entities on the basis of molecular data, they have diverged so recently that it is difficult, if not impossible, to distinguish at least the first two tribes from each other on the basis of any single characteristic.

Bromeliaceae. Bromeliads have traditionally been divided into three subfamilies: Pitcairnioideae with winged (or rarely naked) seeds, Tillandsioideae with plumose seeds, and Bromelioideae with fleshy fruits (Smith and Downs 1974, 1977, 1979; Gilmartin and Brown 1987). Over the past 15 yr, several attempts have been made to infer relationships among these subfamilies and their constituent genera using morphological or molecular data (e.g., Gilmartin and Brown 1987; Clark and Clegg 1990; Givnish et al. 1990, 1992; Ranker et al. 1990; Clark et al. 1993). Importantly, Terry et al. (1997a) using *ndbF* sequences found (i) that *Brocchinia* is sister to the rest of the family, (ii) that Tillandsioideae is monophyletic and sister to remaining elements of the family, (iii) a monophyletic subfamily Pitcairnioideae s.s., and (iv) that *Puya* is sister to a monophyletic Bromelioideae. Horres et al. (2000) using *trnL* sequences identified three major clades whose relationships with each other were unresolved: *Brocchinia* plus *Ayensua*, *Hechtia*, and all remaining bromeliads. The latter clade, in turn, split into an unresolved polytomy of five clades, including a monophyletic Bromelioideae. Finally, Crayn et al. (2000) using partial *matK* sequences found little phylogenetic structure beyond support for individual genera in most cases.

Our phylogeny is consistent with the old suggestion that the bromelioids and tillandsioids arose from within the Pitcairnioideae (Schimper 1888; Mez 1904; Pittendrigh 1948; Tomlinson 1969; Smith and Downs 1974; Benzing et al. 1985; Smith 1989; Benzing 1990). Terry et al. (1997a) 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 their not having sampled three of the eight major clades of Bromeliaceae. They also concluded, on the basis of 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. Benzing's (2000) treatment of the "adaptive radiation" of the bromeliads

based on the phylogeny of Terry et al. (1997b) was premature: too many groups, with crucial biogeographic distributions and physiological/morphological adaptations, were not included. Givnish et al. (2004a) present a detailed scenario for the adaptive diversification of bromeliads on the basis of the phylogeny and biogeographic reconstruction presented here. Contrary to previous claims (e.g., Benzing 2000), until now there had been no phylogenetic evidence within Bromeliaceae that the family arose in the Guayana Shield; the distribution there of earliest divergent *Brocchinia* might have simply been an autapomorphy.

The classical proposals that bromelioids and tillandsioids emerged from a pitcairnioid ancestor were based not on phylogenetic analysis but on the simple observation that epiphytes—an ecologically advanced growth form involving many specializations for life without contact with the soil—were far more numerous outside the pitcairnioids. Not one of the early writers, however, suggested that *Brocchinia* or *Lindmania* might lie at the base of the family or that Pitcairnioideae was not monophyletic or otherwise "unnatural." Smith (1934) proposed that *Puya* might represent something close to the "ur-bromeliad" or ancestral bromeliad, but molecular data show that *Puya* arose quite recently, though it might now be better seen as the "ur-bromelioid." Smith's (1934) suggestion that Rapateaceae evolved from within Bromeliaceae via *Navia* is clearly incorrect (Terry et al. 1997a; Givnish et al. 1999, 2000; this article).

Our results include a number of other important new findings. First, *Ayensua* is embedded within *Brocchinia* with this clade sister to the remainder of the family. *Brocchinia* is a remarkable genus of ca. 20 species endemic to rainy, extremely infertile habitats atop the tepuis and adjacent lowland sandplains of the Guayana Shield. *Brocchinia* has undergone an adaptive radiation in mechanisms of nutrient capture that is unparalleled at the generic level in angiosperms (Givnish et al. 1997). *Brocchinia prismatica* is sister to a clade comprising *Ayensua*, *Brocchinia acuminata*, and *Brocchinia paniculata*. The latter species is a member of the Melanacra clade (Givnish et al. 1997). *Ayensua uaipanensis* shares with another member of the Melanacra clade, *Brocchinia maguirei*, the highly unusual characteristic of a sharply defined abscission zone at the base of each leaf.

Second, the tepui endemic *Lindmania* is the sister to all other bromeliads except *Brocchinia* and *Ayensua*. Third, a hard polytomy exists with Tillandsioideae, *Hechtia*, and all remaining bromeliads. Fourth, we identify a "Cratonic clade," in allusion to its restriction to the single craton on which both the Brazilian and Guayana Shields ride. Givnish et al. (1997) resolved *Brewcaria*, *Navia*, and "*Brocchinia serrata*" as close relatives on the basis of cpDNA restriction site variation; the last species diverges from all other taxa classified as *Brocchinia* in having a superior ovary and spinescent leaves. The association of *Cottendorfia* with *Navia*, among other genera, in the Cratonic clade is supported by the sister relationship of *Cottendorfia florida* with *Navia phelpsiae* on the basis of *matK* sequence variation (Crayn et al. 2000). However, the latter study also placed *Navia igneosicola* sister to almost all species of *Pitcairnia* (including *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 now placed in *Navia* will ultimately be excluded from this genus. Fifth, our results place *Abromeitiella* and *Deuterocohnia* sister to each other and jointly sister to *Dyckia* and *Encholirium*. Sixth, this study confirms *Fosterella* as sister to this larger group of highly xeromorphic genera. Seventh, our *ndbF* phylogeny shows that the large genus *Puya*, native mostly to the Andes, is sister to the monophyletic subfamily Bromelioideae (figs. 3, 5).

Historical Biogeography

Our findings demonstrate that Rapateaceae and Bromeliaceae both arose in the Guayana Shield of northern South America, spread centripetally from there, and reached tropical west Africa via long-distance dispersal relatively recently, 6–8 Ma if we use calculations based on cross-verified PL. Similar dates are obtained if local molecular clocks or lineage-specific mutation rates are employed. We believe that the substantially older estimates that arise from nonparametric rate smoothing reflect a bias based on the method, for two reasons. First, NPRS is known to perform poorly in clades that exhibit clocklike evolution (Sanderson 2002). Thus, while NPRS may be an appropriate method for estimating dates across the monocots as a whole, which exhibit strong heterogeneity in the rate of molecular evolution (Gaut et al. 1993, 1997), it probably is inappropriate for estimations within either Bromeliaceae or Rapateaceae. Second, and more importantly, in both families the lineage containing the sole African taxon has substantially shorter branch lengths than do flanking groups (77.8 ± 1.7 steps for Monotremeae vs. 101.1 ± 5.3 steps for other rapateads; 59.0 ± 1.6 steps for *Pitcairnia* vs. 68.3 ± 3.7 steps for other Pitcairnioideae s.s., *Puya*, and bromelioids). These differences are highly significant ($P < 2 \times 10^{-9}$ for bromeliads, $P < 10^{-5}$ for rapateads, based on two-tailed *t*-tests) despite both families having passed the Felsenstein test for clocklike molecular evolution. Short branches in one lineage flanked by long branches in other lineages are likely to be diluted by nonparametric rate smoothing and might lead to unrealistically ancient ages for dispersal/vicariance events in that lineage. This appears to have happened in both families; it would be useful to conduct simulations to see how sensitive NPRS is to such bias, given its increasing use in phylogenetic and biogeographic reconstructions.

On the basis of *rbcl* sequence data, Givnish et al. (2000) argued that Bromeliaceae, Mayacaceae, and Rapateaceae form a clade and that this group was likely to share a common ancestor from the Guayana Shield. Detailed analyses based on more extensive data—involving *rbcl*, *atpB*, and 18S (Chase et al. 2000) or *ndbF* (this article; Givnish et al. 2004b)—do not, however, support this clade and instead point to a close but nonsister relationship among these families (fig. 3). We note that it is still possible, even likely, that the broader group containing these three families (with Bromeliaceae earliest divergent) may still have arisen in the Guayana Shield, given the origins of both Bromeliaceae and

Rapateaceae there, the likely origin of Xyridaceae there (on the basis of the unique coexistence of all genera of the family there as well as all chromosomal numbers within wide-ranging *Xyris*; Givnish et al. 2000), the occurrence of numerous genera of Eriocaulaceae there, the presence of *Mayaca*, and the position of the Guayana Shield endemic *Thurnia* at the base of the closely related Cyperaceae (Chase et al. 2000; Givnish et al. 2000). *Mayaca* has the same biogeographic pattern as that seen in Bromeliaceae and Rapateaceae, with one species in west Africa and several in the Americas; it would be interesting to reconstruct the evolutionary history of this genus next.

Rapateaceae. The evolutionary chronology of Rapateaceae derived in this article (fig. 4) has several implications for the historical biogeography of the family, all consistent with the detailed discussion provided by Givnish et al. (2000). The latter results are modified by the inclusion of additional taxa, a new estimated time of origin (87 Ma vs. 62 Ma), and new estimated times of cladogenesis within the family, based on the new position of *Spathanthus* and the use of PL versus lineage-specific rates of molecular evolution. We infer that Rapateaceae arose in the Guayana Shield of South America. All genera except *Maschalocephalus* occur in the Guayana Shield, and all of those except *Spathanthus*, *Cephalostemon*, *Rapatea*, *Epidryos*, and *Stegolepis* are restricted to the Guayana Shield (Maguire 1979, 1982, 1984; Givnish et al. 2000; P. E. Berry, in preparation). *Epidryos* is unique in the family in possessing viscid seed appendages (P. E. Berry, in preparation), fitting its epiphytic role and facilitating long-distance seed dispersal and a range including parts of the Guayana Shield, Panama, Colombia, and Ecuador. A disjunct population of *Stegolepis* has also recently been discovered in Ecuador (P. E. Berry, personal communication).

We also infer that Rapateaceae arose in the lowlands and then invaded highland habitats as subfamily Saxofridericioideae diversified or possibly later with the rise of *Stegolepis* and allied genera (Givnish et al. 2000). This finding parallels the patterns documented in *Brocchinia* (Givnish et al. 1997) and Guayana Shield Gentianaceae (Struwe et al. 2002), the two groups endemic to the Guayana Shield with taxa at a variety of elevations that have been the subject of detailed phylogenetic analyses. In Rapateaceae, secondary reinvasions of the lowlands may have happened twice: in tribe Schoenocephalieae (one widespread species of *Kunhardtia* is entirely montane, while the other is rare and occurs in the lowlands) and in *Saxofridericia*. Additional taxa must be studied to determine whether the montane distribution of several *Saxofridericia* and most populations of *Kunhardtia* is a derived trait shared by *Stegolepis* and related genera or whether they instead represent independent colonization(s) of the highlands (Givnish et al. 2000).

The early divergent, low-elevation genera of tribe Rapateae apparently were able to spread early and widely along riverine corridors before the uplift of the northern Andes and resulting shift in the Amazon ca. 20 Ma, separating the Guayana and Brazilian Shields with a band of edaphically distinct, noncratonic sediments (Givnish et al. 2000). Most of these genera are found in swamps, thickets, and caatinga along riverine corridors (Givnish et al. 2000). Given *Rapatea*'s occurrence on siltier substrates, its appearance in

Amazonia and Bahia may well reflect more recent overland dispersal. On the basis of PL, *Spathanthus* appears to have evolved roughly 38 Ma (fig. 4), before the rise of the central and northern Andes and the associated shift of the Amazon ca. 20 Ma. The Amazon has been running its current course to the Atlantic Ocean since at least the Miocene, separating the Guayana and Brazilian Shields with a belt of edaphically distinct, nutrient-rich sediments derived from the Andes (Hoorn 1994; Hoorn et al. 1995; Potter 1997). The apparent divergence of *Cephalostemon* and *Rapatea* later than this, only 21 Ma (fig. 4), indicates that they might each have colonized the Brazilian Shield via short-distance dispersal at that time. *Rapatea*'s occurrence on siltier substrates suggests that it may have colonized (or recolonized) parts of the Amazon basin even more recently.

Maschalocephalus appears to have diverged from its South American relatives 7.3 Ma (fig. 4), long after the opening of the tropical Atlantic ca. 84–102 Ma (Sidder and Mendoza 1991; Edmond et al. 1995). Even if *Maschalocephalus* colonized Africa much earlier, about the time the tribe Monotremeae as a whole arose 29 Ma, it would still have been too late for continental drift to have played a direct role in its occurrence in Africa. Our PL calculation that *Maschalocephalus* arrived in Africa 7.3 Ma is quite close to estimates based on local molecular clocks (6.9 Ma) and lineage-specific mutation rates (7.6 Ma). NPRS generates a substantially older age of 19 Ma; even this is far too late for *Maschalocephalus* to have colonized Africa via vicariance. However, NPRS is probably an inappropriate approach, given that evolution in Rapateaceae is clocklike and that other biases may apply in this case (see "Discussion").

A recent origin of *Maschalocephalus* via long-distance dispersal ca. 7 Ma might help explain the lack of rapatead speciation in Africa (Good 1974). Historical cycles of aridity in Africa (Goldblatt 1993; Querouil et al. 2003) probably played a role in preventing (or subsequently extirpating) other colonists and slowing speciation, given the present restriction of all rapateads to mesic or wet habitats and *Maschalocephalus*'s occurrence in sandstone areas of relatively heavy (albeit seasonal) rainfall from Sierra Leone to Côte d'Ivoire. Our results and those of Givnish et al. (2000) thus indicate that, if continental drift played a role in creating the amphiatlantic distribution of Rapateaceae, it did so by creating similar sandy, wet, nutrient-poor substrates favorable to rapateads on both sides of the Atlantic, not by rafting rapateads across it. Vicariance of habitat, not vicariance of taxa, accounts for the observed intercontinental disjunction.

The invasion of tepui habitats by subfamily Saxofriderioideae appears to have facilitated isolation and rapid speciation atop individual tepuis, driven by vicariance and dispersal (Givnish et al. 2000). Most montane genera and species of Rapateaceae are narrowly endemic to small areas or individual tepuis within the Guayana Shield. *Amphiphylum* and *Marahuacaea* (allied to *Stegolepis*; Givnish et al. 2000) are restricted to the neighboring tepuis of Duida and Marahuaca in central Amazonas, Venezuela (fig. 2), *Phelpsiella* (also allied to *Stegolepis*; Givnish et al. 2000) is restricted to Parú, ca. 60 km to the north, and most species of *Stegolepis* are restricted to one or a few tepuis each, with each tepui having one or more species present (Huber 1988).

The montane clade containing *Stegolepis* and allied genera arose 15 Ma and began to diversify only 9 Ma (fig. 4). Tribe Schoenocephalieae arose more recently, ca. 10 Ma, appears to have begun diversifying 4.3 Ma, and is now restricted to the western Shield: *Kunhardtia* in the Sierra Maigualida, Sipapo, Autana, Cuao, Guanay, Yutajé, Coro-Coro, and nearby lowlands in northern Venezuelan Amazonas; *Schoenocephalum* in Amazonian savannas on white sand in nearby portions of western Amazonas and adjacent Colombia and Brazil, in the drainages of the Orinoco, Guainía, Atabapo, Ventuari, Inírida, Vaupés, Caquetá, and Rio Negro; *Guacamaya* in a small area of Amazonian savannas along the Guainía and Atabapo (fig. 2).

Given that the most diverse montane lineage, the newly recognized Stegolepideae, arose only 15 Ma (fig. 4), it appears that dispersal must have been a dominant factor. Givnish et al. (2000) estimated that chemical dissolution and erosion should cause the margins of adjacent tepuis to retreat from each other at a rate of ca. 2.4 km/Ma. Such low rates would permit vicariance to play a role only on tepuis that are currently quite close to each other (e.g., Duida, Marahuaca, Huachamacari; fig. 2). Vicariance seems unlikely to have played a role in speciation atop tepuis that are now further apart than ca. 35 km. Despite the lack of adaptations for long-distance dispersal in most rapateads, dispersal seems likely to have led to the isolation and subsequent speciation of Stegolepideae populations atop more distant tepuis, which would have been separated from each other long before the stegolepids arose (Givnish et al. 2000). Infrequent long-distance dispersal (perhaps via waterfowl) would be consistent with the recent origin via dispersal of *Maschalocephalus* and with extensive speciation and narrow endemism in montane saxifriderioideids, in which the habitat is naturally separated into "islands in the sky," patches of cool, rainy, exceedingly humid, and extremely infertile habitats scattered in a sea of lowland tropical forests and savannas. Infrequent dispersal over geographic scales comparable to those between large tepuis appears to have spurred speciation and endemism in several plant groups in the Hawaiian Islands (e.g., *Alsinden-dron-Schiedea*: Soltis et al. 1996; the silversword alliance: Baldwin 1997; Baldwin and Sanderson 1998; *Cyanea*: Givnish et al. 1994, 1995; Givnish 1998; Hawaiian violets: Ballard et al. 1998; Hawaiian mints: Lindqvist and Albert 2002) and a number of other oceanic archipelagoes, such as Macaronesia (Böhle et al. 1996; Francisco-Ortega et al. 1996, 1997; Kim et al. 1996, 1999; Mes et al. 1996; Mort et al. 2002) and the Juan Fernandez Islands (Sang et al. 1994, 1995). We plan to examine the role of long-distance dispersal via vicariance in speciation atop the tepuis by developing molecular phylogenies for rapatead and bromeliad genera whose individual species are mostly restricted to single tepuis and then using these trees to test whether close relatives generally occur on adjacent tepuis (as expected from vicariance) or whether there are frequent exceptions to this rule (as expected from long-distance dispersal).

Bromeliaceae. Based on PL estimates, 61 Ma elapsed between the origin of the bromeliad stem group and divergence among the crown group of surviving lineages 23 Ma (fig. 5). This long time period suggests a great deal of extinction over the intervening period and helps account for the morphologically isolated position of the Bromeliaceae. The nesting of

two lineages, *Brocchinia* and *Lindmania*, endemic to the Guayana Shield at the base of Bromeliaceae implies this large (ca. 2600 spp.) family arose there, with subsequent centripetal invasions of other parts of South and Central America as well as tropical west Africa (figs. 5, 7). The current lineages of *Brocchinia* began to diversify 20 Ma (fig. 5). *Brocchinia* originated at low elevations and then evolved adaptations to nutrient poverty (carnivory, ant-fed myrmecophily, N₂ fixation) that depended on evolution of the tank habit and live absorptive trichomes, all of which were contingent on occupying rainy, humid, extremely nutrient-poor habitats at high elevations on the tepuis (Givnish et al. 1984, 1997). *Brocchinia*'s distribution is coextensive with the Guayana Shield, with almost all species occurring on sand or sandstone on the tepuis or sandplains 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).

The northern Andes and Central America appear to have been invaded independently by members of at least three major lineages: the higher tillandsioids (*Guzmania*, *Tillandsia*, *Vriesea*) beginning ca. 15 Ma; *Fosterella*, beginning ca. 10 Ma; and (involving the entire Andean cordillera) *Puya*, beginning at least 10 Ma (figs. 5, 7; all calculations based on stem groups). We have no way of knowing, given the low intensity of sampling at this point, whether each of these lineages involved single or multiple invasions of the Andes. Several additional groups (e.g., some *Pitcairnia*, bromelioids) have also independently colonized the Andes, but we do not have adequate sampling to estimate the time(s) or numbers of their arrivals. The Brazilian Shield was independently invaded at least three times: by *Cottendorfia* from the Guayana Shield ca. 12 Ma, by *Dyckia-Encholirium* from the central Andes ca. 9 Ma, and by higher Bromelioideae ca. 7 Ma (figs. 5, 7). Individual members of other large groups (e.g., higher tillandsioids) have doubtless also colonized this area independently. We estimate that *Pitcairnia felicianae* arrived in tropical west Africa via long-distance dispersal no earlier than 12 Ma. Most of the present-day diversity of the family involves lineages that have appeared only in the past 17 Ma, including the subfamilies Tillandsioideae and Bromelioideae as well as the remaining large genera *Hechtia*, *Dyckia*, *Pitcairnia*, *Navia*, and (perhaps very recently, at least for modern lineages) *Puya*.

This time period around 17 Ma ushered in the rise of essentially xeromorphic lineages, including the genus *Hechtia* (with heavily armed, succulent leaves and CAM photosynthesis), the subfamily Tillandsioideae (many of which are epiphytes, with several members of the *Guzmania-Tillandsia-Vriesea* lineage having CAM photosynthesis), and the remaining higher bromeliads (almost all having spinescent leaves, with several [*Puya*, Bromelioideae] also having CAM photosynthesis). *Hechtia* and the tillandsioids represent the first bromeliad invasions of Neotropical regions outside the Guayana Shield. Both cases appear to involve northern portions of South America, with *Hechtia* invading Central America. Phylogenetic reconstruction suggests that subfamily Tillandsioideae arose in the Guayana Shield (fig. 7), but that is an artifact of the choice of species used to represent *Guzmania*, *Tillandsia*, and *Vriesea*. The latter genera have widespread distributions

and are especially diverse in the Andes (Smith and Downs 1977). More pertinently, *Glomeropitcairnia* is restricted to parts of northern Venezuela and Trinidad immediately adjacent to the Guayana Shield, and some species of *Catopsis* (e.g., *Catopsis berteroniana*) occur on the Guayana Shield as part of a more extensive range (Smith and Downs 1974). Most of the remaining genera have ranges overlapping the Guayana Shield but have invaded several other regions and are more diverse elsewhere, especially in the Andes. This suggests that the subfamily may have originated by dispersing just beyond the periphery of the Guayana Shield to the Caribbean littoral. Origin of the *Guzmania-Tillandsia-Vriesea* clade within Tillandsioideae—including the most highly specialized, “atmospheric” epiphytes in the family, with a center of diversity in the Andes—began ca. 15 Ma (fig. 7), well after the rise of the central and northern Andes ca. 20 Ma (see above).

Three of the four genera of the Cratonic clade—*Brewcaria*, *Navia*, and “*Brocchinia*” *serrata*—are restricted to the Guayana Shield. On the basis of PL, the Cratonic clade originated 17 Ma, after the Amazon is thought to have changed course and ecologically separated the Guayana and Brazilian Shields ca. 20 Ma. We estimate that Brazilian *Cottendorfia* diverged from these other Cratonic clade taxa 12 Ma (fig. 5), raising long-distance dispersal as a likely mechanism of *Cottendorfia*'s distribution.

Pitcairnioideae *sensu stricto* diverged from the ancestor of *Puya* and Bromelioideae 15 Ma (fig. 5). Phylogenetic reconstruction indicates that the ancestor of these three lineages arose in the Andes (fig. 7), but we suspect that Andean distributions arose independently, substantially later, in Pitcairnioideae s.s. and *Puya*. This suspicion is based on (i) the uplift of the northern and central Andes ca. 20 Ma, (ii) the apparent origin of *Puya* much later than this (11 Ma), (iii) the origin of high Andean *Abromeitiella* and *Deuterocohnia* at 10 Ma, and (iv) the origin of *Fosterella* at midelevations in the Andes 10 Ma (fig. 5). 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 12 Ma (fig. 5), long after the northern and central Andes were uplifted.

The distributions of genera within Pitcairnioideae s.s. indicate that the group represents the result of a counterclockwise invasion from the Guayana Shield into the northern Amazon basin and/or northern Andes, then into the central Andes, and finally into their southern foothills and drier portions of the Brazilian Shield and Bahia (figs. 7, 8). Divergence between *Fosterella* and its sister clade may have taken place in southern Bolivia and northern Argentina, where midelevation *Fosterella* overlaps with the Andean genera *Abromeitiella* and *Deuterocohnia* (fig. 8). The latter genera are very 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. An invasion route from the southern Andes eastward to Bahia is indicated by *Dyckia*'s range, which abuts *Deuterocohnia* in the west and *Encholirium* in the east on the horn of Brazil. Further research is required to determine whether highly xeromorphic *Encholirium* is sister to a monophyletic *Dyckia* or

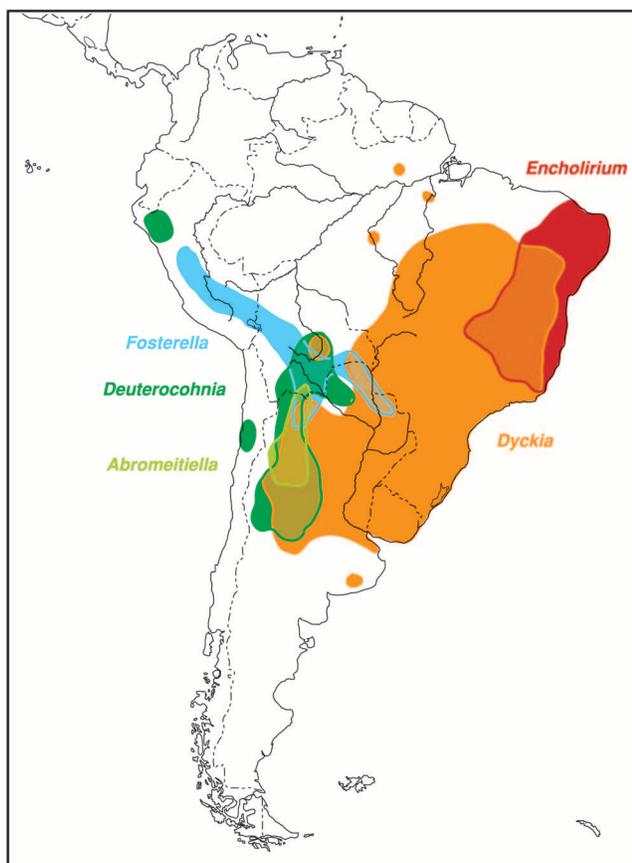


Fig. 8 South American distributions of genera of Pitcairnioideae s.s. excluding *Pitcairnia*, which is widespread in the northern Andes, Central America, Caribbean littoral, Guayana Shield, and northern Amazonia. Note extensive overlap of genera in southern Bolivia and northern Argentina and apparent counterclockwise dispersal from northern Andes, Guayana Shield, and Amazon Basin into the central/southern Andes, Brazilian Shield, and arid Bahia. Distributions adopted from Smith and Downs (1974). A single species of *Fosterella* (*Fosterella micrantha*) occurs disjunctly in Central America.

instead derived from within it. Divergence between the species representing each of these genera occurred quite recently, within the Pleistocene spanning the last 2 Ma; *Abromeitiella* and *Deuterocohnia* appear to have diverged even more recently, ca. 1.7 Ma (fig. 5).

As with *Maschalocephalus*, the PL dates exclude vicariance via continental drift as a possible explanation for the occurrence of *P. felicianae* in Africa and point instead to relatively recent long-distance dispersal. On the basis of PL, African *P. felicianae* diverged from its American counterparts 12 Ma, slightly before *Maschalocephalus* diverged from its relatives (see above). It should be noted, however, that we failed to represent a large amount of morphological diversity within the genus, including *P. felicianae*'s closest relatives from the New World. The latter are thought possibly to include *Pitcairnia fuertesii* from the Caribbean, *Pitcairnia pungens* from Ecuador and Peru (Harms and Mildbraed 1938), or certain unnamed saxicolous species from eastern Brazil (Porembski and Barthlott 1999), though detailed justification for both of

these views is lacking. Porembski and Barthlott (1999) do show, however, that *P. felicianae* diverges from all other *Pitcairnia* studied (which is hardly all of the species of *Pitcairnia*, given the size of the genus) in a number of characteristics. *Pitcairnia felicianae* differs from all Pitcairnoideae in possessing a ligula with two toothlike scales (although the adnate scales in *Pitcairnia pseudopungens*, which the authors presented in their fig. 5, are not that different). The species also has papillae on the stigma lobes that do not occur in other *Pitcairnia*. Its possession of testa cells with perforated outer periclinal walls is also unparalleled in *Pitcairnia*, and indeed only one species of *Puya* is known to share the trait. It is not clear whether these traits are simply autapomorphies of *P. felicianae* or instead imply synapomorphies that unite all other *Pitcairnia* while placing it as the sister to the rest of the genus or even outside it. Resolution of this quandary will require studying a large number of species within *Pitcairnia*. Crayn et al. (2000) have already found, however, that eight of nine species of *Pitcairnia* sequenced for *matK* form a clade. If indeed *P. felicianae* is sister to all other members of the genus, the 12-Ma date is the maximum date for this intercontinental disjunct pattern.

The lineages leading to *Puya* and subfamily Bromelioideae separated 11 Ma, with *Puya* diversifying mostly along the length of the Andes and the bromelioids arising in one of several places, including northern South America, before invading the Brazilian Shield ca. 7 Ma (figs. 5, 6). Some of the early divergent bromelioids (including *Bromelia* and the pineapple *Ananas*) occur in a wide range of areas, including seasonal parts of northern South America and Central America, but a majority of later divergent genera are endemic to seasonal parts of the Brazilian Shield (Smith and Downs 1977). Many of these latter genera, despite their possession of fleshy fruits and possible capacity for long-distance dispersal, have quite limited ranges, and it seems likely that they represent the product of diversification *in situ* within the Brazilian Shield. More species of the large genus *Puya* (ca. 100 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 relatively small, wide-ranging *Puya floccosa* and the gigantic *Puya raimondii* from the central Andes diverged only 700,000 yr ago (fig. 5).

Contrasts, similarities, and their roots. One of the striking biogeographic differences between Bromeliaceae and Rapateaceae is the much larger range of bromeliads in the New World (fig. 1). Almost surely, this reflects the evolution of adaptations to xeric habitats and to epiphytism in Bromeliaceae and the almost total lack of such adaptations in Rapateaceae. Roughly two-thirds of all bromeliads are estimated to possess CAM photosynthesis (Crayn et al. 2000), which, together with associated succulence, provides a potent means of reducing transpiration and enduring intense drought, albeit at the cost of reduced photosynthetic capacity (Winter and Smith 1996). Most tillandsioids and bromeliads have leaf scales (trichomes) that serve as one-way ports that absorb water and nutrients and facilitate life as an epiphyte (McWilliams 1974; Benzing 1980, 2000). Rapateads do not appear to have evolved similar adaptations to drought or epiphytism (except in *Epidryos*, 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.

One of the striking similarities in the biogeography of bromeliads and rapateads is the location of the areas occupied by both families in Africa (fig. 1). *Maschalocephalus* grows in savannas and forests on wet sand from Sierra Leone to Côte d'Ivoire; *P. feliciana* is endemic to sandstone outcrops on the tepuis-like Gangan and other table mountains of the Fouta Djallon massif in Guinea (Porembski and Barthlott 1999), to the northwest of *Maschalocephalus*'s range. *Pitcairnia feliciana* occurs in areas remote from the coast and areas of trade or, indeed, much human activity, so there is little doubt that it (and *Maschalocephalus*) arrived in Africa by nonhuman means (Porembski and Barthlott 1999). The narrow present-day ranges of the lone bromeliad and the lone rapatead in nearly the same portion of tropical west Africa might initially seem puzzling. However, bromeliads and rapateads should be favored by the moist, nutrient-poor conditions at these areas of similar underlying geology—split from the Guayana Shield and Precambrian Roraima sandstones by the rifting Atlantic—given that both families originated under such conditions (and, in the case of rapateads, mainly persist only under such conditions today). The region receives abundant rainfall under tropical conditions but with a 3–5-mo dry season. It is not the wettest lowland region in Africa; that distinction belongs to the disjunct area of heavy rainfall to the southeast along the equator around Cameroon. But tropical west Africa lies more than 1500 km closer to the eastern edge of the Guayana Shield (here taken as the eastern outposts of Monotremata) than the Bight of Africa, which would have required dispersal over 39% more distance across the tropical Atlantic.

Furthermore, on the basis of fossil pollen, the Guinean mountains apparently retained a wet climate during the Pleistocene, even though the savanna border in this region generally moved southward (Jahns et al. 1998; Dupont et al. 2000). The Fouta Djallon district is a center of endemism, with several species (like the treelet sedge, *Microdraoides squammosus*) also occurring disjunctly 1500 km to the west in Cameroon and Nigeria (Porembski and Barthlott 1999). Presumably, during periods of wetter climate, species such as these spread between both of these wet areas and then became isolated as conditions became drier. Other species may have been lost from one (or both) these refugia during arid periods. Geology, present-day climate, and past climate may thus, in concert, have helped bromeliads and rapateads survive in this refugium but killed them or prevented their

spread outside. *Maschalocephalus* appears to have unspecialized entomophilous flowers that might have permitted pollination by a variety of bees or other insects after arrival in Africa. *Pitcairnia feliciana*, on the other hand, appears specialized for avian pollination. While it left hummingbirds behind in South America, there are several species of nectivorous sunbirds in the area that may have substituted for them (Porembski and Barthlott 1999). Regrettably, pollination studies have not been conducted on either species to date.

Finally, it may seem paradoxical to invoke wind dispersal from South America to Africa, either directly or via waterfowl, to account for the presence of both families in Africa, given that the average wind direction at this latitude is strongly in the opposite direction. But recent studies on the tropical Atlantic sea surface temperature dipole, a system somewhat analogous to El Niño in the tropical Pacific, indicate that positive feedback between winds and ocean temperatures can occasionally create west to east wind anomalies veering toward the Guinea coast (Servain 1991; Enfield et al. 1999; Jury et al. 2002). Storms under such conditions would be one candidate for the means by which Rapateaceae and Bromeliaceae (re)colonized Africa.

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