Evolution, 54(6), 2000, pp. 1915–1937

MOLECULAR EVOLUTION, ADAPTIVE RADIATION, AND GEOGRAPHIC DIVERSIFICATION IN THE AMPHIATLANTIC FAMILY RAPATEACEAE: EVIDENCE FROM *ndh*F SEQUENCES AND MORPHOLOGY

T. J. GIVNISH,[1,2] T. M. EVANS,[3] M. L. ZJHRA,[4] T. B. PATTERSON,[1] P. E. BERRY,[1] AND K. J. SYTSMA[1]
[1]*Department of Botany, University of Wisconsin, Madison, Wisconsin 53706*
[2]*E-mail: givnish@facstaff.wisc.edu*
[3]*Department of Biology, Hope College, Holland, Michigan 49423*
[4]*Department of Biology, University of Arizona, Tucson, Arizona 85721*

Abstract.—Rapateaceae (16 genera, ~100 species) is largely restricted to the tepuis and sandplains of the Guayana Shield in northern South America, with *Maschalocephalus* endemic to West Africa. The family has undergone extensive radiation in flower form, leaf shape, habit, and habitat. To analyze the evolution of these distributions and traits, we derived a molecular phylogeny for representatives of 14 genera, based on sequence variation in the chloroplast-encoded *ndh*F gene. The lowland subfamily Rapateoideae is paraphyletic and includes the largely montane subfamily Saxofridericioideae as a monophyletic subset. Overall, the morphological/anatomical data differ significantly from *ndh*F sequences in phylogenetic structure, but show a high degree of concordance with the molecular tree in three of four tribes. Branch lengths are consistent with the operation of a molecular clock. *Maschalocephalus* diverges only slightly from other Monotremae: it is the product of relatively recent, long-distance dispersal, not continental drift—only its habitat atop rifted, nutrient-poor sandstones is vicariant. The family appears to have originated approximately 65 Mya in inundated lowlands of the Guayana Shield, followed by: (1) wide geographic spread of lowland taxa along riverine corridors; (2) colonization of Amazonian white-sand savannas in the western Shield; (3) invasion of tepui habitats with frequent speciation, evolution of narrow endemism, and origin of hummingbird pollination in the western Shield; and (4) reinvasion of lowland white-sand savannas. The apparent timing of speciation in the *Stegolepis* alliance about 6–12 Mya occurred long after the tepuis began to be dissected from each other as the Atlantic rifted approximately 90 Mya. Given the narrow distributions of most montane taxa, this suggests that infrequent long-distance dispersal combined with vicariance accounts for speciation atop tepuis in the *Stegolepis* alliance.

Key words.—Amazonian savannas, continental drift, Guayana Shield, hummingbird pollination, *ndh*F, Rapateaceae, seed dispersal, tepuis, vicariance biogeography.

Received November 30, 1999. Accepted May 18, 2000.

The monocot family Rapateaceae (16 genera, ~ 100 species) is of considerable biogeographic and evolutionary interest. Most genera and species are restricted to the Guayana Shield (Table 1), an ancient core of South America and a center of speciation and endemism in many plant and animal groups (Mayr and Phelps 1967; Steyermark 1986; McDiarmid and Gorzula 1989; Funk and Brooks 1990; Berry et al. 1995; Givnish et al. 1997). Tepuis of sandstones or quartzites of the Roraima Super Group soar 500–2900 m above the tropical lowlands of the Guayana Shield. These ''islands in the sky'' are characterized by cool, wet weather and exceptionally infertile substrates and are separated from each other by up to 200 km (Huber 1995a; Givnish et al. 1997). Many Rapateaceae occupy narrow ranges atop individual tepuis or adjacent sandplains (Maguire 1979, 1982, 1984; Huber 1988), have seeds with no apparent means of long-distance dispersal, and thus appear to be evolutionarily quite sedentary. Yet the family has an amphiatlantic distribution, with monotypic *Maschalocephalus* restricted to West Africa (Good 1974) and native to a sandstone region that abutted the Guayana Shield before continental drift opened the tropical Atlantic 84–102 million years ago (Briceño and Schubert 1990; Gibbs and Barron 1993; Pitman et al. 1993; Potter 1997).

The family has undergone adaptive radiations in floral morphology, habitat, and growth form. Most genera (e.g., *Saxofridericia, Stegolepis*) have yellow, cup-shaped flowers that lack nectar and are buzz-pollinated by bees (Renner 1989), but *Guacamaya, Kunhardtia,* and *Schoenocephalium* have tubular flowers that are red, yellow, or white; secrete nectar; and are visited by hummingbirds (P. E. Berry and T. J. Givnish, pers. obs.); *Spathanthus* has a whitish ''spathe'' and a spicate inflorescence adnate to the involucral bract (Fig. 1). Almost all members of the family are terrestrial herbs native to wet, acidic, highly infertile sands, peats, or mucks, but *Epidryos* is epiphytic. *Stegolepis* and *Marahuacaea* dominate extensive peatlands atop tepuis and neighboring uplands, and bear strap-shaped leaves in bizarre, fan-shaped arrays with closely sheathed leaf-bases (Fig. 1). *Cephalostemon* and *Monotrema* grow in open Amazonian savannas, inundated forests, and caatingas at low to moderate elevations and bear narrow, sometimes terete, and mostly erect leaves. *Potarophytum* and *Rapatea* grow in densely shaded, inundated forests and bear broad, often horizontal foliage (Fig. 1). *Saxofridericia* grows in partly open habitats in lowland swamps, tepui meadows, and granitic slopes, with leaves often less than 8 cm wide but up to 5 m long; remarkably, its flowers pierce a pair of connate involucral bracts, which never open and surround the inflorescence (Fig. 1).

Morphological, anatomical, and palynological characters have been used to recognize four tribes and two subfamilies (Maguire 1958; Carlquist 1961, 1966, 1969; Venturelli and Bouman 1988; Stevenson et al. 1998), but these characters have yet to receive careful phylogenetic analysis. Relationships of rapateads to other monocot families have been among the most controversial issues in higher-level angiosperm systematics, with morphological and anatomical data tieing the

TABLE 1. Current classification, species number (number of those outside Guayana Shield), habitat, and geographic distribution of rapatead genera. Subfamilies and tribes follow Maguire (1982, 1984), Steyermark (1989), and Stevenson et al. (1998); species numbers after these sources and P. E. Berry (unpubl. data). Nomenclature for habitats and elevational ranges (lowland [L] < 500 m; highland [H] > 1500 m; 500 m < upland [U] < 1500 m) after Huber (1982, 1995b). GS, Guayana Shield; A, Amazon Basin; BS, Brazilian Shield; AC, Andes and Central America; WA, West Africa.

Taxon	Species no.[1]	Habitat	Elevation	Geographic distribution
Subfamily Rapateoideae				
Tribe Rapateeae				
Cephalostemon	9 (2)	Amazonian savannas, wet caatinga, similar habitats in Brazilian Shield	L	GS/BS: Colombia, Venezuela, Brazil, Bolivia
Rapatea	23 (8)	Mucky, inundated forests	L	GS/A: Colombia, Venezuela, Trinidad, Guianas, Brazil, Ecuador, Peru, Bolivia
Spathanthus	2 (1)	Stream- and riverbanks, open inundated forests and scrub, wet caatinga	L	GS/A: Colombia, Venezuela, Guianas, Brazil
Tribe Monotremeae				
Maschalocephalus	1 (1)	Wet sandy savannas	L	WA: Liberia, Sierra Leone, Côte d'Ivoire
Monotrema	4 (1)	Amazonian savannas, open inundated forests and scrub	L	GS/BS: Colombia, Venezuela, Brazil
Potarophytum	1 (0)	Streamside forests on white quartz gravel and sand	U	GS: Guyana (Kaieteur Plateau)
Windsorina	1 (0)	Inundated forests	L	GS: Guyana (Potaro River)
Subfamily Saxofridericioideae				
Tribe Saxofridericieae				
Amphiphyllum	1 (0)	Tepui bogs and meadows	H	GS: Venezuela (Cerro Duida)
Epidryos	3 (2)	Cloud forests	U	GS/AC: Panama, Colombia, Venezuela, Guyana, Ecuador, Bolivia
Marahuacaea	1 (0)	Tepui bogs and meadows	H	GS: Venezuela (Cerro Marahuaca)
Phelpsiella	1 (0)	Tepui bogs and meadows	H	GS: Venezuela (Cerro Parú)
Saxofridericia	9 (2)	Ecotones between tepui bogs/ meadows and surrounding scrub, and between riverbanks and lowland inundated forests; peat pockets over granitic outcrops	L → H	GS/A: Colombia, Venezuela, Guianas, Brazil
Stegolepis	35 (0)	Tepui bogs and meadows	H	GS: Venezuela, Guyana, Brazil
Tribe Schoenocephalieae				
Guacamaya	1 (0)	Amazonian savannas	L	GS: Colombia, Venezuela
Kunhardtia	2 (0)	Tepui bogs and meadows; granitic outcrops at low to (mainly) highland elevations	L → H	GS: Venezuela
Schoenocephalium	4 (0)	Amazonian savannas	L	GS: Colombia, Venezuela, Brazil

[1] Most individual species grow only in the Guayana Shield, or exclusively outside it, but a handful of species in *Cephalostemon*, *Rapatea*, and *Spathanthus* range across the margins of the Shield. With the exception of these genera, the number of species growing within the Shield can be obtained by subtracting the number growing outside the Shield from the total number in the genus.

TABLE 2. Species included in the molecular analyses. Nomenclature follows Maguire (1982, 1984), Dahlgren et al. (1985), and Stevenson et al. (1998). NTBG, National Tropical Botanical Garden; SEL, Selby Botanical Garden.

Family/tribe	Species	Initial citation	GenBank accession	Voucher/source
Flagellariaceae	*Flagellaria indica*	Clark et al. 1995	U22008	Clark & Zhang 1305
Joinvilleaceae	*Joinvillea ascendens*	Clark et al. 1995	U21973	NTBG 800379
Poaceae	*Bambusa stenostachya*	Clark et al. 1995	U21967	Zhang 8400174
Bromeliaceae	*Aechmea haltonii*	Terry et al. 1997	L75844	SEL 85-1447
	Brocchinia micrantha	Terry et al. 1997	L75859	SEL 81-1937
	Puya aequatorialis	Terry et al. 1997	L75903	SEL 93-211
	Vriesea viridiflora	Terry et al. 1997	L75910	SEL 78-757
Mayacaceae	*Mayaca fluviatilis*	this paper	AF207639	Delaware Aquatic Plants
Rapateaceae				
Rapateeae	*Cephalostemon flavus*	this paper	AF207624	Smith, Sytsma, Givnish 303
	Rapatea paludosa	this paper	AF207623	Sytsma, Smith, Givnish 5157
	Spathanthus bicolor	this paper	AF207622	Givnish 89-125
Monotremeae	*Maschalocephalus dinklagei*	this paper	AF207628	Assí s.n., Côte d'Ivoire 5/95
	Monotrema bracteatum	this paper	AF207625	Smith, Sytsma, Givnish s.n.
	Monotrema xyridoides	this paper	AF207626	Smith, Sytsma, Givnish 400
	Potarophytum riparium	this paper	AF207627	Givnish 94-3100
Saxofridericieae	*Amphiphyllum rigidum*	this paper	AF207638	Fernández, Stergios, Givnish, Funk 8061
	Epidryos guayanensis	this paper	AF207632	Berry and Brako 5539
	Marahuacaea schomburgkii	this paper	AF207633	Fernández, Stergios, Givnish, Funk 8205
	Saxofridericia regalis	this paper	AF207637	Hahn 4675
	Stegolepis hitchcockii, ssp. *morichensis*	this paper	AF207629	Smith, Sytsma, Givnish 297
	Stegolepis ptaritepuiensis	this paper	AF207631	Lehnhardt 223
	Stegolepis steyermarkii	this paper	AF207630	Smith, Sytsma, Givnish 304
Schoenocephalieae	*Guacamaya superba*	this paper	AF207636	Smith, Sytsma, Givnish 301
	Kunhardtia rhodantha	this paper	AF207635	Smith, Sytsma, Givnish 300
	Schoenocephalium cucullatum	this paper	AF207634	Sytsma, Smith, Givnish 5116

family to Xyridaceae (Hamann 1962), Commelinaceae (Venturelli and Bouman 1988), or the order Commelinales generally (Cronquist 1981; Dahlgren et al. 1985; Stevenson and Loconte 1995), to Thurniaceae of the Cyperales (Tiemann 1985), or to Bromeliaceae (Gilmartin and Brown 1987). In the only study to analyze DNA sequence variation across these groups and their putative relatives, Givnish et al. (1999) identified Bromeliaceae and Mayacaceae as the sister groups of Rapateaceae and redefined the order Bromeliales to encompass these three families.

Here we present the first detailed molecular phylogeny for Rapateaceae, based on a cladistic analysis of sequence variation in the chloroplast-encoded *ndh*F gene. We use this tree to: (1) reconstruct patterns of morphological evolution, adaptive radiation, and geographic diversification within the family in a noncircular fashion; (2) evaluate the congruence of molecular data with morphology and anatomy, and the extent to which traditionally recognized subfamilies and tribes reflect evolutionary relationships; and (3) determine the prospects for using a molecular clock in this group to assess the rates of plant evolution in the Guayana Shield. We test whether: (4) hummingbird pollination has arisen once or many times; (5) similarities between rapatead genera in growth form represent shared ancestry or evolutionary convergence; (6) highland habitats were invaded from the lowlands or vice versa; (7) *Maschalocephalus* represents recent, long-distance dispersal or ancient vicariance via continental drift; and (8) the circumscription of the largest genus *Stegolepis,* which is differentiated from several segregate genera by the absence of involucral bracts, is valid. Our results suggest that that speciation atop tepuis could not have occurred solely via vicariance, given the apparent timing of speciation in tepui rapateads versus the uplift and initial dissection of the tepuis from each other approximately 90 Mya, triggered by the rifting Atlantic Ocean pushing South America against the Pacific Plate (Sidder and Mendoza 1991; Stallard et al. 1991; Edmond et al. 1995; Potter 1997).

METHODS

Taxon Sampling and Outgroup Analysis

Twenty-five *ndh*F sequences were included in our phylogenetic analysis, of which we obtained 17 for species representing 14 of the 16 genera, all four tribes, and both subfamilies of Rapateaceae (Table 2). Species representing all three sections of the large genus *Stegolepis* were included. To maximize the resolution of relationships among ingroup taxa while minimizing the likelihood of artifacts caused by a poor sampling of outgroups (Sytsma and Baum 1996), we used eight outgroup taxa from Bromeliaceae, Mayacaceae, and the order Poales (sensu Dahlgren et al. 1985) to polarize character states within Rapateaceae. Based on a cladistic analysis of *rbc*L cpDNA sequence variation, Givnish et al. (1999) identified Bromeliaceae-Mayacaceae as sister to Rapateaceae, with this larger group (Bromeliales) being sister to a clade consisting of Poales, Xyridaceae-Eriocaulaceae, Cyperales, and Typhales. A combined analysis of *rbc*L sequence data and morphological characters for a less inclusive set of commelinoids produced a phylogeny consistent with these results (Chase et al. 1995). Based on these inferred relationships, we used species representing each of the four subfamilies of Bromeliaceae (Terry et al. 1997) and *Mayaca* as outgroups, and species from three families of Poales as superoutgroups (Table 2).

DNA Extraction, Amplification, and Sequencing

Total DNA was isolated from fresh leaves or frozen material maintained at −80° C, using the CTAB procedure of Doyle and Doyle (1987) as modified by Smith et al. (1991). The chloroplast-encoded *ndh*F gene was amplified in two separate fragments using primer sequences kindly provided by R. Olmstead. The 5′ end was amplified using one primer that anneals approximately 52 nucleotides upstream of the coding region of the gene and another that anneals near po-

←

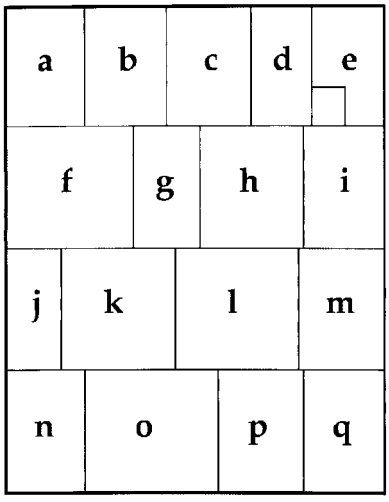


FIG. 1. Floral morphology, inflorescence structure, and growth form in Rapateaceae. **Top row.** Tribe Rapateeae: (a) *Spathanthus bicolor* inflorescence with flowers at anthesis surrounded by single whitish bract; (b) *S. bicolor* habit, growing on wet shore near Canaima (note elongate petioles); (c) *Cephalostemon affinis,* habit, Amazonian savanna at base of Cerro Yapacana; (d) *C. affinis,* inflorescence; (e) *Rapatea paludosa* inflorescence being visited by euglossine bee. **Second row.** Tribe Monotremeae: (f) *Potarophytum riparium,* in streamside forest over quartz gravel, Kaieteur Plateau; (g) *Monotrema xyridoides,* close-up of inflorescence; (h) *M. bracteatum,* inflorescences; (i) *Maschalocephalus dinklagei,* habit with sessile inflorescence, Sierra Leone. **Third row.** Tribe Saxofridericieae: (j) inflorescence of *Stegolepis parvipetala* being visited by weevils, Auyán-tepui, at edge of cloud forest above Angel Falls; (k) habit of *S. hitchcockii,* showing tightly packed leaf bases and distichous fan of strap-shaped leaves, Cerro Yapacana; (l) close-up of *Stegolepis angustata* flower being visited by halictid bee chewing the corrugated anthers; (m) inflorescence of *Saxofridericia grandis,* with flowers piercing saccate involucral bracts from mucilage-filled chamber. **Bottom row.** Tribe Saxofridericieae: (n) habit of *Saxofridericia compressa,* showing exceptionally long, narrow leaves near edge of bog atop Cerro de la Neblina and Elizabeth Burkhart, field assistant, Harvard University; tribe Schoenocephalieae: (o) inflorescence of *Kunhardtia rhodantha,* with long red corollas at anthesis; (p) inflorescence and mature flower of *Guacamaya superba* (note spikelets piercing involucral bracts); and (q) inflorescence and mature flowers of *Schoenocephalium cucullatum.* Photograph credits: T. J. Givnish (b, c, d, f, j, l, n); P. E. Berry (g, h, m, o, p, q); K. J. Sytsma (e, k); G. Romero (a); and A. Carle (i).

TABLE 3. Morphological and anatomical character states used in analyses of phylogenetic relationships and evolutionary trends in Rapateaceae. Characters and character states (all unordered): **1.** placentation: (0) axile/parietal, (1) basal/subbasal axile; **2.** carpels: (0) multiovulate, (1) uniovulate (rarely biovulate, in *Spathanthus*); **3.** seed shape: (0) angular/prismatic, (1) oblong/ovaliform, (2) disciform, (3) ovoid, (4) winged, (5) plumose; **4.** petal shape: (0) obovate/obcordate, (1) lanceolate; **5.** petal color: (0) yellow, (1) red, (2) white, (3) other; **6.** number of bracts: (0) 0, (1) 1, (2) 2, (3) 3 to many, (4) noninvolucral bracts present; **7.** pollen type: (0) bisulcate, (1) zonisulcate, (2) monosulcate diplococcoid, (3) monosulcate simple, (4) monoporate simple; **8.** pollen scrobiculi: (0) absent, (1) present; **9.** pollen size: (0) small, (1) large, (2) very large; **10.** seed striations: (0) absent, (1) present; **11.** scapes: (0) absent, (1) one, (2) two to many; **12.** nectaries: (0) absent, (1) present; **13.** seeds applanate-appendaged: (0) no, (1) yes; **14.** number of anther locules: (0) 2, (1) 4; **15.** seeds white-granulate: (0) no, (1) yes; **16.** bracts saccate: (0) no, (1) yes; **17.** number of carpels, (0) 1, (1) 3; **18.** spikelet bracts showy: (0) no, (1) yes; **19.** asymmetric arm-parenchyma cells in roots: (0) absent, (1) present; **20.** arrangement of tanniniferous cells in roots: (0) radial plates, (1) narrow radial series; **21.** metaphloem sieve tubes

Taxon	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Spathanthus bicolor	1	1	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0
Rapatea paludosa	1	1	1	0	0	2	1	0	0	1	1	0	0	1	0	0	1	0
Cephalostemon flavus	1	1	1	0	0, 2	2	1	0	2	1	1	0	0	1	0	0	1	0
Maschalocephalus dinklagei	1	1	1	0	0	2	2	0	0	0	0	0	1	1	1	0	1	0
Potarophytum riparium	1	1	1	0	0	3	2	0	0	0	1	0	1	1	1	0	1	0
Monotrema bracteatum	1	1	1	1	0	2	2	0	0	0	1	0	1	1	1	0	1	0
Monotrema xyridoides	1	1	1	1	0	2	2	0	0	0	1	0	1	1	1	0	1	0
Amphiphyllum rigidum	0	0	0	0	0	3	3	0	0	0	1	0	0	1	0	0	1	?
Epidryos guayanensis	0	0	2	1	0	0	3	0	0	0	2	0	0	0	0	?	1	?
Marahuacaea schomburgkii	0	0	0	0	0	3	3	0	0	0	2	0	0	1	0	0	1	?
Saxofridericia regalis	0	0	0	0	0	2	3	0	0	0	1	0	0	1	0	1	1	0
Stegolepis hitchcockii	0	0	0	0	0	0	3	0	0	0	2	0	0	1	0	?	1	?
Stegolepis ptaritepuiensis	0	0	0	1	0	0	3	0	0	0	2	0	0	1	0	?	1	?
Stegolepis steyermarkii	0	0	0	0	0	0	3	0	0	0	2	0	0	1	0	?	1	?
Kunhardtia rhodantha	0	0	0	1	1	2	3	0	1	0	1	1	0	0	0	0	1	1
Schoenocephalium cucullatum	0	0	0	1	0	2	3	1	1	0	1	1	0	1	0	0	1	1
Guacamaya superba	0	0	0	1	2	2	3	1	1	0	1	1	0	1	0	1	1	1
Aechmea haltonii	0	0	3	0	2	4	3, 4	?	?	0	1	1	0	?	0	0	1	?
Brocchinia acuminata	0	0	4	0	2	4	3	?	?	0	1	1	0	?	0	0	1	?
Puya aequatorialis	0	0	4	1	3	4	3	?	?	0	1	1	0	?	0	0	1	?
Vriesea viridiflora	0	0	5	0	3	4	3	?	?	0	1	1	0	?	0	0	1	?
Mayaca fluviatilis	0	0	3	0	2	4	3	?	?	0	0	0	0	0, 1	0	0	0	?

Sources of data: Maguire 1982, 1984 (characters 1, 2, 4–6, 10, 11, 13–18); Stevenson et al. 1998, Smith and Downs 1974, P. E. Berry, unpubl. data (3); Carlquist 1966 (7–9); P. E. Berry, unpubl. data (12); Carlquist 1969 (19–23, 25–29); Stevenson and Loconte 1995 (30–44); Stevenson et al. 1998 (24); Venturelli and Bouman 1988 (2).

sition 1318 of the coding region. Primers for amplification of the 3′ end of the gene were located near positions 972 and 2110 of the coding region. Amplifications were conducted on a Cetus DNA Thermocycler (Perkin Elmer, Wellesley, MA), using dGTP nucleotides from United States Biochemical (USB, Cleveland, OH) and either *Taq* polymerase or *Tfl* DNA polymerase from Promega (Madison, WI).

Sequences were obtained from double-stranded amplified products as described by Gyllensten (1989), using the Sanger dideoxy method (Sanger et al. 1977). Sequencing reactions were executed manually using the USB Sequenase kit protocol with the cold-shock modification of Conti et al. (1993), or via cycle-sequencing using the ABI Prism™ dye-terminator kit (Perkin-Elmer). Cycle-sequencing used 25 cycles of 10 sec at 96°C, 5 sec at 48°C, and 240 sec at 60°C. Manual sequencing products were electrophoresed on 6% acrylamide gels and autoradiograms interpreted visually; cycle-sequencing products were run on similar gels and interpreted by an ABI 373A DNA Automated Sequencer (Applied Biosystems, Foster City, CA). Chromatograms for autosequences were inspected using Sequencher™ 3.0 (Gene Codes Corp., Ann Arbor, MI); misinterpreted sites were identified and corrected using established guidelines. The amplification primers, as well as internal primers spaced approximately 300 bases apart, were used to obtain sequence data for all but roughly the last 150 nucleotides of *ndh*F. Overlapping sequence fragments were obtained from both strands using a total of 14 primers. Sequences were aligned visually and indels coded using the guidelines of Baum et al. (1994), and entered into a computer file using MacClade version 3.05 (Maddison and Maddison 1992). Twelve indels (involving the insertion of one to three codons) were detected.

Phylogenetic Analyses

Molecular data

Variation in *ndh*F sequences was used to reconstruct relationships using PAUP* 4.0b2a (Swofford 1999). Global parsimony (Maddison et al. 1984) was employed to polarize character states and search for the shortest tree(s). Nucleotide positions were considered multistate, unordered characters; unknown nucleotides were treated as uncertainties. Bases beyond position 2119 in the aligned sequences were excluded from analysis due to the relatively incomplete coverage across taxa.

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. Setting MULPARS on should facilitate the recovery of all trees within an island (Olmstead et al. 1992, 1993; Conti et al. 1996). Two searches were conducted, using unweighted

TABLE 3. Extended. in roots: (0) wide, (1) narrow; **22.** arrangement of tannin-filled cells in stem cortex and stele; (0) idioblastic; (1) aggregated; (2) absent; **23.** inflorescence position; (0) axillary; (1) terminal; **24.** inflorescence type: (0) indeterminate thyrse, (1) determinate thyrse, (2) solitary flowers, (3) spike or raceme; **25.** slime canals/cavities in root cortex: (0) absent, (1) present; **26.** stelar parenchyma: (0) unlignified, (1) slightly lignified, (2) lignified; **27.** hypodermal fibrous strands: (0) absent, (1) present; **28.** silica in epidermal cells: (0) absent, (1) present; **29.** silica in cortical hypodermis: (0) absent, (1) present; **30.** calcium oxalate raphides: (0) absent, (1) present; **31.** ptyxis: (0) adplicate, (1) supervolute, (2) conduplicate; **32.** hairs in leaf axils: (0) absent, (1) present; **33.** air canals: (0) absent, (1) present; **34.** septae in air canals: (0) absent, (1) present; **35.** number of stamens: (0) 6, (1) 3 from outer whorl; **36.** anther dehiscence: (0) longitudinal, (1) poricidal; **37.** microsporogensis: (0) successive, (1) simultaneous; **38.** endexine: (0) absent; (1) present; **39.** stigmatic surface: (0) dry, (1) wet; **40.** endosperm formation: (0) nuclear, (1) helobial; **41.** fruit: (0) baccate, (1) septicidal capsule, (2) loculicidal capsule; **42.** embryo type: (0) broad, (1) linear; **43.** peltate trichomes: (0) absent, (1) present; **44.** rugose anthers: (0) absent, (1) present.

Character																									
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
0	0	0	2	0	0	0	0	0	1	1	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
0	0	0	0	0	0	0	2	1	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
0	0	0	0	0	0	0	2	1	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
0	0	0	0	0	1	0	0	0	0	1	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
1	1	1	1	0	0	0	1	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
1	1	1	1	0	0	0	1	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
1	1	1	1	0	0	0	1	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
1	1	1	1	0	0	0	1	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	1
1	1	1	1	0	0	0	1	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	1
1	1	1	1	0	0	0	1	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	1
1	1	1	1	0	0	0	1	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	1
1	1	1	1	1	0	1	0	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
1	1	1	1	1	0	1	0	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
1	1	1	1	1	0	1	0	?	1	0	0	2	1	1	0	0	1	1	1	1	0	1	0	0	0
?	?	?	?	1	3	0	?	?	1	?	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0
?	?	?	?	1	3	0	?	?	1	?	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0
?	?	?	?	1	3	0	?	?	1	?	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0
?	?	?	?	1	3	0	?	?	1	?	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0
?	?	?	?	0	2	0	?	?	0	0	0	0	1	1	1	1	1	0	1	1	0	2	0	0	0

(Fitch) parsimony and codon-weighted parsimony (Albert et al. 1993; Hillis et al. 1994). Indels were treated as unweighted characters under Fitch parsimony, and given a weight equal to the average (604 steps) of the weights assigned to various base mutations under codon-weighted parsimony.

Following each search, we formed the strict consensus of all the most parsimonious trees resulting from that search. To explore the relative degree of support for specific relationships, we conducted parsimony jackknife analyses (Farris et al. 1996) on both the equally weighted and codon-weighted phylogenies. Analyses used 1000 replicate deletions of 36.8% of potentially informative characters, based on full heuristic searches in PAUP*; no more than 5000 trees were retained for swapping per replicate. Finally, searches using unweighted and codon-weighted parsimony were conducted after excluding Poales and some or all the other outgroups. A maximum-likelihood analysis was conducted excluding Poales, using a heuristic search strategy and the Hasegawa-Kishino-Yano (Hasegawa et al. 1985) two-parameter model of sequence evolution.

Morphological and combined analyses

Unweighted searches were also conducted using 44 morphological/anatomical characters (Table 3) derived from the literature for the taxa sequenced (Carlquist 1961, 1966, 1969; Maguire 1979, 1982, 1984; Venturelli and Bouman 1988; Stevenson and Loconte 1995; Stevenson et al. 1998) and unpublished data (P. E. Berry), using the five designated outgroups in Bromeliaceae and Mayacaceae. Parsimony-jackknife support values were calculated for all nodes.

We performed a partition-homogeneity test (Farris et al. 1995) on the informative molecular and morphological/anatomical characters to determine if they showed no significant difference in phylogenetic structure and, thus, could be justifiably combined in a total-data analysis (Sytsma 1990; Huelsenbeck et al. 1996; Ballard et al. 1998). The search strategy used in the jackknife analyses was employed. A comparison of the relative power of the two datasets was performed, calculating the highest potential probability that each dataset could lead to correct phylogenetic inference, using the model and equations of Givnish and Sytsma (1997a,b). These probabilities are based on the best-case scenario of a dichotomous phylogeny with branches of equal length and form a ceiling on the actual probability of inferring a correct phylogeny.

Character-State Mapping

We assessed patterns of phenotypic evolution and geographic diversification by overlaying morphological, anatomical, ecological, and distributional character states on the terminal taxa and outgroups and then using MacClade 3.05 (Maddison and Maddison 1992) to infer character-state evolution consistent with all of the most parsimonious changes on the underlying tree. Accelerated transformation was used to minimize the number of apparent convergent gains. Morphological and anatomical characters (Table 3) included all those considered characteristic of the two subfamilies, four

tribes, and 16 genera of Rapateaceae (Carlquist 1961, 1966, 1969; Maguire 1982, 1984; Venturelli and Bouman 1988; Stevenson et al. 1998).

Molecular Clock and Time of Origin of Rapateaceae

Variation in branch length within Rapateaceae, Bromeliaceae, and Poaceae was quantified as the standard deviation divided by the mean of the *ndh*F branch lengths (under Fitch parsimony) from the terminal taxa to the inferred origin of each family in one of the shortest trees obtained under equal- and codon-weighted parsimony and accelerated transformation. Variation in divergence was also calculated using *P*-values (Nei and Li 1979) for all pairs of different species within each family. To test the operation of an *ndh*F molecular clock in Rapateaceae, we first obtained the most parsimonious tree(s) implied by the sequence data after excluding nonrapateads, using the earliest divergent species in the unweighted and weighted analyses as the outgroup(s). We then calculated the log-likelihoods of these shortest trees with and without enforcing a molecular clock. The difference of these log-likelihoods was then compared 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).

We estimated the date of origin of Rapateaceae from the age of known fossils of closely related monocot groups, based on the topology and branch lengths of the *rbc*L tree for commelinoids (Givnish et al. 1999). We assumed the operation of lineage-specific molecular clocks leading back to the common ancestor of Poales, Typhales, Zingiberales, and Bromeliaceae. Average branch lengths were calculated from this ancestor to each terminal member of a lineage, using accelerated transformation. We then estimated the age of Rapateaceae by assuming the operation of an *rbc*L clock within the immediate lineage leading to it. The timing of cladogenetic events within Rapateaceae was then calculated assuming the clocklike evolution of *ndh*F sequences, calibrated against the estimated time of the family's origin. These inferred dates were correlated with the estimated 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; Edmond et al. 1995; Rasanen et al. 1995; Schubert 1995; Potter 1997; Doerr 1999).

Results

Molecular Phylogenetic Analyses

Fitch parsimony resulted in nine shortest trees of length 995 steps and a well-resolved strict consensus (Fig. 2). The same number of trees and tree topology were obtained when Poales, Poales and Bromeliaceae or *Mayaca,* or all outgroups were excluded. The consistency index CI for these trees was 0.78 (CI′ = 0.67 excluding autapomorphies); the standardized CI′*$_9$ (rescaled to nine taxa to eliminate the effect of number of taxa; Givnish and Sytsma 1997a,b) was 0.93; the retention index (RI) was 0.82. In all, 639 sites and 12 indels were variable, of which 360 sites and four indels were phylogenetically informative.

Codon-weighted parsimony resulted in three shortest trees, each one step longer than the unweighted trees under Fitch parsimony. The strict consensus of the codon-weighted trees placed *Spathanthus* sister to *Rapatea-Cephalostemon,* making the basalmost tribe Rapateeae monophyletic (Fig. 2, inset). Tree topology was unaffected by outgroup omission, except that *Spathanthus* became sister to the other rapateads (as with the unweighted analysis) when Poales and either Bromeliaceae or *Mayaca* were excluded. Values of CI, CI′, CI′*$_9$, and RI for the weighted analysis were nearly identical to those for the unweighted analysis. Because the codon-weighted analysis agrees slightly better with the pattern of morphological variation and because simulations suggest that codon-weighted parsimony is more likely than unweighted parsimony to recover the correct phylogeny (Hillis et al. 1994; Hillis 1995), we focus on conclusions drawn from the weighted consensus tree.

Our analysis strongly supports the monophyly of Rapateaceae (100% jackknife support) and Bromeliaceae being sister to Mayacaceae (Fig. 2). However, the subfamily Rapateoideae, which generally grows below 400-m elevation, is paraphyletic, including the monophyletic subfamily Saxofridericioideae (100% support) as a subclade. Saxofridericioideae usually occurs above 1000-m elevation and is sister to the tribe Monotremeae of Rapateoideae (81% support). Within Saxofridericioideae, the tribe Saxofridericieae is paraphyletic, with the monophyletic tribe Schoenocephalieae (100% support) embedded within it and sister to *Saxofridericia* (100% support).

Within tribe Rapateeae, *Spathanthus* is sister to *Rapatea* and *Cephalostemon* in the weighted tree (Fig. 2, inset), and to all other members of the family in the unweighted analysis. These three genera were the earliest to diverge from other rapateads and are notable in having ranges that extend outside the Guayana Shield into the Amazon Basin or (in *Cephalostemon-Rapatea*) the Brazilian Shield (Table 1). Within tribe Monotremeae, the West African endemic *Maschalocephalus dinklagei* is sister to the other genera sampled (Fig. 2). *Potarophytum riparium,* a broad-leaved herb of wet, open forests over quartz sand and gravel along the Potaro River on the Kaieteur Plateau in Guyana, is sister to *Monotrema* (96% support); all *Monotrema* are restricted to Amazonian savannas in the western Guayana Shield.

Within tribe Saxofridericieae, the large genus *Stegolepis* (~ 35 species) appears to be paraphyletic. Species in sections *Pauciflora* and *Guianensis* (*Stegolepis hitchcockii, S. steyermarkii*) cluster with *Amphiphyllum* and *Marahuacaea*; the species sampled in section *Pungens* (*S. ptaritepuiensis*) is part of a basal polytomy with *Epidyros* (Fig. 2). *Stegolepis* has no involucral bracts subtending the inflorescence at maturity, except for the two species of section *Pauciflora* subsection *Gleasoniana.* The segregate tepui genera *Amphiphyllum* and *Marahuacaea* have three or more involucral bracts surrounding the mature inflorescence. Members of Saxofridericieae are generally restricted to wet sand, bogs, and meadows on the summits and slopes of tepuis (see data of Maguire 1982, 1984; Huber 1988). *Epidryos* (three species) is epiphytic in montane forests, and is the only genus of Saxofridericieae to

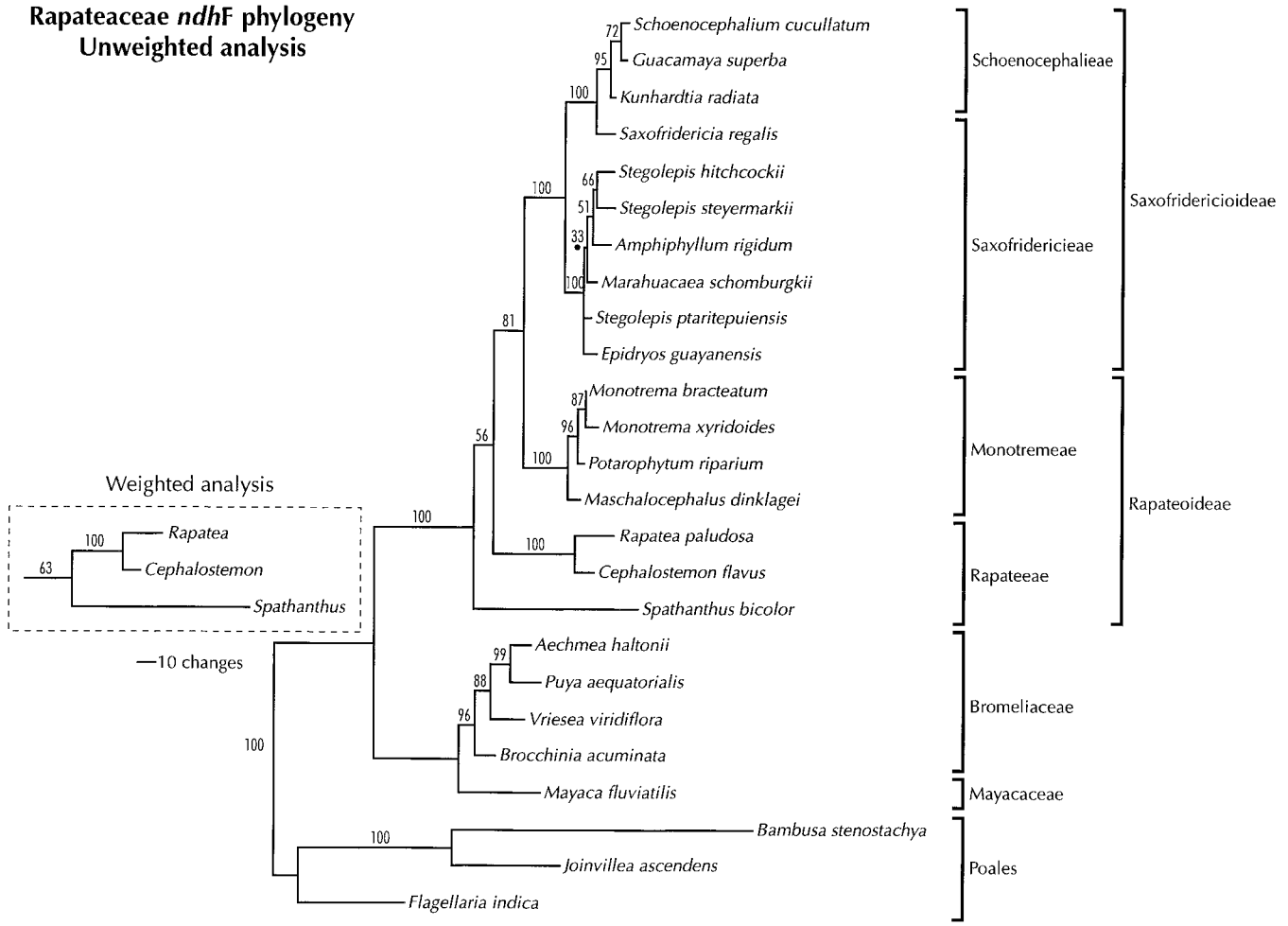


FIG. 2. Phylogram showing relationships among rapateads and outgroups for one of the nine shortest trees inferred from an unweighted cladistic analysis of *ndh* F sequence variation. Branch lengths are proportional to the number of inferred mutations along each branch; jackknife support values are indicated above each node. The tree shown has the same topology as the strict consensus of the unweighted analysis, except that the branch labeled with a dot collapses in the strict consensus. The same topology emerges in the strict consensus of the codon-weighted analysis, except that the labelled branch does not collapse, while *Spathanthus* becomes sister to *Cephalostemon-Rapatea* (inset), preserving the monophyly of the tribe Rapateeae.

range beyond the Guayana Shield, into Panama and Andean Colombia and Ecuador. Individual species of *Stegolepis* are mostly restricted to single tepuis and a fairly narrow elevational range (Huber 1988). *Saxofridericia* grows in partly open microsites at the edges of tepui meadows and lowland swamps, with some lowland species extending into the Amazon Basin. It is not part of the same clade as *Stegolepis*, but instead sister (95% support) to Schoenocephaliae. Within that tribe, the mainly highland *Kunhardtia* is sister (100% support) to the lowland *Guacamaya* and *Schoenocephalium* native to Amazonian savannas in southwestern Venezuela and adjacent Colombia, with *Guacamaya* known from only a few sites within the more extensive range of *Schoenocephalium*. *Kunhardtia* grows in boggy habitats ranging from granitic Sierra Maigualida and Serrania Sipapo in the central Guayana Shield to several tepuis (Autana, Cuao, Guanay, Coro-Coro, Yutajé) at the western limit of the tall Roraima table-mountains (Fig. 3) and a few lowland sites on damp granite nearby, near the northeasternmost of the Amazonian savannas to which *Schoenocephalium* is native.

A two-parameter maximum-likelihood analysis, using members of Bromeliaceae and Mayacaceae as outgroups, recovered essentially the same tree topology as the unweighted parsimony analysis when the molecular-clock hypothesis was not enforced, except that *Mayaca* was embedded in Bromeliaceae (tree not shown). When a molecular clock was enforced, this branching pattern was preserved, except that *Spathanthus* became sister to all other taxa in an unrooted network.

Both the unweighted and weighted maximum-parsimony trees (Fig. 2) appear to show rather clocklike patterns of molecular evolution within Rapateaceae, with similar amounts of genetic change down each lineage. The average Fitch branch length (relative to the inferred divergence point of Bromeliales) was 119.2 ± 8.8 steps (SD/mean = 0.074) across all rapatead lineages in the unweighted analysis, and

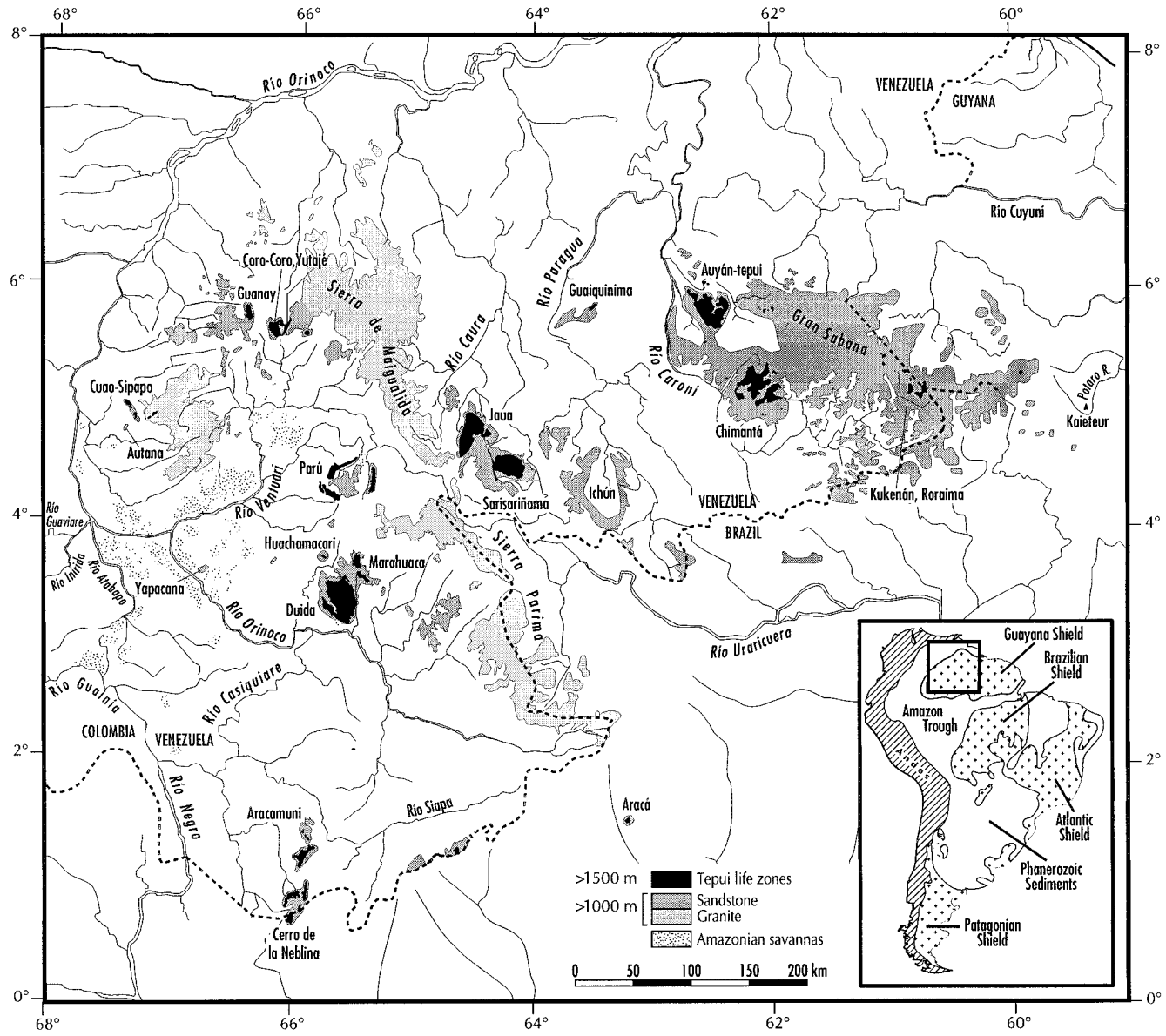


FIG. 3. Distribution of sandstone tepuis, granitic uplands, and lowland Amazonian savannas in the Venezuelan portion of the Guayana Shield (based on maps by Huber 1988, 1995a; Givnish et al. 1997). Location relative to other physiographic regions of South America is shown in the inset. The extensive occurrence of Amazonian savannas in Colombia has not yet been mapped.

110.7 ± 18.0 (SD/mean = 0.162) for the weighted analysis. West African *Maschalocephalus* was only slightly divergent from its closest relatives among the South American Monotremeae (minimum $P = 0.0083$); this is only 3.7% of the maximum divergence ($P = 0.223$) within the family, seen between *Spathanthus* and *Marahuacaea.* The observed amounts of genetic divergence in Rapateaceae ($P = 0.041 \pm 0.032$) appear to be roughly double those in Bromeliaceae ($P = 0.019 \pm 0.003$), with the difference being highly significant ($P < 0.0001$, two-tailed *t*-test with 20 df). These figures may underrepresent the greater divergence in Rapateaceae, given that the data include several within-genus comparisons for Rapateaceae, but only four highly divergent members of Bromeliaceae. For the species of Poales included in this study, the mean genetic divergence ($P = 0.107 \pm 0.024$) was 2.6 times that in Rapateaceae, and 5.6 times that in Bromeliaceae.

A comparison of log-likelihoods, with and without enforcement of a molecular clock, of the unweighted parsimony trees showed no significant departure from clocklike behavior within the family ($P > 0.27$, χ^2 test with 15 df for each of the nine shortest trees, using *Spathanthus* as the outgroup). A similar calculation on the branching patterns resulting from codon-weighted parsimony, however, did show a significant departure from clocklike behavior ($P \leq 0.003$, χ^2 test with 15 df for each of the three shortest trees, using Rapateeae as the outgroup). Inspection of the weighted trees indicated this deviation is ascribable to *Spathanthus* occupying an especially long branch; the ratio of the standard devation/mean branch length drops by nearly half—from 0.163 to 0.088 (this

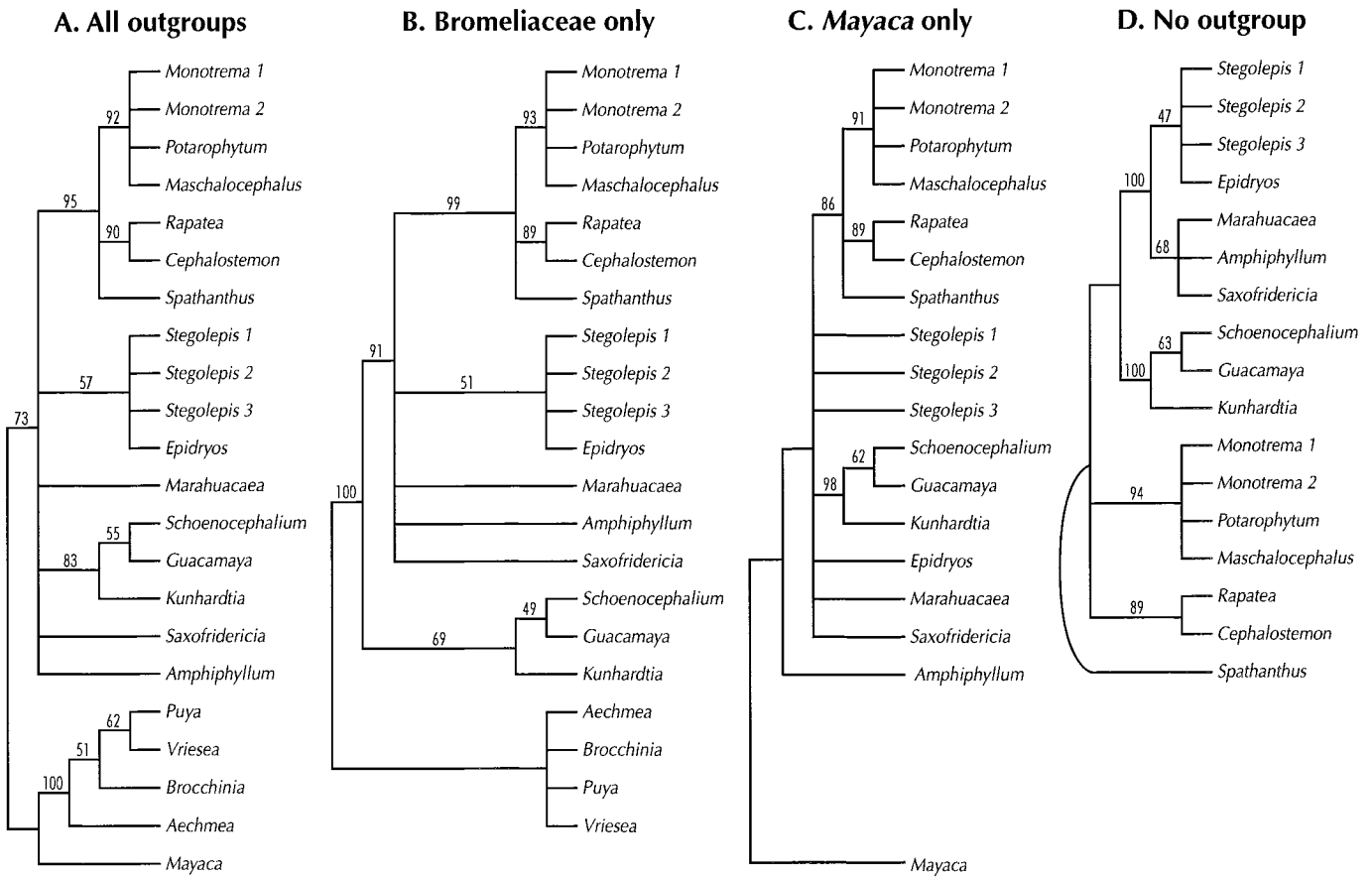


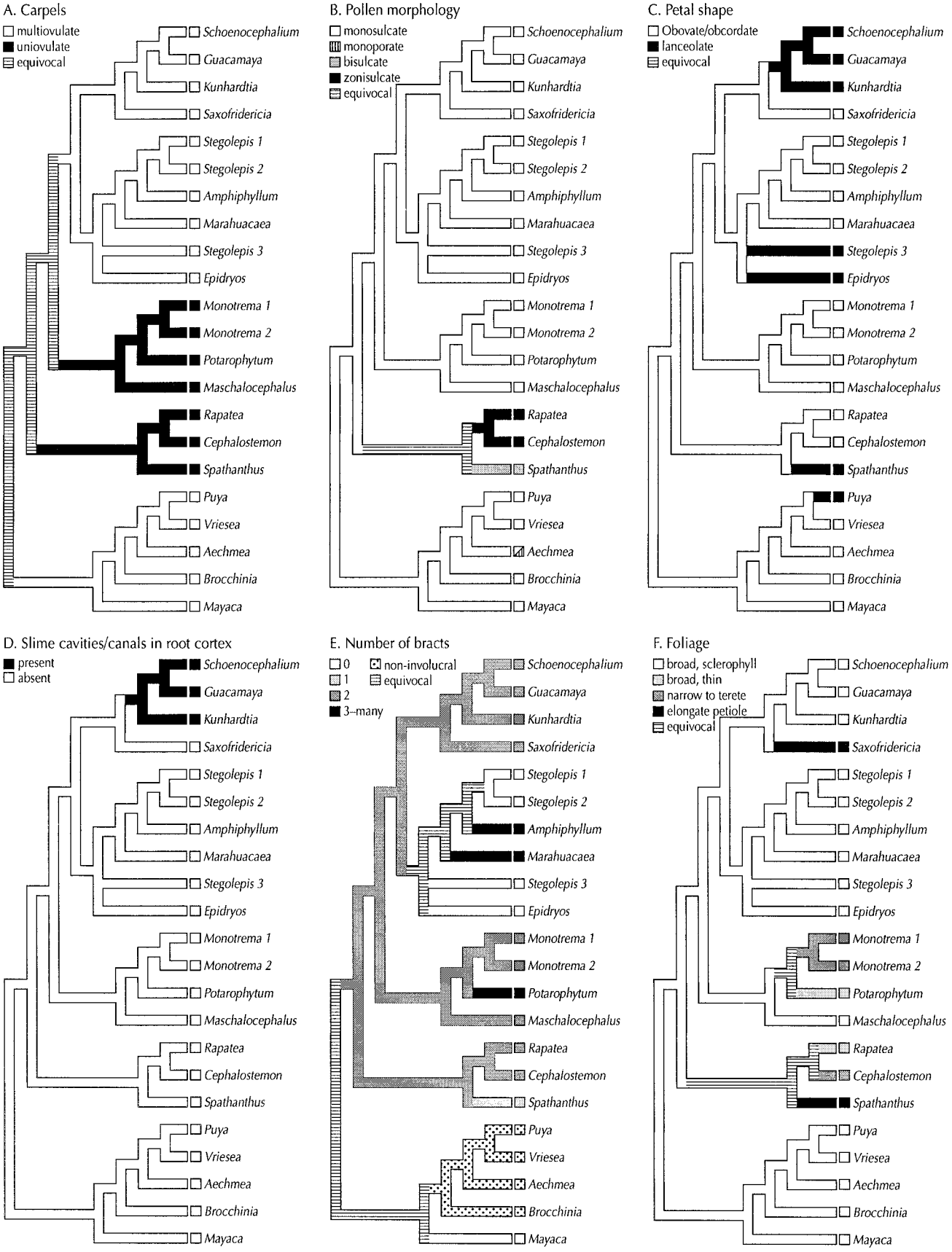
FIG. 4. Strict consensus trees arising from cladistic analyses of morphological data in Rapateaceae and allies, using global parsimony and representative outgroups in (A) Bromeliaceae and Mayacaceae; (B) Bromeliaceae only; and (C) Mayacaceae only. When no outgroups are included an unrooted network emerges (D), polarized here using *Spathanthus* based on the molecular data.

is comparable to the value for the unweighted analysis [0.073], which passes the molecular-clock test)—if it alone is excluded from the calculations.

Morphological Phylogenetic Analyses

When members of both Bromeliaceae and Mayacaceae were used as outgroups, an unweighted search based on 44 morphological and anatomical characters (three of which were uninformative) resulted in 166 shortest trees of length 79 steps, with CI = 0.80 (0.79 excluding uninformative characters), CI'^*_9 = 0.92, and RI = 0.90. The strict consensus tree (Fig. 4A) was poorly resolved, with a sixfold polytomy at the base of the ingroup. Within Rapateaceae, the only clades identified were the subfamily Rapateoideae, the tribes Schoenocephalieae and Monotremeae, *Rapatea-Cephalostemon,* and *Stegolepis-Epidryos*; of these groups, only Schoenocephalieae was fully resolved, with a topology identical to that seen in the *ndh* F analyses. When *Mayaca* was excluded, 112 shortest trees of length 69 steps were detected; with a total of 40 informative characters, CI = CI′ = 0.84, CI'^*_9 = 0.94, and RI = 0.93. In the strict consensus of this narrower group, Rapateaceae was monophyletic, with Schoenocephalieae basalmost and a monophyletic subfamily Rapateoideae sister to the tribe Saxofridericieae (Fig. 4B). When bromeliad outgroups were excluded, 264 trees 58 steps long were obtained; with 29 informative characters, CI = 0.79, CI′ = 0.76, CI'^*_9 = 0.89, and RI = 0.88. The strict consensus in this case had only six nodes resolved, with a ninefold basal polytomy (Fig. 4C). Finally, when all outgroups were excluded and the resulting unrooted network was polarized using *Spathanthus* (based solely on the molecular results), 32 trees 49 steps long were obtained; with 27 informative characters, CI = 0.82, CI′ = 0.80, CI'^*_9 = 0.91, and RI = 0.91. The strict consensus (Fig. 4D) was topologically similar to the molecular tree, except that *Saxofridericia* fell into a polytomy with genera allied to *Stegolepis,* relationships within Monotremeae were unresolved, and a basal trichotomy made it impossible to determine whether Rapateoideae was monophyletic or (as with the molecular data) paraphyletic.

The only clades recognized by all of these analyses and the molecular data were Monotremeae, Schoenocephalieae, and *Rapatea-Cephalostemon.* In several cases, the morphological data confirm the tribal branches of the molecular tree without specifying (or specifying in a fashion contrary to that implied by the molecular data) how those branches are related to each other. Based on the observed differences in overall tree topology, the molecular and morphological data generally appear to be incompatible. Only when all outgroups were excluded did a topology emerge (Fig. 4D) that was nearly compatible with the molecular tree, but less resolved and less well-supported.


A. Carpels
multiovulate
uniovulate
equivocal
B. Pollen morphology
monosulcate
monoporate
bisulcate
zonisulcate
equivocal
C. Petal shape
Obovate/obcordate
lanceolate
equivocal
D. Slime cavities/canals in root cortex
present
absent
E. Number of bracts
0
1
2
3–many
non-involucral
equivocal
F. Foliage
broad, sclerophyll
broad, thin
narrow to terete
elongate petiole
equivocal
Schoenocephalium
Guacamaya
Kunhardtia
Saxofridericia
Stegolepis 1
Stegolepis 2
Amphiphyllum
Marahuacaea
Stegolepis 3
Epidryos
Monotrema 1
Monotrema 2
Potarophytum
Maschalocephalus
Rapatea
Cephalostemon
Spathanthus
Puya
Vriesea
Aechmea
Brocchinia
Mayaca

A partition-homogeneity test demonstrated that there was, in fact, a significant difference in phylogenetic structure between the molecular and morphological datasets ($P < 0.017$ for 1000 random data reshufflings). Following the guidelines advocated by Sytsma (1990), Huelsenbeck et al. (1996), and Ballard et al. (1998), these two datasets were thus not amalgamated for a combined analysis, and character-state evolution was analyzed by overlaying morphological, anatomical, ecological, and biogeographic traits on the weighted *ndh*F tree. According to the equations presented by Givnish and Sytsma (1997a,b), there was at most a 58% chance of inferring the correct tree using the unweighted morphological data (64% if *Mayaca* is excluded), compared with at most a 100% chance for the unweighted molecular data. Both datasets had similar normalized consistency indices (0.89 to 0.94 for morphology, 0.93 for *ndh*F sequences), but the molecular dataset involved nine times as many informative characters.

Patterns of Character-State Evolution

Despite the significant difference in phylogenetic structure in the morphological and molecular datasets, there is a fairly high degree of congruence between *individual* morphological/anatomical characters and the molecular phylogeny, especially at the tribal level and below. Of 44 characters, 29 mapped cleanly onto the *ndh*F tree with no parallel gains or losses; 11, with one parallel gain or loss; three with two parallelisms; and one with four parallelisms (see Fig. 5A–F). Highly homoplasious characters involve pollination and inflorescence structure: lanceolate petals arose five times independently (Fig. 5C), whereas multiple/absent bracts (Fig. 5E), white flowers, and rugose anthers each arose independently three times. Data are currently unavailable for 11 characters in the outgroups, including seven in which there were no parallel gains or losses of state currently apparent in Rapateaceae.

Multiovulate carpels and axile placentation characterize both the outgroups and Saxofridericioideae (Fig. 5A). This implies a transition to uniovulate (rarely biovulate) carpels and basal placentation at the base of Rapateoideae, followed by a reversal to the multiovulate and axile conditions in Saxofridericioideae, concurrent with the evolution of prismatic seeds. However, it must be recognized that these characters may be developmentally interdependent. Multiovulate carpels may favor the evolution (or, more simply, the development) of prismatic seeds and axile versus basal placentation, simply as a result of packing constraints within the carpels. The two saxofridericioid genera with nonprismatic seeds have, as expected, different patterns of placentation and seed packing: *Epidryos*, with discoid seeds, has ovules staggered alternately in a planar array, whereas several *Saxofridericia* have carpels that abort all but one ovule and develop ovoid seeds (P. E. Berry, unpubl. data).

Schoenocephaliae is marked by lanceolate petals (also in *Epidryos*, *Spathanthus*, and some *Monotrema* and *Stegolepis*), and the unique presence of nectaries and reddish or yellowish petals, sepals, and/or spikelet bracts (Fig. 5C). These traits are associated with the evolution of red, yellow, or white tubular flowers pollinated by hummingbirds. Petals are basally connate throughout Rapateaceae, but are fused over a greater length in *Kunhardtia* than in other rapateads. Hummingbird pollination appears to have evolved relatively recently from bee pollination in the western Guayana Shield (see below). Nectar secretion is otherwise unknown in Rapateaceae and Mayacaceae, or in commelinoid monocots distal to Bromeliales (Givnish et al. 1999), but is widespread in Bromeliaceae (Smith and Downs 1974). Monophyly of Schoenocephalieae is also supported by the shared possession of slime canals/cavities in the root cortex (Fig. 5D).

Broad ($>$ 10 cm wide), relatively thin, horizontal leaves evolved independently in *Rapatea* and *Potarophytum* of the tribes Rapateeae and Monotremae, respectively (Fig. 5F). These genera grow in shaded understories of seasonally inundated lowland forests and streamside cloud forests, respectively. Narrow, grass- or sedge-like foliage ($<$ 2 cm wide) evolved independently in *Cephalostemon* and *Monotrema*, both native to open, wet, highly infertile savannas over quartz sand in southwestern Venezuela and adjacent Colombia (and to similar habitats in the Brazilian Shield, in four species of *Cephalostemon*). The leaf bases of both of these genera are sometimes filled with mucilage. Tightly packed, massive, persistent, mucilage-filled leaf bases—associated with a distichous fan of vertically oriented, straplike leaf blades ($\sim$ 5 cm wide) and massive rhizomes—characterize several members of Saxofridericioideae. Observations on Cerro de la Neblina (Givnish et al. 1986) and the Gran Sabana (T. J. Givnish and K. J. Sytsma, unpubl. data) indicate that *Stegolepis*, the most common and widespread saxofridericioid genus, can survive at least modest ground fires in tepui bogs and meadows, with leaves resprouting from among the persistent leaf bases to replace those lost to the flames. The same is true of *Schoenocephalium* and *Guacamaya* in lowland Amazonian savannas (P. E. Berry, pers. obs.). Unusually elongate petioles, devoid of laminar tissue, have evolved in *Spathanthus* (e.g., Mori et al. 1997) and some *Saxofridericia*, both of which occupy habitats that can undergo substantial flooding (Fig. 5F). Such petioles, which are coupled with long (to 2.5 m), *Typha*-like blades in *Spathanthus*, might prolong the time all or part of the leaf surface is held above water. However, both leaf blades and petioles are most elongate in *S. bicolor* under shady conditions (P. E. Berry, pers. obs.).

Ecology and Biogeography

If genera are classified as lowland (occuring mainly below 500-m elevation), upland (500–1500 m) or highland (mainly $>$ 1500-m) following Huber (1995b), we infer that Rapateaceae originated in the lowlands and then invaded highland

←

FIG. 5. Overlays of character states on the weighted rapatead phylogeny. Accelerated transformation (ACCTRAN) was used to minimize the number of apparent independent origins. Boxes indicate character states of terminal taxa; multishaded boxes represent polymorphism, and absence of a box indicates missing data. (A) Placentation; (B) pollen morphology; (C) nectaries; (D) slime canals/cavities in the root cortex; (E) number of involucral bracts; (F) leaf form.

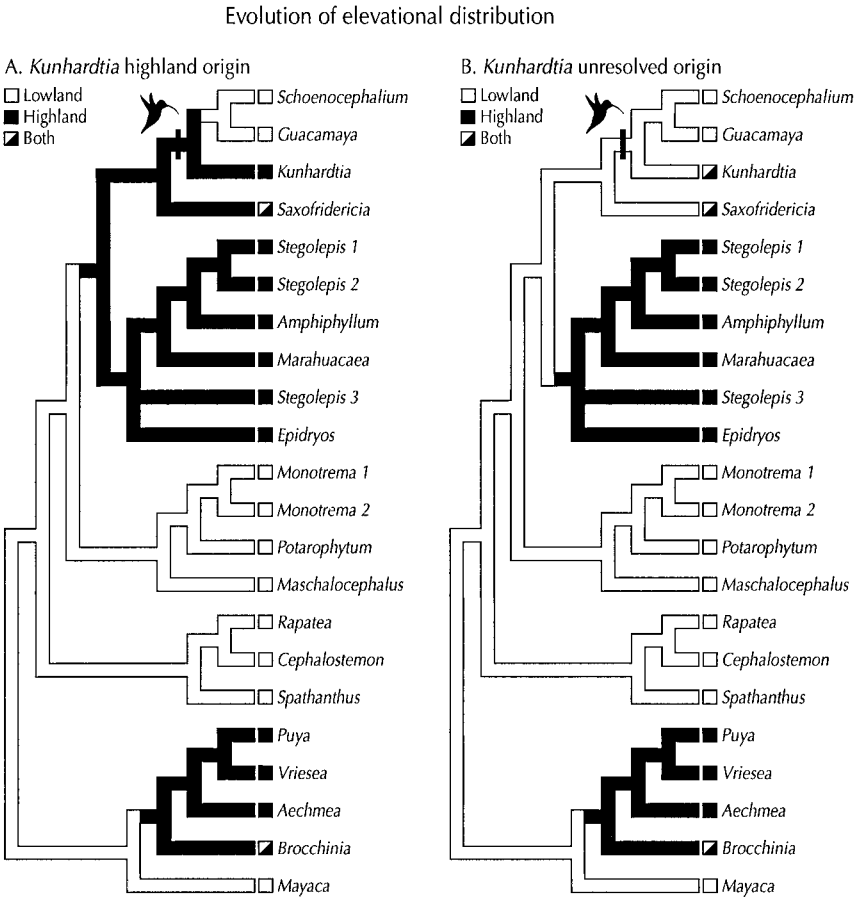


FIG. 6. Evolution of elevational distribution in Rapateaceae. Bar indicates origin of hummingbird pollination. (A) Invasion of high-elevation habitats by ancestral Saxofridericioideae inferred if *Kunhardtia* originated in the highlands, as suspected based on the present-day occurrence there of almost all *Kunhardtia* populations. In this case, hummingbird pollination arose under montane conditions. Note independent highland invasion by *Potarophytum,* secondary invasion of lowlands by *Schoenocephalium-Guacamaya,* and *Saxofridericia* sect. *Saxofridericia.* (B) Independent invasions of highlands by ancestor of *Stegolepis* complex, *Kunhardtia rhodantha, Saxofridericia* sect. *Inermis,* and *Potarophytum* inferred if *Kunhardtia* originated in the lowlands or both lowlands and highlands. In this case, hummingbird pollination arose under lowland conditions in the rainy, western Guayana Shield.

habitats in concert with the diversification of the subfamily Saxofridericioideae or possibly later, with the rise of *Stegolepis* and allied genera (Fig. 6). This finding parallels the pattern recently documented in *Brocchinia* (Bromeliaceae), the only group of plants from the Guayana Shield for which a molecular phylogeny has previously been published (Givnish et al. 1997). Secondary re-invasions of the lowlands may have occurred twice, in Schoenocephaliae (one widespread species of *Kunhardtia* is wholly montane, whereas the other is rare and found in the lowlands) and in *Saxofridericia.* Additional taxa must be sequenced to determine whether the montane distribution of several *Saxofridericia* and most populations of *Kunhardtia* is a derived feature shared with *Stegolepis* and allied genera or whether they instead represent independent colonization(s) of the highlands.

Several genera with wide geographic ranges are lowland taxa that diverged relatively early in the evolution of the family; most of these are found in swamps, thickets, and caatinga along riverine corridors. *Cephalostemon* is found in relatively open, sandy, lowland habitats in both the Guayana and Brazilian Shields, on either side of the Amazon Basin; *Spathanthus* and especially *Rapatea* range from the Guayana Shield into the Amazon Basin, in riverine thickets and mucky forests, respectively. *Epidryos* is an exception: P. E. Berry (pers. obs.) has found that this genus is unique in the family in possessing viscid seed appendages. This feature fits *Epidryos*'s epiphytic role and may coincidentally permit long-distance dispersal and a range including parts of the Guayana Shield, Panama, Colombia, and Ecuador.

Most montane genera and species are narrowly endemic to small areas or individual tepuis within the Guayana Shield. *Amphiphyllum* and *Marahuacaea* are restricted to the neighboring tepuis of Duida and Marahuaca in central Amazonas, Venezuela (Fig. 3); *Phelpsiella* is restricted to Parú, about 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 recently divergent Schoenocephalieae are restricted to the western Shield: *Kunhardtia* in the Sierra Maigualida, Sipapo, Autana, Cuao, Guanay, Yutajé, Coro-Coro and nearby lowlands in northern Venezuelan Amazonas, and *Schoenocephalium* 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* is known from a small area of Amazonian savannas along the Guainía and Atabapo (Fig. 3). Finally, genera of Monotremeae generally have rather narrow geographic ranges. Broad-leaved *Potarophytum* is native only to streamside cloud forests at moderate elevations (~ 800 m) on the Kaieteur Plateau in central Guyana; *Windsorina* is restricted to seasonally inundated forests at low elevations along the Potaro below Kaieteur (Fig. 3). *Monotrema* is restricted to Amazonian savannas and surrounding thickets in western Amazonas in Venezuela and nearby Colombia and Brazil, with most species known from only a few sites (Maguire 1982, 1984). *Maschalocephalus* is the exception, growing in wet sandy savannas across a substantial African range in Liberia, Sierra Leone, and Côte d'Ivoire.

Phylogenetic reconstruction using parsimony implies: (1) the order Bromeliales arose on the Guayana Shield (Givnish et al. 1999); (2) within Rapateaceae, the Amazon Basin was secondarily invaded by the tribe Rapateeae, with *Cephalostemon* extending into the Brazilian Shield; (3) *Epidryos* reached the Andes and Panama from the Guayana Shield; and (4) *Maschalocephalus* evolved after dispersal to West Africa. The tribe Schoenocephalieae appears to have arisen in the western Guayana Shield near the triple confluence of the Orinoco, Atabapo, and Guaviare, based on the close proximity there of the ranges of *Kunhardtia* and *Schoenocephalium.*

Rapateaceae, Bromeliaceae, and Mayacaceae share a strong tendency toward growing on highly infertile substrates (Givnish et al. 1999). Such substrates are generally wet sands in Mayacaceae and wet sands or peats in Rapateaceae—as they are in *Brocchinia* (Givnish et al. 1997), the earliest divergent element of Bromeliaceae (Terry et al. 1997). Within *Brocchinia,* nutrient poverty and high rainfall favored the rise of the tank habit, and the subsequent origins of carnivory, ant-fed myrmecophily, and tank epiphytism (Givnish et al. 1997). The invasion of drier terrestrial substrates and epiphytic perches in other Bromeliaceae appears to be a derived condition within Bromeliales; both Rapateaceae and Mayacaceae grow in mesic to wet sites.

Reconstruction of ancestral habitats implies: (1) Rapateaceae arose in lowland white-sand savannas (as did the earliest divergent species of *Brocchinia*; Givnish et al. 1997); (2) *Spathanthus* invaded open, inundated riverbanks and savannas; (3) *Rapatea* and *Potarophytum* independently invaded more or less closed inundated forests; (4) Saxofridericioideae invaded tepui meadows and bogs; (5) *Epidryos* subsequently became epiphytic in cloud forests; (6) elements of Schoenocephalieae reinvaded lowland, Amazonian white-sand savannas in the western Guayana Shield; and (7) certain species of *Saxofridericia* may have reinvaded lowland inundated forests (Fig. 7).

Discussion

Systematics

Although our molecular data supports the monophyly of the family, they do not support its current infrafamial classification (sensu Maguire 1982, 1984; Steyermark 1989; Stevenson et al. 1998). The subfamily Rapateoideae is paraphyletic, with its tribe Monotremeae sister to the subfamily Saxofridericioideae. Tribe Saxofridericieae is clearly paraphyletic, with *Saxofridericia* sister to the hummingbird-pollinated Schoenocephalieae in the *ndh* F tree. Tribe Rapateeae is weakly supported, being monophyletic only in the weighted molecular analysis, in which *Spathanthus* is sister to *Cephalostemon-Rapatea.* In polarized morphological analyses, *Spathanthus* always lies in an unresolved trichotomy with *Cephalostemon-Rapatea* and the tribe Monotremeae. The tribes Monotremeae and Schoenocephalieae are each strongly supported by both the molecular and morphological data.

The generally strong agreement between many anatomical and palynological characters and the groups recognized in the *ndh*F trees at or below the tribal level suggests that such characters could be used to infer the closest relatives of the two (monotypic) genera we have thus far been unable to collect and sequence. *Windsorina* clearly belongs to Monotremeae based on morphology and anatomy. Furthermore, within Rapateaceae, it shares determinate thyrses and spindle-shaped, diplococcoid pollen only with *Maschalocephalus.* This suggests that Guyanese *Windsorina* is sister to West African *Maschalocephalus* and that Monotremeae (with *Monotrema* sister to *Maschalocephalus-Windsorina* and Guyanese *Potarophytum* basalmost) may have arisen in the eastern Guayana Shield, centered on the Potaro River and its moderately elevated sandstone plateaus. *Phelpsiella* is known only from the summit of Cerro Parú between 1600 m and 2000 m elevation. Except for saccate bracts enveloping the inflorescence, it is remarkably similar to *Stegolepis breweri,* from the sinkholes on Cerro Sarisariñama at about 1000-m elevation. Both taxa have narrow, ribbonlike leaves with auriculate sheaths, as well as flattened, winged scapes with two to four spikelets.

The circumscription of *Stegolepis* and the four segregate genera allied to it need to be reexamined. *Stegolepis* and *Epidryos* have been distinguished by their lack of involucral bracts on mature inflorescences, versus two bracts in *Phelpsiella,* and three to many bracts in *Amphiphyllum* and *Marahuacaea.* However, bract number is one of the two most homoplasious morphological characters within Rapateaceae (Fig. 5D), suggesting that this trait may lack critical systematic value. A key question is how inflorescences develop in the *Stegolepis* alliance. Specifically, how many bract primordia appear early in the ontogeny of inflorescences in different groups? The number of bract primordia seems far more likely to represent a homologous character-state than the number of bracts at maturity, given the ease with which bracts might be shed at intermediate stages of inflorescence development.

Morphological Evolution and Ecological Diversification

Leaf and flower characteristics

Adaptation to densely shaded environments—in the form of broad, thin leaves—appears to have occurred at least twice, in *Rapatea* and *Potarophytum.* Phenotypic traits associated with pollination (number of scapes, number of bracts, showiness of bracts) are, as might be expected, highly homopla-

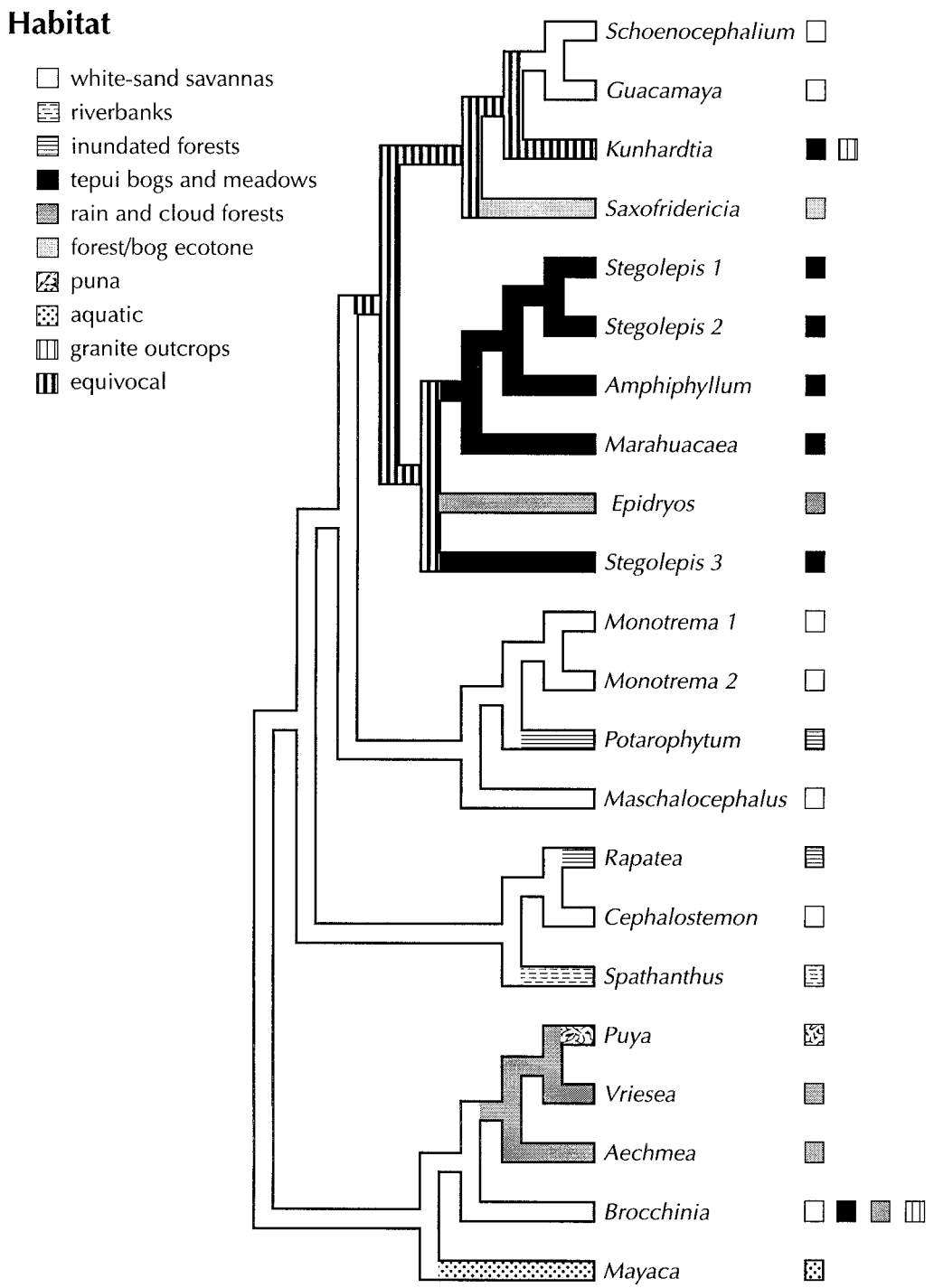


FIG. 7. Historical pattern of ecological diversification in Rapateaceae. Note the inferred origin of the family in lowland white-sand savannas. The same ancestral state is inferred if riverbanks and/or inundated forests are coded as white-sand savannas, into which they grade.

sious. Evans et al. (1999) report similar results for Commelinaceae, in which aspects of floral and inflorescence structure show a high degree of homoplasy relative to their *ndh*F tree, while anatomical traits (perhaps better insulated from external selection) show a high degree of concordance. Givnish et al. (1999) report qualitatively similar results for commelinoid monocots based on an *rbc*L phylogeny.

Numerous adaptations to hummingbird pollination (nectaries; red to yellow petals, sepals, bracts, and/or spikelets) arose once, at the base of the Schoenocephalieae. Lanceolate

petals also evolved in this group (as in *Epidryos, Spathanthus,* and some *Monotrema* and *Stegolepis*) and form moderately long, essentially tubular flowers. In *Kunhardtia,* the petal bases are also fused for 10–15 mm. Nectar production and accumulation is necessary for hummingbird pollination, which favored the evolution of a narrow, tubular corolla and a reddish visual display. The ancestor of Schoenocephalieae may have arisen under montane conditions atop tepuis, given this condition in the *Stegolepis* alliance and many *Saxofridericia,* and in almost all populations of basal *Kunhardtia* (see Fig. 6). If so, hummingbird pollination would have originated under wet, cool conditions, which favor thermoregulating pollinators, and been retained in two genera (*Guacamaya, Schoenocephalium*) that grow in lowlands that receive more rainfall (~ 3 m; Huber 1982) than most similar areas in the Guayana Shield and Amazon Basin. Nectar production is otherwise unknown in Rapateaceae. However, the evolutionary origin and loss of nectaries are not uncommon in monocots. Givnish et al. (1999) inferred that gynoecial nectaries were lost three times in commelinoids and arose twice subsequently (in Bromeliaceae and Rapateaceae [although the exact placement of the nectaries in Schoenocephalieae remains to be determined]), and that petalar nectaries evolved once (in Eriocaulaceae) following the loss of gynoecial nectaries at the base of the Typhales and its graminoid sister groups. In monocots as a whole, Simpson (1998) recently inferred a total of at least 13 parallel gains of septal nectaries.

The pollination biology of Rapateaceae merits further investigation. Renner (1989) reported that species of *Saxofridericia* and *Stegolepis* are buzz-pollinated by bees, with pollen being released from the anthers through apical pores. K. J. Sytsma and A. R. Mast (unpubl. data) observed halictid bees chewing the corrugated anthers of *Stegolepis angustata* in the Gran Sabana (Fig. 1). T. J. Givnish and K. J. Sytsma (unpubl. data) observed euglossine bees visiting *Rapatea paludosa,* and T. J. Givnish has seen weevils visiting the flowers of *Stegolepis parvipetala* on Auyán-tepui (Fig. 1). Whether floral visitation by the last two groups results in pollination is, at present, unknown.

Fire adaptation

Fire atop tepuis may have played a key role in the adaptive evolution of *Stegolepis* and relatives. *Stegolepis* dominates bogs and peaty meadows on tepuis and sandstone plateaus. It possesses massive rhizomes and tough, tightly packed, persistent, mucilage-filled leaf bases that ensheath the stem and bear a distichous fan of strap-shaped leaves. *Stegolepis* can survive moderate ground fires, apparently aided by its protective leaf bases (Givnish et al. 1986, 1997). The three herbaceous genera that are known to survive fires atop tepuis, *Stegolepis, Brocchinia* (tough leaf tips ensheathing the terminal bud), and *Heliamphora* (pitcher leaves ensheathing the rhizome tip; Givnish et al. 1986), are frequent dominants in tepui bogs and meadows. Although it is doubtful that fires are very frequent in such habitats or that even these plants could survive repeated intense fires, occasional fires would favor them and temporarily obliterate fire-intolerant species. Such fires seem inevitable. Infertile conditions atop tepuis favor heavy allocation to antiherbivore defenses, selecting for tough, tannin-laden leaves. The resulting accumulation of slowly decomposing litter would provide ample fuel for fire ignited by lightning during infrequent droughts; lightning strikes might be especially common near tepui escarpments, where convection can be quite strong (Givnish et al. 1997).

Habitat diversification

The ancestral rapateads appear to have arisen in wet, open, nutrient-poor, lowland habitats of the Guayana Shield, like Amazonian savannas and similar sites inhabited today by *Cephalostemon, Monotrema,* and the earliest divergent member of the basal bromeliad genus *Brocchinia* (see Givnish et al. 1997) and like some of the aquatic sites occupied by *Mayaca.* Seasonally inundated, partly open riverine forests, caatingas, and savannas found on peats, sands, and gravels were invaded by *Spathanthus* and *Maschalocephalus*; more densely shaded inundated forests, sometimes on muckier soil, were invaded by *Rapatea* and *Potarophytum.* The subfamily Saxofridericioideae then invaded bogs and similar habitats atop tepuis. A lowland-to-highland shift parallels that recently documented in the Guayana Shield for the basal bromeliad genus *Brocchinia* (Givnish et al. 1997). In Saxofridericioideae, secondary reinvasions of the lowlands appear to have occurred in tribe Schoenocephalieae near the western limit of the tall tepuis, and in *Saxofridericia. Epidryos* diverged early from other taxa in this group, acquiring viscid seeds that presumably are bird dispersed and adapted to an epiphytic habit. Several species of *Stegolepis* and related genera evolved massive, persistent leaf bases and may thereby have become ecological dominants in tepui bogs and meadows swept by infrequent fire. *Saxofridericia* invaded scrubby, partly closed sites transitional from open bogs or streamsides into closed forests. The remarkably long (up to 5 m) but narrow (~ 5 cm) leaves of a few species (e.g., *S. spongiosa*) seem adapted to lean on competitors, overtopping the tall, relatively dense shrubs and herbs in its ecotonal habitat, while using them to support its sprawling, mechanically somewhat unstable foliage. Some taxa (e.g., *Saxofridericia inermis*) have short, narrow leaves and are self-supporting, so it will be interesting to trace biomechanical evolution in this genus once its phylogeny is obtained.

Biogeography

Members of Rapateaceae today are native to six floristic regions: (1) Guayana Shield; (2) Amazon Basin; (3) Brazilian Shield; (4) Andes; (5) Central America; and (6) tropical West Africa. Bromeliaceae occur in these areas, as well as in (7) North America and (8) the Caribbean. Mayacaceae occurs in regions 1, 2, 3, 4, 5, 6, and 7. A cladistic analysis at the continental scale across commelinoid monocots showed that the common ancestor of Bromeliaceae, Mayacaceae, and Rapateaceae was likely to have evolved in the Guayana Shield (Givnish et al. 1999); a similar analysis, using *Mayaca* and the bromeliad outgroups employed in this study, indicates that Rapateaceae initially arose in the Guayana Shield.

Within Rapateaceae, genera of the tribe Rapateeae diverged early from the other lineages, and today range widely from the Guayana Shield into other parts of South America: *Spathanthus* into the Amazon Basin; *Cephalostemon* into the

Brazilian Shield as well; and *Rapatea* into the Amazon Basin, coastal Brazil (Bahia), and Pacific Colombia. *Rapatea* and *Spathanthus* are restricted to low elevations, in seasonally inundated forests and scrub along riverbanks; *Cephalostemon* grows in lowland and upland sites, mainly on open, herb-covered sites on wet, extremely infertile sands. It seems likely that all genera were able to spread widely along riverine corridors of appropriate habitat, before and after silty sediments along the Amazon separated the Guayana and Brazilian Shields. Given *Rapatea*'s growth on siltier substrates, its presence in the Amazon Basin may reflect long-distance dispersal. Its presence in Pacific Colombia may represent vicariance caused by uplift of the northern Andes and eastward shunting of the Amazon 20 Mya (Potter 1997), given the inferred origin of the common ancestor of *Rapatea* and *Cephalostemon* approximately 32 Mya (see below). If so, *Cephalostemon*'s disjunct range likely represents long-distance dispersal, given its restriction to sandy substrates, its inferred divergence from *Rapatea* only nine Mya (see below), and the fact that the Amazon has been running its current course to the Atlantic—thereby separating the Guayana and Brazilian Shields with a band of edaphically distinct, noncratonic sediments—since at least the Miocene, roughly 20 Mya (Hoorn 1994; Hoorn et al. 1995; Potter 1997). An earlier ecological isolation of the shields is possible, given the Mesozoic downwarping of the Trans-Amazonian Platform and the presence of more than 6000 m of terrigenous sediments from the lower Cretaceous in the trough underlying the bed of the lower Amazon (Potter 1997). Roughly 10 Mya, a seaway in this trough separated the Guayana and Brazilian Shields (Rasanen et al. 1995).

Genera of Monotremeae grow on wet, infertile sands at low to intermediate elevations, and all but *Maschalocephalus* are narrowly distributed within the Guayana Shield, with *Monotrema* in the west and *Potarophytum* and *Windsorina* in the east. *Maschalocephalus* inhabits wet sandy savannas from Liberia to Côte d'Ivoire in tropical west Africa. This sandstone region, overlying part of the West African Shield, abutted the Guayana Shield before continental drift opened the Atlantic 84–102 Mya (Sidder and Mendoza 1991; Edmond et al. 1995). However, our sequence data indicate that *Maschalocephalus* is the product of relatively recent long-distance dispersal, not ancient continental drift. Genetic divergence between this genus and its South American relatives represents only 3.7% of the maximum divergence in the family as a whole. Given the clocklike evolution of *ndh*F in Rapateaceae, if *Maschalocephalus* had diverged from South American lineages when the Atlantic became a substantial barrier to dispersal, the family would have had to arisen 2.3–2.8 billion years ago! A recent origin ($\sim$ 6 Mya, see below) of *Maschalocephalus* via long-distance dispersal is in accord with the lack of rapatead speciation in Africa (Good 1974). Historical cycles of aridity on that continent (Goldblatt 1993) may also have played a role, given the present restriction of rapateads to mesic/wet habitats. Continental drift was a potential explanation for the shared amphiatlantic distributions of closely related Rapateaceae, Mayacaceae, and Bromeliaceae. However, our results show that, if continental drift played a role in creating the distribution of Rapateaceae, it did so by creating comparable sandy, wet, nutrient-poor substrates favorable to the family on both sides of the Atlantic, not by rafting rapateads across it. Vicariance of habitat, not vicariance of species, accounts for the observed disjunction. Given that *Mayaca* is favored by highly infertile conditions, and has also undergone no additional, multiplicative speciation in Africa, its amphiatlantic distribution may have a similar explanation (Givnish et al. 1999).

With the origin of Saxofridericioideae, rapateads invaded high-elevation habitats atop tepuis. Coincident with this ecological shift was an apparent acceleration in speciation, with 44 species in tepui Saxofridericieae versus eight in its lowland sister group (Monotremeae) and seven in an embedded, largely lowland clade (Schoenocephalieae). In addition, most highland Saxofridericioideae are narrowly endemic to single tepuis or groups of adjacent tepuis. Vicariance and/or infrequent long-distance dispersal would favor frequent speciation and narrow endemism in this montane group. Chemical dissolution and (to a lesser extent) mechanical erosion have slowly dissected the tepuis one from the other, forming a megakarstic landscape (Briceño and Schubert 1990; Briceño et al. 1990; Edmond et al. 1995; Schubert 1995; Doerr 1999). The resulting fragmentation and isolation of these sky islands—each marked by unusually infertile, rainy, humid, and cool environments in an ocean of lowland tropical forests and savannas—would have helped isolate populations on different tepuis. Over time, such isolation should lead to genetic divergence and ultimately speciation. Poor powers of seed dispersal presumably accelerated this process: epiphytic *Epidryos*, with viscid seeds well-adapted for bird dispersal, has only three species versus 35 in *Stegolepis*.

In Schoenocephalieae, at least one lowland reinvasion (or perhaps a highland colonization, see Fig. 6) appears to have occurred in the western Guayana Shield near where the Orinoco enters the sandstone region, where the westernmost portion of *Kunhardtia*'s range on Cuao and Autana abuts the northernmost Amazonian savannas and approaches the northeastern limit of *Schoenocephalium*'s range (Fig. 3). Such savannas form an archipelago of open habitats on quartz sands and gravels, with a high water table that may vary seasonally several decimeters or more (Huber 1982). Dispersal among these savannas might have occurred as their boundaries fluctuated in response to climatic change or fire. In addition, water dispersal along streams or across the exceedingly flat interfluves during heavy rains seems likely. Several creeks on the middle Orinoco, with Amazonian savannas near their banks, reverse directions seasonally, in response to the earlier start of rains in the equatorial headwaters. Amazonian savannas with *Guacamaya* and *Schoenocephalium* on the Guainía lie a short distance from the Orinoco-Atabapo across a flat interfluve, where the Guainía appears to have recently been captured by the Rio Negro. Many species of *Saxofridericia*, sister to Schoencephalieae, are restricted to the western Guayana Shield on and near Duida (Maguire 1982), reinforcing the conclusion that both groups arose in this general region.

Origin of Rapateaceae and Invasion of Tepui Habitats

When did the Rapateaceae arise? This question is difficult to answer, especially given the absence of rapatead fossils (Herendeen and Crane 1995). Fossil Bromeliaceae are known

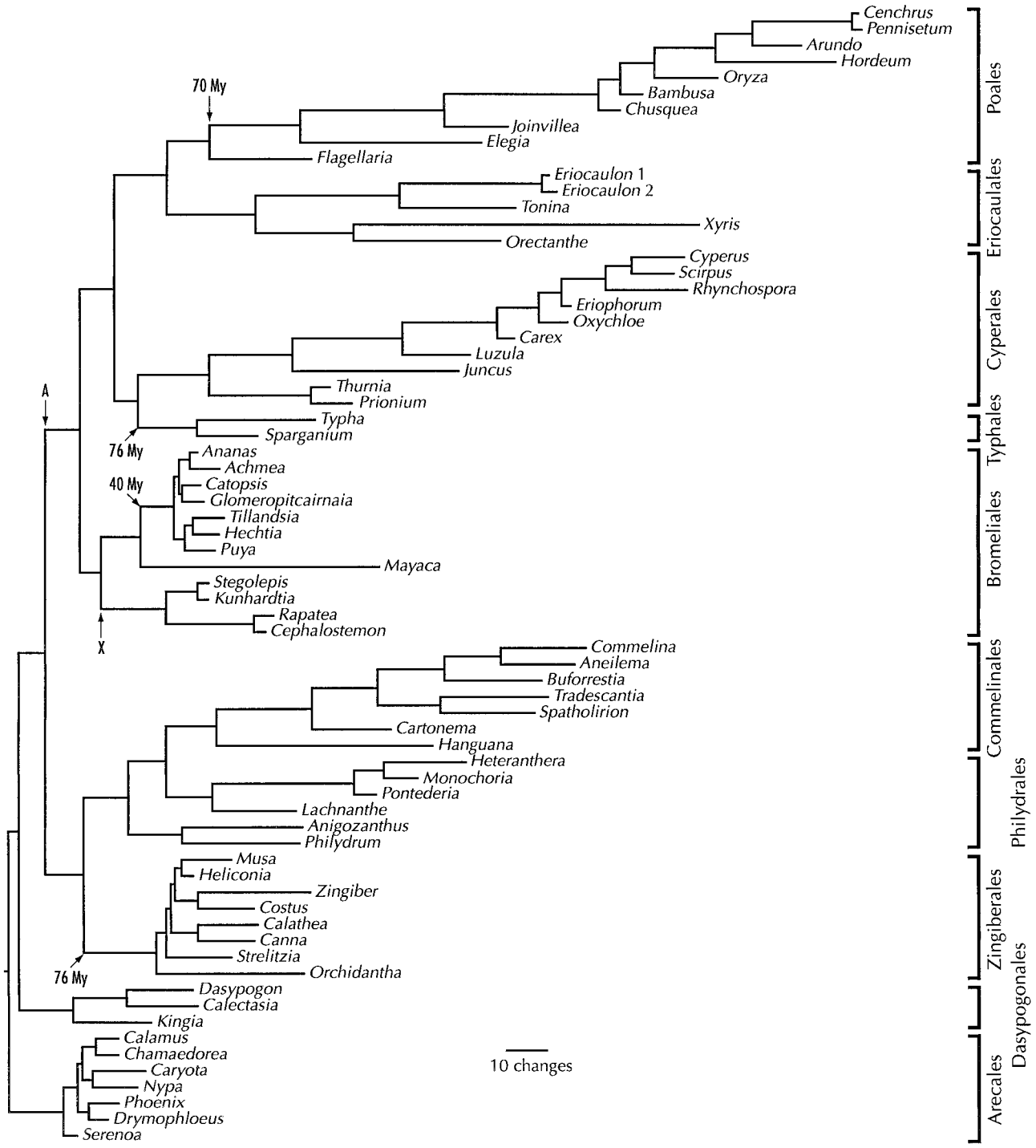


FIG. 8. Phylogram for one of the 20 shortest phylogenies for the commelinoid monocots based on *rbc*L variation (data of Givnish et al. 1999); branch lengths are proportional to the number of mutations inferred along each branch. Ages of oldest known fossils for Poaceae-Restionaceae, Typhales, Bromeliales, and Zingiberales are shown and identified with earliest inferred origin of each group. Branch lengths were used to infer the age of their common ancestor A as 98.6 My, and then infer the age *x* of the Rapateaceae as being 61.2–69.6 My (see text).

from 40 Mya, fossil Poales (Poaceae and Restionaceae) from 70 Mya, and fossil Typhales and Zingiberales from 76 Mya (Herendeen and Crane 1995). The order Bromeliales (Bromeliaceae, Mayacaceae, Rapateaceae) diverged from other commelinoids between when the Zingiberales and allies originated and when the Typhales and Poales arose, based on a codon-weighted analysis of *rbc*L sequence variation (Givnish et al. 1999). Based on branch lengths in that analysis, these groups diverged in a relatively short time (Fig. 8). Although the rates of *rbc*L evolution vary substantially among com-

melinoid lineages (Gaut et al. 1992, 1997), one can extrapolate rates for each lineage a short distance to estimate the age of their common ancestor A (Fig. 8), and then use that age to derive the time of origin for Rapateaceae. Lineage-specific rates were estimated as the mean number of mutations inferred from the earliest common ancestor of each lineage to the present-day taxa, divided by the age of the oldest known fossils. The age of the common ancestor A was estimated as 98.6 My, based on calculated ages of 92.3 My (Poaceae-Restionaceae), 92.9 My (Bromeliaceae, Zingiberales), and 116.4 My (Typhales). This yielded an estimated time of origin for Rapateaceae of 69.6 My; an age of 61.2 My was calculated by extrapolating the rate of *rbc*L evolution in Bromeliaceae extrapolated to the origin of Rapateaceae.

If we thus assume that Rapateaceae arose roughly 65 Mya, then the branch lengths in the clocklike, unweighted *ndh*F tree (Fig. 2) imply that *Maschalocephalus* diverged from other Monotremeae 6 Mya (long after the tropical Atlantic rifted 84–102 Mya), that *Rapatea* and *Cephalostemon* diverged from each other 9 Mya (long after the Amazon assumed its current course ~ 20 Mya), and that the common ancestor of *Rapatea-Cephalostemon* arose 32 Mya. But the *ndh*F clock also implies that the montane saxofridericioids arose about 24 Mya, that the *Stegolepis* alliance (many of whose species are restricted to single tepuis or groups of tepuis) arose 12 Mya, and that the extant stegolepids began to diverge only 6 Mya. These dates are so recent as to create a paradox regarding speciation atop tepuis.

The Roraima sandstones are known to be roughly 1.6 Gy old (Gibbs and Barron 1985; Schubert 1995), and these marine sediments overlie granites more than 2.1 Gy old (Goldstein et al. 1997). The initial uplift of the Roraima Sandstones is widely assumed to coincide with the initial opening of the tropical Atlantic (Sidder and Mendoza 1991; Edmond et al. 1995). Stallard et al. (1991) and Edmond et al. (1995) estimated the denudation rate of the Roraima sandstones and the entire Guayana Shield, averaged over their entire extent in the Orinoco watershed, as 10–20 m My^{-1}; this calculation is predicated on uplift beginning roughly 90 Mya. Based on fluvial geochemistry, Stallard (1988) and Stallard et al. (1991) estimated the denudation rates of flat, sandy lowlands and tepui summits to be roughly 1–5 m My^{-1}. There should have been especially high rates of weathering and erosion in the steep, heavily fissured tepui rims and adjacent talus slopes (Briceño et al. 1990); erosion in these small areas (~ 1% of the total extent of the Guayana Shield in Venezuela; Huber 1995a) would have increased the regional rate of denudation far above that on the tepui summits and extensive lowlands. If we assume an average denudation of 3 m My^{-1} for tepui summits and lowlands and an average denudation of 15 m My^{-1} for the Venezuelan part of the Guayana Shield (see above), then the denudation rate x on the tepui rims and talus slopes must satisfy

$$(3 \text{ m My}^{-1} \times 0.99) + (x \text{ m My}^{-1} \times 0.01) \approx 15 \text{ m My}^{-1}, \quad (1)$$

implying that $x \pm 1.2$ km My^{-1}. This denudation should cause the tepui margins mainly to retreat horizontally, rather than being lowered below the general elevation of the tepui interiors (sandstone tends to shear off in blocks, and tepuis have square edges, not round ones). Thus, we estimate that dissolution and erosion should cause the margins of adjacent tepuis to retreat from each other at a rate of about 2.4 km My^{-1}. If we assume that the same rate of dissection has operated in the past (2-fold variation in rainfall does not appear to affect present-day denudation rates in the Guayana Shield; Stallard et al. 1991), then the margins of adjacent tepuis could have been roughly 200–250 km closer when the central Atlantic began to rift 84–102 Mya. The rifting Atlantic floor, by pushing against the South American and (ultimately) the Pacific Plates, provided the motive force to accelerate the uplift of the Guayana Shield and dissection of the overlying Roraima sandstones. The breadth of the Ventuari valley which separates Sipapo-Cuao in the northwest from Parú and the Duida complex in the southeast, as well as of the gaps between Jaua and Parú and between Chimantá and Cerro Ichún are broadly consistent with this very crude estimate of dissection rate.

If one assumes speciation only by vicariance, it is difficult to reconcile the uplift of tepuis rougly 90 Mya with their apparent invasion by the *Stegolepis* alliance only 6–12 Mya. *Stegolepis* today occurs across all tepuis, and most individual species are narrowly endemic to single tepuis or small groups of neighboring tepuis (Huber 1988), with no obvious means of long-distance dispersal. If vicariance did underlie most speciation in this group, then the uplift of the Roraima sandstones had to commence much more recently than currently thought, and the rate of their dissection had to be at least 10 times greater. Given our estimated rates of dissection, vicariance could (at most) account for the distribution of closely related taxa on tepuis isolated by narrow, recently formed gulfs (e.g., Duida vs. Marahuaca or Huachamacari; or these tepuis vs. Parú).

In contrast, if long-distance dispersal after the tepui landscape had become dissected accounts for the broad distribution of *Stegolepis,* questions arise about the lag between the origin of tepuis and their invasion by saxofridericioids, and about frequent speciation and narrow endemism in *Stegolepis* despite substantial gene flow. Finally, if the *Stegolepis* alliance arose long enough ago (~ 90 Mya) that speciation began with the dissection of the tepuis as the Atlantic rifted, it would imply that the Rapateaceae arose long before any angiosperms are known from the fossil record. Thus, if we assume the operation of a molecular clock in Rapateaceae, we are confronted with unavoidable contradictions, requiring us to rethink the timing of uplift and rate of weathering of the Guayana Shield, or (perhaps better) the process by which speciation occurred in the montane rapateads and, most especially, the role played by long-distance dispersal. Simply abandoning the molecular clock for Rapateaceae does not appear justified, given that *ndh*F sequences within the family evolve in strikingly clocklike fashion. Infrequent long-distance dispersal would be consistent with the recent origin via dispersal of *Maschalocephalus* and with extensive speciation and narrow endemism in montane saxofridericioids. Infrequent dispersal over geographic scales roughly comparable to those between major tepuis has spurred speciation and local endemism in several plant groups in the Hawaiian Islands without gene flow swamping local differentiation (e.g.,

Alsinidendron-Schiedea, Wagner et al. 1995; the silversword alliance, Baldwin 1997; Baldwin and Sanderson 1998; and *Cyanea*, Givnish et al. 1994, 1995; Givnish 1998). Similar processes appear to have shaped plant speciation at similar scales on other oceanic archipelagoes, including Macaronesia (Francisco-Ortega et al. 1996, 1997; Kim et al. 1996, 1999; Mes et al. 1996) and the Juan Fernandez Islands (Sang et al. 1994, 1995).

The geological rate of dissection of the Roraima table mountains from each other needs further study. Some of the larger intertepui gaps (e.g., that between Duida and the southern cluster of Aracamuni, Avispa, and Neblina) could reflect weathering along the margins of intervening tepuis that have since been weathered away themselves (e.g., near present-day Aratitiyope). The added presence of just one intermediate gulf, initiated by weathering along fault lines, could double the apparent rate at which the margins of present-day tepuis receded from each other, so that recession rates of only 0.6 km My^{-1} could account for the observed gaps between major tepuis. The presence of tiny Yapacana roughly halfway between Duida and Cuao/Autana testifies to the presence of at least some intermediate weathering fronts in the large present-day gap between tepuis along the upper Orinoco and Ventuari. Further research, perhaps using Ar^{40}-Ar^{39} and K-Ar analyses to measure the time over which uplifted rocks have been exposed to weathering (Vasconcelos et al. 1994; Vasconcelos 1999), is needed to determine the age of uplift of the tepuis to at or above their current elevation. Such research, together with improvements of the estimated rates of tepui dissection advanced by Edmond et al. (1995), are needed to refine future calibrations of the rates of genetic divergence in rapatead populations atop the tepuis.

Acknowledgements

We thank B. Stergios (Universidad de los Llanos), G. Romero (Harvard University), C. Brewer, and F. and A. Michelangeli (Fundacion Terramar) for helping arrange permits and logistics in Venezuela. V. Funk and C. Kelloff (Smithsonian Institution), C. Ramdass (University of Guyana), M. and M. Chan-a-sue, H. Ameer, and M. Wilson provided critical logistical support in Guyana. Dr. L. Aké Assi graciously supplied material of *Maschalocephalus* from Côte d'Ivoire. G. Romero and A. Carle kindly allowed us to use their photographs of *Spathanthus* and *Maschalocephalus*. J. Smith and A. Fernandez helped collect specimens on two expeditions to Venezuelan Amazonas. B. Stallard and B. Tikoff provided useful comments on geological history. K. Elliot provided outstanding graphical assistance. We gratefully acknowledge the support of grants BSR 9007293 and DEB 9306943 to TJG and KJS from the NSF Systematics and Population Biology Program, as well as a grant from the Smithsonian Institution to V. Funk that helped support a helicopter expedition to several Venezuelan tepuis.

Literature Cited

Albert, V. A., M. W. Chase, and B. D. Mishler. 1993. Character-state weighting for cladistic analysis of protein-coding DNA sequences. Ann. Mo. Bot. Gard. 80:752–766.

Baldwin, B. G. 1997. Adaptive radiation of the Hawaiian silversword alliance: congruence and conflict of phylogenetic evidence from molecular and non-molecular investigations. Pp. 103–128 *in* T. J. Givnish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge Univ. Press, New York.

Baldwin B. G., and M. J. Sanderson. 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). Proc. Natl. Acad. Sci., USA 95:9402–9406.

Ballard, H. E., K. J. Sytsma, and R. R. Kowal. 1998. Shrinking the violets: phylogenetic relationships of infrageneric groups in *Viola* (Violaceae) based on internal transcribed spacer DNA sequences. Syst. Bot. 23:439–458.

Baum, D. A., K. J. Sytsma, and P. C. Hoch. 1994. A phylogenetic analysis of *Epilobium* (Onagraceae) based on nuclear ribosomal DNA sequences. Syst. Bot. 19:363–388.

Berry, P. E., O. Huber, and B. K. Holst. 1995. Floristic analysis and phytogeography. Pp. 161–192 *in* P. E. Berry, B. K. Holst, and K. Yatskievych, eds. Flora of the Venezuelan Guayana. Vol. 1. Timber Press, Portland, OR.

Briceño, H. O., and C. Schubert. 1990. Geomorphology of the Gran Sabana, Guayana Shield, southeastern Venezuela. Geomorphology 3:125–141.

Briceño, H., C. Schubert, and J. Paolini. 1990. Table mountain geology and surficial geochemistry: Chimanta Massif, Venezuelan Guayana Shield. J. S. Amer. Earth Sci. 3:179–194.

Carlquist, S. 1961. Pollen morphology of Rapateaceae. Aliso 5: 39–66.

———. 1966. Anatomy of Rapateaceae: roots and stems. Phytomorph. 16:17–38.

———. 1969. Rapateaceae. Pp. 128–145 *in* P. B. Tomlinson, ed. Anatomy of the monocotyledons. Vol. 3. Oxford Univ. Press, Oxford, U.K.

Chase, M. W., D. W. Stevenson, P. Wilkin, and P. J. Rudall. 1995. Monocot systematics: a combined analysis. Pp. 685–730 *in* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries, eds. Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew.

Conti, E., A. Fischbach, and K. J. Sytsma. 1993. Tribal relationships in Onagraceae: implications from *rbc* L sequence data. Ann. Mo. Bot. Gard. 80:672–685.

Conti, E., A. Litt, and K. J. Sytsma. 1996. Circumscription of Myrtales and their relationships to other rosids: evidence from *rbc* L sequence data. Amer. J. Bot. 83:221–233.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York.

Dahlgren, R., F. N. Rasmussen, and P. F. Yeo. 1985. The families of the monocotyledons: structure, function, and taxonomy. Springer Verlag, Berlin.

Doerr, S. H. 1999. Karst-like landforms and hydrology in quartzites of the Venezuelan Guyana shield: pseudokarst or ''real'' karst? Zeit. Geomorph. 43:1–17.

Doyle, J. J., and J. L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19:11–15.

Edmond, J. M., M. R. Palmer, C. I. Measures, B. Grant, and R. F. Stallard. 1995. The fluvial geochemistry and denudation rate of the Guayana Shield in Venezuela, Colombia, and Brazil. Geochim. Cosmochim. Acta 59:3301–3325.

Evans, T. M., R. B. Faden, and K. J. Sytsma. 1999. Homoplasy in the Commelinaceae: a comparison of different classes of morphological characters. Pp. 547–556 *in* K. A. Wilson, ed. Monocotyledons: systematics and evolution. Vol. II. Royal Botanic Gardens, Sydney, Australia.

Farris, J. S., M. Kallersjo, A. G. Kluge, and C. Bult. 1995. Constructing a significance test for incongruence. Syst. Biol. 44: 570–572.

Farris, J. S., V. A. Albert, M. Källersjo, D. Lipscomb, and A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12:99–124.

Felsenstein, J. 1994. PHYLIP (Phylogeny inference package). Ver. 3.6. Dept. of Genetics, Univ. of Washington, Seattle, WA.

Francisco-Ortega, J., R. K. Jansen, and A. Santos-Guerra. 1996. Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization in the evolution of the Macaronesian flora.

Proceedings of the National Academy of Sciences, U. S. A. 93: 4085–4090.
Francisco-Ortega, J., D. J. Crawford, A. Santos-Guerra, and R. K. Jansen. 1997. Origin and evolution of *Argyranthemum* (Asteraceae: Anthemideae) in Macaronesia. Pp.407–431 *in* T. J. Givnish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge Univ. Press, New York.
Funk, V. A., and D. R. Brooks. 1990. Phylogenetic systematics as the basis of comparative biology. Smithsonian Institution Press, Washington, DC.
Gaut, B. S., S. V. Muse, W. D. Clark, and M. T. Clegg. 1992. Relative rates of nucleotide substitution at the *rbc*L locus of monocotyledonous plants. J. Mol. Evol. 35:292–303.
Gaut, B. S., L. G. Clark, J. F. Wendel, and S. V. Muse. 1997. Comparisons of the molecular evolutionary process at *rbc*L and *ndh*F in the grass family (Poaceae). Molecular Biology and Evolution 14:769–777.
Ghosh, S. K. 1985. Geology of the Roraima group and its implications. Pp. 33–50 *in* M. I. Muñoz, ed. Memoria I Symposium Amazónico. Ministerio de Energía y Minas, Caracas.
Gibbs, A. K., and C. N. Barron. 1993. The geology of the Guiana Shield. Oxford Monographs on Geology and Geophysics no. 22. Oxford Univ. Press, Oxford, U.K.
Gilmartin, A. J., and G. K. Brown. 1987. Bromeliales, related monocots, and resolution of relationships among Bromeliaceae subfamilies. Syst. Bot. 12:493–500.
Givnish, T. J., 1998. Adaptive radiation of plants on oceanic islands: classical patterns, molecular data, new insights. Pp. 281–304 *in* P. Grant, ed. Evolution on islands. Oxford Univ. Press, Oxford, U.K.
Givnish, T. J., and K. J. Sytsma. 1997a. Consistency, characters, and the likelihood of correct phylogenetic inference. Mol. Phylog. Evol. 7:320–330.
———. 1997b. Homoplasy in molecular vs. morphological data: the likelihood of correct phylogenetic inference. Pp. 55–101 in T. J. Givnish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge Univ. Press, New York.
Givnish, T. J., R. W. McDiarmid, and W. R. Buck. 1986. Fire adaptation in *Neblinaria celiae* (Theaceae), a high-elevation rosette shrub endemic to a wet equatorial tepui. Oecol. 70: 481–485.
Givnish, T. J., K. J. Sytsma, J. F. Smith, and W. S. Hahn. 1994. Thorn-like prickles and heterophylly in *Cyanea*: adaptations to extinct avian browsers on Hawaii? Proc. Natl. Acad. Sci. USA 91:2810–2814.
Givnish, T. J., K. J. Sytsma, W. J. Hahn, and J. F. Smith. 1995. Molecular evolution, adaptive radiation, and geographic speciation in *Cyanea* (Campanulaceae, Lobelioideae). Pp. 288–337 in W. L. Wagner and V. A. Funk, eds. Hawaiian biogeography: evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, DC.
Givnish, T. J., K. J. Sytsma, J. F. Smith, W. J. Hahn, D. H. Benzing, and E. M. Burkhardt. 1997. Molecular evolution and adaptive radiation in *Brocchinia* (Bromeliaceae: Pitcairnioideae) atop the tepuis of the Guayana Shield. Pp. 259–311 *in* T. J. Givnish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge Univ. Press, Cambridge, U.K.
Givnish, T. J., T. M. Evans, J. C. Pires, and K. J. Sytsma. 1999. Polyphyly and convergent morphological evolution in Commelinales and Commelinidae: evidence from *rbc*L sequence data. Mol. Phylog. Evol. 12:360–385.
Goldblatt, P. 1993. Biological relationships between Africa and South America: an overview. Pp. 3–14 *in* P. Goldblatt, ed. Biological relationships between Africa and South America. Yale Univ. Press, New Haven, CT.
Goldstein, S., N. T. Arndt, and R. F. Stallard. 1997. The history of a continent from U-Pb ages of zircons from Orinoco River sand and Sm-Nd isotopes in Orinoco basin river. Chem. Ecol. 139: 271–286.
Good, R. 1974. The geography of flowering plants. 4th ed. Longman, London.
Gyllensten, U. B. 1989. PCR and DNA sequencing. Biotechniques 7:700.
Hamann, U. 1962. Weiteres über Merkmalbestand und Verwandtschaftsbeziehungen der ''Farinosae''. Willdenowia 3:169–297.
Hasegawa, M., H. Kishino, and T. A. Yano. 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. J. Mol. Evol. 22:160–174.
Herendeen, P. S., and P. R. Crane. 1995. The fossil history of the monocotyledons. Pp. 1–21 *in* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries, eds. Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew.
Hillis, D. M. 1995. Approaches for assessing phylogenetic accuracy. Syst. Biol. 44:3–16.
Hillis, D. M., J. P. Huelsenbeck, and C. W. Cunningham. 1994. Application and accuracy of molecular phylogenies. Science 264:671–677.
Hoorn, C. 1994. An environmental reconstruction of the palaeo-Amazaon river system (middle–late Miocene), NW Amazonia. Palaeogeog. Palaeoclim. Palaeoecol. 112:187–238.
Hoorn, C., J. Guerrero, G. A. Sarmiento, and M. A. Lorente. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. Geology 23:237–240.
Huber, O. 1982. Significance of savanna vegetation in the Amazon Territory of Venezuela. Pp. 221–244 *in* G. T. Prance, ed. Biological diversification in the tropics. Columbia Univ. Press, New York.
———. 1988. Guayana highlands vs. Guyana lowlands: a reappraisal. Taxon 37:595–614.
———. 1995a. Geographical and physical features. Pp. 1–61 *in* P. E. Berry, B. K. Holst, and K. Yatskievych, eds. Flora of the Venezuelan Guayana, Vol. 1. Timber Press, Portland, OR.
———. 1995b. Vegetation. Pp. 97–160 *in* P. E. Berry, B. K. Holst, and K. Yatskievych, eds. Flora of the Venezuelan Guayana. Vol. 1. Timber Press, Portland, OR.
Huelsenbeck, J. P., J. J. Bull, and C. W. Cunningham. 1996. Combining data in phylogenetic analysis. Trends Ecol. Evol. 11: 152–158.
Kim, S.-C., D. J. Crawford, J. Francisco-Ortega, and A. Santos-Guerra. 1996. A common origin for woody *Sonchus* and five related genera in the Macaronesian Islands: molecular evidence for extensive radiation. Proceedings of the National Academy of Sciences, U. S. A. 93:7743–7748.
———. 1999. Adaptive radiation and genetic differentiation in the woody Sonchus alliance (Asteraceae: Sonchinae) in the Canary Islands. Plant Systematics and Evolution 215:101–118.
Maddison, D. R. 1991. The discovery and importance of multiple islands of most parsimonious trees. Syst. Zool. 40:315–328.
Maddison, W. P., and D. R. Maddison. 1992. MacClade: analysis of phylogeny and character evolution. Ver. 3. Sinauer Assoc., Sunderland, MA.
Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83–103.
Maguire, B. 1958. Rapateaceae. Mem. N. Y. Bot. Gard. 10:19–49.
———. 1979. Additions to the Rapateaceae. Acta Amazonica 9: 267–269.
———. 1982. Rapateaceae. Flora de Venezuela 11(2):85–203.
———. 1984. Flora de la Guayana Venezolana. I. Nuevos taxa de la Guayana Venezolana. Acta Botanica Venezolano 14:5–52.
Mayr, E., and W. H. Phelps Jr. 1967. The origin of the bird fauna of the south Venezuelan highlands. Bull. Amer. Mus. Nat. Hist. 136:275–327.
McDiarmid, R. W., and S. Gorzula. 1989. Aspects of the reproductive ecology and behavior of the tepui toads, genus *Oreophynella* (Anura, Bufonidae). Copeia 2:445–451.
Mes, T. H. M., J. van Brederode, and H. t'Hart. 1996. Origin of the woody Macaronesian Sempervivoideae and the phylogenetic position of the East African species of *Aeonium*. Botanica Acta 109:477–491.
Mori, S. A., G. Cremers, C. Gracie, J. J. De Granville, M. Hoff, and J. D. Mitchell. 1997. Vascular plants of central French Guiana. 1. Pteridophytes, gymnosperms, and monocotyledons. Mem. New York Bot. Gard. 76:1–422.
Nei, M., and W. Li. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc. Natl. Acad. Sci., USA 76:5269–5273.

Olmstead, R. G., H. J. Michaels, K. M. Scott, and J. D. Palmer. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbc*L. Ann. Mo. Bot. Gard. 79:249–265.

Olmstead, R. G., B. Bremer, K. M. Scott, and J. D. Palmer. 1993. A parsimony analysis of the Asteridae sensu lato based on *rbc* L sequences. Ann. Mo. Bot. Gard. 80:700–722.

Pitman, W. C., III, S. Cande, J. LaBrecque, and J. Pindell. 1993. Fragmentation of Gondwana: the separation of Africa from South America. Pp. 15–34 *in* P. Goldblatt, ed. Biological relationships between Africa and South America. Yale Univ. Press, New Haven, CT.

Potter, P. E. 1997. The Mesozoic and Cenozoic paleodrainage of South America: a natural history. J. S. Amer. Earth Sci. 10: 331–344.

Rasanen, M. E., A. M. Linna, J. C. R. Santos, and F. R. Negri. 1995. Late Miocene tidal deposits in the Amazonian foreland basin. Science 269:386–390.

Renner, S. 1989. Floral biological observations on *Heliamphora tatei* (Sarraceniaceae) and other plants from Cerro de la Neblina in Venezuela. Plant Syst. Evol. 163:21–30.

Sang, T., D. J. Crawford, S.-C. Kim, and T. F. Stuessy. 1994. Radiation of the endemic genus Dendroseris (Asteraceae) on the Juan Fernandez Islands: evidence from sequences of the ITS regions of nuclear ribosomal DNA. American Journal of Botany 81:1494–1501.

Sang, T., D. J. Crawford, T. F. Stuessy, and M. S. O. 1995. ITS sequences and the phylogeny of the genus *Robinsonia* (Asteraceae). Systematic Botany 20:55–64.

Sanger, F., S. Nicklen, and A. R. Coulson. 1977. DNA sequencing with chain terminating inhibitors. Proceedings of the National Academy of Sciences, U. S. A. 74:5463–5467.

Schubert, C. 1995. Origin of the Gran Sabana in southeastern Venezuela: no longer a ''lost world''. Scientia Guianiae 5:147–174.

Sidder, G. B., and S. V. Mendoza. 1991. Geology of the Venezuelan Guayana Shield and its relation to the entire Guayana Shield. U.S. Geological Survey Open File Rep. 91-141.

Simpson, M. G. 1998. Aspects of floral morphology and anatomy in monocot systematics. Abstract *in* Second international conference on the comparative biology of the monocotyledons and third international symposium on grass systematics and evolution. Univ. of New South Wales, Sydney, Australia.

Smith, L.B, and R.J. Downs. 1974. Bromeliaceae (Pitcairnioideae). Flora Neotrop. Mongr. 14:1–662.

Smith, J. F., K. J. Sytsma, J. S. Shoemaker, and R. L. Smith. 1991. A qualitative comparison of total cellular DNA extraction protocols. Phytochem. Bull. 23:2–9.

Stallard, R. F., 1988. Weathering and erosion in the humid tropics. Pp. 225–246 *in* A. Lerman and M. Meybeck, eds. Physical and chemical weathering in geochemical cycles. Kluwer Academic Publishers, Boston, MA.

Stallard, R. F., L. Koehnken, and M. J. Johnsson. 1991. Weathering processes and the composition of inorganic material transported through the Orinoco River system, Venezuela and Colombia. Geoderma 51:133–165.

Stevenson, D. W., and H. Loconte. 1995. Cladistic analysis of monocot families. Pp. 543–578 *in* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries, eds. Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew.

Stevenson, D. W., M. Colella, and B. Boom. 1998. Rapateaceae. Pp. 415–424 *in* K. Kubitzki, ed. Flowering plants. IV. Monocotyledons: Alismatanae and Commelinanae (excluding Gramineae). Springer, Berlin.

Steyermark, J. A. 1986. Speciation and endemism in the flora of the Venezuelan tepuis. Pp. 317–373 *in* F. Vuilleumier and M. Monasterio, eds. High altitude tropical biogeography. Oxford Univ. Press, Oxford, U.K.

———. 1989. Flora of the Venezuelan Guayana. VI. Ann. Mo. Bot. Gard. 75:1565–1586.

Swofford, D. L. 1999. PAUP*: Phylogenetic analysis using parsimony (*and other methods). Ver. 4. Sinauer Associates, Sunderland, MA.

Sytsma, K. J. 1990. DNA and morphology: inference of plant phylogeny. Trends Ecol. Evol. 5:104–110.

Sytsma, K. J., and D. Baum. 1996. Molecular phylogenies and the diversification of the angiosperms. Pp. 314–339 *in* D. W. Taylor and L. J. Hickey, eds. Flowering plant origin, evolution and phylogeny. Chapman and Hall, New York.

Terry, R. G., G. K. Brown, and R. G. Olmstead. 1997. Examination of subfamilial phylogeny in Bromeliaceae using comparative sequencing of the plastid locus *ndh* F. Amer. J. Bot. 84:664–670.

Tiemann, A. 1985. Untersuchungen zur Embryologie, Blütenmorphologie und Systematik der Rapateaceen und der Xyridaceen-Gattung *Abolboda* (Monocotyledoneae). Dissertationes Botanicae 52. J. Cramer, Vaduz, Liechtenstein.

Vasconcelos, P. M. 1999. K-Ar and Ar^{40}/Ar^{39} geochronology of weathering processes. Ann. Rev. Earth Planet. Sci. 27:183–229.

Vasconcelos, P. M., P. R. Renne, G. H. Brimhall, and T. A. Becker. 1994. Direct dating of weathering phenomena by Ar^{40}/Ar^{39} and K-Ar analysis of supergene K-Mn oxides. Geochim. Cosmochim. Acta 58:1635–1665.

Venturelli, M., and F. Bouman. 1988. Development of ovule and seed in Rapateaceae. Bot. J. Linn. Soc. 97:267–294.

Wagner, W.L. and V. Funk, Eds. 1995. Hawaiian biogeography: evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, DC.

Corresponding Editor: K. Holsinger