

# Insights into the diversity of the Pantepui Flora and the biogeographic complexity of the Guayana Shield

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A distinctive floristic assemblage is centered in the Guayana region of northern South America, part of an ancient crystalline shield that covers around 1,000,000 km<sup>2</sup> in southern Venezuela, southeastern Colombia, northern Brazil, and the Guianas. This combined area includes as many as 15,000 species of vascular plants, with at least a third of the species endemic to the region. The diversity and endemism is not evenly distributed, however. The Pantepui Province comprises the roughly 50 mountain summits that lie between 1500 m and 3015 m elevation. This province covers a total area of just 5000 km<sup>2</sup>, or less than half of one percent of the Shield area, yet 2450 vascular plant species (17% of the Shield's total) are found there. Of these, 1500 (60%) are endemic to the Guayana Shield, and 1035 (42%) are found nowhere else but in Pantepui. A full 25% of the species in Pantepui are both endemic there and known only from a single mountain. Of the 2450 Pantepui vascular plant species, 10% are orchids, followed by Melastomataceae, Asteraceae, Rubiaceae, and Bromeliaceae, each of which includes between 5% and 6% of the Pantepui flora. Of the major Pantepui groups, the orchids and the sedges have the lowest levels of endemism on Pantepui (22-25% of the species), whereas many families have over 60% of their species endemic there. Unlike the more recently uplifted Andes, only 4% of the 626 genera occurring in Pantepui have temperate-zone affinities, and 5% are considered cosmopolitan. Eighty Pantepui genera are endemic to the Guayana Shield, and 23 are only found in Pantepui. The largest phytogeographic element is the Neotropical one, which includes 70% of the genera. Smaller but significant elements include tropical African, Malesian, and Pantropical genera. Recent molecular-based phylogenies of Guayana plant taxa suggest a diverse array of evolutionary histories that should be expected from an ancient cratonic area like the Guayana Shield.

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## Introduction

The Guayana Region in northeastern South America covers most of southern Venezuela, the three Guianas (Guyana, Suriname, and

French Guiana), and adjacent areas of Colombia and Brazil (Fig. 1). It largely coincides with the underlying Precambrian basement of the Guayana Shield (Gibbs & Barron 1993; Huber 1994; Berry *et al.* 1995), which covers about

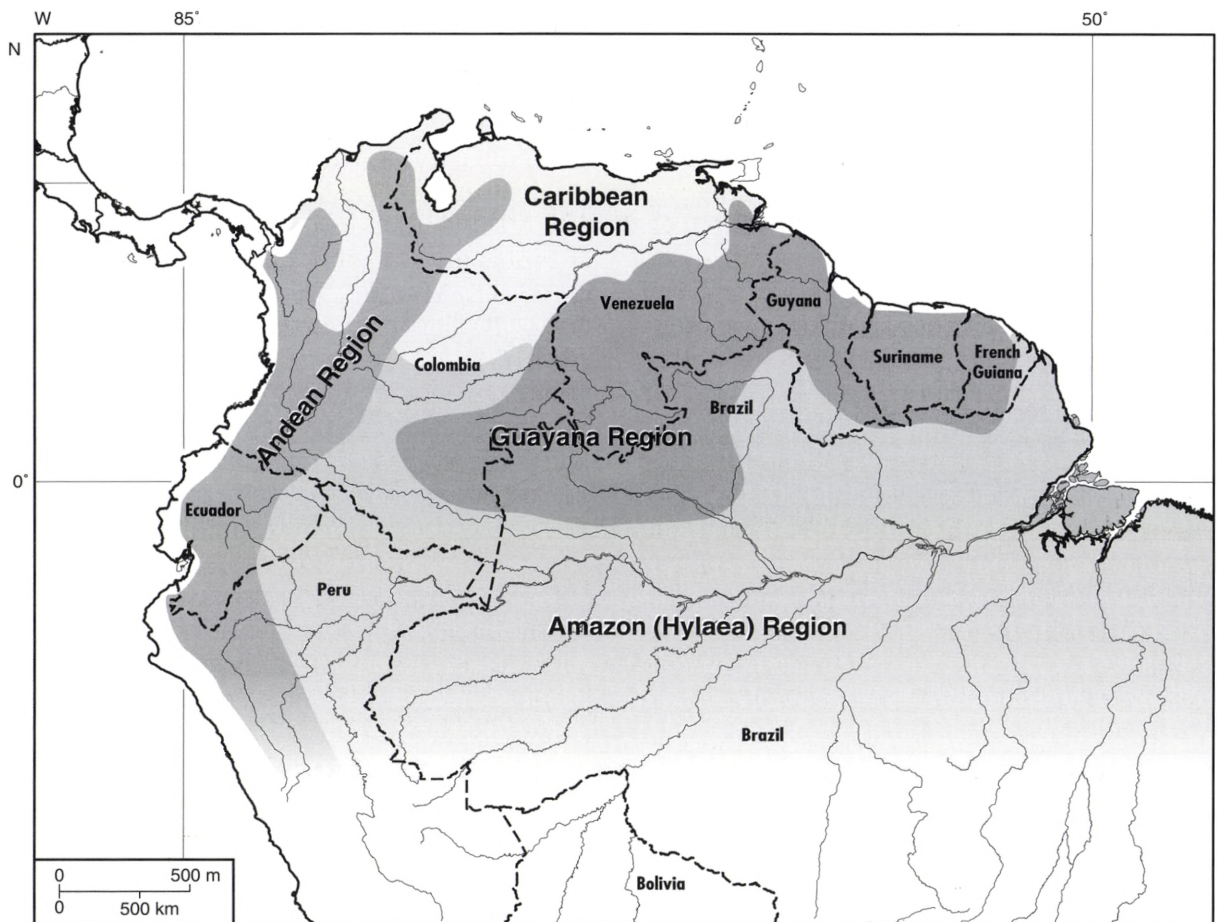


Fig. 1. Map of northern South America showing the approximate limits of the Guayana Region and adjacent phyto-geographic regions (modified after Huber 1994).

1,000,000 km<sup>2</sup> (Berry *et al.* 1995). It is characterized by a very diverse landscape, including forested lowlands and savannas, upland plateaus and the characteristic tabletop mountains (*tepui*) that often emerge as high-elevation 'islands' in the overall landscape. After more than 250 years of botanical explorations in this region, particularly with the exploration of the tepuis carried out in the past 100 years, the area has come to be recognized as a center of plant diversity and endemism (Maguire 1970; Steyermark 1979, 1986; Takhtajan 1986;

Huber 1988, 1995a; Berry *et al.* 1995; Givnish *et al.* 2000).

Much of the focus on plant endemism in the Guayana Shield has centered on the higher-elevation tepuis known as Pantepui, which includes areas mostly above 1500 m elevation (Huber 1987). This area of tepui summits covers a small proportion of the area of the Guayana Region, roughly 5000 km<sup>2</sup> (Huber 1995b), or about 0.5% of the region. Considering this small area, the plant richness and endemism of the tepuis are considerably



higher than those of the uplands and lowlands of the Guayana Region (Berry *et al.* 1995).

The lower elevations of the Guayana Shield share some of the same taxa as the tepuis, but also show additional patterns of endemism and phytogeographical relationships. Since the introductory volume of the *Flora of the Venezuelan Guayana* (Steyermark *et al.* 1995) was published in 1995, seven additional volumes with floristic accounts have been published (Berry *et al.* 1995, 1997, 1998, 1999, 2001, 2003, in press). This information, plus access to manuscripts for families in the final volume, has provided a stronger floristic basis on which to make a phytogeographic reevaluation of the region. Since the *Flora* basically follows the Cronquist system of family classification, we will follow the same system here, except in cases where more recent evidence strongly supports the recognition of different families, such as Bonnetiaceae as distinct from the Theaceae (APG II 2003) or *Pakaraimea* in the Dipterocarpaceae rather than in the Monotaceae (Morton *et al.* 1999).

This paper will focus initially on the flora of Pantepui, because it has been the subject of a recent phytogeographical analysis by Riina (2003). Then it will examine what recent molecular studies are beginning to show about the phylogenetic history of Guayana Shield taxa that have been studied to date.

### Patterns of diversity and endemism of the vascular flora of Pantepui

The phytogeographic province of Pantepui includes high mountain ecosystems of the Guayana Highlands, which extend in altitude mainly between 1500 m and 3000 m (Huber 1994; Berry *et al.* 1995). It has a discontinuous distribution and is part of the phytogeographic region of Guayana located in northeastern South America (Fig. 2). The tepuis are table mountains that often have sheer vertical walls

and mostly flat summits, and most are surrounded by a matrix of generally forested lowlands. Other tepui-like areas located in Guyana (Pakaraima), Suriname (Tafelberg), northern Brazil (Serra Aracá and Serra Tepequem), and southeastern Colombia (Cerro Chiribiquete, Cerro Isibukuri, and Cerro Yapobodá), as well as tepuis in Venezuela such as Cerro Moriche and Cerro Yapacana, have their summits well below 1500 m elevation (except Ayanganna, Kamakusa, Karanang/Morabiakru, and Wokomung in Guyana), so they do not technically belong to the Pantepui Province. Most of these areas correspond to what Huber (1995b) classifies as upland (500-1500 m) or lowland (0-500 m) areas of the Guayana region.

Based on a database of the vascular plants of Pantepui Province that was compiled from current and pending volumes of the *Flora of the Venezuelan Guayana*, the flora of Pantepui comprises 2447 species of angiosperms, gymnosperms, and ferns and fern allies. Of these, 42% are restricted or endemic to Pantepui, and 25% correspond to single-tepui endemics. There are no longer any families considered entirely endemic to Pantepui (*Saccifolium* in the former monotypic Saccifoliaceae is now recognized as part of the Gentianaceae – Struwe *et al.* 2002; and Hymenophyllopsidaceae extends down to 700 m on some tepui slopes), but there are 23 genera endemic to Pantepui (Table 1). Our database includes floristic data from 45 tepuis, of which 38 are considered adequately explored botanically and with a reliable or published floristic record available.

The most recent previous estimate of the Pantepui flora (Berry *et al.* 1995) indicated a total of 2322 species, with 33% endemism. Results of the current study show a slight increase in species richness (2447 species) and a more marked increase in the proportion of endemic species (42%). The estimates of Berry *et al.* (1995) were based on preliminary check-





**Table 1.** Number of Pantepui taxa (occurring above 1500 m in the Guayana Region) and their endemism at different scales.

	Number of taxa in Pantepui	Taxa endemic to the Guayana Shield*	Taxa endemic to Pantepui (%)	Taxa endemic to a single tepui (%)
Families	156	2	0	0
Genera	626	80	23 (3.7)	13 (2)
Species	2447	1517	1034 (42)	617 (25)

\* Updated from Berry *et al.* 1995.

entire area of the *Flora of the Venezuelan Guayana*, where most of the tepuis are located, the Pantepui flora accounts for 25% of all species occurring in the flora area (9411 species, Berry *et al.* 1995, Table 2). This implies that a quarter of the total species occurring in the flora area is present in about 1% (ca. 5000 km<sup>2</sup>) of the total area covered by the flora (ca. 450,000 km<sup>2</sup>). This high concentration of species on the tepuis can be explained in part by the high proportion of Pantepui endemic species. A similar pattern showing high concentrations of endemic species in small areas has been observed in other areas, particularly tropical mountain tops and islands (*e.g.*, Gentry 1986; Ceballos & Brown 1995; Gröger & Barthlott 1996; Crisp *et al.* 2001). Isolation may contribute greatly to the degree of endemism in an area, hence isolated islands and mountains are often rich in endemics (Cox & Moore 2000). The isolation factor applies to the Pantepui case, and the region has been tectonically stable during most of the Tertiary. A paleoecological study of Holocene peat deposits on three tepui summits indicated that the tepuis underwent alternating arid or semi-arid phases with wetter phases during glacial fluctuations, indicating that this area was probably under a climatically variable environment in recent times (Rull 1991). A more recent study (Rull 2004) shows that there was vertical displacement of vegetation zones downwards during

glacial periods as well, similar to what has been amply demonstrated in the northern Andes during the Quaternary.

Steyermark (1986) proposed that the high floristic richness and endemism in Pantepui are the result of a combination of factors such as long geological history and isolation of tepuis into virtual islands, the combination of particular environmental conditions peculiar to Pantepui (low pH, high rainfall, high wind, and high ultraviolet radiation, wide temperature variation, and oligotrophic soils), and both recent connections with floristic elements derived from areas outside the Guayana Shield as well as ancient relationships with western Gondwana or Malesian-Australasian floral elements. The impact of the long geological isolation of the Pantepui flora has been questioned by Huber (1988) and Kubitzki (1990), who argued that plant diversification in the area took place from both the upper regions downwards and from the lowland regions upward.

**Table 2.** Number of taxa for the major taxonomic groups in Pantepui.

	Families	Genera	Species
Angiosperms	130	561	2108
Gymnosperms	2	2	12
Ferns and fern allies	24	63	327

**Table 3.** The 25 largest vascular plant families of Pantepui and their numerical importance. The corresponding figures for the entire Venezuelan Guayana are also shown for the same families for comparative purposes and to provide a broader floristic context that includes the upland and lowland areas surrounding the tepuis.

Family	Number of species in Pantepui	% of the total Pantepui flora	Number of species in the Venezuelan Guayana	% of the Pantepui species out of the total number in the Venezuelan Guayana
Orchidaceae	258	10.5	732	35
Melastomataceae	147	6.0	427	34
Asteraceae	140	5.7	258	54
Rubiaceae	133	5.4	515	25
Bromeliaceae	117	4.8	284	41
Cyperaceae	68	2.8	308	22
Poaceae	67	2.7	409	16
Ericaceae	59	2.4	69	86
Xyridaceae	56	2.3	95	59
Hymenophyllaceae	49	2.0	73	67
Clusiaceae	48	2.0	143	34
Eriocaulaceae	47	2.0	88	53
Araliaceae	46	1.9	64	72
Myrtaceae	46	1.9	183	25
Dryopteridaceae	45	1.8	115	39
Gentianaceae	44	1.8	83	53
Grammitidaceae	43	1.8	55	79
Rapateaceae	40	1.6	70	57
Ochnaceae	39	1.6	120	33
Piperaceae	37	1.5	124	30
Malpighiaceae	36	1.5	153	24
Aquifoliaceae	34	1.4	69	49
Lauraceae	33	1.3	142	23
Euphorbiaceae	30	1.2	239	23
Myrsinaceae	29	1.2	55	53

### *Taxonomic patterns in the vascular plant flora*

The families with the highest number of species (>100) in the Pantepui area are Orchidaceae, Melastomataceae, Asteraceae, Rubiaceae, and Bromeliaceae (Table 3). These five families account for almost 33% of the vascular

plant flora of this area. The next 20 families shown in Table 3 account for 37% of the Pantepui flora, ranging in richness from 68 species to 29 species.

The remaining 131 families represent the other 30% of the species occurring in Pan-



**Table 4.** The 25 largest genera of Pantepui vascular plants, arranged by decreasing size of the genera. This represents 4% of the genera in Pantepui and 29% of the species.

Genus	Family	Species
<i>Psychotria</i>	Rubiaceae	45
<i>Schefflera</i>	Araliaceae	45
<i>Xyris</i>	Xyridaceae	44
<i>Clusia</i>	Clusiaceae	34
<i>Ilex</i>	Aquifoliaceae	34
<i>Navia</i>	Bromeliaceae	33
<i>Lindmania</i>	Bromeliaceae	32
<i>Elaphoglossum</i>	Dryopteridaceae	29
<i>Stegolepis</i>	Rapateaceae	29
<i>Epidendrum</i>	Orchidaceae	28
<i>Bonnetia</i>	Bonnetiaceae	26
<i>Grammitis</i>	Grammitidaceae	26
<i>Miconia</i>	Melastomataceae	26
<i>Myrcia</i>	Myrtaceae	26
<i>Paepalanthus</i>	Eriocaulaceae	26
<i>Trichomanes</i>	Hymenophyllaceae	26
<i>Pleurothallis</i>	Orchidaceae	25
<i>Selaginella</i>	Selaginellaceae	25
<i>Hymenophyllum</i>	Hymenophyllaceae	23
<i>Maxillaria</i>	Orchidaceae	23
<i>Peperomia</i>	Piperaceae	23
<i>Rhynchospora</i>	Cyperaceae	22
<i>Calea</i>	Asteraceae	21
<i>Cybianthus</i>	Myrsinaceae	21
<i>Utricularia</i>	Lentibulariaceae	21
25		713

tepui. Families with high levels of richness in the flora area (*i.e.*, >100 spp.) but poorly represented in Pantepui include: Fabaceae *sensu stricto*, Caesalpiniaceae, Araceae, Mimosaceae, Apocynaceae, Bignoniaceae, Chrysobalanaceae, and Annonaceae. These families are more diverse at medium and low elevations in the Guayana Region, where they are important elements of the forest vegetation. The last column of Table 3 shows the proportion of species in a given family out of its total in the Venezuelan Guayana, showing that families with high percentages (>60%) are better represented in Pantepui than in the surrounding lowlands and uplands. Families strongly exhibiting this

pattern are Ericaceae (85%), Hymenophyllaceae (67%), Araliaceae (72%), and Grammitidaceae (78%). Numerous smaller families also show the same pattern.

The 25 largest plant genera in Pantepui account for almost 30% of the total number of species and are shown in Table 4. *Psychotria* (Rubiaceae), *Schefflera* (Araliaceae), and *Xyris* (Xyridaceae) are the most species-rich genera, followed by *Clusia* (Clusiaceae), *Ilex* (Aquifoliaceae), *Navia*, and *Lindmania* (Bromeliaceae).

Table 5 shows the families with highest levels of endemism, with the percentage of endemic species in relation to the total number of species for each family in Pantepui. The top five families in numbers of endemic species are the same as the top five families in number of Pantepui species (Table 3). However, a number of smaller families in Pantepui have a high proportion of their species endemic to Pantepui, such as Araliaceae (85% endemism), Eriocaulaceae (68%), Aquifoliaceae (71%), Asclepiadaceae (74%), Hymenophyllopsidaceae (88%), Rhamnaceae (85%), Sarraceniacae (75%), and Bonnetiaceae (74%).

### *Distribution patterns*

Many of the species in Pantepui are very restricted in their geographical ranges (Fig. 3). For example, 37% of the Pantepui species are known only from a single tepui, and 28% more occur on just two or three tepuis. Few species are widespread across tepuis (Fig. 3), with 167 (7% of the species) occurring on more than 15 tepuis. We do not have accurate enough records to determine if any species actually occur on all the tepuis, but the more widespread species include: *Cochlidium serrulatum* and *C. tepuiensis* (Grammitidaceae); *Hymenophyllum polyanthos* (Hymenophyllaceae); *Lycopodiella caroliniana* (Lycopodiaceae); *Schizaea elegans* (Schizaeaceae); *Digomphia densicomis* (Bignoniaceae); *Brocchinia acuminata*, *B. hechtoides*, *B. tatei*, *Racinaea spiculosa*, *Vriesea*

**Table 5.** Vascular plant families with most endemic species in Pantepui.

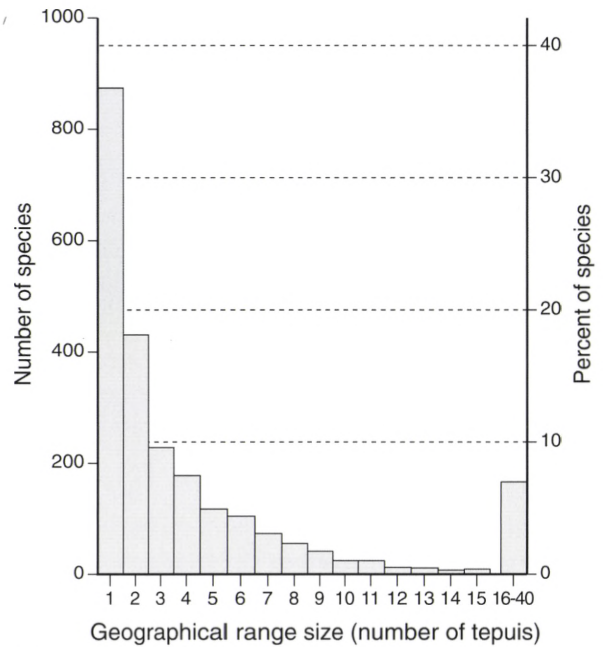
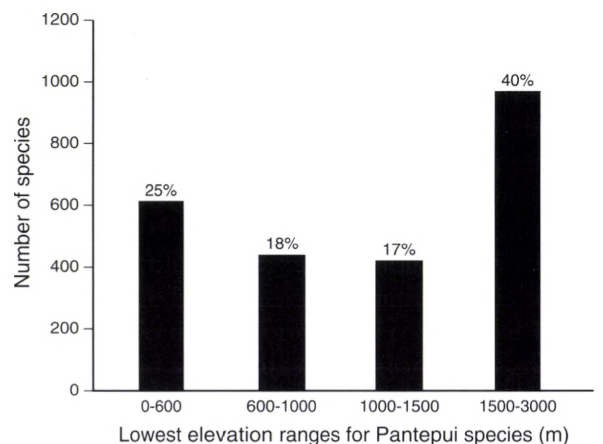
Family	Endemic species	Total number of species	% endemics /total
Asteraceae	84	140	60
Bromeliaceae	75	117	64
Rubiaceae	75	133	56
Melastomataceae	72	147	49
Orchidaceae	58	258	25
Araliaceae	39	46	85
Ericaceae	33	59	56
Xyridaceae	33	56	59
Eriocaulaceae	32	47	68
Poaceae	28	67	42
Gentianaceae	26	44	59
Ochnaceae	26	39	67
Aquifoliaceae	24	34	71
Rapateaceae	24	40	60
Bonnetiaceae	20	27	74
Clusiaceae	20	48	42
Myrtaceae	20	46	44
Malpighiaceae	19	36	53
Myrsinaceae	19	29	66
Asclepiadaceae	18	24	75
Lauraceae	17	33	52
Cyperaceae	15	68	22
Piperaceae	15	37	41
Euphorbiaceae	14	30	47
Selaginellaceae	13	25	52
Rutaceae	12	18	67

*duidae*, and *Tillandsia turneri* (Bromeliaceae); *Cyrilla racemiflora* (Cyrillaceae), *Bejaria sprucei*, *Thibaudia formosa*, and *T. nutans* (Ericaceae); *Myrica sylvatica* (Myricaceae); *Xyris guianensis* and *Oreochanthe sceptrum* (Xyridaceae); *Panicum chnoodes* (Poaceae); *Epidendrum durum*, *E. secundum*, *E. ulei*, *Restrepiopsis tubulosa*, *Sobralia infundibuligera*, and *Trichosalpinx roraimensis* (Orchidaceae).

The elevational pattern of species distribution is shown in Fig. 4. Around 40% of the Pantepui flora is only found at elevations above 1500 m (the lower elevation limit of the Pantepui Province), whereas 15% of the Pantepui

species range from the lowlands (0-600 m) to the highlands (1500-3000 m). Species ranging from the uplands (600-1500 m) to the highlands account for 35% of the total (Fig. 4).

The elevational spectrum of the Pantepui

**Fig. 3.** The geographic range size distribution of Pantepui plant species (number of tepuis where species are found).**Fig. 4.** The lower elevational distributions of the 2447 species occurring in the Pantepui Province.



flora (Fig. 4) supports the view of Huber (1988), who contested the older characterization of isolated tepuis summits as 'islands in the sky,' which was exaggerated by the tower-like appearance of the most conspicuous tepuis of the Guayana region, with steep vertical walls and cliffs contributing to create the impression of strong spatial and perhaps temporal isolation. Even though the spatial isolation is not an impediment for the upward and downward migration of some species, it is nonetheless notable that 40% of the Pantepui flora is distributed exclusively above 1500 m, and another 17% of the species only occur above 1000 m (Fig. 4). This is likely related to intrinsic characteristics of the species, such as limited dispersal capabilities and adaptations to cool, montane environments. Once a population becomes adapted to the tepui summit environment, it is more likely to colonize other areas with similar environmental conditions, so it would need to disperse between tepui summits to expand its geographical range.

Table 6 shows the distribution of the total number of species and the number of endemic species across tepuis ordered by their species richness. The total number of species per tepui ranges from 857 (Chimantá) to 102 (Camani), with an average of 287 species per tepui. Fifty percent or more of the species of the Pantepui flora are present on the three richest tepuis: Chimantá (857), Neblina (690), and Auyán (602), followed by Roraima (541), Marahuaka (504), Ptari (446), Duida (434) and Jaua (393). Not surprisingly, the tepuis with the highest species diversity are the ones with most endemic species. Chimantá, with the highest diversity and endemism, is a huge and very fragmented massif. It probably contains the widest variety of shrubby life forms and vegetation types in the Pantepui province (Huber 1995c). It initially would seem incongruous that a relatively bare-topped tepui like Ptari-tepui appears among the most diverse tepuis,

but there are many taxa that were collected on the talus slopes of the mountain, still above 1500 m and therefore included here as part of the Pantepui flora. In the future, the biogeographical concept of Pantepui may need to be further modified to exclude such species that more likely represent upper altitudinal elements of the upland flora.

The phytogeographical spectrum of the 626 genera occurring in Pantepui is shown in Fig. 5. Appendix 1 provides a complete list of gen-

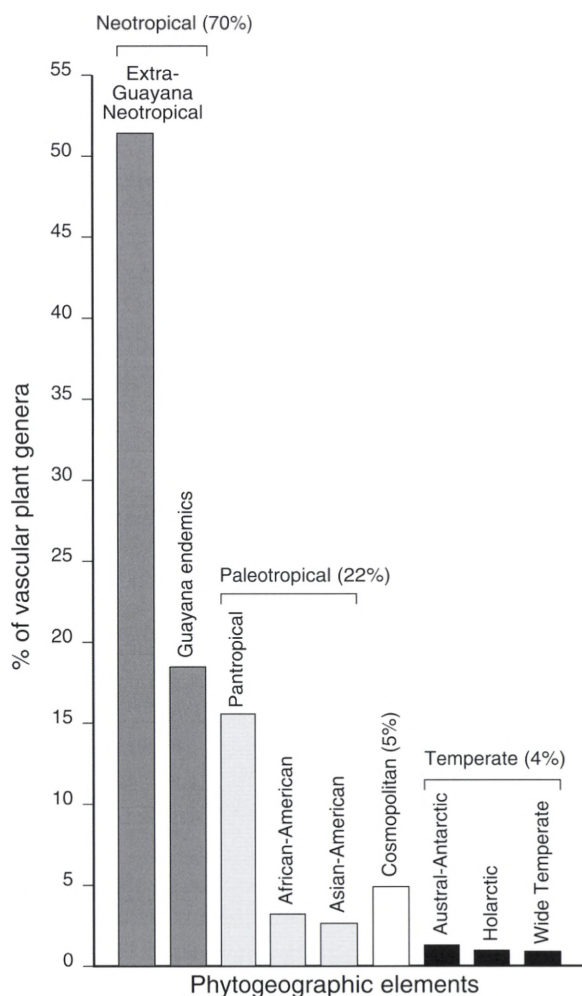


Fig. 5. Phytogeographic affinities of the plant genera occurring in the Pantepui Province.

**Table 6.** Single tepui endemics, Pantepui endemics, and total numbers of vascular plant species found above 1500 m elevation for each major tepui of the Guayana Region. Arranged by decreasing total number of species.

Tepui	Species endemic to this tepui only	Species endemic to Pantepui	Species extending beyond Pantepui	Total number of species
Chimantá	102	258	497	857
Neblina	132	140	416	690
Auyán	32	192	378	602
Roraima	17	146	378	541
Marahuaka	36	149	319	504
Ptari	10	127	309	446
Duida	47	137	250	434
Jaua	38	115	240	393
Sipapo	40	103	184	327
Ilú/Tramén	7	105	213	325
Yutajé	17	83	223	323
Guaiquinima	12	65	242	319
Aracamuni-Avispa	15	71	197	283
Huachamacari	7	72	191	270
Parú	28	76	156	260
Sororopán	8	45	206	259
Sarisariñama	5	63	173	241
Kukenán	4	71	165	240
Corocoro	5	47	178	230
Kamarkawarai	1	70	158	229
Uaipán	1	39	180	220
Aparamán	0	54	164	218
Murispán	2	56	159	217
Maigualida	28	43	139	210
Aprada	2	47	153	202
Tereke-yurén	0	41	158	199
Uei	1	43	151	195
Carrao	0	39	137	176
Marutaní	0	31	140	171
Guanay	6	47	116	169
Karaurín	0	31	134	165
Aracá	0	18	140	158
Yaví	4	30	111	145
Autana	0	31	108	139
Cuao	1	36	102	139
Yapacana	7	11	117	135
Aratitoyope	0	9	118	127
Camani	3	12	87	102



era for each of the selected phytogeographic elements. The tropical component comprises 92% of the genera and is the best represented in the Pantepui flora. About 52% of the flora consists of genera distributed in the Neotropics outside of the Guayana Shield (324), of which 18 (3%) genera are centered in lowland South America or Amazonia, 8 genera (1.3%) are more diverse in the Brazilian Shield, and 26 (4%) have their center of distribution in the Andes (see Appendix 1). The Guayanan element accounts for 18% (110) of the genera. Genera belonging to the Guayanan element include *Brocchinia*, *Celiantha*, *Celianella*, *Chimantaea*, *Connellia*, *Duidaea*, *Duidania*, *Euphronia*, *Gongylolepis*, *Kunhardtia*, *Ledothamnus*, *Lindmania*, *Navia*, *Notopora*, *Orectanthe*, *Pterozonium*, *Raveniopsis*, *Saccifolium*, *Stegolepis*, *Stenopadus*, *Tepuia*, and *Tyleria*. Several Guayanan genera such as *Stenopadus* and *Pterozonium* have outliers, usually a single species, in the Andes or other parts of the Neotropics (see section below).

The Pantropical element is represented by 16% (100) of the genera. Of the other two tropical elements, the Asian-American element represents 2.6% (16) of the genera and the African-American 3.4% (21). Only 3% of the flora includes elements of temperate affinity, whereas the cosmopolitan element accounts for 5% (31) of the genera, including a large proportion of pteridophytes (15) and other genera such as *Cladium*, *Drosera*, *Eleocharis*, *Gnaphalium*, *Juncus*, *Liparis*, *Rhynchospora*, and *Utricularia*.

Steyermark (1986) suggested that there are recent connections of the Guayana (and Pantepui) flora with elements derived from areas outside of the Guayana Shield, as well as ancient relationships with western Gondwana or Malesian-Australasian floral elements, and these contribute to the area's floristic richness and endemism. This idea is supported by the phytogeographic spectrum of the Pantepui

flora at the generic level (Fig. 5). The Pantepui flora is predominantly composed of Neotropical elements shared with different areas (Central America, Andes, Brazilian Shield, and Amazonia), but there are also elements from more distant tropical regions (Fig. 5) that may represent relicts derived from Gondwanan times. It is not informative enough, however, to merely point out a particular distribution pattern, such as the Andean-Guayanan one, and it is also necessary to consider the broader Guayana Shield flora in addition to the more restricted Pantepui flora. The taxa need to be examined individually to determine possible directionality in disjunction patterns or else use phylogenetic tools to try to decipher the past history of a group. The next three sections illustrate variations of Guayanan distribution patterns, and the last six sections emphasize the usefulness of phylogenetic studies to elucidate historical patterns in different plant groups from the Guayana Shield.

#### *Guayanan-based groups disjunct to the Andes*

There are numerous phytogeographical connections linking the Andes and the Guayana Shield (see Appendix 1). Some, such as the high elevation composite *Oritrophium marahuacense*, are known from a single mountain in the Guayana and are evidently outliers of Andean lineages, but there is an expanding list of taxa that are Guayanan-centered, with one or a few outliers that occur in the Andes. This section focuses on a typically Guayanan suite of Andean/Guayanan taxa, that is, the bulk of their species are endemic to the Guayana Shield, and they are restricted in the Andes to sandstone outcrops or their sandy erosion products.

Recent plant explorations in southern Ecuador (the Cordillera del Condor region) and in northern and central Peru have targeted isolated mountains within the Andes that have variable extensions of sandstone outcrops. A number of species have been found



there that are either close relatives of Guayanan groups or in some cases, identical species. For example, *Stenopadus andicola* Pruski is a new species and the first Andean record of an otherwise Guayanan mutisoid genus of 15 species (Pruski 1998). It was described from sandstone outcrops in the Cordillera del Condor near the Peruvian border in southern Ecuador, and subsequently in two sandstone outcrops in Peru, including the Serranía Azul, an isolated massif in Loreto Department (Pruski 2003). *Gongyloplepis colombiana* Maguire is an Andean species of another otherwise entirely Guayana group of mutisoid composites, occurring on sandstone in Venezuela's Táchira State and adjacent areas across the Colombian border.

A remarkable Andean-Guayanan disjunction is the finding in northern Peru of *Aratitiopea lopezii* (L.B. Sm.) Steyerl. & P.E. Berry, a monotypic Xyridaceae genus that was previously known from just a few localities in the Guayana region of Colombia, Venezuela, and Brazil. Other cases of the same taxa occurring in the Guayana Shield and in the Andes include: *Digomphia densicoma* (Mart. ex DC.) Pilg. (Bignoniaceae, with two other species endemic to the Shield); *Euceraea nitida* Mart. (Flacourtiaceae/Salicaceae, with two other species endemic to the Shield); *Bonnetia paniculata* Spruce ex Benth. (Bonnetiaceae, with 25 other species endemic to the Guayana Shield, one more in Cuba and one in coastal Brazil); *Everardia montana* Ridl. ex Thurn (Cyperaceae, with 12 other species endemic to the Shield); *Pterozonium brevifrons* (A.C. Sm.) Lellinger (Pteridaceae, also present in Costa Rica), and *Pterozonium reniforme* (Mart.) Fée, with 12 other species endemic to the Shield; *Podocarpus tepuiensis* J. Buchholz & N.E. Gray (Podocarpaceae, a widespread Guayana Shield species); and *Paepalanthus dichotomus* Klotzsch ex Körn. (Eriocaulaceae, a widespread Guayana Shield species).

There is also an undescribed species in southern Ecuador of *Phainantha* (Melastomataceae, with four other species endemic to the Guayana Shield), the same as with *Lissocarpa* (Lissocarpaceae/Ebenaceae, a genus with one other Andean species and several endemic Guayanan ones). Lastly, *Perissocarpa ondox* B. Walln. (Ochnaceae) was recently described from a montane area of Huánuco, Peru (Wallnöfer 1998); the other two species in the genus are endemic to the Guayana Shield as well as parts of the Venezuelan Andes and coastal cordilleras.

In addition to these clear disjunctions, there are more widespread genera that are most diverse in sandy substrates of the Guayana Shield, but occur in similar substrates in eastern Brazil; Amazonian Brazil and Peru, and occasionally into the montane sandstone areas of northern Peru. These include Rubiaceae taxa such as *Pagamea guianensis* Aubl., *Retiniphyllum fuchsoides* K. Krause, and *Retiniphyllum martianum* Muell. Arg.

#### *Recent Guayana-western Africa disjuncts*

There are many examples of genera and even species that are disjunct between tropical South American and tropical Africa (Goldblatt 1993), but there is a recurring pattern in which a single species of an otherwise entirely Neotropical clade is found in tropical West Africa. In most cases, this pattern has been shown to be the result of long-distance dispersal events from America to Africa. This is the case for *Maschalocephalus dinklagei*, in the Rapateaceae, which is part of a lowland Guayanan lineage that appears to have diverged from its South American relatives about 6 million years ago (Givnish *et al.* 2004). Similarly, *Pitcarinia feliciana*, in the Bromeliaceae, appears to have diverged from South American ancestors about 8 million years ago (Givnish *et al.* 2004). In Vochysiaceae, which has two genera occurring in western Africa (*Erismadelphus* and *Korupodendron*), Syts-



ma *et al.* (2004) estimated that *Erismadelphus* diverged from its closest American ancestor around 41 million years ago, too late for this to be the result of a Gondwanan vicariant event.

Other groups with a similar trans-Atlantic distribution with a sole outlier in western Africa include *Mayaca* (Mayacaceae), *Sacoglottis* (Humiriaceae), *Rhipsalis* (Cactaceae), and *Voyria* and *Schultesia* (Gentianaceae). So far the African taxa in these groups have not been included in molecular-based cladistic studies, but Albert and Struwe (1997) performed a morphologically based cladistic analysis of *Voyria*, a saprophytic genus with 18 species centered in the Guayana Shield region and one species disjunct to tropical West Africa (*V. primuloides*). The African species was nested well within the American taxa, in the same pattern found in Rapateaceae and Bromeliaceae, but instead of invoking long-distance dispersal, Albert and Struwe hypothesized a boreotropical distribution. In *Schultesia*, a similar pattern occurs, with *S. stenophylla* native to western Africa, yet in this case Struwe *et al.* (2002) invoked recent long-distance dispersal to account for the disjunction. In the case of *Voyria*, which has dust-like seeds dispersed by wind or by rain wash (Albert & Struwe 1997), and for which there is no fossil record from North America, it appears more likely it is simply another case of long-distance dispersal from South America to Africa.

#### *Guayana-Malesian disjuncts*

Several genera that are endemic or most diverse in the Guayana Region have their closest relatives in the Malesian region, generally without extant representatives elsewhere. In the Ericales, the monotypic *Pentamerista neotropica* is a tree known only from edges of sandy savannas along the Venezuelan-Colombian border, and it is sister to *Tetramerista*, a genus of three Malesian species in the Tetrameristaceae (J. Schonenberg unpubl. data). These in turn are sister to *Pelliciera rhizophorae*, a monotypic

mangrove genus occurring on either side of the Isthmus of Panama. Before its close relationship to *Tetramerista* was recognized, *Pelliciera* was treated as the sole member of the Pellicieraceae, but it has since been merged into the Tetrameristaceae (Bremer *et al.* 2002).

*Tepuianthus* is a shrubby genus of six species endemic to sandy savannas and tepui summits of the Guayana Shield. When first described, it was placed in its own family, Tepuianthaceae (Maguire & Steyermark 1981) and allied to either the Celastrales or Theales. After sequencing three gene regions, Wurdack and Horn (2001) placed it instead in the Malvales, sister to Thymelaeaceae. They propose placing *Tepuianthus* in a new subfamily of Thymelaeaceae, with the Malesian *Gonystylus* as its closest relative.

The Bonnetiaceae, as currently circumscribed (APG II 2003), contains three genera, the Malesian *Ploiarium* (3 species), the Guayana Shield endemic *Archytaea* (2 species), and *Bonnetia* (28 species), the latter confined to the Guayana Shield except for *B. cubensis* (Cuba, Puerto Rico), *B. stricta* (eastern Brazil), and *B. paniculata* (Andes of Venezuela, Colombia, Ecuador, and Peru, as well as the Guayana Shield). Only *Bonnetia roraimae* has been reliably sequenced to date (APG II 2003), yet this group is richer in genera and species than the other families discussed above, and future molecular studies should address the relationships of the extra-Guayan species of *Bonnetia* to the more numerous and diverse Guayana Shield taxa, as well as the relationships among the three genera in the family. On morphological grounds, it appears that *Ploiarium* and *Archytaea* are more closely related to each other than either is to *Bonnetia* (A. Weitzman pers. com.).

#### *Commelinid monocots*

The commelinid monocot families (*sensu* APG II 2003) are particularly diverse in the Guayana Region, including groups that have much of



their diversity there, such as Bromeliaceae, Eriocaulaceae, Mayacaceae, Rapateaceae, Thurniaceae, and Xyridaceae. Two of these families, Bromeliaceae and Rapateaceae, have been the subject of molecular phylogenetic studies by Givnish *et al.* (1997, 2000, 2004, in press). *Brocchinia*, a genus of 20 species entirely endemic to the Guayana Shield, has been shown by analyses of the chloroplast *ndhF* molecular region to be the basalmost lineage within the Bromeliaceae, constituting a new subfamily Brocchinioideae. *Lindmania*, another genus endemic to the Guayana Region with about 20 species, is the next diverging lineage and may represent an additional subfamily. Besides this, there is a "cratonic clade" that is endemic to the Guayana and secondarily the Brazilian Shields, comprising the genera *Navia*, *Brewcaria*, *Connellia*, and *Cottendorfia*. A preliminary molecular clock analysis dates the diversification of the extant lineages of Bromeliaceae at ca. 17 million years ago, suggesting that the family as a whole has undergone a relatively recent radiation (Givnish *et al.* in press). The basal positions of *Brocchinia* and *Lindmania* indicate that the family originated in the Guayana Shield area, possibly spreading westwards from there into the Andes and south and east into Brazil for some of the other major lineages. The sole Old World member of the family, *Pitcairnia feliciana* from western tropical Africa, is a basal member of the Pitcairnioideae *sensu stricto* and most likely arrived there via long-distance transatlantic dispersal, around 8 million years ago according to initial molecular clock calibrations.

The exclusively Guayanian Bromeliaceae genus *Brocchinia* was examined in detail by Givnish *et al.* (1997), and several evolutionary trends are apparent. The earliest diverging species in the genus occur in the sandy lowlands, and the genus apparently invaded upland and highland habitats at the same time that certain lineages developed a diverse array

of adaptations such as epiphytism, tank formation, myrmecophily, and carnivory. A morphologically distinctive species formerly known as *Ayensua uaipenensis* has also been shown to belong to *Brocchinia* (Givnish *et al.* in press).

The Rapateaceae comprise 17 genera and about 100 species, with all genera but one present or endemic to the Guayana Shield (*Maschalocephalus dinklagei* is endemic to sand plains in west tropical Africa). An *ndhF* analysis of the family shows an analogous situation to *Brocchinia*, with the basal lineages all lowland in distribution, and the more advanced *Stegolepis* alliance restricted to uplands and highlands (Givnish *et al.* 2000). A possible secondary occupation of lowland sand-savannas is evidenced by *Guacamaya* and *Schoenocephalum* (tribe Schoenocephalieae). Within the predominantly high-elevation subfamily Saxofridericioideae, tribe Saxofridericieae is now restricted to the genus *Saxofridericia*, which no longer groups with *Stegolepis* but rather is the sister group to the three hummingbird-pollinated genera that comprise the Schoenocephalieae (Berry 2004). The validity of some of the genera in the new tribe Stegolepideae is also in doubt, particularly the monotypic high elevation genera *Amphiphyllum*, *Phelpsiella*, and *Marahuacaea*.

A molecular clock analysis of the family suggests a recent, long-distance dispersal event to Africa, between 5 and 6 million years ago, to account for the presence of *Maschalocephalus* there (Givnish *et al.* 2004). According to the same analysis, one of the earliest diverging genera in the family, the lowland genus *Spathanthus*, split from the rest of the family around 29 million years ago. Without a doubt, the most interesting and controversial implication of the molecular clock analysis is that the mostly high-montane genus *Stegolepis*, which is now the most diverse genus in the family (with ca. 36 species) and a typical inhabitant of most tepui summits, only began to diversify as little



as 6 million years ago. This young age needs to be further tested with other gene regions and more rigorous molecular clock analyses, but if it is corroborated, then *Stegolepis* and its immediate ancestors should not be perceived as ancient inhabitants of the original highland tepui surface. Just how *Stegolepis* could have come to inhabit virtually all of the tepui summits in this time span is problematical, especially considering the low dispersability of its seeds, but there is currently an opportunity for migration between tepuis across intermediate elevations such as the Gran Sabana in southeastern Venezuela (see Fig. 2). Furthermore, Rull (1994, 2004) demonstrated significant lowering of tepui vegetation zones on the summit of the Chimantá massif during cooler periods of the Holocene, which would have further facilitated migrations among the eastern tepuis. However, it does little to explain how *Stegolepis* could have reached the summits of more isolated mountains in the western sector of Pantepui, such as Neblina and Marahuaka, which are separated from other tepui summits by hundreds of kilometers of lowland forest habitats.

#### *Mutisioid Asteraceae*

The Guayanan mutisioid genera of the Asteraceae are some of the most characteristic members of the endemic Guayana flora, but only *Duidaea* has been sequenced and was included in a preliminary molecular analysis of the tribe by Kim *et al.* (2002). In the latest phylogenetic reevaluation of the subfamilies of the Asteraceae (Panero & Funk 2002), the Guayana mutisioid genera are included as part of the “*Stiffia* group” of the Mutisieae tribe. Although the predominantly southern Andean tribe Barnadesieae is the earliest diverging lineage in the Asteraceae, the Guayanan mutisioids are part of the next diverging clade within the family and comprise a significant early radiation of the family in the Guayana

Shield region. Most of the Guayanan genera are restricted to either the Pantepui Province or the adjacent upland portions of the shield. Many of the bilabiate-flowered genera are endemic to the western part of Pantepui, such as *Duidaea*, *Eurydochus*, *Glossarion*, and *Neblinea*. *Gongylolepis* occurs throughout Pantepui, as well as some lowland white-sand areas, with one species disjunct to the Andes of Venezuela and adjacent Colombia. The actinomorphic-flowered Guayanan Mutisieae include *Chimantaea*, *Quelchia*, *Stenopadus*, and *Stomatochaeta*, which are mostly confined to the eastern part of Pantepui, although *Stenopadus* includes one species that is endemic to sandstone mountains in the Andes of southern Ecuador and north-central Peru (Pruski 1998). A better molecular sampling of the Guayanan genera is a high priority if we wish to understand the relationships among the mutisioids in general and among the bilabiate and actinomorphic-flowered genera endemic to the Guayana region, which are an important early diverging lineage within the family.

#### *Sarraceniaceae*

The Sarraceniaceae include three genera of carnivorous New World pitcher plants. *Heliamphora* is a genus of about nine species endemic to high elevations of the Guayana Shield. *Sarracenia* includes nine species widespread in boggy areas of North America, particularly in the southeastern United States. *Darlingtonia* has one species endemic to boggy areas on serpentine outcrops in Oregon and Washington states. Morphologically based studies grouped *Darlingtonia* and *Sarracenia* as sister taxa, with *Heliamphora* supposedly having more plesiomorphic characters (Maguire 1970, 1978). Thus it was assumed that the family had originated in South America and spread from there to North America (Maguire 1970; Juniper *et al.* 1989). Albert *et al.* (1992) performed the first phylogenetic study across



groups of carnivorous plants, and they included members of the three genera of Sarraceniaceae. Their results, which were confirmed by Bayer *et al.* (1996) with both chloroplast and nuclear gene regions, showed that *Darlingtonia* is the earlier-diverging lineage, and that *Heliampora* and *Sarracenia* are sister taxa. The South African carnivorous *Roridula* (Roridulaceae) was the closest sister group to Sarraceniaceae, raising interesting biogeographic scenarios for the evolution of the three New World pitcher plant genera. Parsimoniously, the family would be more likely to have had a North American origin, with vicariance or dispersal to South America. Although there is no fossil record for members of the Sarraceniaceae, their current distribution and the presence of fossil seeds of the related *Actinidia* from the Eocene of Oregon (Manchester 1994) suggests a boreotropical distribution (Lavin & Luckow 1993). Within *Heliampora*, in which three species were sampled by Bayer *et al.* (1996), the western tepui species *H. tatei* was embedded in an eastern tepui lineage, which suggests for this group that the genus evolved from the east to the west. This also agrees with the higher diversity of the genus in the eastern tepuis. Similar hypotheses should be explored with other groups occurring on a wide geographical range of tepuis.

#### *Gentianaceae*

This is a key family, with many endemic genera in the Guayana Shield. Thiv *et al.* (1999) used molecular results from several gene regions to show that *Saccifolium bandeirae*, which was formerly placed as the sole member of the Saccifoliaceae, belongs in a basal clade of the Gentianaceae together with *Curtia*, the saprophytic *Voyriella*, and presumably *Hockinia* and *Tapeinos-tonon* (the latter two not sampled in their molecular study). *Saccifolium* is perhaps the finest example of a restricted Guayanan endemic – with a single population known only from the

upper slopes of the highest peak of the Guayana Shield, Pico de Neblina, which reaches 3014 m elevation. It has alternate, saccate leaves and imbricate corolla aestivation, both unusual characters for the Gentianaceae. Biogeographically, all five members of the early-diverging tribe Saccifolieae are Neotropical and centered on the Guayana and Brazilian Shields, which may be the area where the family originated (Struwe *et al.* 2002).

The Helieae is an entirely Neotropical tribe of about 23 genera that contains several Guayanan endemic genera (*Celiantha*, *Chorisepalum*, *Irlbachia*, *Neblinantha*, and *Sipapoantha*) and additional endemic species in genera such as *Chelonanthus*, *Macrocarpaea*, *Rogersonanthus*, *Symbolanthus*, and *Wurdackanthus*. There appear to be several biogeographic patterns of different ages in this tribe, but the hypothesis that Pantepui and the Guayana Shield are an ancient area of diversification and speciation for part of the tribe is supported by the early-diverging position of *Chorisepalum*. Andean-dominated lineages such as *Macrocarpaea* and *Symbolanthus* may represent a more recent diversification with subsequent dispersal to the tepui region for the taxa that are endemic there now (Struwe *et al.* 2002).

Tribe Potalieae comprises 13 diverse tropical genera grouped into three subtribes (Struwe *et al.* 2002). Subtribe Potaliinae was formerly assigned to Loganiaceae and includes the Neotropical genus *Potalia* (9 species), as well as the African-Malagasy *Anthocleista* (14 species) and the Australasian-Pacific *Fagraea* (70 species). Within this subtribe, the three genera form a grade, with *Fagraea* sister to *Potalia* and *Anthocleista*. Molecular clock analysis has not been performed yet in this group, but this kind of distribution could reflect either a more ancient Gondwanan vicariance pattern or a mid-Tertiary boreotropical pattern, if the distribution is due primarily to vicariance events.



### *Dipterocarpaceae*

The Dipterocarpaceae was considered an exclusively Old World family until 1977, when *Pakaraimaea dipterocarpacea* was described from the Guayana Shield in Guyana and Venezuela and assigned to its own subfamily (Maguire *et al.* 1977). The familial placement of this genus was later disputed, and a new family Monotaceae was described by Kostermans (1989) to differentiate it and other African genera from the more numerous Asian dipterocarps (it was treated as Monotaceae in Vol. 6 of the *Flora of the Venezuelan Guayana*). Subsequently, a second South American genus (*Pseudomonotes tropenbosii*) was described from the western end of the Guayana Shield (Londoño *et al.* 1995). On morphological criteria, *Pseudomonotes* is more closely related to African and Malagasy genera than it is to *Pakaraimaea*. Molecular studies were conducted on slightly different subsets of the dipterocarp alliance by Morton *et al.* (1999) and Dayanandan *et al.* (1999). These results showed *Pseudomonotes* to be strongly supported as the sister clade to African *Monotes*, and these were sister to a moderately supported clade composed of *Pakaraimaea* plus the rest of the family, namely the diverse Asian subfamily Dipterocarpoideae. Contrary to what one would expect from the present-day diversity of the family in Asia, these studies suggest that Dipterocarpaceae is west Gondwanan in origin and confirm that the two South American genera belong to separate lineages within the family.

### *Lecythidaceae*

*Asteranthos brasiliensis* Desf. is the only member of a genus endemic to the upper Río Negro basin in the Guayana Shield, and it is part of a clade with five tropical west African genera that formerly composed the Scytopetalaceae. Based on molecular and morphological cladistic analyses, these six genera are now treated as the subfamily Scytopetaloidae in the Lecythi-

daceae (Morton *et al.* 1998). This is an early-diverging clade within the family, along with the subfamily Napoleoneoideae, which has two genera that are also restricted to tropical west Africa.

Since the Guayana Shield is a remote, tropical region where it is arduous to make even traditional herbarium collections, it is not surprising that so few molecular-based phylogenetic studies have been carried out on plants from this region. Because there are many interesting phytogeographic and ecogeographic relationships that could be elucidated with robust phylogenies in different groups, it is an extremely apt area to use modern molecular tools. The previous sections show some of the promise that molecular studies have for understanding the evolution and biogeography of plant groups that are restricted to this ancient geological shield.

## Conclusions

The Guayana Shield and its tepuis have long been considered a major center of diversity and endemism in the Neotropics. A database of the vascular plant species present in the Pantepui Province (above 1500 m elevation) has refined the figures for endemism since the publishing of the introductory volume of the *Flora of the Venezuelan Guayana* in 1995. It is now possible to compare the species composition for each of the 38 tepuis for which we have reliable data and to show which tepuis have the most diverse flora and highest degrees of endemism. The Pantepui flora has a strong endemic component, with 42% of its 2447 species endemic there, and 25% of all species occurring there are both endemic and known so far from a single tepui. At the genus level, 70% of the Pantepui genera are restricted to the Neotropics, which includes 18% of the genera endemic to Pantepui Province. This paper discriminates certain patterns into clearly



Guayana-based disjunctions, such as disjuncts between Guayana and Africa, and Guayana and the Andes. Some patterns, such as Malesian-Guayan groups, are more noticeable at the level of the Guayana Shield, rather than Pantepui alone. Phylogenetic studies based on molecular analyses have begun to present evolutionary scenarios for different groups of Guayan taxa, and the results to date show a diverse array of patterns that appear specific to each particular group. A number of plant families appear to have their basalmost lineages present in, or restricted to, the Guayana Region, which suggests an important role of the region in the early evolution of those families. It is still too early to date the evolution of many tepui lineages, but initial data on families such as Bromeliaceae and Rapateaceae suggests that some groups that are now speciose and endemic in Pantepui may represent secondary radiations, with the earliest diverging extant members of the groups occurring now in lowland areas of the Shield.

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**Appendix 1.** List of genera (total = 626) for each of the phylogeographic elements present in Pantepui (see Fig. 5).

### NEOTROPICAL (434)

#### ANDEAN (26)

Asteraceae: *Ageratina*, *Baccharis*, *Oritrophium*, *Pentacalia*; Bromeliaceae: *Puya*; Brunelliaceae: *Brunellia*; Campanulaceae: *Burmeistera*, *Centropogon*, *Siphocampylus*; Ericaceae: *Cavendishia*, *Disterigma*, *Orthaea*; Gentianaceae: *Macroparapa*, *Symbolanthus*; Liliaceae: *Ecremis*; Magnoliaceae: *Dugandiodendron*; Marcgraviaceae: *Sarcopera*; Melastomataceae: *Chaetolepis*, *Monochaetum*; Orchidaceae: *Gomphichis*, *Pterichis*; Poaceae: *Chusquea*, *Neurolepis*; Polygalaceae: *Monina*; Pteridaceae: *Eriosorus*; Rosaceae: *Hesperomeles*.

#### BRAZILIAN SHIELD (8)

Eriocaulaceae: *Leiothrix*; Melastomataceae: *Bertolonia*, *Marsetia*, *Microlicia*, *Tibouchina*; Scrophulariaceae: *Velloziella*; Velloziaceae: *Barbacenia*, *Vellozia*.

#### GUAYANAN ENDEMIC (110)

Apocynaceae: *Salpinctes*; Asteraceae: *Achnopogon*, *Chimantaea*, *Duida*, *Glossarion*, *Gongyolopsis* (1 sp. in the N Andes), *Guayana*, *Huberopappus*, *Imeria*, *Neblinaea*, *Quelchia*, *Stenopadus* (1 sp. in central Andes), *Stomatochaeta*, *Tyleropappus*; Bignoniaceae: *Digomphia* (1 sp. in central Andes); Bonnetiaceae: *Archytaea*, *Bonnetia* (1 sp. in Greater Antilles, a second sp. in the Brazilian Shield, a third one in the Andes); Bromeliaceae: *Ayensua*, *Brewcaria*, *Brocchinia*, *Connellya*, *Lindmania*, *Navia*, *Steyerbromelia*; Caesalpiniaceae: *Dicymba*; Clusiaceae: *Moronobia* (1 sp. in lowland Peru), *Neotatea*; Cyclanthaceae: *Stelestylis*; Cyperaceae: *Cephalocarpus*, *Didymiandrum*, *Everardia* (1 sp. in central Andes), *Rhynchocladium*, *Trilepis*; Ericaceae: *Ledothamnus*, *Mycerinus*, *Notopora*, *Tepuia*; Eriocaulaceae: *Rondonanthus*; Euphorbiaceae: *Celianella*, *Dendrothrix*, *Senefeldersopsis*; Euphroniaceae: *Euphronia*; Fabaceae: *Aldina*; Flacourtiaceae: *Euceraea* (1 sp. in central Andes); Gentianaceae: *Celiantha*, *Chelonanthus* (1 sp. widespread in the Neotropics), *Chorisepalum*, *Irlbachia*, *Neblinantha*, *Rogersonanthus*, *Saccifolium*, *Sipapoantha*, *Wurdackanthus* (1 sp. in the Lesser Antilles); Gesneriaceae: *Rhoogeton*; Haemodoraceae: *Pyrrothiza*; Humiriaceae: *Humiria*; Hymenophylloidsaceae: *Hymenophyllopsis*; Liliaceae: *Nietneria*; Malpighiaceae: *Blepharandra*, *Diacidia*; Melastomataceae: *Acanthella*, *Comoliopsis*, *Macairea*, *Macrocentrum*, *Mallophyton*, *Neblinantha*, *Tateanthus*, *Phainantha* (1 sp. in Ecuador); Ochnaceae: *Adenanthe*, *Adenarake*, *Philacra*, *Poecilandra*, *Tyleria*; Orchidaceae: *Aracamunia*, *Duckeella*, *Guanchezia*, *Helonoma*; Poaceae: *Myriocladus*; Podostemaceae: *Jemmaniella*; Pteridaceae: *Pterozonium* (2 spp. in central Andes, 1 in Costa Rica); Rapateaceae: *Amphiphyllyum*, *Kunhardtia*, *Marahuacaea*, *Phelpsella*, *Rapatea* (mostly lowlands), *Saxofridericia*, *Stegolepis*; Rubiaceae: *Aphanocarpus*, *Cephalodendron*, *Chalepophyllum*, *Coccochondra*,

*Coryphothamnus*, *Duidania*, *Maguireocharis*, *Maguireothamnus*, *Merumea*, *Neblinathamnus*, *Pagameopsis*, *Platycarpum* (1 sp. in lowland Peru), *Retiniphyllum*, *Sipanea*; Rutaceae: *Decagonocarpus*, *Raveniopsis*, *Rutaneblina*; Sarracenaceae: *Heliampora*; Tepuianthaceae: *Tepuianthus*; Xyridaceae: *Abolboda*, *Achlyphila*, *Aratitiopea* (also in Peruvian Andes), *Orectanthe*.

#### LOWLAND AMAZONIAN SOUTH AMERICA (18)

Apocynaceae: *Galactophora*, *Macropharynx*; Bombacaceae: *Catostemma*; Burmanniaceae: *Hexapterella*; Caesalpiniaceae: *Dimorphandra*; Clusiaceae: *Caraipe*, *Mahurea*; Fabaceae: *Alexa*, *Diptotropis*; Hugoniaceae: *Roucheria*; Icacinaceae: *Emmotum*; Melastomataceae: *Ernestia*, *Salpinga*; Olacaceae: *Dulacia*; Ochnaceae: *Elvasia*; Rubiaceae: *Emmeorhiza*, *Gleasonia*; Vochysiaceae: *Ruizterania*.

#### WIDE NEOTROPICAL (273)

Annonaceae: *Guatteria*, *Duguetia*; Apocynaceae: *Aspidosperma*, *Couma*, *Mandevilla*; Araceae: *Anthurium*, *Dieffenbachia*, *Philodendron*, *Stenospermation*; Araliaceae: *Oreopanax*; Arecaceae: *Bactris*, *Dictyocaryum*, *Euterpe*, *Geonoma*, *Maripa*, *Prestoea*; Asclepiadaceae: *Blepharodon*, *Ditassa*, *Macroditassa*, *Matelea*, *Nephradenia*; Asteraceae: *Ageratum*, *Ayapana*, *Calea*, *Chionolaena*, *Chromolaena*, *Erechtites*, *Fleischmannia*, *Gamochaeta*, *Koanophyllum*, *Lepidaploa*, *Oyedaea*, *Piptocarpha*, *Piptocoma*, *Praxelis*, *Verbesina*; Balanophoraceae: *Helosis*; Bignoniaceae: *Distictella*, *Tabebuia*; Bombacaceae: *Matisia*; Bromeliaceae: *Aechmea*, *Guzmania*, *Mezobromelia*, *Pitcairnia* (1 sp. in W Africa), *Racinaea*, *Tillandsia*, *Vriesea*; Burmanniaceae: *Dictyostegia*; Caesalpiniaceae: *Macrobium*; Caryocaraceae: *Anthodiscus*, *Caryocar*; Cecropiaceae: *Cecropia*, *Coussapoa*, *Pourouma*; Clusiaceae: *Tovomita*, *Vismia*; Combretaceae: *Buchenavia*; Commelinaceae: *Tradescantia*; Cucurbitaceae: *Gurania*; Cyclanthaceae: *Asplundia*, *Dicranopygium*, *Sphaeradenia*; Cyperaceae: *Calyptrocarya*, *Lagenocarpus*, *Pleurostachys*; Cyrillaceae: *Cyrilla*, *Purdiaea*; Chrysobalanaceae: *Couepia*; Dennstaedtiaceae: *Ormoloma*; Dicksoniaceae: *Culcita*; Dilleniaceae: *Doliocarpus*; Dryopteridaceae: *Cyclodium*, *Stigmatopteris*; Eremolepidaceae: *Antidaphne*, *Eubrachion*; Ericaceae: *Bejaria*, *Gaylussacia*, *Psammisia*, *Satyrina*, *Sphyrospermum*, *Thibaudia*; Euphorbiaceae: *Conceveiba* (1 sp. in Africa), *Hyeronima*, *Mabea*, *Richeria*; Fabaceae: *Swartzia*, *Taralea*; Gentianaceae: *Curtia*, *Schultesia* (1 sp. in W Africa), *Tachia*, *Tapeinostemon*, *Tetrapollinia*, *Voyria* (1 sp. in Africa); Gesneriaceae: *Alloplectus*, *Besleria*, *Columnnea*, *Corytoplectus*, *Diastema*, *Drymonia*, *Episcia*, *Nautilocalyx*; Grammitidaceae: *Ceradenia*, *Cochlidium*; Haemodoraceae: *Xiphidium*; Hippocrateaceae: *Cheiloclinium*, *Peritassa*; Icacinaceae: *Discophora*; Iridaceae: *Trimezia*; Lamiaceae: *Hyptis*; Lauraceae: *Aniba*, *Endlicheria*,



*Licaria*, *Nectandra*, *Rhodostemonodaphne*, *Sextonia*; Liliaceae: *Isidrogalvia*; Lissocarpaceae: *Lissocarpa*; Loasaceae: *Klaprothia*; Loranthaceae: *Byrsonima*, *Cladocolea*, *Gaiadendron*, *Phthirusa*, *Psittacanthus*, *Struthanthus*, *Tripodanthus*; Malpighiaceae: *Banisteriopsis*, *Eriopsis*, *Hiraea*, *Pterandra*, *Tetrapteryx*; Marantaceae: *Ischnosiphon*; Marattiaceae: *Danaea*; Marcgraviaceae: *Marcgravia*; Mayacaceae: *Mayaca* (1 sp. in W Africa); Melastomataceae: *Aciotis*, *Adelobotrys*, *Centronia*, *Clidemia*, *Comolia*, *Conostegia*, *Graffenrieda*, *Henriettella*, *Leandra*, *Maieta*, *Meriania*, *Miconia*, *Tococa*, *Topobea*, *Siphanthera*; Metaxyaceae: *Metaxya*; Mimosaceae: *Abarema*, *Calliandra*, *Inga*; Monimiaceae: *Mollinedia*; Myristicaceae: *Virola*; Myrsinaceae: *Cybianthus*; Myrtaceae: *Blepharocalyx*, *Calycolpus*, *Calyptanthes*, *Marlierea*, *Myrcianthes*, *Siphoneu-gena*; Nyctaginaceae: *Neea*; Ochnaceae: *Perissocarpa*; Orchidaceae: *Acineta*, *Baskervilla*, *Bletia*, *Brachionidium*, *Catasetum*, *Cattleya*, *Cleistes*, *Comparettia*, *Coryanthes*, *Cryptocentrum*, *Cyrtopodium*, *Dichaea*, *Dryadella*, *Elleanthus*, *Encyclia*, *Epidendrum*, *Epistephium*, *Galeottia*, *Gongora*, *Hexisea*, *Houlletia*, *Jacquinella*, *Lepanthes*, *Lepanthopsis*, *Lockhartia*, *Lueddemannia*, *Lycaste*, *Masdevallia*, *Myoxanthus*, *Octomeria*, *Oncidium*, *Ophidion*, *Otoglossum*, *Otostylis*, *Peristeria*, *Phragmipedium*, *Pinelianne*, *Pleurothallis*, *Polycycnis*, *Ponthieva*, *Prescottia*, *Prosthechea*, *Psilochilus*, *Restrepipsis*, *Scaphosepalum*, *Scaphyglottis*, *Scelochilus*, *Selenipedium*, *Sievekingia*, *Sobralia*, *Stanhopea*, *Stelis*, *Trichosalpinx*, *Vargasiella*, *Xylobium*, *Zygosepalum*; Poaceae: *Aegopogon*, *Arthrostylidium*, *Aulonemia*, *Axonopus* (1 sp. in Africa), *Ichnanthus*, *Merostachys*, *Parodiolyra*, *Thrasya*; Polygonaceae: *Coccoloba*; Polypodiaceae: *Campyloneurum*, *Pectuma*; Proteaceae: *Euplassa*; *Panopsis*; *Roupala*; Quinaceae: *Froesia*, *Quiina*; Rhizophoraceae: *Sterigmataleum*; Rubiaceae: *Coccocypselum*, *Chiococca*, *Duroia*, *Elaeagia*, *Fareamea*, *Hillia*, *Kotchubaea*, *Ladenbergia*, *Malanea*, *Palicourea*, *Pagamea*, *Perama*, *Remijia*, *Rudgea*; Rutaceae: *Spathelia*; Sapindaceae: *Cupania*, *Matayba*; Sapotaceae: *Ecclinusa*, *Elaeoluma*, *Micropholis*, *Pradosia*; Scrophulariaceae: *Achetaria*, *Escobedia*; Simaroubaceae: *Picramnia*; Solanaceae: *Cestrum*, *Markea*, *Solandra*; Theaceae: *Freziera*; Thymelaeaceae: *Daphnopsis*; Verbenaceae: *Aegiphila*, *Amasonia*, *Duranta*; Viscaceae: *Dendrophthora*, *Phoradendron*; Vochysiaceae: *Qualea*, *Vochysia*.

**AFRICAN-AMERICAN (21)** (some genera with single species in Africa are included in the Guayanian or wide Neotropical elements)

Asteraceae: *Achyrocline*; Chrysobalanaceae: *Hirtella*; Clusiaceae: *Symphonia*; Dennstaedtiaceae: *Blotiella*; Dryopteridaceae: *Megalastrum*; Eriocaulaceae: *Syngonanthus*; Euphorbiaceae: *Amanoa*; Grammitidaceae: *Enterosora*, *Zygothlebia*; Lentibulariaceae: *Gentisea*; Malpighiaceae: *Heteropteryx*;

Meliaceae: *Guarea*, *Trichilia*; Poaceae: *Echinolaena*, *Lasiacis*, *Olyra*; Pteridaceae: *Pityrogramma*; Rubiaceae: *Sabicea*; Turneraeaceae: *Turnera*; Verbenaceae: *Lippia*; Zingiberaceae: *Renealmia*.

#### ASIAN-AMERICAN (16)

Asteraceae: *Austroeupeatorium*; Chloranthaceae: *Hedyosmum*; Clethraceae: *Clethra*; Cyperaceae: *Uncinia*; Dennstaedtiaceae: *Paesia*; Fabaceae: *Desmodium*, *Ormosia*; Gleicheniaceae: *Diplopterygium*; Heliconiaceae: *Heliconia*; Lauraceae: *Persea*; Orchidaceae: *Erythrodus*; Plagiogyriaceae: *Plagiogyria*; Rubiaceae: *Schradera*; Sabiaceae: *Meliosma*; Symplocaceae: *Symplocos*; Theaceae: *Gordonia*.

#### PANTROPICAL (100)

Apocynaceae: *Rauvolfia*, *Tabernaemontana*; Aquifoliaceae: *Ilex*; Araliaceae: *Schefflera*; Aristolochiaceae: *Aristolochia*; Asclepiadaceae: *Cynanchum*; Asteraceae: *Conyza*, *Mikania*; Balanophoraceae: *Langsdorffia*; Begoniaceae: *Begonia*; Bombacaceae: *Pachira*; Boraginaceae: *Cordia*; Burmanniaceae: *Burmannia*; Burseraceae: *Dacryodes*, *Protium*; Caesalpinaceae: *Chamaecrista*; Celastraceae: *Maytenus*; Chrysobalanaceae: *Licania*; Clusiaceae: *Clusia*; Combretaceae: *Terminalia*; Connaraceae: *Rourea*; Cyatheaceae: *Alsophila*, *Cyathea*; Cyperaceae: *Hypolytrum*, *Mapania*, *Scleria*; Davalliaceae: *Nephrolepis*; Dennstaedtiaceae: *Dennstaedtia*, *Histiopteris*, *Hypolepis*, *Lindsaea*, *Saccoloma*; Dioscoreaceae: *Dioscorea*; Dryopteridaceae: *Arachniodes*, *Diplazium*, *Elaphoglossum*, *Lastreopsis*, *Oleandra*, *Tectaria*; Ebenaceae: *Diospyros*; Elaeocarpaceae: *Sloanea*; Eriocaulaceae: *Paepalanthus*; Erythroxylaceae: *Erythroxylum*; Euphorbiaceae: *Croton*, *Dalechampia*, *Phyllanthus*; Fabaceae: *Dioclea*; Flacourtiaceae: *Casearia*; Gleicheniaceae: *Dicranopteris*, *Sticherus*; Gnetaceae: *Gnetum*; Grammitidaceae: *Grammitis*; Haloragaceae: *Laurembergia*; Hymenophyllaceae: *Hymenophyllum*, *Trichomanes*; Lauraceae: *Ocotea*; Lythraceae: *Cuphea*; Malvaceae: *Sida*; Moraceae: *Ficus*; Myrsinaceae: *Myrsine*; Myrtaceae: *Eugenia*; Ochnaceae: *Ouratea*, *Sauvagesia*; Olacaceae: *Schoepfia*; Orchidaceae: *Bulbophyllum*, *Eulophia*, *Habenaria*, *Maxillaria*; Oxalidaceae: *Biophytum*; Passifloraceae: *Passiflora*; Phytolaccaceae: *Phytolacca*; Piperaceae: *Peperomia*, *Piper*; Poaceae: *Andropogon*, *Eriochrysis*, *Isachne*, *Oplismenus*, *Pennisetum*, *Saccharum*, *Paspalum*; Polygalaceae: *Securidaca*; Polypodiaceae: *Pleopeltis*; Pteridaceae: *Doryopteris*; Rubiaceae: *Borreria*, *Psychotria*; Rutaceae: *Zanthoxylum*; Santalaceae: *Thesium*; Sapotaceae: *Chrysophyllum*, *Pouteria*; Schizaeaceae: *Anemia*; Selaginellaceae: *Selaginella*; Simaroubaceae: *Simarouba*; Smilacaceae: *Smilax*; Theaceae: *Ternstroemia*; Thelypteridaceae: *Thelypteris*; Urticaceae: *Pilea*; Vitaceae: *Cissus*; Vittariaceae: *Antrophyum*; Vittariaceae: *Vittaria*; Xyridaceae: *Xyris*.



**AUSTRAL-ANTARCTIC (11)**

Cyperaceae: *Oreobolus*; Cunoniaceae: *Weinmannia*; Dryopteridaceae: *Rumohra*; Ericaceae: *Gaultheria*, *Pernettya*; Myrtaceae: *Myrteola*, *Ugni*; Poaceae: *Cortaderia*; Podocarpaceae: *Podocarpus*; Rubiaceae: *Nertera*; Winteraceae: *Drimys*.

**HOLARCTIC (6)**

Caprifoliaceae: *Viburnum*; Ericaceae: *Vaccinium*; Myricaceae: *Myrica*; Scrophulariaceae: *Castilleja*; Rosaceae: *Prunus*; Rhamnaceae: *Rhamnus*.

**WIDE TEMPERATE (6)**

Cyperaceae: *Carex*; Hypericaceae: *Hypericum*; Myrtaceae: *Myrcia*; Rosaceae: *Rubus*; Rubiaceae: *Galium*; Valerianaceae: *Valeriana*.

**COSMOPOLITAN (31)**

Acanthaceae: *Justicia*; Aspleniaceae: *Asplenium*; Asteraceae: *Gnaphalium*; Blechnaceae: *Blechnum*; Cyperaceae: *Cladium*, *Eleocharis*, *Rhynchospora*; Dennstaedtiaceae: *Pteridium*; Droseraceae: *Drosera*; Dryopteridaceae: *Polystichum*; Eriocaulaceae: *Eriocaulon*; Isoetaceae: *Isoetes*; Juncaceae: *Juncus*; Lentibulariaceae: *Utricularia*; Lycopodiaceae: *Huperzia*, *Lycopodiella*, *Lycopodium*; Ophioglossaceae: *Ophioglossum*; Orchidaceae: *Liparis*, *Malaxis*; Osmundaceae: *Osmunda*; Poaceae: *Panicum*; Polygalaceae: *Polygala*; Polypodiaceae: *Polypodium*; Pteridaceae: *Adiantum*, *Cheilanthes*, *Pteris*; Ranunculaceae: *Clematis*; Schizaeaceae: *Schizaea*; Solanaceae: *Solanum*; Styracaceae: *Styrax*.

