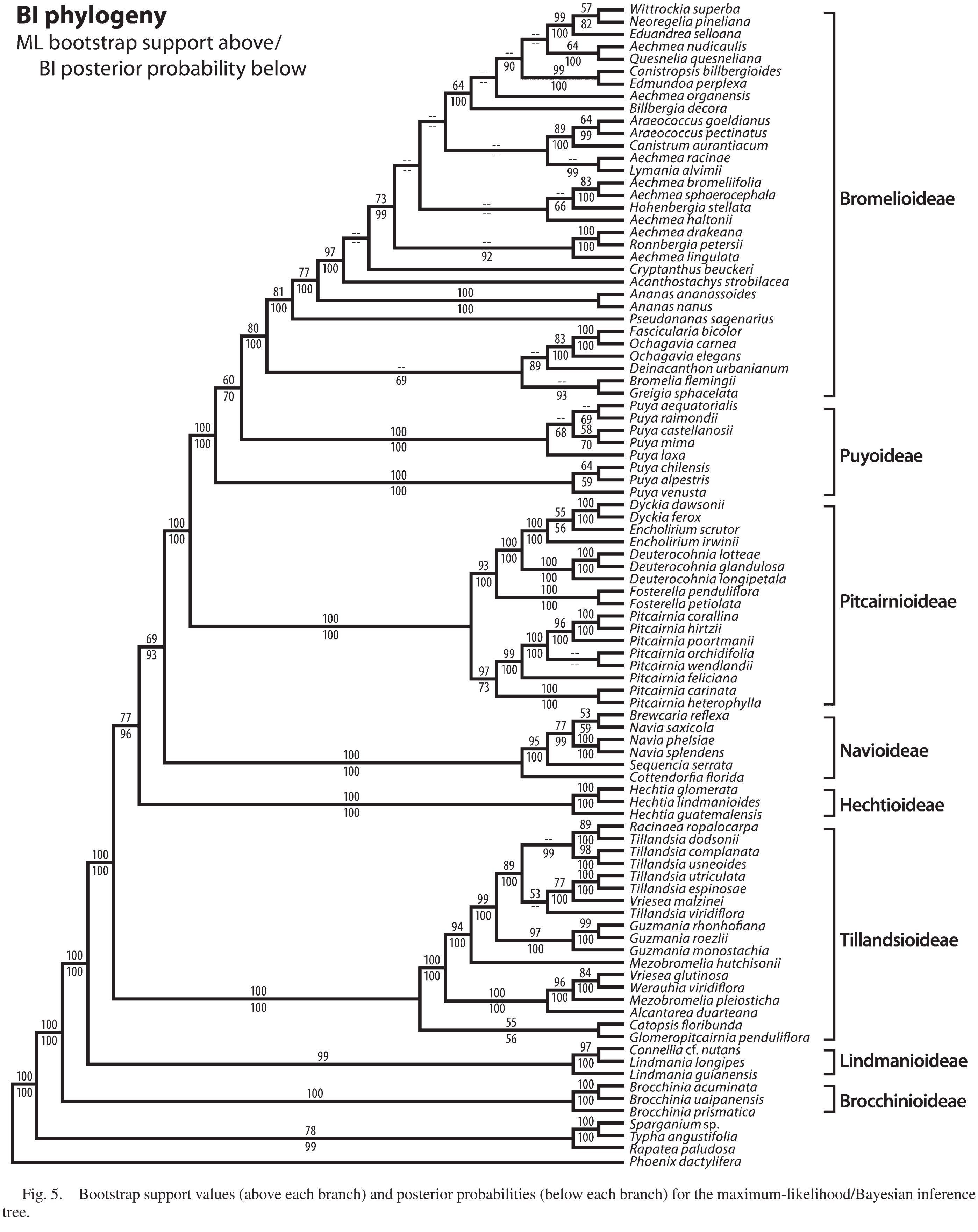

Fig. 5. Bootstrap support values (above each branch) and posterior probabilities (below each branch) for the maximum-likelihood/Bayesian inference tree.

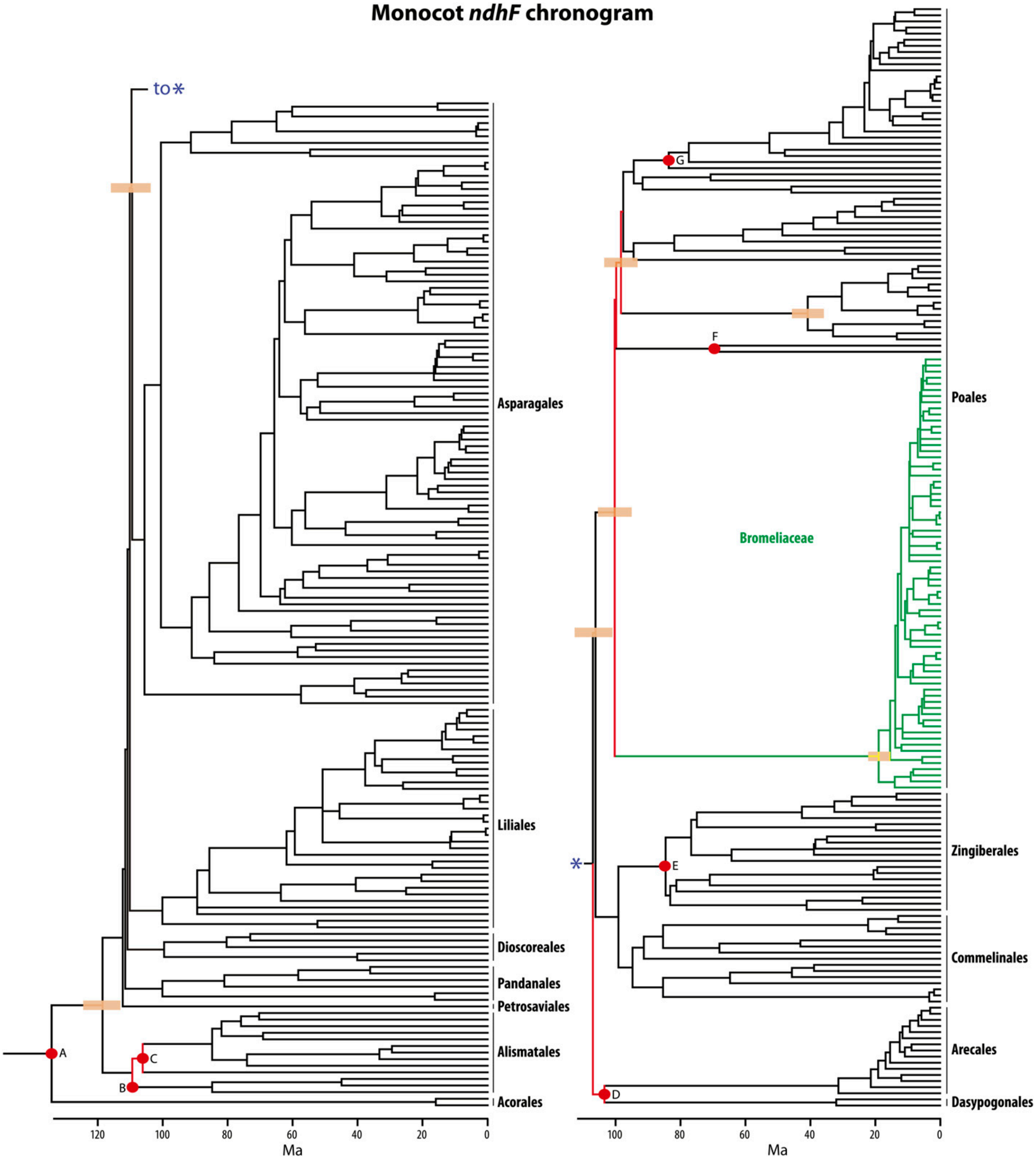

Fig. 6. Cross-verified penalized-likelihood chronogram across monocots based on the maximum-likelihood analysis of *ndhF* sequence variation. A = age of monocot root = 134 Ma (Janssen and Bremer, 2004): B–G = ages of the six Cretaceous fossils (Givnish et al., 2004; Janssen and Bremer, 2004) used to calibrate the monocot phylogeny against time. Bromeliaceae are highlighted in green. Tan boxes indicate ±1 SD, based on bootstrap resamplings, around the estimated ages of several key nodes (red dots), including the core monocots (excluding Acorales and Alismatales), commelinid monocots, order Poales, families Bromeliaceae and Rapateaceae, and remaining Poales sister to Rapateaceae. Red branches indicate those whose topology was constrained based on the plastome tree of Givnish et al. (2010).

Cryptanthus-Acanthostachys—is nearly restricted to this region and arose 9.1 Ma, with present-day taxa diverging from each other ca. 5.5 Ma (Fig. 8).

Reconstruction of the geographic spread of bromeliads under Bayesian inference tells largely the same story. Bayesian inference is, however, somewhat more specific than maximum parsimony about the likely origins of the tillandsioids and navioids. This portion of the tree is the largest that is not fully resolved biogeographically under MP, involving the rapid-fire divergence of four major lineages between 15.4 and 15.0 Ma, and accounting today for all but 2% of all bromeliad species. Bayesian inference reconstructed this portion of the bromeliad spine as being most probably Andean in origin (Fig. 8). Together with the BI reconstruction of the distribution of the stem tillandsioids and navioids, this suggests that tillandsioids arose in the Andes with many subsequent dispersals to other regions, especially Central America, the northern littoral of South America, and the Caribbean. It also suggests that ancestral navioids were, at some point, restricted to the Guayana Shield, with later dispersal or vicariance leading to occupancy of the Brazilian Shield by *Cottendorfia* (Fig. 8). BI suggests that the Guayana Shield or the Andes characterized the stem group for all bromeliads except Brocchinioideae and Lindmanioideae. Maximum parsimony instead points to this group's origin—as well as that of the common ancestor of Hechtioideae and its sister group—being in the Guayana Shield, Andes, or Central America. Maximum parsimony identifies these three areas, as well as the northern littoral of South America and the Caribbean, as possible ancestral areas for Tillandsioideae and *Catopsis-Glomeropitcairnia* (Fig. 8). Maximum parsimony identifies the Guayana Shield, Brazilian Shield, Andes, and Central America as possible ancestral areas for Hechtioideae and the common ancestor of Hechtioideae and the subfamilies to which it is sister. Bayesian inference is less certain than MP in reconstructing the biogeographic origins of *Pitcairnia*, assigning it to one of five areas while MP assigns it to the Andes. Bayesian inference is also less certain than MP in reconstructing the ancestral area of *Bromelia* and *Greigia,* making it equally likely that their common ancestor arose in Central America, the northern littoral of South America and the Caribbean, or the Andes. Bayesian inference reconstructs the stem region of Bromelioideae as being nearly equally likely to be the Andes or Brazilian Shield, with the taxa in the clade sister to the Brazilian Shield clade all being native to the southern Andes/Chile and the Gran Chaco, in the extreme southwest of the Rio de la Plata basin.

Finally, when outgroups are excluded, S-DIVA implies that the Guayana Shield is the ancestral area for Bromeliaceae, Brocchinioideae, and Lindmanioideae (Fig. 8). S-DIVA estimates the chance that the ancestral area for Tillandsioideae is the northern littoral of South America or Caribbean as 29%; that area fused to the Andes, 31%; and that same area fused to Central America, 40%. The chance that the ancestor of Tillandsioideae and its sister groups arose in the Guayana Shield fused to the northern American littoral and Caribbean is 31%; in the Andes alone, 33%; and in Central America alone, 36%. *Catopsis-Glomeropitcairnia* originated in Central America fused to the northern littoral of South America and Caribbean (Fig. 8). S-DIVA identifies the Andes fused to Central America as the ancestral area for Hechtioideae and its sister clade and the ancestral area of Navioideae and its sister clade as the Andes fused to the Brazilian Shield. Under this approach, Navioideae arose in the Guayana Shield fused to the Brazilian Shield, while the extant bromelioids arose in the Andes fused to the Brazilian Shield (Fig. 8). At other nodes, S-DIVA without outgroups usually reconstructs the same ancestral areas as MP and BI, except for *Pitcairnia,* which it implies arose in the Andes. Including outgroups changed the S-DIVA reconstruction little except at the base of Bromeliaceae, where a greater range of possible source regions were identified.

DISCUSSION

Phylogenetic relationships—Our analysis—based on more sequence data per taxon and wider sampling of genera than any previous study—supports the eight-subfamily classification advanced by Givnish et al. (2007) based on *ndhF* sequences (Fig. 2), and further clarifies the relationships among those subfamilies (Figs. 3–5). In the MP strict consensus, six subfamilies received bootstrap support ≥96%. Bromelioideae had 55% bootstrap support; Puyoideae, <50%. Support for five subfamilies increased relative to the *ndhF* study, but that for Lindmanioideae, Puyoideae, and Bromelioideae decreased as a result of the greater breadth of taxonomic sampling, including *Connellia,* the three Chilean *Puya* species, and several Chilean bromelioids. When we excluded the latter from our analysis, bootstrap support for both Puyoideae and Bromelioideae jumped to 100%; when we excluded *Connellia*, support for Lindmanioideae also reached 100%.

The MP, ML, and BI trees all support a stepped phylogeny for the bromeliad subfamilies: (Brocchinioideae, (Lindmanioideae, (Tillandsioideae, (Hechtioideae, (Navioideae, (Pitcairnioideae, (Puyoideae, Bromelioideae))))))). In Givnish et al. (2007), *Hechtia* instead formed a hard trichotomy with Tillandsioideae and all subfamilies sister to and including Navioideae. Our results clarify the position of Hechtioideae and, thus, the relationships of all bromeliad subfamilies. Support for the position of Navioideae is less than 50% under maximum parsimony, compared with 69% under maximum likelihood and 93% under Bayesian inference (Fig. 5).

Our results concur with the general finding that tree resolution and support for most angiosperm clades increase in combined vs. separate plastid gene analyses (e.g., Soltis et al., 1998, 2000; Savolainen et al., 2000; Olmstead et al., 2000, 2001; Bremer et al., 2002; Chase et al., 2006; Graham et al., 2006). Furthermore, simulations show that phylogenetic resolution and support can also improve with more taxa sampled within a given clade (Hillis, 1996; Graybeal, 1998), particularly when taxa are added strategically to break up long branches (Hendy and Penny, 1989; Leebens-Mack et al., 2005). While a number of ILD tests suggest that some plastid regions sequenced in this study show conflict in phylogenetic structures, we believe that this conflict is illusory. First, the plastid genome is inherited as a unit, so individual plastid regions should not conflict in the phylogenetic history their sequences reflect (Doyle, 1992). Second, trees based on each individual region generally do not differ from the combined-data phylogenies at nodes resolved and well supported in the individual-region trees. However, it must be realized that the limited number of informative sites in several data partitions (Table 1) result in few resolved and well-supported nodes in many individual-region trees. For example, we found that sequences for *atpB-rbcL* resolve only 40% of the nodes within Bromeliaceae; of those, 63% have bootstrap support from 50 to 90%, and only 21% (8 nodes) have bootstrap values greater than 90%. The whole point of concatenating plastid data are that individual genes and spacers each contain

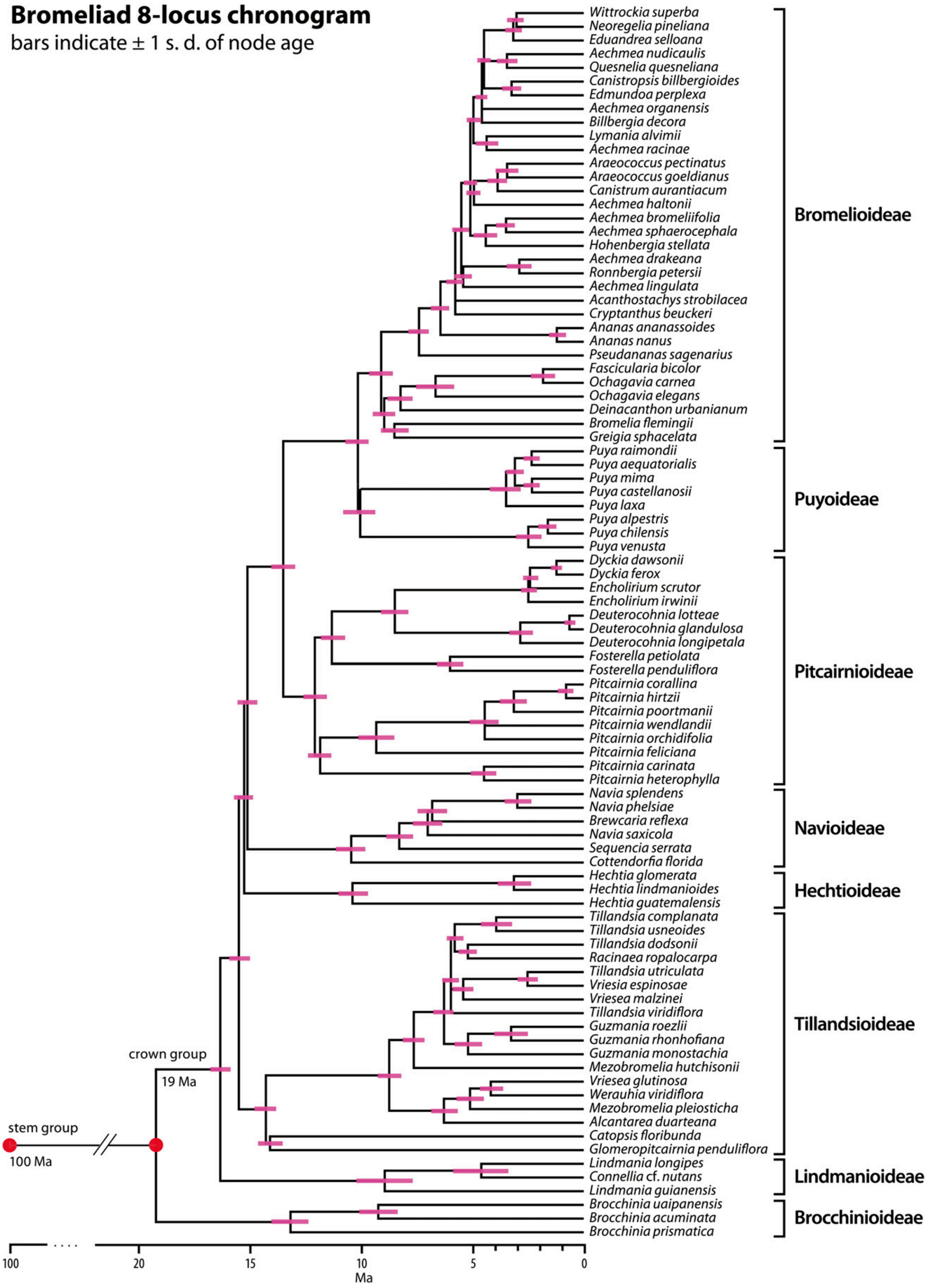
Bromeliad 8-locus chronogram
bars indicate ± 1 s. d. of node age
Wittrockia superba
Neoregelia pineliana
Eduandrea selloana
Aechmea nudicaulis
Quesnelia quesneliana
Canistropsis billbergioides
Edmundoa perplexa
Aechmea organensis
Billbergia decora
Lymania alvimii
Aechmea racinae
Araeococcus pectinatus
Araeococcus goeldianus
Canistrum aurantiacum
Aechmea haltonii
Aechmea bromeliifolia
Aechmea sphaerocephala
Hohenbergia stellata
Aechmea drakeana
Ronnbergia petersii
Aechmea lingulata
Acanthostachys strobilacea
Cryptanthus beuckeri
Ananas ananassoides
Ananas nanus
Pseudananas sagenarius
Fascicularia bicolor
Ochagavia carnea
Ochagavia elegans
Deinacanthon urbanianum
Bromelia flemingii
Greigia sphacelata
Bromelioideae
Puya raimondii
Puya aequatorialis
Puya mima
Puya castellanosii
Puya laxa
Puya alpestris
Puya chilensis
Puya venusta
Puyoideae
Dyckia dawsonii
Dyckia ferox
Encholirium scrutor
Encholirium irwinii
Deuterocohnia lotteae
Deuterocohnia glandulosa
Deuterocohnia longipetala
Fosterella petiolata
Fosterella penduliflora
Pitcairnia corallina
Pitcairnia hirtzii
Pitcairnia poortmanii
Pitcairnia wendlandii
Pitcairnia orchidifolia
Pitcairnia feliciana
Pitcairnia carinata
Pitcairnia heterophylla
Pitcairnioideae
Navia splendens
Navia phelsiae
Brewcaria reflexa
Navia saxicola
Sequencia serrata
Cottendorfia florida
Navioideae
Hechtia glomerata
Hechtia lindmanioides
Hechtia guatemalensis
Hechtioideae
Tillandsia complanata
Tillandsia usneoides
Tillandsia dodsonii
Racinaea ropalocarpa
Tillandsia utriculata
Vriesia espinosae
Vriesea malzinei
Tillandsia viridiflora
Guzmania roezlii
Guzmania rhonhofiana
Guzmania monostachia
Mezobromelia hutchisonii
Vriesea glutinosa
Werauhia viridiflora
Mezobromelia pleiosticha
Alcantarea duarteana
Catopsis floribunda
Glomeropitcairnia penduliflora
Tillandsioideae
Lindmania longipes
Connellia cf. nutans
Lindmania guianensis
Lindmanioideae
Brocchinia uaipanensis
Brocchinia acuminata
Brocchinia prismatica
Brocchinioideae
crown group
19 Ma
stem group
100 Ma
100
20
15
10
5
0
Ma

Table 2. Stem and crown ages of bromeliad subfamilies and subsets thereof, based on penalized-likelihood analyses of the across-monocots *ndhF* tree and the eight-locus plastid phylogeny.

	Stem age (Myr)		Crown age (Myr)	
Taxon	*ndhF*	8-locus	*ndhF*	8-locus
Brocchinioideae	19.1	19.1	14.2	13.1
Lindmanioideae	15.6		16.3	8.9
Tillandsioideae	14.0	15.4	11.8	14.2
Core tillandsioids	11.8	14.2	6.8	8.7
Hechtioideae	14.0	15.2	12.1	10.3
Navioideae	14.0	15.0	9.4	10.4
Navia-Brewcaria	9.3	8.3	8.6	7.0
Pitcairnioideae	13.3	13.4	9.4	11.8
Pitcairnia	13.2	12.0	9.4	11.8
Puyoideae	9.8	10.1	8.7	10.0
Bromelioideae	9.8	10.1	9.5	8.9
Brazilian Shield clade	9.5	9.1	9.3	7.4
Tank epiphyte clade	7.1	5.7	5.7	5.5
Puyoideae + Bromelioideae	13.2	13.4	10.1	10.0
Puy + Brom + Pitc	13.4	15.0	13.2	13.4

relatively little phylogenetic signal in slowly evolving bromeliads, so several regions must be sampled to obtain a reliable phylogenetic estimate. Finally, the pairs of plastid regions showing "significant" conflict in the ILD tests in this study are those in which one or both regions have few informative sites (Table 1). Incongruence length difference tests involving such regions are inherently unstable due to sampling error in determining the universe of characters sampled; branches supported by limited data can easily be reversed in larger data sets as the signal in individual bases is overruled by that in additional bases sampled (e.g., see Darlu and Lecointre, 2002). The fact that the apparent conflict between regions occurred only among those involving one or two regions with limited numbers of informative characters in the combined analysis, combined with the fact that such conflict should be most likely when limited numbers of characters are sampled in a phylogeny with short branches argues that the "conflict" detected by ILD tests for some pairs of regions is simply a sampling artifact and should thus be ignored.

Implications for classification—Our results confirm that the traditional division of Bromeliaceae into three subfamilies—Pitcairnioideae s.l., Tillandsioideae, and Bromelioideae (Harms, 1930), defined by possession of winged seeds, plumose seeds, and fleshy fruits, respectively—must be abandoned. Pitcairnioideae sensu Harms (1930) is paraphyletic and must be split into Brocchiniodeae, Lindmanioideae, Hechtioideae, Navioideae, Pitcairnioideae s.s., and Puyoideae to produce monophyletic subfamilies. Each of the new subfamilies is easily diagnosed based on morphology (Givnish et al., 2007), and the relationships among subfamilies found here are consistent with those demonstrated in other recent analyses (Terry et al., 1997; Crayn et al., 2000, 2004; Horres et al., 2000, 2007; Givnish et al., 2004, 2007; Barfuss et al., 2005; Schulte et al., 2005; Schulte and Zizka, 2008), but better resolved and more taxonomically inclusive.

Our results raise the question of *Puya's* monophyly. *Puya* is monophyletic but weakly supported under MP, and paraphyletic under ML and BI (Figs. 3–5). Jabaily and Sytsma (2010) found support for the monophyly of *Puya* in a combined analysis of sequences for three plastid regions (*matK, rps16, trnS-trnG*) and one single-copy nuclear gene (*PhyC*) with a far more extensive sampling of the genus. *PhyC* alone supports the monophyly of *Puya*, while the plastid data do not contradict monophyly. Given these results, *Puya's* monophyly in our MP trees, and *Puya's* possession of a striking morphological synapomorphy—e.g., petals that spiral tightly after anthesis (Smith and Downs 1974)—we consider *Puya* and Puyoideae to be monophyletic, but recognize that further tests of relationships among Chilean *Puya*, other *Puya*, and Bromelioideae would be useful. The possibility of sinking *Puya* into Bromelioideae, as suggested by Terry et al. (1997), is not appealing, given that both Bromelioideae and Puyoideae as currently defined are characterized by obvious morphological synamorphies, while the clade consisting of both subfamilies appears to lack such defining traits.

Our findings add to a growing case, developed by Schulte et al. (2005, 2009), Schulte and Zizka (2008), Zizka et al. (2009), and Jabaily and Sytsma (2010) that three small terrestrial genera from temperate Chile and the southern Andes (*Fascicularia*, *Ochagavia*, *Greigia*) are among the earliest-divergent members of subfamily Bromelioideae, together with two small terrestrial genera, wide-ranging *Bromelia* and monotypic *Deinacanthon* endemic to the semiarid Gran Chaco of southern Bolivia, Paraguay, and northern Argentina. These genera form a weakly supported clade in our ML, BI, and MP majority-rule trees, and a largely unresolved grade in our MP strict consensus tree (Figs. 3–5). All three analyses identify a further grade of small terrestrial genera sister to the remaining bromelioids, including *Pseudananas*, *Ananas*, and *Cryptanthus*; the single species of epiphytic (but nontank forming) *Acanthostachys* is closely related to *Cryptanthus.* Taxa sister to and including *Pseudananas* form the Brazilian Shield clade (61% MP bootstrap support, 81% ML bootstrap support, 100% BI bootstrap support), which arose 9.1 Ma (see *Results*). In contrast to our results, Sass and Specht (2010) recovered *Ananas* and *Araeococcus* as not being monophyletic. However, this is a result solely of those authors sampling a far greater number of species in the known "trash-can" genus *Aechmea*; almost surely, their findings will result in the errant *Aechmea* species being reclassified as members of *Ananas* or *Araeococcus.*

Almost all species in the Brazilian Shield clade—represented by the 21 species in our study, sister to and including *Aechmea drakeana-A. lingulata-Ronnbergia petersii*—form a clade of tank epiphytes endemic to the Brazilian Shield, based on the possession of tanks and the epiphytic habit by almost all these species (see Smith and Downs, 1974, 1977, 1979; Schulte et al., 2009). All three analyses support this clade, with <50% support under MP, 73% under ML, and 99% under BI (Figs. 3–5). Among these taxa, only *Araeococcus pectinatus* lacks a tank; only *Aechmea bromeliifolia*, *A. sphaerocephala*, *and Billbergia*

←

Fig. 7. Cross-verified penalized-likelihood (PL) chronogram for bromeliad evolution based on the maximum-likelihood phylogeny, using the crown and stem ages derived from the across-monocots PL analysis (see Fig. 6). Each magenta bar indicates ±1 SD around the estimated age of the corresponding node based on bootstrap resamplings.

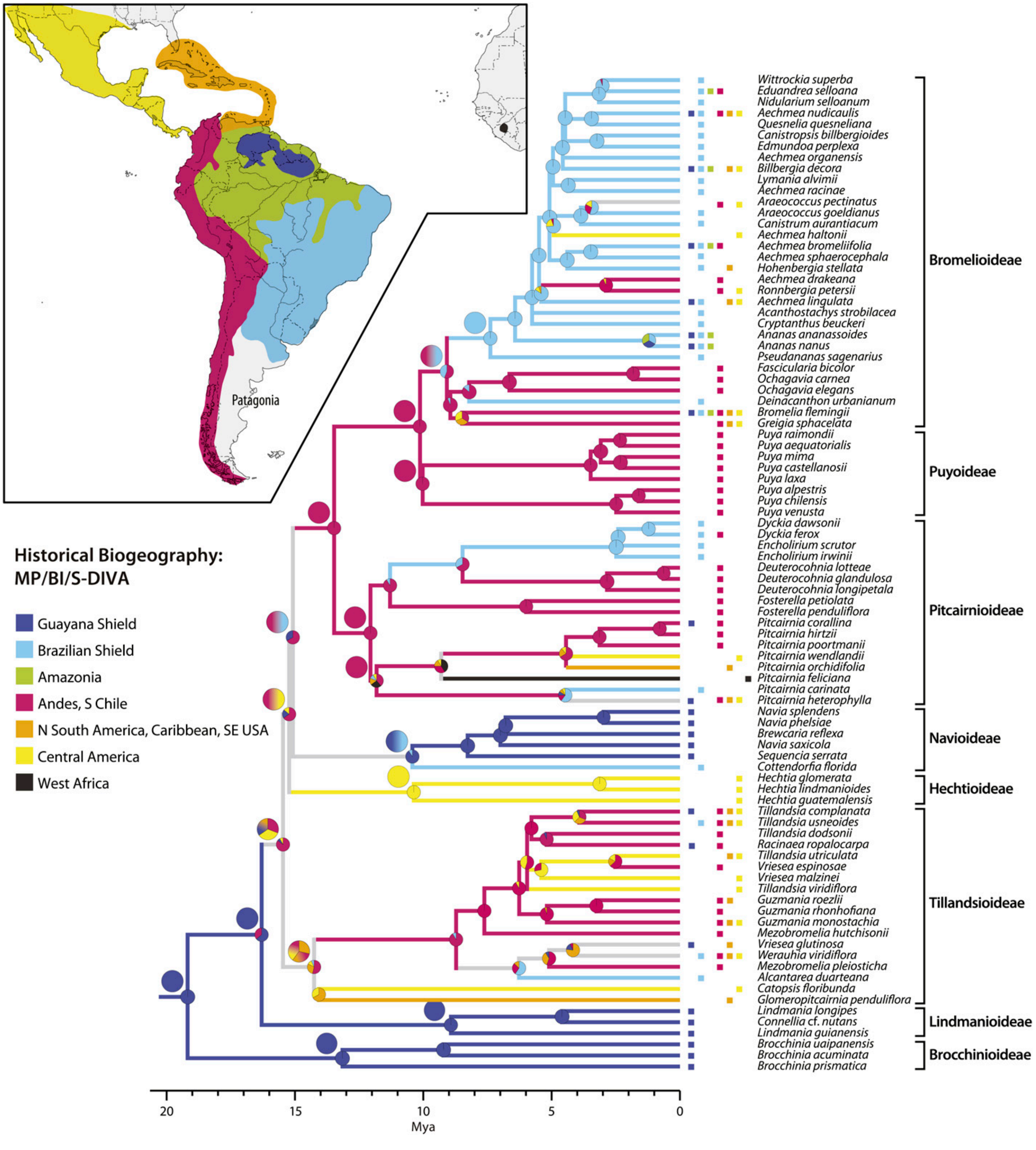

Fig. 8. Geographic evolution of Bromeliaceae calibrated against time. Present-day distribution of individual species (or of genera, in cases where wide-ranging groups are represented by one or two placeholder taxa) indicated by colored boxes. Branch colors indicate the inferred distributions of ancestral taxa under maximum parsimony (MP); gray indicates ambiguity. Pie diagrams at nodes indicate the inferred ancestral distributions under Bayesian inference (BI), with width of wedges delimited by black lines showing likelihood of alternative inferences. Larger pie diagrams displaced northwest of nodes indicate the inferred ancestral distributions under S-DIVA, with wedges delimited by black lines showing likelihood of alternative inferances, and a blend of colors within wedges signifying vicariance involving a fusion of two regions represented by those colors. Analyses involving the possible fusion of more than two areas yield similar results except for a few backbone nodes.

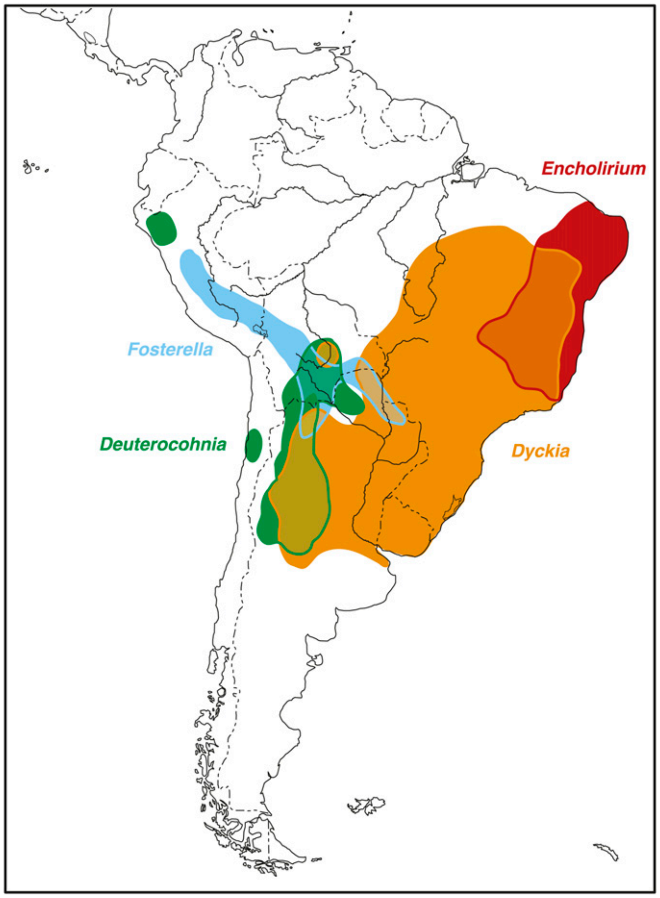

Fig. 9. Geographic distribution of genera of Pitcairnioideae minus *Pitcairnia*; the latter is broadly distributed throughout the Andes and nearby regions. Note the regional overlap of three of the four genera in the "knee" of the Andes.

decora are almost never epiphytic; and only *Aechmea drakeana*, *A. haltoni*, and *Ronnbergia petersii* are not native, at least in part, to the Brazilian Shield (Smith and Downs, 1974, 1977, 1979). Schulte et al. (2009) similarly found tanks ubiquitous (except in *Araeococcus flagellifolius*) in a clade of 28 core bromelioids sister to *Aechmea drakeana-Hohenbergia eriostachya* based on sequence data from one nuclear gene (*PRK*) and five plastid loci. That clade has a membership consistent with our bromelioid tank-epiphyte clade, but also included species of *Androlepis*, *Neoglaziovia*, *Portea*, and *Ursulaea*—four of the 12 genera not included here. Schulte et al. (2009) found that two other genera—*Orthophytum* and *Fernseea*, both species-poor terrestrial groups from the Brazilian Shield—are part of our Brazilian Shield clade. *Fernseea* is sister to all remaining elements of the Brazilian Shield clade, and *Orthophytum* is sister to *Cryptanthus*; only one species of *Fernseea* from these three genera are epiphytes or tank-formers (Schulte et al., 2009).

Our study generally agrees with Barfuss et al. (2005) on relationships within Tillandsioideae. Consistent with our ML tree, Barfuss et al. (2005) found that *Catopsis* and *Glomeropitcairnia* were sister to each other and together sister to all other tillandsioids. Also largely consistent between the two studies is the split of the remaining taxa into the tribes Vrieseeae (*Alcantarea*, *Vriesea*, *Werauhia*) and Tillandsieae (*Guzmania*, *Racinaea*, *Tillandsia*, *Viridantha*). However, in our study one species of *Vriesea* fell into Tillandsieae with 100% bootstrap support, and *Mezobromelia pleiosticha*—replacing a misidentified *Guzmania variegata* sequenced by Barfuss et al. (2005)—fell into Vrieseeae with 95% bootstrap support (Fig. 3).

Brewcaria reflexa appears to be embedded in *Navia* (Figs. 3, 4). Holst (1997) moved several species from *Navia* into *Brewcaria* based on their possessing a spicate or paniculate inflorescence, rather than the capitulate inflorescences seen in other *Navia*. This decision is not supported in the case of *Brewcaria reflexa*, the only species of that genus included in this study. Our study confirms the highly polyphyletic nature of *Aechmea,* with six independent origins indicated by our study. Sass and Specht (2010) found an even greater degree of polyphyly and paraphyly in *Aechmea* based on a much more extensive sampling of species (150) within Bromelioideae.

In a way, our findings confirm the traditional view that bromelioids and tillandsioids arose from within Pitcairnioideae s.l. (Schimper, 1888; Mez, 1904; Pittendrigh, 1948; Tomlinson, 1969; Smith and Downs, 1974; Benzing et al., 1985; Smith, 1989; Benzing, 1990). Terry et al. (1997) reached a similar conclusion, but had a different view of relationships of bromelioids to tillandsioids and the seeming isolation of *Brocchinia* because they did not sample two of our subfamilies and undersampled two others. Terry et al. (1997) also concluded that *Hechtia* was closely allied to *Dyckia*, *Encholirium*, *Abromeitiella*, and *Deuterocohnia*, rather than being a convergent lineage. Horres et al. (2000) did not exclude a close tie of *Hechtia* to xeromorphic pitcairnioids and *Puya,* but their data placed *Hechtia* in a position consistent with that found here. Givnish et al. (2007) noted that the shared possession of four to six leaf anatomical traits by *Hechtia* with *Puya* and the xeromorphic pitcairnioids as a striking instance of concerted convergence.

The classical view that bromelioids and tillandsioids emerged from within Pitcairnioideae s.l. was based not on phylogenetic analysis, but on observing that epiphytism—a highly specialized habit, with several adaptations for life on twigs and branches—is almost absent among pitcairnioids as previously circumscribed. No early writer proposed that *Brocchinia* or *Lindmania* were sister to the rest of the family, or that Pitcairnioideae s.l. were not monophyletic. Terry et al. (1997) were the first to conclude that *Brocchinia* was sister to all other bromeliads and that the traditional Pitcairnioideae were paraphyletic. That view, based on an analysis including exemplars of only 28 of 58 bromeliad genera, is confirmed and greatly amplified by the present analysis.

The remarkably long period of ca. 81 My between the rise of the bromeliads and the divergence of modern lineages from each other suggests that much extinction occurred during the intervening period, and explains the morphologically isolated position of the family and the difficulty, even with extensive molecular data sets, of identifying its sister group (see Givnish et al., 2005, 2007; Chase et al., 2006; Graham et al., 2006). Restriction of Brocchinioideae and Lindmanioideae to the Guayana Shield, the occurrence of some *Catopsis* and *Glomeropitcairnia* in or immediately adjacent to the Guayana Shield, and the near restriction to that region of Navioideae, combined with the phylogenetic relationships shown here, place the origin of Bromeliaceae in the Guayana Shield, consistent with the evidence and arguments presented by Givnish et al. (2007). The divergence of most bromelioid genera in just the last 5.5 Myr, coupled with very low rates of molecular evolution in bromeliads, explains the great difficulty investigators have had in obtaining a well-resolved phylogeny for bromelioids (Terry et al., 1997; Horres et al., 2000, 2007; Crayn et al., 2004; Givnish et al., 2004, 2007; Schulte et al., 2005) and the relatively limited and homoplastic morphological variation in this group (Smith and Downs, 1979; Smith and Kress, 1989, 1990; de Faria et al., 2004; Schulte and Zizka, 2008; Sass and Specht, 2010).

Historical biogeography—Our analyses show that bromeliads arose in the Guayana Shield roughly 100 Ma, spread from that hyperhumid, extremely infertile center to other parts of tropical and subtropical America starting ca. 15.4 Ma, and arrived in tropical Africa ca. 9.3 Ma. Our PL chronology implies that the extant subfamilies began to diverge from each other beginning only about 19 Ma and that invasion of drier peripheral areas in Central America (*Hechtia*) and northern South America (Tillandsioideae) began roughly 15.2 to 15.4 Ma. Brocchinioideae, Lindmanioideae, and Navioideae except *Cottendorfia* remained entirely within the Guayana Shield. The northern Andes and Central America were independently colonized by two major lineages: the core tillandsioids (*Alcantarea*, *Tillandsia*, *Vriesea*, *Werauhia*) beginning about 14.2 Ma; and *Fosterella,* beginning about 11.3 Ma. In addition, *Puya* and the early-divergent bromelioids colonized throughout the Andes, extending into temperate coastal Chile, beginning ca. 10.1 Ma (Fig. 5; all calculated ages based on stem groups). Other groups—including some *Pitcairnia* and species in several bromelioid genera (e.g., *Aechmea*, *Araeococcus*, *Neoregelia*, *Ronnbergia*)—also invaded the Andes independently, but we have not sampled enough taxa to estimate the timing and/or numbers of such events reliably. At least five additional colonizations, however, appear to be involved.

Uplift of the northern Andes beginning in the mid-Miocene, causing a shift in the course of the Amazon from a northerly route via the paleo-Orinoco toward Lake Maracaibo to an easterly course toward its present mouth (Hoorn, 1994; Hoorn et al., 1995, 2010; Potter, 1997), appears to correspond roughly to when bromeliad subfamilies began to diverge outside the Guayana Shield. This Andean uplift appears to have occurred at about the same time as the first split of modern hummingbird lineages in the Andes ca. 13 Ma, with several other Andean lineages diverging during the Pliocene and Pleistocene (Bleiweiss 1998), just as the uplift of the Columbian Andes accelerated starting ca. 3.9 Ma (Gregory-Wodzicki, 2000).

As the central and northern Andes continued to rise, they were colonized by the largely epiphytic tillandsioids between ca. 14.2 and 8.7 Ma, after that subfamily began diversifying in the northern littoral of South America, the Caribbean, and Central America. Speciation in Andean tillandsioids was explosive, resulting in ca. 1250 present-day species (Luther, 2008), more than 60 times the numbers of taxa seen in Brocchinioideae. Tillandsioids today have their great species richness in Andean Colombia, Ecuador, and Peru and range along the length of the Andes, into arid habitats on the Pacific and Caribbean littorals, and into Central America and North America north to Virginia (Smith and Downs, 1977).

How *Hechtia* colonized arid areas of Central America is unclear. The Isthmus of Panama did not close until roughly 4.4–3.1 Ma (Ibaraki, 1997; Kirby et al., 2008), so colonization from the Guayana Shield, the Caribbean or Caribbean littoral, or the Andes almost surely involved one or more bouts of long-distance seed dispersal, either directly to Central America, or via a series of arid habitats in the Lesser and Greater Antilles, or on the west slope of the Andes. Such long-distance dispersal appears plausible, given the inferred dispersal of *Fosterella* from the central Andes to dry forests in Mexico, El Salvador, and Guatemala in Central America (Rex et al., 2007), of *Greigia* and *Ochagavia* to the Juan Fernandez Islands and *Racinaea* to the Galápagos from the Andes (Smith and Downs, 1974), and of *Pitcairnia* across the tropical Atlantic to West Africa (Givnish et al., 2004, 2007). We favor direct dispersal of ancestral *Hechtia* to Central America, given the persistence of arid habitats in the Caribbean as well as coastal Peru and Chile, and the absence of *Hechtia* there. Today, *Hechtia* is restricted to arid habitats in Central America, while tillandsioids there are more broadly distributed ecologically and are especially diverse in humid montane habitats (see Smith and Downs, 1974, 1977).

Deposition of nutrient-rich Andean sediments in the Amazon basin, separating the Guayana and Brazilian Shields ecologically, accelerated ca. 11.8–11.3 Ma, corresponding to continued uplift of the northern Andes and filling of the vast Pebas wetlands of western Amazonia, as well as erosion finally cutting through the Purus Arch in central Amazonia (Figueiredo et al., 2009). Divergence of monotypic *Cottendorfia* from remaining Navioideae of the Guayana Shield about 10.4 Ma suggests that *Cottendorfia* may have arrived in the Brazilian Shield via long-distance dispersal. However, the timing of the deposition of Amazonian sediments separating the Guayana and Brazilian Shields on the Amazonian Platform is close enough in time, and the proximity of both shields close enough in space then that we should not exclude vicariance–short-distance dispersal as an alternative explanation. Three other groups also appear to have colonized the Brazilian Shield: *Dyckia*-*Encholirium* from the central Andes 8.5 Ma (Fig. 7); the Brazilian Shield bromelioids, most likely from the southern Andes ca. 9.1 Ma (see below); and certain species of *Bromelia*, probably from the Amazon basin, also ca. 9.1 Ma (Fig. 8). Individual species of several wide-ranging genera (e.g., *Guzmania*, *Tillandsia*, *Vriesea*) almost surely colonized the Brazilian Shield from other areas as well.

Our reconstruction suggests that Pitcairnioideae dispersed counterclockwise through time, first from the Guayana Shield to the (northern) Andes and its lowland slopes for *Pitcairnia*, then to the central Andes for the split between lineages giving rise to *Fosterella* and to the remaining genera, with a split between the puna cushion-plants of *Deuterocohnia* and arid-zone *Dyckia* in south-central Bolivia roughly 9.1 Ma, and subsequent dispersal of *Dyckia* to the Brazilian Shield and its divergence from *Encholirium* in the Horn of Brazil about 2.4 Ma (Figs. 7 and 8; see also Givnish et al., 2004, 2007).

The cradle of *Puya* appears to be Andean, but our analysis samples too few species within the genus to locate its geographic origin (see Jabaily and Sytsma, 2010). Jabaily (2009) used AFLP data to argue that *Puya* spread northward from the southern and central Andes soon after the split from the Chilean taxa. Based on our calculations, that split occurred around 10 Ma, soon after the uplift of the northern Andes began to accelerate. Divergence between Puyoideae and Bromelioideae seems likely to have occurred in and around the southern Andes, given the basal split in *Puya* between Chilean and Andean taxa, the apparent origin of *Puya* generally from the southern Andes, and the presence in the southern Andes and nearby Pacific lowlands of several members of basal grade or clade of bromelioids, including *Fascicularia*, *Greigia*, and *Ochagavia* (see Results and Schulte et al., 2005). Subsequent diversification of Bromelioideae entailed dispersal of *Bromelia* and *Ananas* throughout much of lowland South and Central America, with colonization of the Brazilian Shield independently by *Bromelia* and by the ancestor(s) of *Fernseea* (see Schulte et al., 2005) and the large number of genera sister to it (Fig. 8). This last lineage—the Brazilian Shield clade—apparently arose 9.1 Ma (Fig. 8).

We propose that the origin of the bromelioid epiphytic clade in and around the Serra do Mar roughly 5.5 Ma corresponds to three key events, involving (1) uplift of the Serra do Mar mainly during Pliocene-Pleistocene times (Almeida, 1976; Amorim and Pires, 1996), (2) uplift of the central Andean Altiplano toward the end of the Miocene (Garzione et al., 2008), and (3) origin of a cooler, rainier climate in the Serra do Mar/Atlantic rain-forest region predicted to result from the impact of central Andean uplift on wind circulation, with increased advection of moisture from the Atlantic as winds from the Pacific were blocked (Ehlers and Poulsen, 2009). The climate models of Ehlers and Poulsen (2009) assume all other factors remained constant as the height of the Andes varied, so the actual uplift of the Serra do Mar mainly from the Pliocene to the present most likely would have caused the observed onset there of cooler, rainier, more humid conditions congenial to epiphytes starting around 5.6 Ma (Vasconcelos et al., 1992; Grazziotin et al., 2006), corresponding nearly exactly with the calculated time of origin of the bromelioid epiphytic clade. Today the Atlantic forest region, including highly diverse but largely destroyed Atlantic rain forests and cloud forests, sandy coastal restingas, mangroves, campos de altitude, and granitic outcrops of the Serra do Mar and Serra da Mantiqueira and adjacent coastal plains, are the wettest part of eastern South America, and the montane habitats are the coolest (Safford, 1999). The Serra do Mar and Serra da Mantiqueira represent the elevated southeastern rim of the tilted Brazilian Shield, and these "seas of hills" ("mares do morros") between roughly 22° and 29°S intercept heavy rainfall and fog from moisture carried by winds off the tropical south Atlantic, as well as occasional cold fronts spawned in Antarctica. Strong climatic fluctuations occurred in this montane region during the Pleistocene (e.g., Behling and Negrelle, 2001), much as they did in the northern Andes (van der Hammen, 1995).

Most bromelioids that arrived in the Brazilian Shield earlier than the origin of the epiphytic clade, during a drier phase and presumably by gradual, short-distance dispersal from the southern Andean region via a corridor of semiarid habitats, are highly xeromorphic terrestrial taxa (*Bromelia*, *Pseudananas*, *Ananas*, *Cryptanthus*, *Orthophytum*). *Fernseea*, sister to all other members of the Brazilian Shield clade (Schulte et al., 2009), is restricted to cool, moist, rocky microsites on the lofty Itatiaia Massif (2800 m a.s.l.) in the Serra da Mantiqueira (Medina et al., 2006), a mountain chain inland of the Serra do Mar in the Atlantic forest region and uplifted somewhat earlier (Amorim and Pires, 1996; Modenesi-Gauttieri and Motta de Toledo, 1996). *Fernseea* may thus have arrived directly from cool, moist habitats in the southern Andes via long-distance seed dispersal. Climatic oscillations throughout the Pleistocene included rainier phases during which the isolation of Amazonian and Atlantic rain forests from each other by semiarid vegetation may have been greatly reduced (Auler and Smart, 2001; Wang et al., 2004), which would have promoted the later dispersal of bromelioids from the Serra do Mar to other areas, and dispersal of other bromeliads (e.g., *Guzmania*, *Tillandsia*, *Vriesea*) into the Serra do Mar.

Dispersal of ancestral bromelioids from the southern Andes to the mountains of southeastern Brazil is consistent with the proposal of Schulte et al. (2005), although we envision at least two colonizations, involving a long-distance, mesic "high road" for *Fernseea* (as argued by Schulte et al., 2005) and a gradual, semiarid "low road" for the remaining taxa, with subsequent evolution of mesomorphic epiphytic taxa in the Atlantic forest region. The defining disjunction of Bromelioideae between the southern Andes and the Atlantic forest region is similar that seen in several other plant groups, including *Araucaria*, *Cordyline*, *Drimys*, *Fuchsia* sect. *Quelusia*, and *Griselinia* (Zinmeister, 1987; Berry, 1989; Katinas et al., 1999; Berry et al., 2004). Most of these cases, however, probably involved a mesic "high road" to the Brazilian Shield, either via long-distance dispersal or (more likely in these ancient groups) as relicts of more widespread mesic temperate forests in the southern hemisphere during the Tertiary. In more recently dispersed groups, gradual spread of mesic-adapted taxa from the Andes to the Brazilian Highlands during glacial cycles of the last few million years is another possibility (Safford, 1999). Although glacial/interglacial cycles had much less amplitude prior to ca. 2.8 Ma (Lisiecki and Raymo, 2005), Antarctic ice sheets are known to have advanced and retreated until at least ca. 4.9 Ma (Naish et al., 2009), so dispersal of bromelioids from the southern Andes to southeastern Brazil during a glacial period cannot be excluded.

The initial diversifications of the tillandsioid and epiphytic tank bromelioid radiations roughly 14.0–8.7 Ma and 5.5 Ma, respectively, associated with independent origins of the tank habit (Givnish et al., 2007), corresponds well with the independently derived dates of origin of diving-beetle lineages endemic to bromeliad tanks ca. 12 Ma in northern South America and ca. 4 Ma in the Serra do Mar region (Balke et al., 2008 and inferences regarding ancestral distributions). In addition, the estimated origin of *Bothrops* (fer-de-lance) species endemic to Atlantic rain forests ca. 3.8 Ma (Grazziotin et al., 2006) agrees fairly well with our estimate of the origin there of the epiphytic tank bromelioids in wet forests ca. 5.5 Ma.

Pitcairnia feliciana apparently arrived in tropical West Africa via recent long-distance dispersal from South America no earlier than about 9.3 Ma. This accords with *Maschalocephalus dinklagei* of Rapateaceae also being a product of recent long-distance dispersal, not ancient vicariance via continental drift (Givnish et al., 2000, 2004). Recent colonization might partly explain the lack of African speciation in both groups, but that seems quite unlikely; the bromelioid epiphytic clade spawned nearly 600 species in less than half the time that we estimate *Pitcairnia* and *Maschalocephalus* have been in Africa. Historical cycles of aridity (Goldblatt, 1993; Querouil et al., 2003) probably played a more important role, given that neither Rapateaceae nor *Pitcairnia* are especially drought-tolerant (Givnish et al., 2004, 2007) and that neither clade contains species with fully developed CAM photosynthesis (Crayn et al., 2001, 2004).

The African endemics of these families occupy nearly adjacent ranges: *Mascalocephalus* in savannas and forests on wet sand from Sierra Leone to Côte d'Ivoire; *Pitcairnia feliciana* on sandstone outcrops of the Fouta Djalon massif in Guinea a few hundred kilometers to the northwest (Porembski and Barthlott, 1999; Givnish et al., 2000, 2004). The Guinean Mountains maintained a wet climate during the Pleistocene, serving as a refugium for wet-climate taxa (Jahns et al., 1998; Dupont et al., 2000). Both Rapateaceae and Bromeliaceae are also likely to have been favored by infertile soils, given their origin and continued abundance in the Guayana Shield. Therefore, early vicariance of habitat—through rafting of sandstone deposits to either side of the Atlantic—followed, much later, by long-distance dispersal appears to have caused the disjunct distributions of rapateads and bromeliads (Givnish et al., 2004). There are roughly 10 other angiosperm families with amphiatlantic distributions (Thorne, 1972, 1973); the use of fossil-calibrated molecular clocks shows that recent, long-distance dispersal probably accounts for this pattern in Melastomaceae (Renner and Meyer, 2001) and Vochysiaceae (Sytsma et al., 2004) as well, with trans-Atlantic dispersal having occurred in these families well before it did in bromeliads or rapateads.

It might be argued that, even with a sample of 90 bromeliad stratified across all subfamilies and most genera, that it would be premature to reconstruct biogeographic (or, in other contexts, morphological or ecological) ancestral character states, given that less than 3% of all extant bromeliad species are included in our analysis. We disagree. First, the full range of geographic distributions have been considered for all genera included, and less than 3% of bromeliad species have been excluded in that process. More importantly, a detailed study of biogeographic and morphological variation with Bromelioideae, based on a substantially denser sampling of taxa (150 species, ca. 17.5% of all bromelioids), showed that both groups of characters were phylogenetically highly conserved (Sass and Specht, 2010). Such conservatism supports the placeholder approach used here.

What morphological and physiological traits adapted bromeliads for life outside the Guayana Shield? How frequently did they arise? Were they acquired sequentially or nearly simultaneously? To what extent is variation among the eight bromeliad subfamilies in species number and diversification rate correlated with these traits and the environments invaded by those subfamilies? What factors make the Tillandsioideae and Bromelioideae, with 40 and 27% of all bromeliad species, respectively, especially diverse? Each of these questions will be addressed in a companion paper, building on the phylogenetic, chronological, and biogeographic reconstructions presented here and new reconstructions of the ancestral states of various morphological, physiological, and ecological characters.

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APPENDIX 1. Species, vouchers, and GenBank accessions for taxa included in this study. Taxa are grouped by subfamily within Bromeliaceae and by family outside Bromeliaceae. Sequences newly generated for this study begin with HQ or JF. Taxa for which sequences were concatenated in the combined analyses are listed sequentially with an asterisk (*). Sequences for different loci obtained from different accessions of the same species are listed after the corresponding vouchers. Missing sequences are indicated by –.

Taxon; *Voucher specimen*, Herbarium; GenBank accessions: *matK*; *ndhF*; *rps16*; *atpB-rbcL*; *psbA-trnH*; *rpl32-trnL*; *trnL* intron/*trnL-trnF* intergenic spacer

Brocchinioideae

Brocchinia acuminata L.B.Sm.; SEL 81-1937; AF162228.2; L75859; HQ913837; JF280690; HQ913663; HQ913751; HQ882715. ***Brocchinia prismatica*** L.B.Sm.; *T. Givnish s.n.*, WIS; HQ900681; AY438600; HQ913838; JF280691; HQ913664; HQ913752; HQ882716. ***Brocchinia uiapanensis*** (Maguire) Givnish; *T. Givnish 4200*, WIS; HQ900682; AY438599; HQ913839; JF280692; HQ913665; HQ913753; HQ882717.

Lindmanioideae

Connellia cf. ***nutans*** L.B.Sm.; *P. E. Berry 7741*, WIS; –; HQ895740; –; –; –; –; –. ***Lindmania guianensis*** (Beer) Mez; *W. Till 16018a*, WU; AY614019; –; AY614141; AY614385; HQ913695; –; AY614263. ***Lindmania longipes*** (L.B.Sm.) L.B.Sm.; *T. Givnish s.n.*, WIS; HQ900683; AY438605; HQ913866; JF280719; HQ913696; HQ913783; HQ882736.

Tillandsioideae

Alcantarea duarteana (L.B.Sm.) J.R.Grant; *W. Till 11052*, WU; AY614031; –; AY614153; AY614397; HQ913656; HQ913744; –; *E. Leme 2891*, HB; –; HQ895732; –; –; –; –; HQ882711. ***Catopsis floribunda*** L.B. Sm.*; MSBG 91-3; AF539963; –; –; –; –; –; –; ***Catopsis morreniana*** Mez*; *H.B.V. B176/80*, WU; –; HQ895739; AY614147; AY614391; HQ913669; HQ913757; HQ882721. ***Glomeropitcairnia penduliflora*** (Griseb.) Mez; *T. Givnish s.n.*, WIS; –; L75864; –; –; –; –; –; *W. Till 12012*, WU; AY614030; –; AY614152; AY614396; HQ913686; HQ913774; AY614274. ***Guzmania monostachia*** (L.) Rusby ex Mez; SEL 82-225; –; L75865; HQ913859; JF280713; HQ913688; HQ913776; HQ882732; *R. Horres H016*, FR; AY949990; –; –; –; –; –; –. ***Guzmania rhonhofiana*** Harms; SEL 80-1130; –; L75934; –; –; –; –; –; *B224/80*, WU; AY614064; –; HQ913860; AY614430; HQ913689; HQ913777; AY614308/AY614308. ***Guzmania roezlii*** (E.Morren) Mez; *H.B.V. 166/96*, WU; –; –; HQ913861; JF280714; HQ913690; HQ913778; HQ882733. ***Mezobromelia hutchisonii*** (L.B.Sm.) W.Weber & L.B.Sm.; *W. Rauh 40104*, HEID; AY614050; HQ895753; AY614172; AY614416; HQ913698; HQ913785; HQ882738. ***Mezobromelia pleiosticha*** (Griseb.) Utley & H.Luther; SEL 81-1986; AF539970; L75891; HQ913868; JF280721; HQ913699; HQ913786; HQ882739. ***Racinaea ropalocarpa*** (André) M.A.Spencer & L.B.Sm.; *B256/96*, WU; AY614083; –; AY614205; AY614449; HQ913720; HQ913807; AY61437. ***Tillandsia complanata*** Benth.; SEL 79-0519; –; L75899; –; –; –; –; –; *L. Hromadnik 2137*, WU; –; –; HQ913893; –; HQ913725; HQ913812; HQ882757; *W. Till 21085a*, WU; –; –; –; JF280746; –; –; –. ***Tillandsia dodsonii*** L.B.Sm.; *Brown 3218*, RM; –; L75879; –; –; –; –; –; *W. Rauh 34183*, WU; AY614072; –; AY614194; AY614438; HQ913726; –; –; SEL 1973-0004-033; –; –; –; –; –; HQ913813; HQ882758. ***Tillandsia usneoides*** (L.) L.; *G. Palim s.n.*, WU; AY614122; –; –; –; –; –; AY614366; *M. Barfuss s.n.*, WU; –; –; AY614243; AY614487; HQ913727; HQ913814; –; ex cult. UW-Madison greenhouses; –; HQ895767; –; –; –; –; –. ***Tillandsia utriculata*** L.; *G. Brown 3211*, RM; –; L75939; –; –; –; –; –; *W. Till 17007*, WU; AY614090; –; AY614212; AY614456; HQ913728; HQ913815; AY614334. ***Tillandsia viridiflora*** (Beer) Baker; *H.B.V. B87/80*, WU; AY614066; HQ895768; AY614188; AY614432; HQ913729; HQ913816; HQ882759. ***Vriesea espinosae*** (L.B.Sm.) Gilmartin; *G. Brown 3218*, RM; AF539978.2; –; HQ913895; JF280748; HQ913731; HQ913818; HQ882760. ***Vriesea glutinosa*** Lindl.; SEL 86-0303; –; L75914; –; –; –; –; –; *H.B.V. B444/80*, WU; GU475471; –; HQ913896; JF280749; HQ913732; HQ913819; HQ882761. ***Vriesea malzinei*** E.Morren; SEL 78-757; AF162265.2; L75915; HQ913897; JF280750; HQ913733; HQ913820; HQ882762. ***Werauhia viridiflora*** (Regel) J.R.Grant; SEL 90-0282; AF539979.2; L75910; HQ913898; JF280751; HQ913734; HQ913821; HQ882763.

Hechtioideae

Hechtia glomerata Zucc.; *M. Remmick 139*, SEL; AF162245.2; HQ895752; HQ913862; JF280715; HQ913691; HQ913779; HQ882734. ***Hechtia guatemalensis*** Mez; SEL 81-1891; –; AY438604; –; –; –; –; –; *D. Crayn s.n.*, SEL; AF162246.2; –; –; –; –; –; –; *R. Horres 088*, FR; –; –; HQ913863; JF280716; HQ913692; HQ913780; AF188821/DQ084656. ***Hechtia lindmanioides*** L.B. Sm.; *D. Crayn s.n.*, SEL; AF162247.2; –; HQ913864; JF280717; HQ913693; HQ913781; HQ882735.

Navioideae

Brewcaria reflexa (L.B.Sm.) B.Holst; Givnish et al., 1997; HQ900680; –; HQ913836; JF280689; HQ913662; HQ913750; HQ882714. ***Cottendorfia florida*** Schult. & Schult.f.; SEL 96-0695; –; AY438602; –; –; –; –; –; *E. Leme 3692*, HB; AF162230.2; –; –; –; –; –; –; *T. Givnish s.n.*, WIS; –; –; HQ913843; JF280697; HQ913671; HQ913759; HQ882722. ***Navia phelpsiae*** L.B.Sm.; MSBG 1986-0523A; AF162249.2; HQ895754; HQ913869; JF280722; HQ913700; HQ913787; HQ882740. ***Navia saxicola*** L.B.Sm.; *T. Givnish s.n.*, WIS; HQ900684; AY208983; HQ913870; JF280723; HQ913701; HQ913788; HQ882741. ***Navia splendens*** L.B.Sm.; SEL 83-0288; –; L75892; –; –; –; –; –; *R. Horres 034*, FR; GU475468; –; HQ913871; JF280724; HQ913702; HQ913789; HQ882767. ***Sequencia serrata*** (L.B.Sm.) Givnish; *T. Givnish s.n.*, WIS; HQ900688; AY438601; HQ913891; JF280744; HQ913723; HQ913810; HQ882756.

Pitcairnioideae

Deuterocohnia glandulosa E.Gross; *L. Hromadnik 5167*, HEID; EU681893; –; –; –; –; –; –; *R. Horres 090*, FR; –; HQ895742; HQ913846; JF280700; HQ913674; HQ913762; AF188784/DQ084652. ***Deuterocohnia longipetala*** (Baker) Mez; *Marnier-Lapostelle s.n.*; –; AY208984; –; –; –; –; –; MSBG 075767; AF162231.2; –; HQ913847; JF280701; HQ913675; HQ913763; HQ882724. ***Deuterocohnia lotteae*** (Rauh) M.A.Spencer & L.B.Sm.; MSBG 94-142; AF162232.2; –; –; –; –; –; –; *R. Horres 084*, FR; –; HQ895743; HQ913848; JF280702; HQ913676; HQ913764; AF188783/DQ084566. ***Dyckia dawsonii*** L.B.Sm.; MSBG 1994-0146A; AF162234.2; HQ895744; HQ913849; JF280703; HQ913677; HQ913765; HQ882725. ***Dyckia ferox*** Mez; MSBG 1996-0211A; AF162235.2; HQ895745; HQ913850; JF280704; HQ913678; HQ913766; HQ882726. ***Encholirium irwinii*** L.B.Sm.; *E. Leme 2881*, HB; AF162237.2; HQ895748; HQ913854; JF280708; HQ913682; HQ913770; HQ882729. ***Encholirium scutor*** (L.B.Smith) Rauh; MSBG 1995-0113A; AF162239.2; HQ895747; HQ913853; JF280707; HQ913681; HQ913769; HQ882728. ***Fosterella penduliflora*** (C.H.Wright) L.B.Sm.; SEL 69-1976-12; –; L75863; –; –; –; –; –; *R. Horres 086*, FR; AY949996; –; HQ913856; JF280710; HQ913684; HQ913772; AF188782/DQ084571. ***Fosterella petiolata*** (Mez) L.B.Sm.; MSBG 1995-0007A; AF162242.2; HQ895750; HQ913857; JF280711; HQ913685; HQ913773; HQ882731. ***Pitcairnia carinata*** Mez; *G. Brown 3173*, RM; AF539974.2; L75902; HQ913875; JF280728; HQ913706; HQ913793; HQ882745. ***Pitcairinia corallina***

Linden & André; SEL 86-0574; AF162252; AY438608; –; –; –; –; –; *R. Horres 094*, FR; –; –; HQ913876; JF280729; HQ913707; HQ913794; HQ882768. ***Pitcairinia feliciana*** (A.Chev.) Harms & Mildbr.; SEL 98-0116; –; AY438609; –; –; –; –; –; *T. Givnish s.n.*, WIS; HQ900685; –; HQ913877; JF280730; HQ913708; HQ913795; HQ882746. ***Pitcairnia heterophylla*** (Lindl.) Beer; *R. Horres 2024*, FR; AF162254.2; HQ895757; HQ913878; JF280731; HQ913709; HQ913796; AF188789/DQ084649. ***Pitcairnia hirtzii*** H. Luther; SEL 93-294; AF539972; L75901; HQ913879; JF280732; HQ913710; HQ913797; HQ882747. ***Pitcairnia orchidifolia*** Mez; MSBG 1994-0036A; AF162255.2; –; HQ913880; JF280733; HQ913711; HQ913798; HQ882748. ***Pitcairnia poortmanii*** André; MSBG 1991-0018A; AF539975.1; –; HQ913881; JF280734; HQ913712; HQ913799; HQ882749. ***Pitcairnia wendlandii*** Baker; MSBG 1996-0529A; AF539976.1; HQ895758; HQ913882; JF280735; HQ913713; HQ913800; HQ882750.

Puyoideae

Puya aequatorialis André; SEL 93-211; AF162260.2; L75903; HQ913884; JF280737; HQ913715; HQ913802; HQ882752. ***Puya alpestris*** (Poepp.) Gay; *R. S. Jabaily 177*, WIS; –; HQ895760; JF280754; JF280764; –; JF280758; JF29926; *R. Horres 060*, FR; AY949998; –; –; –; –; –; –. ***Puya castellanosii*** L.B.Sm.; *R. S. Jabaily 149*, WIS; FJ968190; HQ895761; JF280755; –; JF280762; JF280759; JF299261. ***Puya chilensis*** Molina; *R. S. Jabaily 164*, WIS; HQ900686; –; –; –; –; –; –; *T. Givnish s.n.*, WIS; –; HQ895762; HQ913885; JF280738; HQ913716; HQ913803; HQ882753. ***Puya laxa*** L.B.Sm.; Crayn et al., 2004; AF162262; –; –; –; –; –; –; *R. Horres 006*, FRP; –; HQ895763; HQ913886; JF280739; HQ913717; HQ913804; AF188794/DQ084563. ***Puya mima*** L.B.Sm. & Read; *R. S. Jabaily 228*, WIS; FJ968231; HQ895764; JF280756; JF280765; JF280763; JF280760; JF299262. ***Puya raimondii*** Harms; *T. Givnish s.n.*, WIS; HQ900687; AY438611; HQ913887; JF280740; HQ913718; HQ913805; HQ882754. ***Puya venusta*** (Baker) Phil.; *R. S. Jabaily 166*, WIS; FJ968194; HQ895765; JF280757; –; –; JF280761; JF299263.

Bromelioideae

Acanthostachys strobilacea (Schult. & Schult.f.) Klotzsch; *R. Horres 019*, FR; AY950021; HQ895726; HQ913823; JF280677; HQ913648; HQ913736; AF188765/DQ084606. ***Aechmea bromeliifolia*** (Rudge) Baker; *K. Schulte 051202-4*, FR; GU475466; HQ895727; HQ913824; JF280678; HQ913649; HQ913737; HQ882707. ***Aechmea drakeana*** André; *G. Zizka 1100*, FRP; AY950043; HQ895728; HQ913825; JF280679; HQ913650; HQ913738; AF188772/DQ084588. ***Aechmea haltonii*** H.Luther; SEL 85-1447; AF539960.2; L75844; HQ913826; JF280680; HQ913651; HQ913739; HQ882708. ***Aechmea lingulata*** (L.) Baker; *Faria 81*, RFA; JF295091; HQ895729; –; –; –; –; –; *K. Schulte 101203-1*, FR; –; –; HQ913827; JF280681; HQ913652; HQ913740; HQ882709. ***Aechmea nudicaulis*** (L.) Griseb.; *K. Schulte 200603-1*, FR; –; –; HQ913828; –; HQ913653; –; DQ084689/DQ084589; *W. Till 18094*, WU; AY614024; –; –; AY614390; –; HQ913741; –. ***Aechmea organensis*** Wawra; *Wendt 342*, RFA; JF295090; HQ895730; –; –; –; –; –; *K. Schulte 250205-1*, FR; –; –; HQ913829; JF280682; HQ913654; HQ913742; HQ882710. ***Aechmea racinae*** L.B.Sm.; *Faria 80*, RFA; JF295089; HQ895731; –; –; –; –; –; *K. Schulte 120203-1*, FR; –; –; HQ913830; JF280683; HQ913655; HQ913743; DQ084691/DQ084583. ***Aechmea sphaerocephala*** Baker; *R. Horres 030b*, FR; AY950045; –; HQ913842; JF280696; HQ913670; HQ913758; AF188770/DQ084578. ***Ananas ananassoides*** (Baker) L.B.Sm.; *G. Brown 3129*, RM; AF162227.2; L75845; HQ913831; JF280684; HQ913657; HQ913745; HQ882712. ***Ananas nanus*** (L.B.Sm.) L.B.Sm.; *R. Horres & K. Schulte 050401-9*, FR; AY950054; –; HQ913832; JF280685; HQ913658; HQ913746; DQ084695/DQ084573; SEL 1991-0469; –; HQ895733; –; –; –; –; –. ***Araeococcus goeldianus*** L.B.Sm.; *Moonen s.n.*, SEL; –; HQ895734; –; –; –; –; –; *K. Schulte 100203-1*, FR; AY950002; –; HQ913833; JF280686; HQ913659; HQ913747; DQ084630/DQ084697. ***Araeococcus pectinatus*** L.B. Sm.; SEL 85-231; AF539961.2; L75846; HQ913834; JF280687; HQ913660; HQ913748; HQ882713. ***Billbergia decora*** Poepp. & Endl.; *R. Horres 129*, FR; AY950050; HQ895735; HQ913835; JF280688; HQ913661; HQ913749; DQ084698/DQ084624. ***Bromelia chrysantha*** Jacq.*; MSBG 1983-0286A; AF539962; –; JF280753; –; –; –; –. ***Bromelia flemingii*** I.Ramirez & Carnevali*; SEL 1997-0231; –; HQ895736; –; JF280693; HQ913666; HQ913754; HQ882718. ***Canistropsis billbergioides*** (Schult. & Schult.f.) Leme; *E. Leme 171*, RFA; JF295092; HQ895737; –; –; –; –; –; *K. Schulte 061202-1*, FR; –; –; HQ913840; JF280694; HQ913667; HQ913755; HQ882719. ***Canistrum aurantiacum*** E.Morren; *E. Leme 567*, RFA ; JF295094; HQ895738; –; –; –; –; –; K. Schulte 300508-4, FR; –; –; HQ913841; JF280695; HQ913668; HQ913756; HQ882720. ***Cryptanthus beuckeri*** E.Morren; SEL 89-499; AF539965.2; L75856; HQ913844; JF280698; HQ913672; HQ913760; HQ882723. ***Deinacanthon urbanianum*** (Mez) Mez; *R. Horres H018*, FRP; AY950017; HQ895741; HQ913845; JF280699; HQ913673; HQ913761; AF188781/DQ084607. ***Edmundoa perplexa*** (L.B.Sm.) Leme; MSBG 1987-264; AF539967.2; HQ895746; HQ913851; JF280705; HQ913679; HQ913767; HQ882727. ***Eduandrea selloana*** (Baker) Leme, W.Till, G.K.Br., J.R.Grant & Govaerts; *E. Leme 1830*, HB; JF295093; L75894; –; –; –; –; –; *H.B.V. B00B95-1*, WU; –; –; HQ913852; JF280706; HQ913680; HQ913768; HQ882743. ***Fascicularia bicolor*** (Ruiz & Pav.) Mez; *G. Zizka 1790*, FRP; AY950023; –; –; –; –; –; –; *D. Vandervoort s.n.*, WU; –; HQ895749; HQ913855; JF280709; HQ913683; HQ913771; HQ882730. ***Greigia sphacelata*** (Ruiz & Pav.) Regel; *K. Schulte 230305-4*, FR; AY950015; HQ895751; HQ913858; JF280712; HQ913687; HQ913775; AF188779/DQ084599. ***Hohenbergia stellata*** Schult. & Schult.f.; *R. Horres 037*, FRP; AY950026; –; HQ913865; JF280718; HQ913694; HQ913782; AF188774/DQ084609. ***Lymania alvimii*** (L.B.Sm. & Read) Read; SEL 90-297; –; L75907; HQ913867; JF280720; HQ913697; HQ913784; HQ882737; *R. Horres & K. Schulte 050401-4*, FR; AY950000; –; –; –; –; –; –. ***Neoregelia pineliana*** (Lem.) L.B.Sm.; SEL 86-261; AF539971; L75893; –; –; –; –; –; *R. Horres & K. Schulte 210601-1*, FR; –; –; HQ913872; JF280725; HQ913703; HQ913790; HQ882742. ***Ochagavia carnea*** (Beer) L.B.Sm. & Looser; *R. Horres 117*, FR; –; HQ895755; HQ913873; JF280726; HQ913704; HQ913791; HQ882744; *R. Horres 115*, FR; EU681905; –; –; –; –; –; –. ***Ochagavia elegans*** Phil.; *R. Horres 23a*, FR ; AY950006; HQ895756; HQ913874; JF280727; HQ913705; HQ913792; AF188778/DQ084603. ***Pseudananas sagenarius*** (Arruda) Camargo; *M. W. Chase 24447*, K; GU475470; HQ895759; HQ913883; JF280736; HQ913714; HQ913801; HQ882751. ***Quesnelia quesneliana*** (Brongn.) L.B.Sm.; *K. Schulte 300508-6*, FR; –; –; HQ913888; JF280741; HQ913719; HQ913806; HQ882755; *Wendt 335*, RFA; JF295095; HQ895766; –; –; –; –; –. ***Ronnbergia petersii*** L.B.Sm.; SEL 78-907; –; L75897; –; –; –; –; –; *K. Schulte 170203-5*, FR; AY950001; –; HQ913890; JF280743; HQ913722; HQ913809; DQ084718/DQ084632. ***Wittrockia superba*** Lindm.; *R. Horres & K. Schulte 050401-8*, FR; AY950025; HQ895769; HQ913899; JF280752; HQ913735; HQ913822; AF188767/DQ084611.

Rapateaceae

Rapatea paludosa Aubl.; *K. J. Sytsma et al. 5157*, WIS; –; AF207623; HQ913889; JF280742; HQ913721; HQ913808; HQ882764.

Sparganiaceae

Sparganium sp.; *T. Givnish s.n.*, WIS; AB088802; AY191213; HQ913892; JF280745; HQ913724; HQ913811; HQ882765.

Typhaceae

Typha angustifolia L.*; *Graham 1040*, TRT; –; U79230; –; –; –; –; –. ***Typha latifolia*** L.*; *T. Givnish s.n.*, WIS; DQ069587; –; HQ913894; JF280747; HQ913730; HQ913817; HQ882766.