SYSTEMATICS AND EVOLUTION OF THE Ronnbergia ALLIANCE (BROMELIACEAE): HISTORY OF DISJUNCT DIVERSIFICATION IN THREE BIODIVERSITY HOTSPOTS OF THE NEOTROPICS

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SYSTEMATICS AND EVOLUTION OF THE Ronnbergia ALLIANCE
(BROMELIACEAE): HISTORY OF DISJUNCT DIVERSIFICATION IN THREE
BIODIVERSITY HOTSPOTS OF THE NEOTROPICS

by

JULIÁN ANDRÉS AGUIRRE SANTORO

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment
of the requirements for the degree of Doctor of Philosophy,
The City University of New York
2015
This manuscript has been read and accepted for the Graduate Faculty in Biology to satisfy the dissertation requirement for the degree of Doctor of Philosophy.

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THE CITY UNIVERSITY OF NEW YORK
Abstract

SYSTEMATICS AND EVOLUTION OF THE Ronnbergia ALLIANCE (BROMELIACEAE): HISTORY OF DISJUNCT DIVERSIFICATION IN THREE BIODIVERSITY HOTSPOTS OF THE NEOTROPICS

by

Julián Andrés Aguirre Santoro

Adviser: Dr. Fabián Michelnageli

The systematics, biogeography and evolution of the “Ronnbergia Alliance,” a nested lineage within the Core Bromelioideae, were investigated. In the first chapter, the phylogenetic relationships of the Ronnbergia Alliance were reconstructed using three chloroplast and three nuclear DNA sequence markers in combination with a wide species sampling across the Core Bromelioideae and a nearly complete species-level sampling of the five species complexes that likely comprise the Ronnbergia Alliance. The analysis indicates that the Ronnbergia Alliance is a robust monophyletic group sister to the remaining Core Bromelioideae, and it is composed by species of the polyphyletic genera Aechmea, Hohenbergia and Ronnbergia. The first of main lineage within the Ronnbergia Alliance, here called the Pacific Clade, contains species of that occur exclusively in the forests of southern Central America to northwestern South America. The second clade, called the Atlantic Clade, contains species mostly limited to the central corridor of the Atlantic Forest and the Greater Antilles. The combination of apically spreading tubular corollas and unappendaged ovules are diagnostic for the Ronnbergia Alliance, whereas flower size, corolla tube length, and petal pigmentation are important characters to differentiate the Pacific and Atlantic Clades. A new taxonomic reorganization and synopsis for this clade was
proposed in the second chapter. Here, all the species of the Pacific Clade were placed in *Ronnbergia*, whereas the species of the Atlantic Clade were relocated in the resurrected genus *Wittmackia*. In the third chapter, a complete taxonomic revision of the Caribbean clade of *Wittmackia* was conducted. In the fourth chapter, the biogeographic history and evolutionary rate dynamics of the *Ronnbergia* Alliance were analyzed. These analyses showed that one vicariant event that separated *Ronnbergia* from *Wittmackia* in South America, and a later long-distance dispersal event allowed the separation of *Wittmackia* between the Atlantic Forest and Jamaica. Although the evolutionary rate dynamics remained constant during the diversification of *Ronnbergia*, these rates were heterogeneous during the radiation of *Wittmackia*. This is the first species-level approach that combines phylogenetic, ecological, geographic and morphological information to reveal fine-scale processes that shaped the evolution of highly diverse lineages of Bromeliaceae.
Acknowledgements

I want to express my most sincere gratitude to my advisor and friend, Dr. Fabián Michelangeli, who gave me his unconditional support and guidance during the development of this dissertation and throughout my doctoral studies. I am thankful to Dr. Dennis W. Stevenson, Dr. Lawerence M. Kelly and Dr. Dwight Kincaid for their commitment to make my doctoral studies successful and provide me with their knowledge and support when I needed it. I also want to thank my other committee members, Dr. Ana Carolina Carnaval, Dr. Wendy Clement, and Dr. Wayt Thomas, for helping me achieve a successful dissertation as the main product of five years of doctoral studies.

The completion of my doctoral studies could not have been possible without the full financial and logistic support of the following institutions: the Administrative Department of Science, Technology and Innovation of Colombia (COLCIENCIAS); The New York Botanical Garden (Oliver Hazard Perry Fellowship); The Graduate Center of the City University of New York; and the Academic and Professional Programs for the Americas (LASPAU). Additionally, I want to thank the following agencies for their partial financial support to execute the fieldwork and training of my dissertation: the American Society of Plant Taxonomists, The Botanical Garden of Rio de Janeiro (Brazil), The Explorers Club of America, The Systematic Association and Linnaean Society of London, The Torrey Botanical Society, and the National Science Foundation.

I want to thank my colleagues and friends who shared their knowledge, ideas, and advice with me, especially Nelson Salinas, Marcelo Reginato, Ricardo Kriebel, Fernando Matos, Fernanda Dos Santos Silva, Marcela Thadeo, Vinson Doyle, Jessica Allen, Donald McClelland, Jenna Dorey, and Annie Virnig.
I thank the following colleagues who provided logistic support in the field and in the laboratory, and others who contributed with photographs, samples and specimens for the successful execution of this dissertation: André Amorim, Michael Baxter, Eldis Becquer, Julio Betancur, Keron Campbell, Lisa Campbell, Laura Clavijo, Tracy Commock, Lukas Daneu, Rafaela C. Forzza, Favio González, Bruce K. Holst, Elton Leme, Raquel Monteiro, Antoine Nicholas, Andreas Oberli, Paola Pedraza, Gregory Plunkett, Ivón Ramírez-Morillo, Lauren Raz, Wes Rouse, Eugenio Santiago, Matthew Sewell, Wayt Thomas, Tania Wendt, and Alejandro Zuluaga.

Finally, I am grateful to my family in Colombia and my Timm family in the U.S. for their loving and enthusiastic support to my career as a botanist. This thesis is dedicated to my wife, Jennifer Timm, who gave me all her love and support during these five years and had the patience and genuine interest in helping me with the writing and analytic process of this dissertation.
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Chapter 1

1 Molecular Phylogenetics of the *Ronnbergia* Alliance

(Bromeliaceae, Bromelioideae) and insights about its morphological evolution

1.1 Abstract

The tank-epiphytic clade of berry-fruited bromeliads, also known as the Core Bromelioideae, represents a remarkable adaptive radiation within the Bromeliaceae; the details of this radiation, however, have been difficult to study because this lineage is plagued with generic delimitation problems. In this study, a species-level phylogenetic approach was used to investigate a stable, albeit poorly understood, lineage nested within the Core Bromelioideae, here called the “*Ronnbergia* Alliance.” In order to assess the monophyly and phylogenetic relationships of this group, three chloroplast and three nuclear DNA sequence markers were combined with an exhaustive sampling across five taxonomic complexes predicted to comprise the *Ronnbergia* Alliance. Because of the lack of conflicting signal between the chloroplast and nuclear markers, the datasets were combined to produce a robust phylogenetic hypothesis. The main results indicate that the *Ronnbergia* Alliance is a robust monophyletic group sister to the

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1 Manuscript follows the guidelines of *Molecular Phylogenetics and Evolution.*
remaining Core Bromelioidae, and is comprised of species in the polyphyletic genera *Aechmea*, *Hohenbergia* and *Ronnbergia*. Two major internal lineages with high geographic structure were identified within the *Ronnbergia* Alliance. The first of these lineages, the Pacific Clade, contains species of *Aechmea* and *Ronnbergia* that occur exclusively from southern Central America to northwestern South America. The second clade, the Atlantic Clade, contains species of *Aechmea*, *Hohenbergia* and *Ronnbergia* mostly limited to the Atlantic Forest and the Caribbean. The diagnostic and evolutionary importance of 13 selected characters was also explored using ancestral character reconstructions on the phylogenetic hypothesis. It was found that the combination of apically spreading tubular corollas and unappendaged ovules are diagnostic for the *Ronnbergia* Alliance, whereas flower size, length of the corolla tube, and petal pigmentation and apex are important characters to differentiate the Pacific and Atlantic Clades. This study opens new perspectives to propose taxonomic reorganizations and provide a framework for future evolutionary and biogeographic studies.

**Keywords**

Atlantic Forest, Bromeliaceae, Bromelioidae, Caribbean, Choco Forest, *Ronnbergia* Alliance
1.2 Introduction

Recent developments on the fields of phylogenetics, biogeography, and comparative biology have permitted exploring exciting evolutionary questions across many taxonomic groups. The Bromeliaceae have received special attention because of their clear shifts in adaptive regimes across lineages, high species diversity (ca. 3300 species), and almost exclusive Neotropical geographical distribution (Benzing 2000; Givnish et al. 2014; Bouchenak-Khelladi et al. 2015). Consequently, recent studies have provided significant advances in the understanding of the phylogenetic relationships and major evolutionary events across the main lineages in the family (Givnish and Sytsma 2000; Crayn 2004; Givnish et al. 2004, 2007, 2011, 2014; Quezada and Gianoli 2011; Silvestro et al. 2014). At a finer infra-generic scale, however, the taxonomy and phylogenetic relationships of the Bromeliaceae are still poorly understood (Faria et al. 2004; Barfuss et al. 2005; Schulte et al. 2009; Sass and Specht 2010). In recent years, different studies have approached this problem by focusing on the subfamily Bromelioideae, a monophyletic lineage plagued with generic delimitation problems, but at the same time, highly attractive for evolutionary studies because of its high species diversity (ca. 900 species), large mosaic of phenotypic and adaptive variation, and high levels of narrow endemism across the neotropics (Smith and Downs 1979; Faria et al. 2004; Schulte et al. 2005, 2009; Horres et al. 2007; Sousa et al. 2007; Schulte and Zizka 2008; Almeida et al. 2009; Sass and Specht 2010; Silvestro et al. 2014; Evans et al. 2015). The present study aims to elucidate relationships in the family by bringing clarity to a localized case of problematic generic circumscription in Bromelioideae using a phylogenetic approach.

The problems with generic delimitation in Bromelioideae have been discussed since the early taxonomic treatments of Bromeliaceae. In the latest comprehensive revision of the family,
for instance, Smith & Downs (1979) recognized that although characters such as inflorescence ramification, flower pedicels, and petal appendages are important to diagnose genera within Bromeliioideae, they could occasionally occur in isolated species placed within the most poorly circumscribed genera of the subfamily, such as Aechmea. Morphological studies later provided further evidence showing that these “diagnostic” characters are prone to evolve rapidly and should not be used as delimiters of genera (Brown and Terry 1992; Faria et al. 2004; Schulte and Zizka 2008). The limitations posed by the lack of unequivocal diagnostic characters have been progressively approached with the advent of phylogenetics. Recent studies have shown that the early-diverging lineages of Bromeliioideae are generally tankless, strict terrestrial species, whereas the most recent and diverse lineage encompasses mostly tank-forming, epiphytic species (Schulte et al. 2009; Sass and Specht 2010; Givnish et al. 2011; Silvestro et al. 2014; Evans et al. 2015). While the early-diverging lineages of Bromeliioideae are represented by relatively stable genera, the tank-epiphytic clade, also known as the “Core Bromeliioideae” (sensu Sass and Specht 2010), contains the most confusing genera of Bromeliioideae. This clade includes, for the most part, the large genus Aechmea (ca. 280 spp.), which is highly polyphyletic and intermingles with the other ca. 18 genera in the clade (Faria et al. 2004; Schulte et al. 2009; Sass and Specht 2010; Silvestro et al. 2014).

The level of resolution on the phylogenetic relationships within the Core Bromeliioideae is still insufficient to propose a stable taxonomic classification; independent phylogenetic studies, however, have revealed common patterns that can serve as a starting point for further investigation. One such pattern is that the most robust lineages within the Core Bromeliioideae are composed by species that share a similar, narrow geographical distribution, rather than undisputable morphological similarities. In this context, one of these lineages, here called
“Ronnbergia Alliance,” is thorroughly investigated in this dissertation. This study is, therefore, the first attempt to consolidate the knowledge about the specific events that gave rise to lineages within the Core Bromelioideae and its taxonomic implications.

The preconceived definition of the Ronnbergia Alliance used here is based on a consensus of prior phylogenetic studies that show a small and well supported clade, frequently sister to the remaining Core Bromelioideae, and contains representative species of Ronnbergia, Hohenbergia subgenus Wittmackiopsis, the Aechmea lingulata complex (Siqueira Filho and Leme 2006), and species of Aechmea subgenus Chevaliera and Aechmea subgenus Pothuava endemic to the rainforests of northwestern South America and southern Central America (Aguirre-Santoro et al., 2015; Givnish et al., 2011; Maia et al., 2012; Sass and Specht, 2010; Schulte et al., 2009, 2005; Schulte and Zizka, 2008; Silvestro et al., 2014; Fig. 1.1). Except for the widespread species Aechmea lingulata, these five taxonomic complexes are characterized by their narrow endemism within three highly biodiverse regions of the neotropics: 1) the rainforests of northwestern South America and southern Central America; 2) the central and northern Atlantic Forest and adjacent semi-deciduous forests and Caatinga; and 3) the region of the Caribbean that includes the Greater Antilles (except Hispaniola), the Cayman and Providencia islands, and the Yucatán Peninsula. Although the species across these taxonomic complexes also share morphological affinities, taxonomic treatments have rarely placed them together because they do not strictly fit within traditional generic limits. For example, species of Ronnbergia and Aechmea subgenus Pothuava that co-occur in the forests of northwestern South America and southern Central America exhibit simple inflorescences, long-tubular subspradung corollas, and similar patterns of corolla coloration; these species, however, have long remained in different genera because Aechmea subgenus Pothuava has petal appendages whereas
Ronnbergia lacks them. None of these five taxonomic complexes has been comprehensively represented in phylogenetic studies, and their phylogenetic relationships and monophyly have not been formally tested. For this reason, this study assesses the monophyly and phylogenetic relationships of the Ronnbergia Alliance by including a near-complete species sampling of the five taxonomic complexes discussed above.

Using a robust phylogenetic hypothesis for the Ronnbergia Alliance will serve as a framework to study unexplored characters and reassess the importance of traditional taxonomic ones. This is relevant because previous morphology-based phylogenetic analyses suggested that overlooked characters such as corolla shape, ovary surface, stigma types, pollen ornamentation, and seed structure are good sources of potential diagnostic characters to define clades across Bromelioidae (Faria et al. 2004; De Sousa et al. 2008; Almeida et al. 2009). Moreover, traditional taxonomic characters such as sepal armature, petal appendages, ovule appendages, placentation, and pollen aperture must be revisited because they seem to be stable across major lineages within Bromelioidae, but have been rarely explored in a phylogenetic context (Mez 1896; Smith and Downs 1979; Schulte and Zizka 2008). The present study explores some of these characters using ancestral character state reconstructions in order to test their stability and diagnostic value. This approach will help future taxonomic decisions for the Ronnbergia Alliance and detect traits that were important for the diversification of its lineages.

This study can be summarized in two main objectives: 1) to reconstruct the phylogenetic relationships of the Ronnbergia Alliance using multilocus DNA sequence data and a comprehensive species sampling in order to test its monophyly, confirm its placement within the Core Bromelioidae, and identify its internal subclades; and 2) to explore the taxonomic and evolutionary importance of 13 morphological characters that show potential as diagnostic
characters for the *Ronnbergia* Alliance and its subclades. This study aims to demonstrate that it is possible to approach the taxonomic and phylogenetic complexity of the Core Bromelioidae by targeting robust lineages and understanding the morphological trends in each lineage. A better understanding of these groups will open new perspectives to propose taxonomic reorganizations and provide a framework for future evolutionary and biogeographic studies.
1.3 Materials and methods

1.3.1 Taxon sampling

A total of 168 terminals representing 129 species were included in the phylogenetic analyses (Table 1.1). Three species of Bromelia were chosen for rooting the trees, because this genus has been identified as one of the earliest-diverging lineages within Bromelioideae (Givnish et al. 2007, 2011; Schulte and Zizka 2008; Schulte et al. 2009; Evans et al. 2015). In order to generate a nearly complete species-level phylogenetic hypothesis for the relationships of the Ronnbergia Alliance, ninety-four terminals to represent 60 species of the following five taxonomic complexes were selected: 1) *Ronnbergia* (12 spp. included out of 13 spp. recognized here); 2) *Hohenbergia* subgenus Wittmackiopsis (17 spp. included out of 19 spp. recognized here); 3) the *Aechmea lingulata complex* as defined by Siqueira Filho and Leme (2006) (23 spp. included out of 26 spp. recognized here); 4) *Aechmea* subgenus *Pothuava* from southern Central American and northwestern Andes (6 spp. included out 9 spp. recognized here); and 5) *Aechmea* subgenus *Chevaliera* endemic to the rainforests of northwestern South America (2 spp. included out of 3 spp. recognized here). Although *Aechmea* subgenus *Pothuava* also includes 12 species endemic to eastern Brazil, the widespread *Aechmea nudicaulis*, and the northern Central American-endemic *Aechmea maria-reginae*, these species are not predicted to be part of the Ronnbergia Alliance because previous studies showed them as related to distant and scattered lineages of the Core Bromelioideae (Schulte et al. 2005, 2009; Schulte and Zizka 2008; Sass and Specht 2010; Evans et al. 2015). Similarly, only tank-forming, epiphytic species of *Aechmea* subgenus *Chevaliera* from northwestern South America are predicted to be part of the Ronnbergia Alliance, because the other species of this subgenus have been shown as distant
relatives within and outside the Core Bromelioideae (Schulte et al. 2009; Sass and Specht 2010; Silvestro et al. 2014; Evans et al. 2015). This comprehensive species sampling of the Ronnbergia Alliance corresponds to 86% of the total species described across the five taxonomic complexes.

A large selection of Bromelioideae species (71 terminals; 67 spp.) was used in order to include the most likely sister lineages of the Core Bromelioideae, and a thorough representation of the Core Bromelioideae. For the former, seven terminals (six spp.) of the genera Acanthostachys, Ananas, Disteganthus, and Orthophytum were sampled; for the latter, sixty-four terminals (61 spp.) were selected to represent the main lineages and genera of the Core Bromelioideae (excluding the Ronnbergia Alliance). This sampling includes several species of Aechmea subgenus Chevaliera and Aechmea subgenus Pothuava not predicted to be part of the Ronnbergia Alliance. Sequences for several species were downloaded from GenBank and are mostly based on the study of Sass & Specht (2010) (Table 1.1).
<table>
<thead>
<tr>
<th>Genus/subg./complex</th>
<th>Taxon</th>
<th>Collector (herbarium). (Liv. = Accession living plant)</th>
<th>ETS</th>
<th>g3pdh</th>
<th>rpb2</th>
<th>matk-trnK</th>
<th>rps16-trnK</th>
<th>trnL-F</th>
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</thead>
<tbody>
<tr>
<td>Acanthostachys</td>
<td>Acanthostachys pitcairnioides (Mez) Rauh &amp; Barthlott</td>
<td>Leme s.n (SEL)</td>
<td>Pending</td>
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<tr>
<td>Aechmea lingulata complex</td>
<td>Aechmea altocaririensis Leme &amp; L. Kollmann</td>
<td>Leme 8217-TYPE (RB)</td>
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<td>Pending</td>
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</tr>
<tr>
<td>Aechmea amorimii Leme</td>
<td>Montenegro 703 (RB)</td>
<td>Pending</td>
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<td>Lymania spiculata Leme &amp; Forzza</td>
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Table 1.1. Sampled taxa, vouchers and GenBank accession numbers. Species names in bold correspond to taxa predicted to comprise the *Ronnbergia* Alliance.
1.3.2 Sample collection, DNA extraction, amplification, and sequencing

Most samples were collected from wild plants in the main centers of diversity of the five taxonomic complexes of the Ronnbergia Alliance: Jamaica, Puerto Rico, the Yucatan Peninsula in Mexico, Southeastern Brazil, and Colombia (including the island of Providencia). Samples that could not be collected in the field were collected \textit{ex situ} at the Mary Selby Botanical Gardens in Sarasota, Florida and the private collection of Elton Leme in Teresópolis, Brazil (Table 1.1). All samples for DNA extraction were obtained from young leaves quickly dried in silica gel, and subsequently stored at -20ºC. Only one sample of \textit{Aechmea lingulata} from the lesser Antilles was obtained from herbarium material given the importance of including a Caribbean representative of this species in the analyses (permission for DNA extraction granted by the Gray Herbarium).

DNA was extracted using the DNeasy kit from Qiagen following the manufacturer’s standard procedures. Sequences for six DNA sequence markers were generated in this study, three from the nuclear genome and three from the chloroplast genome. These molecular markers were previously used in phylogenetic studies of Bromeliaceae, showing good potential for phylogenetic resolution, and not exhibiting detectable problems of paralogy. The nuclear markers correspond to the nuclear ribosomal external transcribed spacer (\textit{ETS}), the 23\textsuperscript{rd} intron of RNA polymerase beta subunit II (\textit{rpb2}), and the 8\textsuperscript{th} and 10\textsuperscript{th} exons of glyceraldehyde-3-phosphate dehydrogenase (\textit{g3pdh}). The three chloroplast molecular markers are the \textit{matK} gene and part of the adjacent 3’\textit{trnK} intron (\textit{matK-trnK}), the intergenic spacer between \textit{rps16} and \textit{trnK} (\textit{rps16-trnK}), and the intergenic spacer between \textit{trnL} and \textit{trnF} (\textit{trnL-F}).
The primers, references and temperature profiles for the PCR reactions are described in Table 1. All PCR reactions were conducted in 15 μl volumes using Eppendorf Mastercycler Pro thermocyclers. The master mix for all reactions contained 0.5 μl of template DNA, 0.75 μl of each pair of forward and reverse primers (10 μM), 1.5 μl of BSA (0.25 μg/μl), 7.5 μl of GoTaq Green Master Mix (Promega), and 4 μl of water. Only the master mix for trnL-F additionally contained 3 μl of Betaine (1 M) and 1 μl of water. Final PCR products were sequenced using the Sanger method for DNA sequencing and the same primers of the PCR reactions through the High-Throughput service at University of Washington, U.S.A. In order to avoid the limitations of having large amounts of missing data, the final dataset contains only taxa from which four or more sequences were generated. The only exception is the herbarium sample of Aechmea lingulata, from which it was only possible to obtain partial sequences of the chloroplast markers. No chimeric terminals were used in this study.
<table>
<thead>
<tr>
<th>DNA sequence</th>
<th>External primers</th>
<th>Internal primers</th>
<th>Reference</th>
<th>PCR temperatures (first reaction)</th>
<th>PCR temperatures (second reaction)</th>
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</thead>
<tbody>
<tr>
<td>ETS</td>
<td>ETS-Fwd and ETS-Rev.</td>
<td>Sass &amp; Specht (2010)</td>
<td>95°C × 3 min, 35 cycles (95°C × 1 min, 54°C × 1 min, 64°C × 1 min), 72°C × 5 min</td>
<td>95°C × 3 min, 8 cycles (95°C × 45 sec, 59°C × 45 sec, 72°C × 1 min), 30 cycles (95°C × 1 min, 65°C × 1 min, 72°C × 1 min), 72°C × 5 min</td>
<td></td>
</tr>
<tr>
<td>g3pdh</td>
<td>g3pdh-Fwd. and g3pdh-Rev.</td>
<td>Sass &amp; Specht (2010)</td>
<td>95°C × 3 min, 30 cycles (95°C × 30 sec, 50°C × 30 sec, 72°C × 45 sec), 72°C × 5 min</td>
<td>95°C × 3 min, 30 cycles (94°C × 1 min, 50°C × 2 min, 72°C × 2 min), 72°C × 10 min</td>
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</tr>
<tr>
<td>rpb2</td>
<td>rpb2-Fwd. Intern.-Fwd. and rpb2-Rev.</td>
<td>Sass &amp; Specht (2010)</td>
<td>95°C × 5 min, 25 cycles (95°C × 30 sec, 50°C × 30 sec, 72°C × 45 sec), 72°C × 5 min</td>
<td>95°C × 5 min, 30 cycles (94°C × 1 min, 50°C × 2 min, 72°C × 2 min), 72°C × 10 min</td>
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</tr>
<tr>
<td>matK-trnK</td>
<td>390F and 1710R</td>
<td>Barfuss et al. (2005)</td>
<td>94°C × 5 min, 30 cycles (94°C × 1 min, 50°C × 2 min, 72°C × 2 min), 72°C × 10 min</td>
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<tr>
<td>rps16-trnK</td>
<td>c and f</td>
<td>Taberlet et al. (1991)</td>
<td>80°C × 5 min, 30 cycles (94°C × 1 min, 52°C × 1 min, 65°C × 2 min), 65°C × 10 min</td>
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<td>trnL-F</td>
<td>rpS16x2F2 and trnK(UUU)x1</td>
<td>Shaw et al. (2007)</td>
<td>98°C × 5 min, 35 cycles (95°C × 30 sec, 60°C × 2 min), 72°C × 5 min</td>
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</tr>
</tbody>
</table>

Table 1.2. Primers, references, and temperature profiles for all the PCR reactions conducted in this study.

1.3.3 Sequence alignment and phylogenetic analyses

Editing of sequences and generation of contigs were conducted in *Sequencher* version 5.2.4 (Gen Codes Corp. Ann Arbor, MI, USA). The alignments for each individual maker were
performed online with MAFFT version 7 (Katoh and Standley 2013), using the global homology option and default parameters. These alignments were subsequently inspected in Mesquite version 3.01 (Maddison and Maddison 2014) for obvious misalignments of large blocks, which were manually adjusted. The summary of alignment statistics was calculated for each alignment using the R packages Ape and Phangorn (Paradis et al. 2004; Schliep 2011; R Development Core Team 2015).

The best-fit substitution model of nucleotide evolution was determined for each DNA sequence region using jModelTest (Guindon and Gascuel 2003; Darriba et al. 2012). A neighbor-joining tree was used to compute the likelihood scores of the data across different models of substitution. Subsequently, the best model for each partition was chosen using the corrected Akaike Information Criterion (AICc). The substitution model GTR + Γ was selected for ETS, g3pdh, and matK-trnK; the model GTR + Γ + I was chosen for rps16-trnK and trnL-F; and the model HKY + Γ was specified for rpb2.

Apart from the alignments of the individual markers, three concatenated datasets were generated for the analyses: one combining the three chloroplast markers (cpDNA); one combining the three nuclear markers (nrDNA); and one combining all markers together (combined matrix). These matrices were generated with the program 2matrix (Salinas and Little 2014), which constructs concatenated datasets and automatically generates files for further analyses using the most popular phylogenetic software available (e.g. MrBayes, Garli, RaxML, TNT, etc). For each concatenated dataset, independent phylogenetic analyses using three different approaches were conducted: Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI). Only ML analyses were performed for the alignments of individual molecular markers in order to visually detect potential causes of incongruence.
Maximum Parsimony analyses were executed with the program \textit{TNT} (Goloboff et al. 2008). Heuristic searches were conducted using ten replicates of ratchet coupled with tree-drifting, and a final round of tree bisection and reconnection (TBR) (Goloboff 1999; Nixon 1999). First, for each of 200 Ratchet iterations, a random set of characters was upweighted and downweighted ten magnitudes. One optimal tree was searched and saved using the reweighted matrix and TBR as a tree perturbation strategy. After setting the matrix to its original weights, a new optimal tree was searched with TBR using the saved tree from the previous phase. Second, tree-drifting was conducted for 200 iterations using the saved trees of the ratchet phase. This method is similar to ratchet, but instead of reweighting a random set of characters, it saves optimal or suboptimal trees per iteration based on the values of the Raw Length Difference and Relative Fit Difference metrics described by Goloboff (1999). The final set of trees obtained from the ratchet plus tree-drifting searches were subsequently used for a final heuristic search using TBR to completion, saving a maximum of 10,000 trees if necessary. A strict consensus tree was generated from the final set of most parsimonious trees. Node confidence was estimated using 1000 pseudoreplicates of bootstrap (BS) with similar parameters of the initial ratchet search but using only 20 iterations per pseudoreplicate.

Maximum Likelihood analyses were performed with the program \textit{RAxML-Blackbox} (Stamatakis 2014) through the Cipres Science Gateway service (Miller et al. 2011). The GTRGAMMA model of evolution was independently specified for each DNA sequence marker alignment. Node confidence was estimated using the “rapid bootstrapping” option of \textit{RAxML}.

Bayesian Inference analyses were conducted with \textit{MrBayes 3.2.3} (Ronquist et al. 2012) through the Cipres Science Gateway service (Miller et al. 2011), and the high performance computer cluster of the New York Botanical Garden. The models of evolution selected by
were set for each independent partition. Default priors of model parameters were also defined for each partition. Two parallel MCMC runs of 30,000,000 generations were conducted, each run containing three heated chains and one cold chain. The default value of temperature coefficient was used for all analyses. Trees and estimated parameter values were sampled every 1000 generations, thus obtaining a total of 30,000 samples from which the first 7500 were discarded as burn-in. Convergence between the two independent runs and inspection of appropriate parameter mixing was assessed with Tracer version 1.5 (Rambaut and Drummond 2003). A 50 % majority-rule consensus tree, with mean branch lengths, and posterior probabilities of clades (PP) was generated to summarize the results of the post burn-in posterior distribution of trees.

1.3.4 Congruence

The main discussion of this paper is based on the results of the phylogenetic analyses using the combined dataset. This approach ensures the use of all available information for reconstructing a robust phylogeny, which otherwise would be poorly informed by datasets containing a limited number of informative sites. Nevertheless, it is possible that individual markers or separate genomes contain conflicting phylogenetic signals that could affect the results of the combined analysis. In order to identify major disagreements among the phylogenetic hypotheses generated with the separate datasets, pairwise comparisons of well-supported incongruent clades were performed (Mason-Gamer and Kellogg 1996). Topological conflicts were considered significant if the same set of taxa showed two different relationships supported with BS values of 75 % or more and PP ≥ 0.95. A lack of well-supported conflict among datasets is a good indication for combining all genes in a concatenated phylogenetic analysis.
To further explore incongruence, a primary concordance tree was constructed through a Bayesian Concordance Analysis (BCA) with the program Bucky version 1.4.3. (Ané et al. 2007; Larget et al. 2010). This method explores and integrates the posterior distribution of trees obtained through Bayesian Inference analyses of the individual partitions without making assumptions on the causes for gene incongruence (e.g. incomplete lineage sorting, hybridization, paralogy, sequencing error, etc.). The primary concordance tree summarizes the clades with the largest concordance factors, thus providing an estimate of the dominant vertical phylogenetic signal among genes. A comparison of incongruent clades between the primary concordance tree and the combined tree will serve as further evidence for problematic results. For this analysis, a new round of MrBayes analyses was performed for each individual partition but including only taxa not missing any of the molecular markers. The three chloroplast markers were treated as a single partition. The posterior distributions of trees from each MrBayes analysis were used as input for Bucky. The primary concordance tree was obtained by conducting two MCMC runs of 1 million generations, using a discordance parameter alpha value of 1 and a burn-in of 100,000 samples.

1.3.5 Phylogenetic hypothesis testing

Phylogenetic studies of the Core Bromelioidae suggest that groups of species that co-occur in similar geographic regions tend to be closely related and, in many cases, comprise monophyletic groups, regardless of their current taxonomy (Schulte et al. 2009; Sass and Specht 2010; Givnish et al. 2014). Based on this conclusion, an Approximately Unbiased test of phylogenetic tree selection (AU test; Shimodaira 2002) was used for testing alternative competing hypotheses of monophyly within the Ronnbergia Alliance against our empirical
results. For the first alternative hypothesis, three monophyletic groups are proposed: 1) a clade containing all the species from Northwestern South America and southern Central America; 2) a clade containing all the species from the Atlantic Forest plus the widespread *Aechmea lingulata*; and 3) a clade comprising the Caribbean species. For the second alternative hypothesis, a monophyletic clade containing only Caribbean species nested with the widespread *A. lingulata* was constrained. This second alternative hypotheses is proposed because *Aechmea lingulata* is the only species of that is distributed in the Caribbean and the Atlantic Coast of Tropical South America (Smith and Downs 1979). In order to obtain sitewise log-likelihood values for the alternative hypotheses, Maximum Likelihood analyses were conducted with *RAxML-Blackbox* (Stamatakis 2014) using the concatenated dataset and the same parameters of the original ML analyses but constraining the topologies accordingly. The AU test was conducted with the program *CONSEL* (Shimodaira and Hasegawa 2001), which uses the sitewise log-likelihood values from the empirical and constrained ML analyses as input. *P*-values below 0.05 indicate that the hypothesis of monophyly is not supported by the data.

1.3.6 **Morphological character data**

A morphological survey was conducted in order to identify potential characters for circumscribing the *Ronnbergia* Alliance and its main subclades. Morphological data were obtained from examination of herbarium material, liquid collections, photographs, literature, and living plants when possible. The first author determined all the examined specimens, most of them corresponding to the same terminals used for the phylogenetic analyses. A final set of 13 characters, 9 discrete and 4 continuous, was selected for further analysis because of their relative stability within clades (Table 1.3).
The following is a list of the selected discrete characters: **Character 1**: pseudopetiole (0) present and (1) absent. Pseudopetiole refers to the abrupt narrowing of the leaf blades above the sheaths. **Character 2**: inflorescence ramification (0) simple (not branched) and (1) paniculate (branched). **Character 3**: dorsiventral floral compression (0) terete and (1) compressed. **Character 4**: corolla apex (0) reflexed, (1) erect, and (2) cucullate. **Character 5**: petal apex: (0) acuminate to acute and (1) obtuse to retuse. **Character 6**: petal color (0) pigmented, other than white and (1) white. **Character 7**: petal appendages (0) absent and (1) present. Petal appendages correspond to two laminar structures of variable morphology that originate at the base of the petal adaxial surface, prolong parallel to the sides of the antipetalous filaments, and detach from the petals apically. **Character 8**: filament apex: (0) much narrower than the anthers and (1) as wide as the anthers. **Character 9**: chalazal ovule appendages: (0) absent (or rudimentary) and (1) present (long-appendaged).

Continuous characters were measured on one to five specimens per species, depending on material availability. The measurements used in the analyses correspond to the log-transformed mean values of the following characters: **Character 10**: flower length. **Character 11**: corolla tube exposition to flower length ratio. **Character 12**: sepal connation to flower length ratio. **Character 13**: sepal mucro length to flower length ratio.
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<th>Floral compression</th>
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<th>Petal apex</th>
<th>Petal color</th>
<th>Petal appendages</th>
<th>Filament apex ovule</th>
<th>Appadage</th>
<th>Flower length (mm)</th>
<th>Sepal length</th>
<th>Sepal connation/flower length</th>
<th>Sepal micro/flower length</th>
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Table 1.3. Morphological data matrix. Scores in brackets represent polymorphic character states. Question mark (?) represents unknown data.

### 1.3.7 Ancestral character state reconstructions

Ancestral character state reconstructions were conducted for the 13 surveyed characters on a subsampled phylogeny of the *Ronnbergia* Alliance. In order to take phylogenetic uncertainty into account for the ancestral character state reconstructions, a random subset of 1000 trees was selected from the post burn-in posterior distribution of trees from the *MrBayes* analysis of the combined dataset. Subsequently, all the trees were pruned, conserving the original branch lengths in order to obtain the following subset of taxa: 1) all the species of the *Ronnbergia* Alliance; 2) ten representatives of the sister group of the *Ronnbergia* Alliance (*Aechmea blumenavii, A. bromeliifolia, A. contracta, A. dactylina, A. mariae-reginae, Aechmea*...
nudicaulis, Hohenbergia andina, H. correia-araujoi, Lymania spiculata, and Ursulaeautensis); and 3) three representatives of the possible sister groups of the Core Bromelioidae (Acanthostachys strobilacea, Ananas comosus, and Disteganthus morii). These species were selected in order to include an estimation of the morphological diversity outside the Ronnbergia Alliance. Within the Ronnbergia Alliance, duplicate accessions per species that formed monophyletic groups were also pruned, giving priority to type and field-collected specimens. For the non-monophyletic species, the accessions were conserved and scored independently in the morphological survey.

Two methods of ancestral state reconstruction were used for the discrete characters: Maximum Likelihood ancestral character state reconstruction (ML-ASR) and Bayesian ancestral character state reconstruction (BI-ASR). Maximum Likelihood ancestral state reconstructions were performed on the 1000 trees for all discrete characters fitting one-rate model and two-rate models of character evolution in BayesTraits version 2.0 (Meade and Pagel 2014). A two-rate model was chosen as the best-fit model for all binary characters based on the likelihood ratio test. The model for character 4, the only multistate character, corresponds to a six-rate model. Bayesian ancestral reconstructions were also conducted in BayesTraits version 2.0 using the options MultiState and MCMC. Reverse Jump MCMC was performed in order to integrate over the space of parameters across different models of evolution. An exponential prior distribution was chosen for the analyses. Because little is known about the mean values of the exponential prior distribution, this parameter was seeded from a uniform hyper-prior. The approximate interval of this hyper-prior was estimated from the empirical values of rate change obtained from the ML-ASR analyses for each character. For each character reconstruction, two MCMC runs were conducted for 10 million generations, sampling every 10,000 generations, and setting a
burn-in of 100,000 generations. The mean values of the ML-ASR and BI-ASR probabilities were calculated for the most robust selected nodes of the phylogeny. The corresponding values for these nodes across the 1000 trees were summarized with the option addMRCA. The final results of the ML-ASR and BI-ASR were plotted in the 50% majority rule of the combined MrBayes analysis.

Ancestral maximum likelihood reconstruction of the continuous characters was conducted with the function ContMap from the R package Phytools (Revell 2012; R Development Core Team 2015) using a Brownian model of trait evolution to estimate ancestral values in the internal nodes of the phylogeny. These reconstructions were mapped on the best tree of the combined ML analysis, which was transformed to ultrametric using the function chronopl from the R package Ape (Paradis et al. 2004; R Development Core Team 2015), with a lambda value of 0.1. This function uses the semi-parametric smoothing, penalized likelihood method described by Sanderson (2002).

1.4 Results

1.4.1 Phylogenetic analysis of the individual markers, cpDNA and nrDNA datasets, and congruence

The general statistics of the alignments for the individual and combined datasets are shown in Table 1.4. The nuclear markers exhibit the largest amount of variable and parsimony-informative sites. ETS stands as the most informative region among all the individual markers. In contrast, the chloroplast markers show lower percentages of variable and parsimony-informative characters, with matK-trnK being the most variable of the chloroplast markers.
The ML analyses of the individual markers resulted in topologies with different degrees of resolution and support (trees not shown). No significant incongruences were detected among the topologies; most of the conflict corresponds to shallow clades with low bootstrap support values. Except for ETS, none of the individual analyses recovered the monophyly of the Ronnbergia Alliance; the topologies obtained with each marker, however, tend to group the species of the Ronnbergia Alliance in medium to low supported clades.

The combined chloroplast molecular markers produced a phylogenetic hypothesis more robust than any of the individual markers alone (Fig. 1.2). Phylogenetic analyses using MP, ML, and BI showed highly similar topologies that differed in the degree of resolution for some clades and did not produce well-supported incongruent clades (MP and ML trees not shown). The phylogenetic analyses of the cpDNA dataset did not provide enough information to resolve the monophyly of the Ronnbergia Alliance. The 50% majority rule consensus tree of the BI analysis shows that the backbone topology is a polytomy formed by seven lineages, from which all the
species of the *Ronnbergia* Alliance encompass the two largest clades (Fig. 1.2). The first of these two clades received medium to high statistical support (BS 94/68, PP 0.82), and it is composed exclusively by species endemic to northwestern South America and southern Central America of *Aechmea* subgenus *Chevaliera*, *Aechmea* subgenus *Pothuava* and *Ronnbergia*. The second clade is highly supported (BS 100/94, PP 1) and contains all the species of the *Ronnbergia* Alliance endemic to Eastern Brazil and the Caribbean, in addition to the widespread *Aechmea lingulata*. Within this clade, the species of the Caribbean-endemic *Hohenbergia* subgenus *Wittmackiopsis* form a well-supported monophyletic group (BS 100/76, PP 1).

The phylogenetic analyses of the three nuclear molecular markers produced relatively robust overall topologies, especially at the deeper nodes (Fig. 1.2). No major conflicts were detected among the MP, ML and BI analyses, although the MP consensus tree shows less resolved clades (MP and ML trees not shown). The 50% majority rule consensus tree of the Bayesian analysis shows the *Ronnbergia* Alliance as monophyletic with high values of node confidence (BS 93/98; PP 0.99). This clade is part of a medium to highly supported clade (BS 100/51, PP 1) that also contains a lineage comprised by the remaining tank-forming species of the Core Bromelioidae, excluding *Aechmea* subgenus *Chevaliera* (BS 55/78, PP 1). As in the cpDNA analyses, the species in the *Ronnbergia* Alliance are grouped in the same two relatively robust clades (BS 100/58, PP 1; and BS 100/75, PP 0.99). The monophyly of the Caribbean-endemic *Hohenbergia* subgenus *Wittmackiopsis* is also supported by the nrDNA dataset (BS 72/85, PP 1).

The main differences between the phylogenetic hypotheses obtained with the cpDNA and nrDNA datasets are mostly associated with the level of resolution. The cpDNA dataset produced a polytomic backbone topology whereas the nrDNA analyses resolved the basal relationships of the phylogeny with low to medium support. Although the polytomy obtained with the cpDNA
analysis does not provide information about the monophyly of the *Ronnbergia* Alliance, it does not represent a conflicting scenario for this hypothesis. Both analyses support the same main clades across the phylogeny and exhibit relatively low resolution within these clades. No well-supported incongruent clades were detected among the topologies generated with these datasets.
Figure 1. 50% Majority rule consensus tree of the Bayesian Inference analysis using the cpDNA and nrDNA datasets independently. Left: cpDNA topology. Right: nrDNA topology. Names in red correspond to species of the Ronnbergia Alliance. Numbers on the nodes correspond to posterior probabilities.
1.4.2 Phylogenetic analysis of the combined dataset and primary concordance tree

The lack of well-supported incongruences and frequent clade similarities among the separated phylogenetic hypotheses of the cpDNA and nrDNA datasets are signs of confidence to perform combined phylogenetic analyses. The analyses conducted with the combined dataset provided more robust topologies compared to those of the individual markers, cpDNA, and nrDNA datasets alone (Fig. 1.3). The MP, ML, and BI exhibit non-conflicting and highly similar topologies (Fig. 1.3, supplementary Figs. 1.10–1.11).

Figure 1.3 illustrates the main results of the combined phylogenetic analyses represented on the 50% majority rule consensus tree of the BI analysis. Here, the species of the Core Bromelioidae form a medium supported clade (BS 42/66, PP 1). This clade excludes several species of *Aechmea* subgenus *Chevaliera*, which appeared at the early-diverging branches of the tree, as well as *Acanthostachys*, *Ananas*, *Disteganthus*, and *Orthophytum*. Two robust major lineages can be identified within the Core Bromelioidae clade. One comprises all the species of the *Ronnbergia* Alliance, from now on called the “*Ronnbergia* Alliance clade” (BS 100/100, PP 1), whereas the second lineage contains the remaining species of the Core Bromelioidae (BS 99/99, PP 1).

The *Ronnbergia* Alliance clade is formed by two strongly supported clades with high geographic structure, the “Pacific Clade” (BS 100/100, PP 0.72) and the “Atlantic Clade” (BS 100/100, PP 1). The Pacific Clade contains species of *Aechmea* and *Ronnbergia* endemic to the forests of northwestern South America and Southern Central America. Two subclades are strongly supported within the Pacific Clade, one containing only species of *Ronnbergia* (Clade
A; BS 99/99, PP 0.99), and another containing species of both Ronnbergia and Aechmea subgenus Pothuava (Clade B; BS -/95, PP 1). The placement of the remaining species in the Pacific Clade is unresolved and low to medium supported. The Atlantic Clade comprises species of Aechmea and Ronnbergia endemic to eastern Brazil, the Caribbean-endemic Hohenbergia subgenus Wittmackiopsis and the widespread Aechmea lingulata. Within the Atlantic Clade, the two Brazilian species of Ronnbergia are grouped with three species of the Aechmea lingulata complex in a clade with medium support (Clade C; BS 44/68, PP 0.88). This clade is sister to a robust lineage that contains the bulk of species of the Atlantic Clade (Clade D; BS 100/100, PP 1). Most of Clade D is composed by a grade of species of the Brazilian-endemic Aechmea lingulata complex and the widespread Aechmea lingulata. Nested within Clade D, Hohenbergia subgenus Wittmackiopsis forms a robust monophyletic group, here called the “Caribbean Clade” (BS 100/97, PP 1). The Caribbean Clade contains two robusts lineages, one with Hohenbergia antillana from Puerto Rico grouped with two species mostly restricted to the Blue Mountains in Jamaica (H. eriostachya and H. polycephaala), and another lineage that comprises species endemic to Jamaica, Puerto Rico, Cuba, and the western Caribbean (Yucatán Peninsula, Cayman Islands, and Providencia).
Figure 1.3. 50% Majority rule consensus tree of the Bayesian Inference analysis using the combined dataset. Numbers on the nodes correspond to posterior probabilities, followed by a representation of node confidence of the MP/ML analyses; the start symbol (*) represents bootstrap values ≥ 60%; hyphen (-) represents bootstrap values below 60%. Nodes are labeled according to clade names: Core Bromelioidae (C.B.), Pacific Clade (P.C.), Atlantic Clade (A. C.), Caribbean Clade (C.C.), Clade A (A), Clade B (B), Clade C (C), and Clade D (D). **Bottom left:** geographic distribution of the species in the *Ronnbergia* clade; colors correspond to the clades that the species belong to, except for the widespread *Aechmea lingulata* (red). Data source: Global Biodiversity Information Facility (GBIF).

The primary concordance tree exhibits the same main clades of the combined phylogenetic analyses with concordance factors of 0.5 or below (Supplementary Fig. 1.12). The primary concordance tree summarizes the overall signal of the individual genes; therefore, its similarity with the combined tree provides further confidence for preferring the combined analyses to the independent ones.

1.4.3 **Hypothesis testing**

The AU test produced a $p$-value of 0.279 for the hypothesis where three monophyletic clades are endemic to northwestern South America and southern Central America, eastern Brazil, and the Caribbean, respectively. This result indicates that this is a competing hypothesis compared to the unconstrained analyses and can be explained by our data. The second hypothesis, where *A. lingulata* is nested within the Caribbean Clade, received a $p$-value of 0.04, which means that this is not a competing hypothesis compared to the unconstrained analyses, and cannot be explained with our data.
1.4.4 Morphological analysis

The two methods implemented for ancestral reconstruction of discrete characters showed similar results across all characters (Figs. 1.4–1.9; supplementary Table 1.5). However, ML-ASR and BI-ASR disagree on the reconstruction of inflorescence ramification, filament apex, and ovule appendages at the node that represents the ancestor of the Core Bromeliioideae (node C.B. in Figs. 1.4-1.9).

**Character 1.** Pseudopetiolate leaves are present in all the species of Clade A and two species within the Atlantic Clade (Fig. 1.7). It is uncertain if this character arose early in the history of the *Ronnbergia* Alliance; the ancestral reconstructions, however, suggest that the ancestor of the Pacific Clade also had this character state. Within this clade, pseudopetiolate leaves became fixed in Clade A and reversed to non-pseudopetiolate leaves in the remaining species outside this clade. The Atlantic Clade likely arose from an ancestor without pseudopetiolate leaves and this character appeared independently twice during the diversification of this lineage. **Character 2.** The species of the Pacific Clade always exhibit simple inflorescences, whereas the Atlantic Clade contains species with both simple and paniculate inflorescences (Fig. 1.6). Simple inflorescences are the most likely state for the ancestor of the *Ronnbergia* Alliance clade. This character became fixed in the Pacific Clade without further transformations to paniculate inflorescences. In the case of the Atlantic Clade, the ancestral state is uncertain. One reversal to simple inflorescences is supported for the ancestor of Clade C. Paniculate inflorescences are the most likely ancestral state of Clade D, with several independent reversals to simple inflorescences across the clade. All the species of the Caribbean Clade exhibit paniculate inflorescences and this is also its most likely ancestral state. There is uncertainty on
the ancestral state of inflorescence ramification for the ancestor of the Core Bromeliioideae, whereas the ancestor of the sister lineage of the *Ronnbergia* Alliance clade likely exhibited simple inflorescences. **Character 3.** Dorsiventral floral compression is present in all the species of the Caribbean Clade and four species within the Pacific Clade (Fig. 1.7). The ancestral reconstructions show that this character state only became fixed in the diversification of the Caribbean Clade and appeared independently three times in the Pacific Clade. **Character 4.** All the species of the *Ronnbergia* Alliance clade exhibit corollas with reflexed apices; the only exception is *Aechmea bicolor*, which has erect apices (Fig. 1.4). This character is also frequently present in the sister lineage of the *Ronnbergia* Alliance clade. The corolla with a reflexed apex is strongly supported as the ancestral character for almost all clades in the phylogeny, except for the sister lineage of the *Ronnbergia* Alliance clade, where there is a significant amount of uncertainty about its ancestral state. **Character 5.** Obtuse to retuse petals are more common in the species of the Pacific Clade than in the ones of the Atlantic Clade; acuminate to acute petals are more frequent in the latter. The same pattern is observed in the ancestors of these clades. The most likely ancestral state of the *Ronnbergia* Alliance clade is obtuse to retuse petals (Fig. 1.5). **Character 6.** Pigmented petals are more common in the Pacific Clade than in the Atlantic Clade (Fig. 1.5). Ancestral state reconstructions suggest that the ancestor of the *Ronnbergia* Alliance clade likely exhibited pigmented flowers. This is also the ancestral character state for the Pacific Clade, although several independent reversals to white flowers occurred within this lineage. A transformation to white flowers occurred for the ancestor of the Atlantic Clade followed by fixation of this state across its subclades. Nevertheless, a few cases of independent reversals to colored flowers occurred in this clade. **Character 7.** Most species of the *Ronnbergia* Alliance clade lack petal appendages; however, the presence of this character is not rare in the group (Fig.
Ancestral reconstructions strongly suggest that the lack of petal appendages is the ancestral state for the *Ronnbergia* Alliance clade and most of its lineages. Several independent acquisition of petal appendages occurred within this lineage. Presence of petal appendages was reconstructed as the ancestral state for Clade B, followed by one reversal. **Character 8.** Most species across the phylogeny exhibit filament apices narrower than the anthers (Fig. 1.7). However, many species of the Pacific Clade and two species outside the *Ronnbergia* Alliance clade have filament apices as wide as the anther. The filament apex as wide as the anther is reconstructed as the most likely ancestral state of the *Ronnbergia* Alliance clade and the Pacific Clade. Two transformations from wide to narrow filament apices occurred during the diversification of the *Ronnbergia* Alliance clade. One transformation arose with the ancestor of the Atlantic Clade, followed by fixation along the history of this lineage. The second transformation occurred for the ancestor of Clade B within the Pacific Clade. The ancestral state of this character is uncertain for the Core Bromelioideae. **Character 9.** Chalazal ovule appendages are absent or rudimentary in the *Ronnbergia* Alliance clade and are reconstructed as the ancestral state for this lineage (Fig. 1.4). Long chalazal appendages appeared only in several species outside the *Ronnbergia* Alliance clade and it is the ancestral state of the sister lineage of the *Ronnbergia* Alliance clade. The reconstruction of this character is uncertain for the ancestor of the Core Bromelioideae.

The ancestral reconstruction of continuous characters revealed four patterns. First, the ancestor of the Pacific Clade likely had longer flowers than the ancestor of the Atlantic Clade (Fig. 1.8). Second, the ancestors of both Clade A and Clade B exhibited longer projections of the corolla tube in proportion to flower length compared to other lineages (Fig. 1.8). Third, Clade A and Clade C likely arose from an ancestor with highly connate sepals in relation to flower length.
(Fig. 1.9). Finally, the ancestors of both the Atlantic Clade and clade B had longer sepal mucros in proportion to flower length compared to other lineages (Fig. 1.9).
Figure 1.4. Bayesian ancestral character state reconstruction (BI-ASR) of corolla apex and chalazal ovule appendages. Nodes are labeled according to clade names: Core Bromelioideae (C.B.), Pacific clade (P.C.), Atlantic clade (A. C.), Caribbean clade (C.C.), Clade A (A), Clade B (B), Clade C (C), and Clade D (D). Start symbol (*) shows the results of the ML-ASR for a given node.
Figure 1.5. Bayesian ancestral character state reconstruction (BI-ASR) of petal apex and petal color. Nodes are labeled according to clade names: Core Bromelioideae (C.B.), Pacific clade (P.C.), Atlantic clade (A. C.), Caribbean clade (C.C.), Clade A (A), Clade B (B), Clade C (C), and Clade D (D).
Figure 1.6. Bayesian ancestral character state reconstruction (BI-ASR) of inflorescence ramification and petal appendages. Nodes are labeled according to clade names: Core Bromeliioideae (C.B.), Pacific clade (P.C.), Atlantic clade (A. C.), Caribbean clade (C.C.), Clade A (A), Clade B (B), Clade C (C), and Clade D (D). Start symbol (*) shows the results of the ML-ASR for a given node.
Figure 1.7. Bayesian ancestral character state reconstruction (BI-ASR) of pseudopetiole, dorsiventral floral compression, and filament apex. Nodes are labeled according to clade names: Core Bromelioidae (C.B.), Pacific clade (P.C.), Atlantic clade (A.C.), Caribbean clade (C.C.), Clade A (A), Clade B (B), Clade C (C), and Clade D (D). Start symbol (*) shows the results of the ML-ASR for a given node.
Figure 1.8. Maximum likelihood ancestral character state reconstruction of flower length and corolla tube exposition to flower length ratio. Nodes are labeled according to clade names: Core Bromelioideae (C.B.), Pacific clade (P.C.), Atlantic clade (A.C.), Caribbean clade (C.C.), Clade A (A), Clade B (B), Clade C (C), and Clade D (D).
Figure 1.9. Maximum likelihood ancestral character state reconstruction of sepal connation to flower length ratio and sepal mucro length to flower length ratio. Nodes are labeled according to clade names: Core Bromelioideae (C.B.), Pacific clade (P.C.), Atlantic clade (A.C.), Caribbean clade (C.C.), Clade A (A), Clade B (B), Clade C (C), and Clade D (D).
1.5 Discussion

1.5.1 Monophyly, phylogenetic position, and diagnosis of the Ronnbergia Alliance

Although most of the independent molecular markers and the cpDNA dataset did not provide enough information to resolve the monophyly Ronnbergia Alliance, they did not conflict with this hypothesis. This lack of resolution is the result of the low variation across the molecular markers, especially those of the chloroplast genome (Table 1.4), a phenomenon already discussed in previous phylogenetic studies of Bromelioidae (Schulte et al. 2005, 2009; Horres et al. 2007; Schulte and Zizka 2008; Sass and Specht 2010; Evans et al. 2015). Some of these studies suggested that to overcome these limitations it is important to increase the number of molecular markers and include both nuclear and chloroplast DNA sequences (Schulte et al. 2009; Sass and Specht 2010; Silvestro et al. 2014). This observation is confirmed by our study, as the nrDNA dataset alone provided sufficient information to support the monophyly of the Ronnbergia Alliance with medium to high values of confidence. Moreover, combining this dataset with the cpDNA alignment further increased the robustness of the results, and provided good resolution for the phylogenetic placement and internal relationships of the Ronnbergia Alliance clade.

A remarkable achievement of this study is that our predictions about the composition of the Ronnbergia Alliance allowed reconstructing a phylogenetic hypothesis for this group using a species-level taxonomic sampling. The Ronnbergia Alliance was represented in earlier studies with two or three species that included Aechmea drakeana, A. lingulata, Hohenbergia eriostachya, and Ronnbergia petersii (Horres et al. 2007; Schulte and Zizka 2008; Schulte et al. 2009; Givnish et al. 2011). Sass and Specht (2010) placed 16 species in this clade but were
unable to resolve their internal relationships. In contrast, our comprehensive taxonomic sampling allowed placing with confidence 60 species in the *Ronnbergia* Alliance and provided a framework for the inclusion of about ten additional species not sampled in this study. Moreover, this large species representation in combination with our DNA sequence sampling contributed to increase the resolution of the relationships within the group compared with other studies.

Although our results are not categorically contradicted by other studies, three recent studies were unable to support the monophyly of the *Ronnbergia* Alliance. In the first study, Silvestro et al. (2014) placed eight species of the *Ronnbergia* Alliance in a clade that also included *Hohenbergiopsis guatemalensis* and *Billbergia tweediana*. Moreover, a ninth species, *Aechmea turbinocalyx*, was placed in a distant clade with other species of *Aechmea* and *Quesnelia*. Because they only used one nuclear marker (*PhyC*), they did not provide the topologies produced by the cpDNA dataset, and their samples were mostly collected from cultivated plants in botanical gardens, it is difficult to discuss the causes of this conflict. In the second study, Evans et al. (2015) included eight species of the *Ronnbergia* Alliance that appeared grouped in two medium supported clades; these lineages correspond to the Pacific and Atlantic Clades of our analyses. Despite this result, the molecular dataset used in this study did not provide sufficient resolution to reconstruct the *Ronnbergia* Alliance clade. Lastly, Aguirre-Santoro et al. (2015) included 20 species of the *Ronnbergia* Alliance. Despite their relatively large species sampling, their combined morphological and molecular dataset lacked power to resolve the monophyly of the group. However, they recovered three polytomic clades composed exclusively by species of the *Ronnbergia* Alliance.

The monophyly of the *Ronnbergia* Alliance highlights the generic delimitation problems across Bromeliioideae. It includes fragments of the genera *Aechmea* and *Hohenbergia*, and shows
the polyphyly of the entire genus *Ronnbergia*. From the five species complexes sampled here, only the two species of *Aechmea* subgenus *Chevaliera*, and the Caribbean-endemic *Hohenbergia* subgenus *Wittmackiopsis* form monophyletic groups. The remaining species of *Aechmea* are scattered and intermingle with species of *Ronnbergia* (Fig. 1.3). The polyphyly of *Ronnbergia* had already been discussed by Aguirre-Santoro et al. (2015) and Evans et al. (2015), whereas the polyphyly of *Hohenbergia, Aechmea* subgenus *Pothuava* and *Aechmea* subgenus *Chevaliera* was mentioned in the studies of Faria et al. (2004), Schulte and Zizka (2008), and Sass and Specht (2010), and Evans et al. (2015). In the case of the *Aechmea lingulata* complex, our results strongly suggest that this is not a monophyletic group. However, Siqueira Filho and Leme (2006) were correct in predicting that the species of this complex are very closely related.

Our combined analyses agree with previous phylogenetic studies by showing the *Ronnbergia* Alliance clade as one of the two main lineages of the Core Bromeliioideae (Fig. 1.3). Although the Core Bromeliioideae has not been formally circumscribed, most studies recognize this group as the most diverse clade of Bromeliioideae. It has been suggested that this lineage experienced an exceptional diversification because of the acquisition of two key adaptations: the epiphytic habit and the formation of tank rosettes (Schulte et al. 2009; Givnish et al. 2014; Silvestro et al. 2014). The *Ronnbergia* Alliance clade fits within this radiation because it includes several epiphytic and tank-forming species; however, reversions to terrestrial habitats and lack of tanks also occurred in the group (e.g. the terrestrial *Aechmea lingulatoides* and the tank-less *Ronnbergia killipiana*). There is not a single character that helps unambiguously diagnose the *Ronnbergia* Alliance clade; however, our morphological ancestral reconstructions suggest that characters such as the reflexed corolla apex and the lack of chalazal ovule appendages are traits that appeared in the ancestor of this lineage and became fixed along the history of the group (Fig.

57
1.4). These two characters are also present in the sister group of the *Ronnbergia* Alliance clade, but they do not seem to occur in combination in any species within this lineage.

1.5.2 *Phylogenetic relationships within the Ronnbergia Alliance clade and diagnostic characters*

One of the main results of the present study is that the relationships of the main lineages within the *Ronnbergia* Alliance clade showed a high level of resolution and support. Two major robust clades were identified within the *Ronnbergia* Alliance clade: the Pacific Clade and the Atlantic Clade (Fig. 1.3). These clades received these labels to illustrate the distinctive geographic disjunction and internal geographic structure of their included species. Both clades were recovered independently by the cpDNA and nrDNA datasets (Fig. 1.2) but received better resolution and support in the combined analysis.

1.5.2.1 *Pacific Clade*

All the species in the Pacific Clade are endemic to northwestern South America and southern Central America. They are currently placed in *Aechmea* subgenus *Chevaliera, Aechmea* subgenus *Pothuava*, and *Ronnbergia*. Apart from recent phylogenetic studies, the close affinity among species of *Aechmea* subgenus *Pothuava* and *Ronnbergia* had already been detected in earlier taxonomic treatments. For instance, these two groups can only be differentiated by the presence or absence of petal appendages; for this reason, Smith and Downs (1979) included *Ronnbergia* within the taxonomic key of *Aechmea* subgenus *Pothuava* because of the difficulty in separating these two groups when petal characters are not available. Moreover, in the absence of petal characters, *R. petersii* looks so similar to the sympatric *A. allenii* that recent taxonomic
treatments proposed them as synonyms (Davidse et al. 1995). Despite the importance of petal appendages in taxonomic treatments, our results do not support the use of this character as diagnostic for any group. Nevertheless, we recognize that the absence of petal appendages is the ancestral and most common state across the Ronnbergia Alliance clade and its main lineages. The presence of petal appendages appeared repeatedly during the diversification of the group and can be useful to separate species or small species complexes (Fig. 1.6).

The morphological survey of the species in the Pacific Clade did not permit identifying exclusive diagnostic characters that separate this lineage from the Atlantic Clade. However, ancestral reconstructions indicate that the combination of characters that support this group are the presence of simple inflorescences, long flowers, sepals exhibiting short mucro length to flower length ratios, and colored petals with obtuse to retuse apices. Transformations of all these characters are observed within the Pacific Clade but correspond to isolated, independent events (Figs. 1.5-1.6 and 1.8-1.9). The presence of pseudopetiolate leaves and filament apices as wide as the anther are reconstructed as ancestral states of the Pacific Clade; these characters, however, only became fixed in the strongly supported Clade A, which contains the bulk of species of Ronnbergia, including the type species, R. morreniana (Fig. 1.7). These characters, combined with long sepal connation in relation to flower length, make Clade A the only clearly diagnosable lineage within the Pacific Clade.

The most dissimilar species in the Pacific Clade correspond to the members of Aechmea subgenus Chevaliera from the forests of southern Costa Rica to northwestern South America: A. germinyana and A. veitchii. They are sister species but their phylogenetic position in the Pacific Clade is unresolved. These species fit within the Pacific Clade because of their simple inflorescences, subreflexed apices of the corollas, shorter sepal mucros in relation to sepal
length, and absence of long chalazal ovule appendages. Nevertheless, they also exhibit unusual characters within this lineage such as short, compressed flowers and white petals with acute apices. From a traditional taxonomic point of view, these species are also unusual in _Aechmea_ subgenus _Chevaliera_ because of their tank-forming rosettes, short subspreading flowers, well-developed petal appendages, and unappendaged ovules, characters mostly absent in the other species of this subgenus. The geographic distribution of these species in the same geographic range of the other species in the Pacific Clade further supports their inclusion within this lineage.

1.5.2.2 **Atlantic Clade**

The Atlantic Clade is the largest lineage within the _Ronnbergia_ Alliance clade (Fig. 1.3). Like in the Pacific Clade, the species within the Atlantic Clade also exhibit very restricted patterns of geographic distribution with most of the species being endemic to eastern Brazil and the Caribbean. This clade also includes _Aechmea lingulata_, which is mostly distributed through the Atlantic coast of the Neotropics and the Caribbean, from northeastern Brazil to the Caribbean. Ancestral reconstructions suggest that the ancestor of the Atlantic Clade differed from that of the Pacific Clade by their paniculate inflorescences, shorter flowers, sepals exhibiting long mucro length to sepal length ratios, and white petals with acuminate to acute apices (Figs. 1.5–1.6 and 1.8–1.9).

Within the Atlantic Clade, the _Aechmea lingulata_ complex is polyphyletic and intermingles with the Brazilian species of _Ronnbergia_. This is not an unexpected result as recent taxonomic studies have emphasized that using the lack of petal appendages to describe species of _Ronnbergia_ in Brazil should be avoided; instead, these species should be placed in the _Aechmea lingulata_ complex (Siqueira Filho and Leme 2006; e.g. Leme and Kollmann 2011). The results
of the present study permitted identifying two main lineages of the Atlantic Clade: Clades C and Clade D. Clade C is a clade with medium to low support composed of five species of *Aechmea* and *Ronnbergia* endemic to the Central Atlantic forest. No diagnostic morphological characters were found to support this clade; however, character reconstructions suggest that the ancestor of this group likely exhibited simple inflorescences, long flowers, medium-exposed corolla tubes to flower length ratio, and long connation of sepals to flower length ratio (Figs. 1.6 and 1.8–1.9). Clade D, on the other hand, is strongly supported and comprises the remaining species of the *Aechmea linguata* complex and the Caribbean Clade. This lineage mostly contains species with paniculate inflorescences; short flowers; long sepal mucros in relation to flower length; corolla tubes shortly exposed; and white flowers (Figs. 1.5–1.6 and 1.8–1.9). The relationships among the species of the *Aechmea linguata* complex are highly unresolved in a polytomy that also includes a medium supported clade that comprises *A. bicolor* as sister to the Caribbean Clade. The widespread *Aechmea linguata* is related to other Brazilian species of *Aechmea* and does not seem to be directly related to the Caribbean Clade. This pattern is further supported by the AU test, which rejects a scenario where *A. linguata* forms a monophyletic group with the Caribbean Clade.

1.5.2.3 **Caribbean Clade**

Both the combined and independent datasets strongly support the monophyly of the Caribbean Clade; a lineage entirely formed by all the species of *Hohenbergia* subgenus *Wittmackiopsis* (Figs. 1.2–1.3). The ancestral character reconstructions suggest that this clade can be diagnosed within the *Ronnbergia* Alliance clade by its strongly compressed flowers. This character is not unique to the Caribbean Clade, as it also appeared once within the Pacific Clade
and outside the *Ronnbergia* Alliance clade (Fig. 1.7). The Caribbean Clade also conserves the
diagnostic characters of Clade D: paniculate inflorescences, long sepal mucros in relation to
flower length, short exposure of the corolla tube to flower length ratio, and white petals (except
for three species that exhibit green petals), which allows its easy identification (Figs. 1.5–1.6 and
1.8–1.9). In taxonomic classifications, the combination of some of these characters, such as the
presence of paniculate inflorescences, strongly compressed flowers forming strobilate spikes,
and presence of petal appendages, corresponds to the current diagnosis of the genus *Hohenbergia*
(Smith and Downs 1979). However, our results highlight that the lack of ovule appendages and
the presence of white (rarely green) petals are more important diagnostic characters to place
*Hohenbergia* subgenus *Wittmackiopsis* within the *Ronnbergia* Alliance rather than *Hohenbergia*.
Moreover, the diagnostic value of the presence of petal appendages is not supported by our data,
as the ancestral state of the Caribbean Clade is the absence of these structures (Fig. 1.6).

The close relationship of the Caribbean Clade with a grade of species mostly endemic to
eastern Brazil reveals a major disjunction within the *Ronnbergia* Alliance. As discussed above,
only the range of *Aechmea lingulata* overlaps with these two areas of geographic distribution;
however, a close relationship between this species and the Caribbean Clade is not supported by
our data. This pattern suggests that the diversification of the Caribbean Clade likely
corresponded to an event of long-distance dispersal.

1.5.3 Trends in biogeography and morphological evolution

The *Ronnbergia* Alliance is part of the Core Bromelioideae, one of the most recent
adaptive radiations in Bromeliaceae. This diversification has been suggested to be triggered by
the combined acquisition of CAM photosynthesis, epiphytic habit, tank-forming rosettes, and the
production of large numbers of small, appendaged seeds, which increased ecological opportunity and permitted the colonization of unexploited niches (Quezada and Gianoli 2011; Givnish et al. 2014; Silvestro et al. 2014). Other characters such as the acquisition of asymmetrical sepals are also associated to the diversification of this group but have received less attention (Schulte and Zizka 2008). Because they are part of the Core Bromeliioideae radiation, the members of the Ronnbergia Alliance clade also exhibit these characters; this group, however, contains cases of independent reversals to C3 photosynthesis, terrestrial habit, and lack of tank-forming rosettes (Smith and Downs 1979; Crayn 2004; Silvestro et al. 2014). This phenotypic plasticity indicates that instances of adaptive diversification are common in this group and respond to colonization of ecosystems that range from super-humid forests in the Choco region to dry Caatingas in eastern Brazil. The ancestral character reconstructions identified two characters that remain stable within the Ronnbergia Alliance clade: tubular corollas with reflexed apices and lack of chalazal ovule appendages (Fig. 1.4). The functionality of these floral characters has not been formally studied in Bromeliaceae; however, chalazal ovule appendages have been described to remain present in the seeds in order to favor adhesion to animals for dispersal or surfaces such as tree bark for the establishment of seedlings (Benzing 2000; Givnish et al. 2014). Perhaps the lack of these structures in the Ronnbergia Alliance explains why the species have such narrow ranges of geographic distribution and can only grow as terrestrials, on rocks, or as epiphytes in the lower strata of the forest.

Another remarkable result obtained here is the clear geographical separation of the main lineages in the Ronnbergia Alliance clade. The phylogenetic hypotheses suggest two major disjunctions. The first disjunction occurred early in the history of the group, separating the Pacific and Atlantic Clades between the northwestern South America and eastern Brazil. The
second disjunction occurred later in the diversification of the Atlantic Clade, separating the Brazilian species from the Caribbean Clade. Although our analyses provided evidence that show the occurrence of these disjunctions, only a biogeographic approach can provide appropriate hypotheses to explain the causes and sequence of these events.

The ancestral character reconstructions suggest that the characters that exhibit major transformations after the early split of the Pacific and Atlantic Clades are inflorescence ramification, floral size, sepal mucro size in relation to flower length, petal color, and petal apex. Assuming adaptive evolution, these shifts in reproductive characters indicate that both lineages diversified under different influence of pollinators, herbivores, and fruit dispersers. In the case of the Brazilian-Caribbean disjunction, the most conspicuous character transformation is related to the compression of flowers in the Caribbean Clade (Fig. 1.7). All the species in the Caribbean Clade exhibit strobilate spikes that contain flowers with different levels of compression, frequently protected by large or spiny floral bracts. On the other hand, the Brazilian species exhibit lax to sublax spikes with terete flowers and short floral bracts, either spiny or smooth. The causes that led to floral compression have not yet been studied in Bromeliaceae; this pattern, however, suggests that the diversification in the Caribbean islands favored floral compression in combination with floral bract protection and development of sepal mucros, characters that contribute to restrict access to flower herbivores or undesired fruit dispersers.

Another likely case of diversification associated to character change occurred in Clade A within the Pacific Clade (Figs. 1.3 and 1.7). Our results show that the origin of this group is associated with the presence of pseudopetiolate leaves, the complete lack of petal appendages, and two characters not studied here: the lack of leaf margin serration and the presence of explosive berries. It is possible that these traits are associated with the diversification of the
group in the understory of highly humid forests of the Choco region. Explosive dry fruits are relatively common across the Angiosperms; nevertheless, explosive berries are very rare characters. In Bromeliaceae, this mechanism of seed dispersal has only been reported in *Ronnbergia* but has been poorly documented and needs further understanding.

### 1.6 Conclusions

Our comprehensive taxonomic sampling and use of six DNA sequence markers provided evidence to support the monophyly of the *Ronnbergia* Alliance, reveal the relationships within this clade, and explore the importance of selected morphological characters. These robust results will serve as framework for future studies focused on proposing a stable and predictive classification of genera within the conflictive Core Bromelioideae. Moreover, the phylogenetic hypotheses show that the diversification of the *Ronnbergia* Alliance clade is the result of two major geographic disjunctions across the neotropics. These disjunctions were followed by subsequent, highly localized radiations in three centers of diversity: (1) northwestern South America and southern Central America; (2) eastern Brazil; and (3) the Caribbean. These results set an ideal scenario for future biogeographic studies that aim to understand the processes that produced this exceptional diversification. Finally, ancestral state reconstructions show that although the *Ronnbergia* Alliance is a phenotypically variable lineage, there are characters that became fixed in the major lineages. It is possible that these characters provided adaptive advantages that promoted the diversification of the clades. However, it is necessary to use further morphological and ecological data combined with modern comparative methods to test evolutionary questions associated to trait evolution.
### 1.7 Supplementary table and figures

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Table 1.5. Probabilities of ancestral state reconstruction for the selected nodes in figures 1.4–1.7
Figure 1.10. Best tree of the Maximum Likelihood analysis. Names in red correspond to species of the *Ronnbergia* Alliance. Numbers on the nodes correspond to bootstrap values.
Figure 1.11. Strict consensus tree of the Maximum Parsimony analysis. Names in red correspond to species of the *Ronnbergia* Alliance. Numbers on the nodes correspond to bootstrap values.
Figure 1.12. Primary concordance tree. Names in red correspond to species of the *Ronnbergia* Alliance. Numbers on the nodes correspond to concordance factors. Names in red correspond to species of the *Ronnbergia* Alliance. Numbers on the nodes correspond to concordance factors.
Chapter 2

2  Taxonomy of the *Ronnbergia* Alliance (Bromeliaceae): New combinations, synopsis, and new circumscriptions of *Ronnbergia* and the resurrected genus *Wittmackia*

2.1  Abstract

The *Ronnbergia* Alliance is a recently described lineage composed by two highly supported and diagnosable clades with strong geographic structure: the Pacific and the Atlantic Clades. These clades, however, comprise species currently placed in the polyphyletic genera *Aechmea, Hohenbergia* and *Ronnbergia*. This study aims to reorganize the species that comprise both the Pacific and Atlantic Clades into stable and predictable taxonomic categories. In this context, the 26 species that compose the Pacific Clade are here circumscribed in the genus *Ronnbergia*, whereas the 44 species grouped in the Atlantic Clade are assigned to the resurrected genus *Wittmackia*. An updated circumscription of these two genera is presented, including a taxonomic key to recognize the species. Additionally, the respective taxonomic transfers and general information about each species are presented in the form of a synopsis. This taxonomic treatment will facilitate future studies of the systematics, conservation and evolution of *Ronnbergia* Alliance.

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2 Manuscript follows the guidelines of *Plant Systematics and Evolution*
2.2 Introduction

The majority of species that compose the subfamily Bromelioideae (Bromeliaceae) make part of the highly diverse, albeit taxonomically conflictive, Core Bromelioideae clade (Schulte et al. 2009). Phylogenetic studies have shown that most genera that form the Core Bromelioideae are polyphyletic and intermingled with the trash-can genus Aechmea, suggesting that their taxonomic limits, and the characters that they are based on, must be reconsidered (Faria et al. 2004; Schulte et al. 2005, 2009; Horres et al. 2007; Sass and Specht 2010; Silvestro et al. 2014; Evans et al. 2015). In an effort to resolve this issue, Aguirre-Santoro (in preparation; see chapter 1) conducted a molecular-based phylogenetic study focused on a robust clade of the Core Bromelioideae, informally called the “Ronnbergia Alliance.” This study included a nearly complete species-level sampling for the taxa putatively in the clade, which combined with the use of six molecular markers and the ancestral reconstruction of potentially diagnostic characters permitted the recognition of the Ronnbergia Alliance as a diagnosable and robust lineage awaiting formal taxonomic restructuring (Fig. 2.1).
Figure 2.1. Phylogenetic relationships and geographic distribution of the *Ronnbergia* Alliance. Black circles in the map represent species of *Ronnbergia*. Red circles represent species of *Wittmackia* (Source of the phylogeny: Aguirre-Santoro (in preparation; see chapter 1))
According to Aguirre-Santoro (in preparation; see chapter 1) the *Ronnbergia* Alliance can be diagnosed by the combination of an apically spreading tubular corolla and the lack of chalazal ovule appendages. The *Ronnbergia* Alliance comprises species of the genera *Aechmea*, *Hohenbergia*, and *Ronnbergia*, all of which appeared as polyphyletic and, in the case of the first two genera, very distantly related to their corresponding type species. Despite this apparent lack of taxonomic stability in the genera nested within the *Ronnbergia* Alliance, it was possible to determine that this clade is composed by two robust lineages with high geographic structure (Fig. 2.1). The first lineage, also called the Pacific Clade (Aguirre-Santoro in preparation; see chapter 1), includes species of *Aechmea* and *Ronnbergia* endemic to the forested regions from Costa Rica to central Peru. This clade can be roughly diagnosed by the combination of simple inflorescence, long corolla tubes, and pigmented petals (except green). The second lineage, named the Atlantic Clade, comprises several species of *Aechmea* and *Ronnbergia* mostly endemic to the central Atlantic forest in southeastern Brazil, and species of the Caribbean-endemic *Hohenbergia* subgenus *Wittmackiopsis*. The ancestral character reconstructions suggested that this clade is generally recognizable by its relatively short flowers, short corolla tubes, and white petals. The robustness of this phylogenetic evidence, combined with the geographically congruent distributions of the species and the exploration of potentially diagnostic characters, provides a framework to give these lineages their own taxonomic identity. Therefore, in this study the species nested within the Pacific and Atlantic Clades are formally assigned to the genera *Ronnbergia* and *Wittmackia*, respectively.

Given that the species composition of these newly expanded genera is unprecedented, this taxonomic study is organized in the form of a synopsis that includes descriptions of the
genera, taxonomic keys for the identification of each species, and a general overview of the
taxonomy and geographic distribution of the species. This study does not aim to be a
comprehensive revision of the group, but a guide that can be used for future taxonomic,
evolutionary and conservation studies of this lineage of bromeliads. For instance, a more
comprehensive taxonomic revision of the Caribbean species nested in the Atlantic Clade is
currently in preparation (Aguirre-Santoro in preparation; see chapter 3).

2.3 Materials and Methods

Most of the new combinations presented here correspond to species sampled for the
Ronnbergia Alliance in the study by Aguirre-Santoro (in preparation; see chapter 1). New
combinations of species not sampled by Aguirre-Santoro (in preparation; see chapter 1) were
included in this synopsis according to three criteria: 1) the species exhibit the diagnostic
characters that support inclusion in the Ronnbergia Alliance and the Pacific or Atlantic Clades;
2) their morphological affinities with species sampled in the phylogeny were discussed in
protologues and taxonomic treatments (e.g. Smith & Downs (1979) for Ronnbergia and Leme &
Siqueira Filho (2007) for Wittmackia); and 3) the species share similar geographic distributions
with the species sampled in the phylogeny.

The taxonomic keys and the information used to construct the synopsis was obtained
from observation of the species in the field, revision of protologues, and examination of type
specimens and selected collections from the herbaria B, RB, CEPEC, COL, G, GH, JAUM, HB,
HUA, IJ, K, NY, P, SEL, UCWI, and US. Some of these herbarium collections were examined
using electronic resources such as http://plants.jstor.org and high-resolution photographs
provided by curators. This synopsis is far from being an exhaustive taxonomic revision; for this
reason, many collections in world and local herbaria still remain to be examined. Geographic coordinates used to map the distribution of genera were obtained from observed material and information downloaded from the Global Biodiversity Information Facility (GBIF Data Portal, http://www.gbif.org/) and CRIA (http://splink.cria.org.br) databases after cleaning unlikely occurrences and including specimens determined by specialists.

2.4 Taxonomic Treatment

2.4.1 Diagnosis of the Ronnbergia Alliance

Plants epiphytic, rupicolous or terrestrial. Leaf blades lingulate to narrowed towards the base. Inflorescence exposed, occasionally concealed in the rosette, simple to 1-divided, occasionally 2-divided. Corolla tubular, apically spreading, rarely suberect. Ovules unappendaged.

Species composition, taxonomy, and geographic distribution: the Ronnbergia Alliance contains 70 species grouped in two genera, *Ronnbergia* and *Wittmackia*. The most distinctive characters that separate *Ronnbergia* from *Wittmackia* are its generally longer flowers ([20-]25-50 mm vs. 9-20[-37] mm long), longer corolla tubes ([6-]11-27 mm vs. 2.5-7 mm long), frequently pigmented flowers (vs. frequently white or green), and petal appendages arising from the base of the petal when present (vs. above 2 mm or more from the petal base when present). The species of the *Ronnbergia* alliance are concentrated in three disjunct centers of geographic distribution: 1) Costa Rica to the central Andes of Peru, 2) the northern and central Atlantic Forest in Brazil, including adjacent areas of caatinga and semi-deciduous forest, and 3) the Caribbean (Fig. 2.1).
2.4.2 Artificial key for the identification of genera in the Ronnbergia Alliance

1 Inflorescence branched….*Wittmackia*

1* Inflorescence simple…2

2 Exposed portion of the corolla tube > 11 mm long….*Ronnbergia*

2* Exposed portion of the corolla tube < 8 mm long…3

3 Medial floral bracts bright red at anthesis….*Ronnbergia*

3* Medial floral bracts green, cream or yellow at anthesis…4

4 Ovaries red or pink in anthesis, turning dark purple to black in fruit; sepals becoming as fleshy as the carpels of the fruit….*Ronnbergia*

4* Ovaries green, cream, yellow or light purple at either anthesis or in fruit; sepals persistent but not as fleshy as the carpels of the fruit….*Wittmackia*

2.4.3 Recircumscription and synopsis of Ronnbergia

*Ronnbergia* E. Morren & André, Ill. Hort. 21: 120. 1874.

≡ *Ronnbergia* subgen. *Euronnbergia* Mez, Monogr. Phan. 9: 157. 1896.—Type species:

*Ronnbergia morreniana* Linden & André, Ill. Hort. 21: 120, pl. 177. 1874.

≡ *Ronnbergia* subgen. *Aechmeopsis* Mez, Monogr. Phan. 9: 158. 1896.—Type:

*Ronnbergia columbiana* E. Morren, Belgique Hort. 35: 82. 1885.

*Plants* terrestrial or epiphytic, cespitose or solitary, stoloniferous or acaulescent; rosette broad and forming phytotelmata or narrow and basally elongated, not forming phytotelmata.

*Leaves* clearly differentiated between sheath and blade; sheaths elliptic, oblong or ovate, green,
pale brown or irregularly purplish, lepidote on both sides, entire or serrate towards the apex; blades lingulate, in some cases narrowed towards the base to slenderly pseudopetiolate, giving the blades an ovate to lanceolate shape, chartaceous to coriaceous, green or becoming reddish, concolorous, discolorous, maculate or clearly mottled, lepidote on both sides but more densely on the abaxial side, channeled or without a median channel, margins entire to serrate, apex attenuate to rounded, apiculate to mucronate. **Inflorescence** visible or concealed in the rosette, erect to inclined: peduncle green or whitish, glabrescent to densely floccose; bracts of the peduncle persistent, chartaceous, green, green with blue apex, pink or bright red, glabrous to densely floccose, always longer than the internodes, lightly imbricate to forming an involucre at the inflorescence base, erect to ascending, elliptic, lanceolate, ovate or oblanceolate, margins entire to serrate, apex attenuate to obtuse, apiculate or mucronate; fertile portion of the inflorescence simple, subcapitate, strobiliform or cylindrical, rachis visible or concealed by the floral bracts or flowers, sparsely to densely floccose. **Floral bracts** gradually to abruptly diminishing in size towards the inflorescence apex, shorter than the ovaries to surpassing the sepals, symmetric, persistent, polystichous, laxly separated to densely imbricate, erect to divaricate, sometimes reflexed apically, linear, triangular, lanceolate, ovate or oblanceolate, chartaceous to strongly coriaceous, green, blue or bright red, lepidote to densely floccose, margins entire to serrulate, apex attenuate to rounded, apiculate, caudate or mucronate. **Flowers** lax to densely congested, 5 to ca. 100 per spike, erect to divaricate, 20–50 mm long. **Calyx** conical, occasionally dorsiventrally compressed, convolute; sepals basally connate, strongly asymmetric, forming a membranous lateral wing that overlaps the adjacent sepal, white, green, dark blue, purple, pink or bright red, becoming white, yellow, brown or blue in fruit, glabrous to densely floccose, coriaceous, sometimes becoming as fleshy as the carpels of the fruit, unarmed.
to strongly mucronate. **Corolla** tubular, spreading apically, exserted 5–27 mm beyond the calyx; petals free, elliptic or subspatulate, white, yellow, purple, blue or pink, apex rounded, occasionally acute, petal appendages absent or present, when present fimbriate, arising at the very base of the petal or below the first third of the petal. **Stamens** included to partially exserted; filaments flattened, occasionally broadening at the apex; anthers sagittate to rectangular, apiculate to mucronate. **Ovary** globose to subcylindrical, green, whitish, yellow, pink or bright red, glabrous to densely floccose; placentation apically-axile, ovules > 30 per ovary, unappendaged. **Stigma** conduplicate-spiral, papillose. **Fruit** globose or ellipsoidal, yellow or blue, the sepals persistent and sometimes becoming fleshy, in some cases the seeds released explosively when the ripe fruit is mechanically removed (Fig. 2.2).

*Species composition and geographic distribution:* Ronnbergia includes 26 species, 22 of which are named species, and four correspond to new species being described for publication. Of these 26 species, 16 were sampled in the phylogenetic study by Aguirre-Santoro (in preparation; see chapter 1). The species of *Ronnbergia* are distributed from Costa Rica to the central Andes of Peru. The northern distribution of the genus is mostly restricted to the rainforests of the Chocó/Darién region and the western Andean Cordillera of Colombia and northern Ecuador. The second center of distribution is located in southern Ecuador and northern Peru, mostly in the Amotape-Huancabamba zone (Weigend 2002), where the species inhabit mountainous areas of semideciduous to humid forests from the Pacific coast to the Amazonian slopes of the Andes. Most species of *Ronnbergia* occur at low to medium elevations of about 1200–1500 m. Only two species, *R. maidifolia* and *R. veitchii*, reach 2600 m.

*Taxonomic Comments.* Ronnbergia is the oldest generic name available for this group and includes the type species of the genus, *R. morreniana*. The new circumscription presented
here includes all the extra-Brazilian species of Ronnbergia, nine species previously placed in Aechmea subgenus Pothuava, three species formerly included in Aechmea subgenus Chevaliera, and four unpublished new species. The inclusion of these species of Aechmea in Ronnbergia does not dramatically change the diagnosis of the genus because the presence of petal appendages was the only character that kept them apart from Ronnbergia. It could be argued that the species here transferred from Aechmea subgenus Chevaliera are particularly different because of their strobiliform inflorescences covered with broad and rigid floral bracts, and strongly compressed flowers. Their traditional placement in Aechmea subgenus Chevaliera, however, is weakly supported, as it is known that this taxon is phenotypically diverse, highly polyphyletic, and requires a more narrow delimitation (Silva 2003; Faria et al. 2004; Schulte et al. 2009; Sass and Specht 2010). Moreover, the transferred species fit within the limits of Ronnbergia because of their combination of suberect to apically spreading corollas and unappendaged to short-appendaged ovules, a combination of characters not observed in other species of Aechmea subgenus Chevaliera, including the type species of this subgenus, Aechmea spaherocephala Baker.
2.4.3.1 *Taxonomic key to the species of Ronnbergia*

1. Floral bracts of the medial portion of the inflorescence > 1.5 cm wide, much wider than the flowers, completely concealing the ovaries in anthesis; flowers dorsiventrally compressed…2

1* Floral bracts of the medial portion of the inflorescence < 1.2 cm wide, about equaling to much narrower than the flowers, partially to completely exposing the ovaries at anthesis; flowers slightly compressed to circular in cross section…6

2. Floral bracts strongly arcuate-reflexed at the apex…3

2* Floral bracts erect …4

3. Sepals 10–13 mm long…*Ronnbergia veitchii*

3* Sepals 20–25 mm long…*Ronnbergia sp. nov. 1*

4. Floral bracts bright red, 15–30 mm long; sepals 10–13 mm long…*Ronnbergia germinyana*

4* Floral bracts completely green to apically orange, 35–65 mm long; sepals 20–30 mm long…5

5. Leaf blades not narrowed towards the base; floral bracts and sepals completely green; calyx tightly convolute, sepals entire…*Ronnbergia viridispica*

5* Leaf blades strongly narrowed towards the base; floral bracts and sepals orange, at least at the apex; calyx subspreading, loosely convolute at the apex, sepals serrulate…*Ronnbergia sp. nov. 2*

6. Floral bracts of the medial portion of the inflorescence lanceolate, linear or filiform, apex acuminate to attenuate-caudate turning gradually into an apicule or mucro…7

6* Floral bracts of the medial portion of the inflorescence round to shortly ovate, apex round to broadly acute, smooth or abruptly apiculate…19

7* Sepal mucro > 5 mm long…8
7 Sepal mucro 1–4.5 mm long…13

8 Sepals completely green at anthesis; petals unappendaged…9

8* Sepals white-pink, pink, red, orange or magenta at anthesis; petals bearing two basal appendages…10

9. Leaves forming a semi-erect funnelform rosette; leaf blades not channeled; peduncle 11–17 cm long; inflorescence elevated above the rosette; sepal mucro 8–15 mm long; petals 2.5–3 cm long, white, the apex obtuse to rounded… *Ronnbergia petersii*

9* Leaves forming a spreading funnelform rosette; leaf blades channeled; peduncle 6–9 cm long; inflorescence sunken in the rosette; sepal mucro 6–7 mm long; petals 4 cm long, lavender, the apex acute… *Ronnbergia nidularioides*

10 Fertile portion of the inflorescence cylindrical with the flowers laxly distributed along the visible rachis; sepals 13–18 cm long (excluding the mucros)…11

10* Fertile portion of the inflorescence capitate to subcapitate with the flowers densely distributed and imbricate along the concealed rachis; sepals 23–30 cm long (excluding the mucros)…12

11 Teeth along the leaf blade margin > 1 mm long; floral bracts 16–22 mm long (including mucro); sepal mucro 8–12 mm long… *Ronnbergia weberbaueri*

11* Teeth along the leaf blade margin 0.4–0.8 mm long; floral bracts 5–6 mm long (including mucro); sepal mucro 4–6 mm long… *Ronnbergia sp. nov. 3*

12 Bracts of the peduncle red to bright pink, forming an involucre extending above the medial half of the fertile portion of the inflorescence; sepals red to bright pink at anthesis, floccose… *Ronnbergia allenii*
12* Bracts of the peduncle green, forming an involucre partially covering the basal third of the fertile portion of the inflorescence; sepals probably purple at anthesis, glabrescent... *Ronnbergia* sp. nov. 4

13 Leaf blades lanceolate to elliptical, strongly narrowed towards the base... 14

13* Leaf blades lingulate, not at all narrowed to slightly narrowed towards the base... 15

14 Leaf blades 2.5–6(–7.3) cm wide; peduncle completely concealed by the rosette; apical bracts of the peduncle broadly ovate, forming an involucre; petal unappendaged... *Ronnbergia deleonii*

14* Leaf blades 7.5–8.5 cm wide; peduncle exposed above the rosette; apical bracts of the peduncle lanceolate and imbricate, but not forming an involucre; petals bearing two basal appendages... *Ronnbergia subpetiolata*

15 Flowers 10–12 mm long; sepals 3–5 mm long... *Ronnbergia aciculosa* [p.p.]

15* Flowers > 20 mm long; sepals > 8 mm long... 16

16. Ovary verrucose... *Ronnbergia drakeana*

16* Ovary smooth... 17

17 Flowers up to 35 mm long; sepals 8–10 mm long... 18

17* Flowers 40–50 mm long; sepals 12–17 mm long... *Ronnbergia involucrata*

18 Apical bracts of the peduncle forming a conspicuous involucre, inconspicuously serrulate to entire, the teeth < 0.5 mm long; sepals white to pink... *Ronnbergia wuelfingerhoffii*

18* Apical bracts of the peduncle imbricate but not forming a conspicuous involucre, conspicuously serrate, the teeth 0.8–2 mm long; sepals orange to red... *Ronnbergia fraseri*

19 Floral bracts 0.9–1.5 × 0.8–1 cm; sepals turbinate, marcescent in fruit; fruits ovoid, greenish... *Ronnbergia campanulata*
19* Floral bracts 0.2–0.4 × 0.2–0.4 cm; sepals tightly convolute, becoming as fleshy as the carpels in fruit; fruits globose, dark blue to black ...20

20 Leaf blades not narrowed at the base to slightly narrowed towards the base, not clearly pseudopetiolate...21

20* Leaf blades conspicuously pseudopetiolate...24

21 Sepals and petals pink to magenta in anthesis, at least at the apex; exposed portion of the corolla tube shorter or as long as the sepal length; petals bearing two basal appendages...22

21* Sepals green to purple-blue at anthesis; petals white, blue-purple or yellow; exposed portion of the corolla tube > 1.5 times longer than the sepal length; petals unappendaged...23

22 Floral bract mucro 0.5–3 mm long; sepal mucro < 1 mm long...Ronnbergia tonduzii

22* Floral bract mucro ca. 10 mm long (according to the protologue); sepal mucro > 2 mm long...Ronnbergia aciculosa [p.p.]

23 Leaf blades not narrowed towards the base; sepals 1.2–1.7 cm long; petals white to purple-blue at the apex...Ronnbergia columbiana

23* Leaf blades slightly and gradually narrowed towards the base; sepals 0.4–1 cm long; petals yellow, sometimes purple-blue at the apex...Ronnbergia explodens

24 Leaf blades broadly elliptic or ovate, rounded at the base; flowers 2.7–3.5 cm long...Ronnbergia morreniana

24* Leaf blades oblong, lanceolate or long-elliptic, cuneate at the base; flowers 1.5–2.5 cm long...25

25 Medial bracts of the peduncle 4.5 cm long; sepals 0.4–0.5 cm long...Ronnbergia hathewayi

25* Medial bracts of the peduncle 5.5–9 cm long; sepals 0.7–1 cm long...26
Peduncle 20–30 cm long; sepals bearing an inconspicuous mucro; petals yellow… *Ronnbergia killipiana*

Peduncle 35–50 cm; sepals clearly mucronate; petals purple… *Ronnbergia maidifolia*

### 2.4.3.2 Synopsis

1. *Ronnbergia aciculosa* (Mez & Sodiro) Aguirre-Santoro, **comb. nov.** ≡ *Aechmea aciculosa*


*Habitats:* montane humid forests.

*Distribution area:* given the obscure taxonomy of this species, the type locality is the only certain area of occurrence of *Ronnbergia aciculosa*. This area is located in the western slopes of the Andes Cordillera in central-western Ecuador at about 1000 m elevation.

*Notes:* According to the protologue, *Ronnbergia aciculosa* is unique by its floral bracts bearing an acicular mucro of 10 mm long, a character clearly absent in the very similar *Ronnbergia tonduzii*. I observed the holotype of *Ronnbergia aciculosa* from the herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B); however, the inflorescence of this specimen was destroyed and no floral bracts were visible. The only available material corresponded to fragments of flowers, which look very similar to those of *R. tonduzii* but exhibit slightly longer sepal mucros. In the revision of the Bromelioidae of Ecuador by Manzanares (2002), many specimens were identified as *R. aciculosa* (*Aechmea aciculosa*) likely based on their elongate inflorescences, pink to magenta flowers, sepals exhibiting a somehow conspicuous mucro, and round fruits turning dark purple to black. Examination of the specimens of *R.*
Aciculosa cited by Manzanares (2002) housed at MO did not yield any characters that separate them from *R. tonduzii*, especially because they did not exhibit the enigmatic floral bracts with 10 mm mucros of *R. aciculosa*. However, some of these specimens exhibit slightly long sepal mucros, which are normally very short or absent in *R. tonduzii*. At this time I hesitate to propose a synonymization of *R. aciculosa* under *R. tonduzii* because it is impossible to be certain of the morphology of the floral bracts in the holotype of *R. aciculosa*. Moreover, I did not examined material deposited in Ecuadorian herbaria, including a possible isotype located at the QPLS herbarium in Quito.


*Habitats*: montane humid forests.

*Distribution area*: endemic to central Panama at 300–1300 m elevation.

*Representative specimens examined*: Panama: *Allen* 2467 (US).

*Notes*: *Ronnbergia allenii* is a very distinctive species within *Ronnbergia* distinguished by its capitate inflorescence covered for about half its length by an involucre formed by the bright red to pink bracts of the peduncle.

3. **Ronnbergia campanulata** Gilmartin & H. Luther, J. Bromeliad Soc. 40: 206, fig. 7. 1990.—TYPE: Ecuador, Morona-Santiago, NW range of Cordillera del Condor, trail from crest or ridge to base camp overlooking Río Zamora, 1950 m, 4 January 1972, *B. Macbryde* 954 (holotype, US!).
Habitats: montane humid forests.

Distribution area: endemic to the Cordillera del Cóndor in Ecuador at 1800–2000 m elevation.

Representative specimens examined: Ecuador: Manzanares 7201 (MO).

Notes: this species is distinguished within Ronnbergia by its blue, turbinate calyx.


Habitats: edges or understory of lowland to montane humid forests.

Distribution area: Ronnbergia columbiana is found from western Colombia to the eastern slopes of the Andes Cordillera in northern Peru at 0–700 m.

Representative specimens examined: Colombia: Aguirre-Santoro 210 (COL).


Habitats: understory of montane humid forests.

Distribution area: Ronnbergia deleonii is found from western Colombia to the southeastern slopes of the Andes in Ecuador at 550–1150 m.

Representative specimens examined: Colombia: Forero 3137 (COL, MO); Ecuador: Galo Tipaz 1915 (MO).

*Habitats:* humid montane forests.

*Distribution area:* endemic to the eastern slopes of the Andes cordillera in southeastern Ecuador and northern Peru at 600–2000 m elevation.

*Representative specimens examined:* Ecuador: *Clark 3121* (SEL); Peru: *Smith 4777* (MO).

*Notes:* this species is very distinctive within *Ronnbergia* because of its verrucose ovary.


*Habitats:* understory of montane humid forests.

*Distribution area:* *Ronnbergia explodens* is found from southern Panama to the eastern slopes of the Andes in central Peru at 80–1400 m elevation.

*Representative specimens examined:* Panama: *Croat 67205* (MO); Colombia: *Forero 7422* (COL); Ecuador: *Cerón 19218* (MO); Peru: *Foster 8635* (F, SEL).
8. Ronnbergia fraseri (Baker) Aguirre-Santoro, comb. nov. \(\equiv\) Aechmea fraseri Baker, Handb. Bromel. 61. 1889.—TYPE: Ecuador, Andes of Ecuador, 1860, L. Fraser s.n. (holotype, BM [web]!).

*Habitats:* semideciduous forests.

*Distribution area:* endemic to the inter-Andean slopes of Ecuador and northern Peru at 1200–1500 m elevation.

*Representative specimens examined:* Ecuador: Camp E-3465 (NY, US); Peru: Diaz 5991 (MO).


*Habitats:* understory of montane humid forests.

*Distribution area:* endemic to the Chocó/Darién region from southern Panama to western Colombia at 0–1740 m elevation.

*Representative specimens examined:* Panama: Williams 960 (NY, US); Colombia: Aguirre-Santoro 209 (COL)

*Notes:* this species is very distinctive within Ronnbergia because of its strobiliform inflorescence covered with bright red, serrate, and ascending floral bracts.

Habitats: understory of montane humid forests.

Distribution area: Ronnbergia hathewayi is found from Costa Rica to northwestern Colombia at 300–1500 m elevation.

Representative specimens examined: Costa Rica: Gómez 20844 (MO); Panama: Thompson 5059 (SEL); Colombia: MacDougal 4045 (MO, HUA).


Habitats: semideciduous forests.

Distribution area: endemic to the western and inter-Andean slopes of southern Ecuador at 1200–1500 m elevation.

Representative specimens examined: Ecuador: Foster 2593 (US)


Habitats: understory of montane humid forests.
Distribution area: endemic to the Chocó/Darién region from western Colombia to northwestern Ecuador at 50–1500 m elevation.

Representative specimens examined: Colombia: Forero 3392 (COL); Ecuador: Hoover 1251 (MO).

Notes: According to the protologue, the presence of serrate leaf blades was used as one of the diagnostic characters to delimit Ronnbergia killipiana. Recent collections, however, revealed individuals of this species with entire leaves, complicating its differentiation from R. hathewayi. Ronnbergia killipiana can be distinguished from R. hathewayi by its longer medial scape bracts (5–7 cm vs. 4.5 cm), longer sepals (7–9 mm vs. 4–5 mm), and yellow petals (vs. white and tipped purple to complete purple).

13. **Ronnbergia maidifolia** Mez, Monogr. Phan. 9: 158. 1896.—TYPE: Colombia, Valle del Cauca, West Andes above Cali, 2000 m, F.C. Lehmann 6386 (3015) (holotype, B [web]!).

Habitats: understory of montane humid forests.

Distribution area: Ronnbergia maidifolia is found from Panama to western Colombia at 500–2350 m elevation.

Representative specimens examined: Panama: Allen 4493 (MO); Colombia: Aguirre-Santoro 1920 (COL).

14. **Ronnbergia morreniana** Linden & André, Ill. Hort. (1874) 120. t. 177. 1874.—TYPE: Colombia, No locality, 1873, Linden Hortus s.n. (Lectotypified from the original description and illustration by Smith & Downs (1979)).

Habitats: edges or understory of montane humid forests.
Distribution area: endemic to the Chocó/Darién region from western Colombia to northwestern Ecuador at 100–1100 m elevation.

Representative specimens examined: Colombia: Betancur 12782 (COL); Ecuador: Galo Tipaz 1875 (MO).

Notes: this species is distinguished within Ronnbergia by its abruptly pseudopetiolate and mottled leaf blades.


Habitats: understory of montane humid forests.

Distribution area: endemic to the Chocó/Darién region from southwestern Colombia to western Ecuador at 200–2000 m elevation.

Representative specimens examined: Ecuador: Hoover 2009 (MO).

16. Ronnbergia petersii L.B. Sm., J. Bromeliad Soc. 23: 46, fig. 1973.—TYPE: Panama, Cerro Jefé, 750 m, K. Peters s.n. (holotype, US!).

Habitats: montane humid forests.

Distribution area: this species is only known from the type collection in Cerro Jefe, Panama at 750 m elevation.

Notes: in the revision of Bromeliaceae for Flora Mesoamericana (Davidse et al. 1995), Ronnbergia petersii was proposed as a synonym of the sympatric R. allenii (Aechmea allenii);
however, this synonymy is not well justified because *R. petersii* exhibits green bracts (vs. bright red to hot pink), much longer sepal mucros (up to 15 mm vs. up to 7 mm long), and unappendaged petals (vs. petals bearing two basal appendages).

### 17. *Ronnbergia subpetiolata* (L.B. Sm.) Aguirre-Santoro, **comb. nov.** $\equiv$ *Aechmea subpetiolata* L.B. Sm., Contr. Gray Herb. 124: 8, pl. 1939. $\equiv$ *Pothuava subpetiolata* (L.B. Sm.) L.B. Sm. & W.J. Kress, Phytologia 66(1): 76. 1989.—**TYPE:** Colombia, Cauca, Ad pag. El Tambo, in silva primaeva ad La Costa., 1500 m, 29 March 1938, *K. von Sneidern* 1593 (holotype, S [web]!).

*Habitats:* montane humid forests.

*Distribution area:* this species is only known from the type collection in El Tambo, Cauca, Colombia at 1700–1800 m elevation.


*Habitats:* montane humid forests.

*Distribution area:* *Ronnbergia tonduzii* is found from Costa Rica to the slopes of the Andes Cordillera in southern Ecuador at 200–2500 m elevation.

*Notes:* This species is very similar to *Ronnbergia aciculosa*. See the “Notes” section of *R. aciculosa* for more details.
Representative specimens examined: Costa Rica: *Smith 15308* (US); Panama: *Knapp 4920* (MO); Colombia: *Gentry 23969* (COL, MO); Ecuador: *Tirado 517* (SEL).

19. *Ronnbergia veitchii* (Baker) Aguirre-Santoro, **comb. nov.** ≡ *Aechmea veitchii* Baker, Bot. Mag. 103: t. 6329. 1877.—**TYPE:** Cultivated at Kew from material collected in Colombia, no date, *Kew Hortus s.n.* (holotype, K [web]!).

*Habitats:* edges or understory of montane humid forests.

*Distribution area:* *Ronnbergia veitchii* occurs from Costa Rica to the Andean slopes of central Peru at 800–2600 m elevation.

*Representative specimens examined:* Costa Rica: *Croat 36183* (MO); Panama: *Croat 69046* (MO); Colombia: *Aguirre-Santoro 1916* (COL, NY); Ecuador: *Gentry 80261* (MO); Peru: *Schunke 9843* (MO).

*Notes:* *Ronnbergia veitchii* is distinguished by its strobiliform inflorescence covered with bright red, serrate, and arcuate-reflexed floral bracts.

20. *Ronnbergia viridispica* (Aguirre-Santoro & Betancur) Aguirre-Santoro, **comb. nov.** ≡ *Aechmea viridispica* Aguirre-Santoro & Betancur, Brittonia 63(2): 310, fig. 5. 2011.—**TYPE:** Colombia, Antioquia, Mpio. Amalfí, vereda Las Animas, 6°56’02”N, 75°00’32”W, 24 August 1999, *D. Tuberquia & A. Zapata 1057* (holotype, JAUM!).

*Habitats:* montane humid forests.

*Distribution area:* this species is known from two collections in Antioquia, near Almalfí and Anorí, in the northern Andes of Colombia at 1450–1600 m elevation.

*Representative specimens examined:* Colombia: *López-A. 830* (HUA)
Conservation status: this species is endangered (EN), according to Aguirre-Santoro & Betancur (2011).

21. Ronnbergia weberbaueri (Harms) Aguirre-Santoro, comb. nov. = Aechmea weberbaueri

Habitats: relict humid forests near dry areas.

Distribution area: endemic to the Amotape-Huancabamba Zone in the northwestern Andean slopes of Peru at about 1200 m elevation.

Representative specimens examined: Peru: Rauh 20347 (US)


Habitats: humid montane forest.

Distribution area: Ronnbergia wuelfinghoffii occurs in the eastern side of the Andes Cordillera in southeastern Ecuador and northern Peru at 600–2300 m elevation.

Representative specimens examined: Ecuador: Clark 8945 (US); Peru: Vásquez 26627 (MO).

23. Ronnbergia sp nov. 1
Habitats: understory of montane humid forests.

Distribution area: endemic to the Chocó/Darién region in western Colombia at about 1200 m elevation.

Representative specimens examined: Silverstone-S. 1506 (MO).

Notes: this species is similar to *R. veitchii* but exhibits flowers and sepals more than two times longer.

24. *Ronnbergia* sp nov. 2

Habitats: understory of montane humid forests.

Distribution area: endemic to the Chocó/Darién region in western Colombia at about 1800-2000 m elevation.

Representative specimens examined: Clavijo 1618 (COL).

Notes: this species can be distinguished within *Ronnbergia* by its spreading-convolute calyx and orange sepals.

25. *Ronnbergia* sp nov. 3

Habitats: understory of lowland humid forests.

Distribution area: endemic to the Chocó/Darién region in western Colombia at about 100 m elevation.

Representative specimens examined: Gentry 37055 (MO).

Notes: this species is similar to *R. weberbaueri* from northwestern Peru but mainly differs from it by its shorter inflorescence, shorter floral bracts, less numerous flowers, and shorter sepal mucros.
26. **Ronnbergia sp nov. 4**

*Habitats:* understory of lowland humid forests.

*Distribution area:* endemic to the Chocó/Darién region in western Colombia at about 0-100 m elevation.

*Representative specimens examined:* Fuchs 21901 (COL).

*Notes:* this species can be distinguished within *Ronnbergia* by its subcapitate inflorescence, and unusually long and strongly mucronate sepals.

### 2.4.4 Resurrection, recircumscription, and synopsis of *Wittmackia*


**Plants** terrestrial, rupicolous or epiphytic, cespitose or solitary, stoloniferous or acaulescent; rosette broad, forming phytotelmata. **Leaves** clearly differentiated between sheath and blade; sheaths elliptic, oblong or ovate, green, pale brown or irregularly purplish, lepidote on both sides, entire or serrate towards the apex; blades linear to lingulate, occasionally narrowed towards the base (e.g. *W. canaliculata*), green, occasionally vinaceous (e.g. *W. brasiliensis*),
lepidote on both sides but more densely on the abaxial side, channeled or without a median channel, margins entire to strongly serrate, apex attenuate to rounded, apiculate to mucronate. **Inflorescence** visible or partially concealed in the rosette, erect to pendulous: peduncle green, dull purple or whitish, glabrescent to densely floccose; bracts of the peduncle marcescent, chartaceous, green, dull purple or pale brown, glabrous to densely floccose, shorter to longer than the internodes, erect to ascending, linear-lanceolate, lanceolate or oblanceolate, margins entire to serrate, apex attenuate to acute, apiculate or mucronate; fertile portion of the inflorescence simple to 2-divided, 4–70 cm long, rachis visible or concealed by the bracts, flowers or branches, sparsely lepidote to densely floccose. **Primary bracts** gradually to abruptly diminishing in size towards the apex of the inflorescence, diverging from the rachis to divaricate, marcescent, chartaceous, shorter to longer than the branches; ovate to linear-lanceolate, green, cream, dull purple or pale brown, occasionally bright red (*W. tentaculifera*), lepidote to floccose, entire to serrulate, apex attenuate to acute. **Spikes** globose-strobilate to long-cylindrical; sessile or stipitate, the stipe exposed or concealed by bracts, 0.5–15 cm long, terete to slightly flattened, glabrous to floccose; rachis of the spike straight, exposed or concealed by the flowers or floral bracts. **Floral bracts** gradually to abruptly diminishing in size towards the inflorescence apex, shorter than the ovaries to surpassing the sepals, symmetric, persistent, polystichous, laxly separated to densely imbricate, erect to divaricate, linear, triangular, lanceolate, ovate or orbicular, chartaceous to strongly coriaceous, green, cream, yellow, orange, vinaceous, occasionally bright red (*W. tentaculifera*), margins entire to serrulate, apex attenuate to retuse, apiculate, caudate or mucronate. **Flowers** lax to densely congested, 3 to about 100 per spike, erect to divaricate. **Calyx** conical to dorsiventrally compressed, convolute, occasionally turbinate-convolute (*W. turbinocalyx*); sepals basally connate, strongly asymmetric, forming a
membranous lateral wing that overlaps the adjacent sepal, white, cream, green, yellow, purple, lilac, pink or bright red, glabrous to densely floccose, occasionally brown-tometose-lepidote (*W. eriostachya* and *W. polycephala*), coriaceous, unarmed to strongly mucronate. **Corolla** tubular, spreading apically, occasionally suberect (e.g. *W. bicolor*) exserted 2–8 mm beyond the calyx; petals free, elliptic or subspatulate, white, green, occasionally lilac or purple (e.g. *W. brasiliensis*), apex acute to obtuse, petal appendages absent or present, when present lobulate, arising above 2 mm or more from the petal base. **Stamens** included; filaments flattened, subconstricted at the insertion point of the anther; anthers rectangular, apiculate to mucronate. **Ovary** ovoid-compressed, ellipsoidal, cylindrical, obovoid or clavate, white, cream, green, yellow, orange, pink, purple or bright red, glabrous to densely floccose; placentation apically-axile, ovules > 30 per ovary, unappendaged. **Stigma** conduplicate-spiral, papillose. **Fruit** ovoid, ovoid-compressed, ellipsoidal, cylindrical, obovoid or clavate, yellow, red, blue or black, the sepals persistent and sometimes becoming basally fleshy (Fig. 2.3).

**Species composition and geographic distribution:** *Wittmackia* includes 44 species, forty-three of which are named species, and one corresponds to a new species awaiting publication. Aguirre-Santoro (in preparation; see chapter 1) sampled 41 of these 44 species in their phylogenetic study. The species of *Wittmackia* are mainly distributed in two centers of diversity. The first area is located in the central corridor of the Brazilian Atlantic Forest in southeastern Bahia state, with a few species occurring farther north from Ceará to Sergipe states. The second center of diversity is Jamaica in addition to a small group of species occurring in the remaining Greater Antilles (except Hispaniola), their adjacent islands west of the Caribbean, and the Yucatan Peninsula. *Wittmackia lingulata* is the only widespread species in the group, occurring along the tropical Atlantic coast, Panama and the Caribbean, except for the major islands of the
Greater Antilles. The species of *Wittmackia* inhabit a wide variety of environments from hygrophilous mountainous forests to dry habitats in semi-deciduous forests and tropical dry forest. Most species of *Wittmackia* occur in lowlands to medium-low elevations of about 600–800 m. However, species such as *W. fawcetii* and *W. eriostachya* can grow up to 1600 m elevation in the Blue Mountains of Jamaica.

**Taxonomic comments:** *Wittmackia* is the oldest generic name available for this group as *W. lingulata* and *W. patentissima* were the first species assigned to this genus by Mez (1891). *Wittmackia* has been a synonym of *Aechmea* for almost 60 years, since Smith (Smith 1956a) considered that the lax spikes and mucronate sepals of the species were the most relevant characters for their generic placement. However, it is currently known that *Aechmea* is an artificial, polyphyletic genus that requires major restructuring. For this reason, and based on the phylogenetic evidence presented by Aguirre-Santoro (in preparation; see chapter 1), here we resurrect and recircumscribe *Wittmackia*. The lack of ovule appendages is the most remarkable similarity between the original diagnosis of *Wittmackia* and the new circumscription proposed here. However, our new delimitation rejects the usage of the absence of petal appendages to separate this genus from others, as this is a character that evolved several times in the group (Aguirre-Santoro in preparation; see chapter 1).

Within *Wittmackia*, there is a morphological gap between the Caribbean-endemic species and the remaining species. The former exhibit strongly compressed flowers grouped in strobilale spikes, whereas the latter have lax to subcongested spikes and flowers not compressed. Moreover, Aguirre-Santoro (in preparation; see chapter 1) confirmed that this morphological gap corresponds to an evolutionary event that separated the Caribbean-endemic species from their mostly Brazilian-endemic relatives. Despite this clear morphological differentiation and the
evidence of monophyly for the Caribbean-endemic species, I do not propose an infrageneric classification for *Wittmackia*. This decision is based on the results by Aguirre-Santoro (in preparation; see chapter 1), which did not provide evidence for the monophyly of the mostly Brazilian-endemic species (including *W. lingulata*). These results, however, did not reject the hypothesis that they form a monophyletic group, which leaves open the possibility of a future infrageneric classification of *Wittmackia* when more robust phylogenetic studies become available.

### 2.4.4.1 Taxonomic key to the species of *Wittmackia*

1 Inflorescence simple…2

1* Inflorescence branched…15

2 Flowers > 35 mm long, forming an angle of 0° to 15° with the inflorescence rachis at anthesis…3

2 Flowers < 32 mm long, forming an angle of 30° to 130° with the inflorescence rachis at anthesis…5

3 Peduncle up to 10 cm long; fertile portion of the inflorescence up to 4 cm long (excluding the corollas of terminal flowers); sepals 9–10 mm long…4

3* Peduncle > 12 cm long; fertile portion of the inflorescence 5–7 cm long (excluding the corollas of terminal flowers); sepals > 12 mm long… *Wittmackia silvana*

4 Leaves 7–19 cm long, 1.3–2 cm wide, not channeled; flowers ca. 6 per spike; petals ca. 21 mm, acute, lilac at the apex. *Wittmackia neoregelioides*

4* Leaves 20–40 cm long, > 2 cm wide, canaliculate towards the base; flowers 8–20 per spike; petals ca. 30 mm long, obtuse to emarginate, white… *Wittmackia carvalhoi*

5 Inflorescence > 3.5 cm wide (excluding the corollas of the most external flowers); flowers > 25 mm long; sepals > 11 mm long (including the mucro); petals > 18 mm long…6
5. Inflorescence < 3 cm wide (excluding the corollas of the most external flowers); flowers < 20 mm long; sepals < 9 mm long (including the mucro); petals < 14 mm long…8

6 Leaf blades 50–100 × 5.5–6.5 cm, not channeled, margins serrate; peduncle partially to completely concealed by the rosette; fertile portion of the inflorescence > 4 cm wide (excluding the corollas of the most external flowers); sepals and ovaries green at anthesis…7

6* Leaf blades 30–45 × 1.8–2 cm, canaliculate, margins entire; peduncle almost completely exposed out of the rosette; fertile portion of the inflorescence ca. 3.5 cm wide (excluding the corollas of the most external flowers); sepals and ovaries yellow at anthesis…*Wittmackia canaliculata*

7 Inflorescence up to 10 cm long; flowers congested along the rachis; medial floral bracts 20–25 mm long; sepal mucro ca. 4 mm long…*Wittmackia amorimii*

7* Inflorescence ca. 20 cm long; flowers subdistantly separated to each other along the rachis; medial floral bracts 9–11 mm long; sepal mucro 2–3 mm long…*Wittmackia gregaria*

8 Sepals and ovaries bright yellow to orange; corolla tube apex suberect to slightly reflexed …9

8* Sepals and ovaries green, cream, greenish purple or purple; corolla tube apex strongly reflexed …11

9 Leaf blade 2.3–3 cm wide; floral bracts 3–5 mm long; sepals 2–5 mm long; petals 9–10 mm long, bearing two basal appendages; stigma white…10

9* Leaf blade 1.4–1.7 cm wide; floral bracts 6–15 mm long; sepals ca. 7 mm long; petals ca. 14 mm long, unappendaged; stigma greenish yellow…*Wittmackia andersoniana*

10 Leaves strongly coriaceous; blades conspicuously serrate along the margins; inflorescence erect or slightly inclined; petal apex obtuse to emarginate…*Wittmackia bicolor*
10* Leaves chartaceous to subcoriaceous; blades subentire, inconspicuously serrulate at the apex; inflorescence pendulous; petal apex acute... *Wittmackia pendulispica*

11 Leaf blades densely cinereous lepidote on the abaxial surface; sepals turbinate... *Wittmackia turbinocalyx*  [p.p]

11* Leaf blades sparsely covered by lepidote indument on the abaxial surface; sepals tightly convolute... 12

12 Leaf blades frequently vinaceous abaxially; inflorescence strongly inclined to pendulous; floral bracts 1.5–4 mm long; sepals green with purple apex or completely purple... *Wittmackia brasiliensis*  [p.p]

12* Leaf blades green abaxially; inflorescence erect to slightly inclined; floral bracts 5–23 mm long; sepals green to cream, never purple... 13

13 Peduncle 30–45 cm long; fertile portion of the inflorescence 11–20 cm long, long-cylindrical; flowers > 40 per spike; petals 11–12 mm long; stigmas white... 14

13* Peduncle ca. 17 cm long; fertile portion of the inflorescence 4.5–5 cm long, subcylindrical; flowers < 30 per spike; petals ca. 15 mm long; stigmas green... *Wittmackia limae*

14 Leaf blades minutely serrulate at the apex; flowers 15–16 mm long; sepals 6–7 mm long, exhibiting a mucro 2–3 mm long; petals lilac to purple... *Wittmackia altocaririensis*

14* Leaf blades entire; flowers ca. 20 mm long; sepals ca. 9 mm long, exhibiting a mucro 1–1.5 mm long; petals white... *Wittmackia ituberaensis*

15 Flowers subconcongested to laxly distributed along the spike rachis, never strobilate; calyx circular in cross section, sepals all ecarinate and similar... 16
15* Flowers densely congested along the spike rachis, forming a strobilate spike; calyx
dorsiventrally compressed, posterior sepals strongly carinate, the anterior sepal ecarinate…32
(Caribbean-endemic Wittmackia spp)
16 Ovaries and sepals bright yellow to orange at anthesis…17
16* Ovaries and sepals green, greenish yellow, cream, pink, lilac or bright red at anthesis…19
17 Basal inflorescence branches 2–3.5 cm long, bearing 2 to 8 flowers; petals
unappendaged….18
17* Basal inflorescence branches (3-) 4–7 cm long, bearing 9 to 25 (-33) flowers; petals bearing
two basal appendages….Wittmackia burle-marxii
18 Blade margin entire; bracts of the peduncle shorter than the internodes; sepals orange, mucro
1 mm long; petal apex obtuse-emarginate; stigma white; ovary orange…Wittmackia laevigata
18* Blade margin minutely serrulate at the apex; bracts of the peduncle equaling or slightly
longer than the internodes; sepals yellow, mucro 2 mm long; petal apex acute; stigma green;
ovary yellow…Wittmackia viridostigma
19 Ovaries and sepals bright red in anthesis, terminal spike > two times longer than the
inflorescence rachis…Wittmackia tentaculifera
19* Ovaries and sepals green, greenish yellow, cream, pink or lilac in anthesis, terminal spike
much shorter than the inflorescence rachis or up to 1.5 times longer…20
20 Petals lilac to light purple, at least at the apex…21
20* Petals white or green…24
21 Leaf blades 1.2–1.5 cm wide, frequently vinaceous abaxially, entire to minutely serrulate at
the apex; inflorescence bearing no more than 4 branches; sepals 6–9 mm long, mucro < 1 mm
long…Wittmackia brasiliensis [p.p]
21* Leaf blades > 3 cm wide, always green abaxially, conspicuously serrate; inflorescence bearing 7 to 40 branches; sepals 3–5.5 mm long, mucro > 1.5 mm long …22

22 Leaf spines 1–3 mm long; inflorescence bearing 7 to 22 branches; flowers 14–19 mm long….23

22* Leaf spines ca. 0.5 mm long; (17-)23 to 40 branches; flowers 12 mm long Wittmackia pernambucensis

23 Leaves > 30 cm long; inflorescence bearing more than 8 branches; sepals 2–5 mm (excluding the mucro), green to greenish-yellow….Wittmackia lingulata [p.p]

23* Leaves < 30 cm long; inflorescence bearing 5 to 7 branches; sepals > 5.5 mm (excluding mucro), lilac-white to purple at apex…Wittmackia maranguapensis

24 Plants flowering up to 55 cm tall; blades 1.4–4.3 cm wide; inflorescence 4–15 cm long……25

24* Plants flowering 60–130 cm tall; blades 5–12 cm wide; inflorescence 20–54 cm long……28

25 Calyx turbinate, sepals 6.5–8 mm long; petals bearing two basal appendages…Wittmackia turbinocalyx [p.p]

25* Calyx tightly convolute, sepals 1.5–4 mm long; petals unappendaged…26

26 Lepidote indument of the blades forming transverse bands; inflorescence rachis slightly geniculate; flowers 16 mm long; sepals 4 mm long; petals 11–13 mm long….Wittmackia incompta

26* Lepidote indument uniformly distributed on the blades; inflorescence rachis straight; flowers 10–11 mm long; sepals 1.5–2.5 mm long; petals 6–6.5 mm long….27

27 Blades subdensely to densely lepidote, 2.4–3.8 cm wide, apex mucronate, margins subdensely serrulate; basal branches of the inflorescence 6.5–11 cm long; floral bracts mucronate; petals white, apex broadly acute and slightly apiculate…Wittmackia sulbahianensis [p.p]
27* Blades glabrescent, 2–2.5 cm wide, apex slightly apiculate, margins sparsely spinulose; basal branches of the inflorescence ca. 4 cm long; floral bracts acuminate-caudate; petals green, apex rounded… _Wittmackia linharresiorum_

28 Ovary globose to ovoid, ca. 4 mm in diameter…29

28* Ovary oboviod to clavate, 2–3 mm in diameter…30

29 Mucro of the floral bracts shorter than their basal blades, flexible; sepals 5–7 mm long, mucro up to 1.5 mm long… _Wittmackia froesii_

29* Mucro of floral bracts longer than their basal blades, rigid; sepals 2–4 mm long, mucro > 1.8 mm long… _Wittmackia lingulata_ [p.p]

30 Basal spikes bearing 28–90 flowers…..31

30* Basal spikes of bearing 10–20 flowers …._Wittmackia subbahianensis_ [p.p]

31 Xerophytic plants, stoloniferous; sepals 5 mm long, including the 2–3 mm mucro; petals ca. 11 mm long, apex acuminate; ovary cylindrical or nearly so, ca. 5 × 2 mm… _Wittmackia lingulatoides_

31* Mesophytic or higrophylic plants, cespitose; sepals 4 mm long, including the 1–1.5 mm mucro; petals ca. 8–9 mm long, apex broadly acute to obtuse emarginated; ovary ellipsoid to oboval, ca. 4 × 2.5 mm… _Wittmackia patentissima_

32 Stipes of the basal branches longer or equaling the length of the spikes…33

32* Stipes of the basal branches shorter than the length of the spikes…36

33 Inflorescence erect to inclined in anthesis; primary bracts surpassing the basal branches…34

33* Inflorescence pendulous in anthesis; primary bracts shorter than the basal branches…35

34 Medial bracts of the peduncle shorter than the internodes, peduncle diameter 6–8 mm; stipes of the basal branches 40–42 mm long, spikes bearing 12–18 flowers… _Wittmackia laesslei_
34* Medial bracts of the peduncle longer than the internodes, peduncle diameter 9–14 mm; stipes of the basal branches 17–39 mm long, spikes bearing 25 to 35 flowers... *Wittmackia sp. nov. aff negrilensis* [p.p]

35 Fertile portion of the inflorescence 36–51 × 9.4–20 cm; primary bracts 4.7–7.4 cm long; stipes 51–63 mm long, spikes bearing 9–25 flowers; floral bracts green to cream in anthesis, 3.8–4.9 mm long; petal appendages arising at 2–2.5 mm from the petal base... *Wittmackia abbreviata*

35* Fertile portion of the inflorescence 52–91 × 23–36 cm; primary bracts 7.5–9 cm long; stipes 85–133 mm long, spikes bearing 26–50 flowers; floral bracts yellow in anthesis, 6.5–11 mm long; petal appendages arising at 4 mm from the petal base... *Wittmackia distans*

36 Sepals > 7 mm long, narrowly triangular, the winged side enlarged towards the medial region of the sepal... 37

36* Sepals < 7 mm long, deltate, the winged side enlarged towards apical region of the sepal... 39

37 Stipes 24–49 mm, 1.8–3.2 mm in diameter... *Wittmackia inermis*

37* Stipes 4–20 mm, 4–10 mm in diameter... 38

38 Bracts of the peduncle and basal primary bracts serrate; floral bracts floccose to sparsely floccose, green, serrulate; petals 11–13.8 cm long, petal appendages absent. Puerto Rico and British Virgin Islands... *Wittmackia antillana*

38* Bracts of the peduncle and basal primary bracts entire; floral bracts glabrous, bright yellow to orange in anthesis, entire; petals 14.5–18 cm long, petal appendages present. Jamaica... *Wittmackia urbaniana*

39 Floral bracts, ovaries and sepals brown-tomentose-lepidote... 40

39* Floral bracts, ovaries and sepals glabrous to white-floccose-lepidote... 41
40 Leaf teeth < 1 mm long; primary bracts longer than the spikes; spikes sessile... *Wittmackia polycephala*

40* Leaf teeth > 1 mm long; primary bracts shorter than the spikes; spikes stipitate...5

*Wittmackia eriostachya*

41 Floral bracts obtuse to truncate; sepal mucro 0.2–0.8 mm long...42

41* Floral bracts acuminate to acute; sepal mucro 1–5 mm long...43

42 Peduncle 10–12 mm in diameter; bracts of the peduncle serrulate; fertile portion of the inflorescence 15–25 cm wide, rachis glabrous; spikes 5.8–7.8 cm long, bearing 40–50 flowers; floral bracts glabrous, mucro 1.7–4.7 mm long; sepals 3–4.5 mm long... *Wittmackia jamaicana*

42* Peduncle 4–9 mm in diameter; bracts of the peduncle entire; fertile portion of the inflorescence 7.8–12.8 cm wide, rachis sparsely floccose; spikes 2.9–4.7 cm long, bearing 18 to 35 flowers; floral bracts sparsely floccose, mucro 0.2–0.9 mm long; sepals 5.8–7 mm long... *Wittmackia fawcettii*

43 Apical bracts of the peduncle < 8.2 cm long; basal primary bracts 3–7.1 cm long...44

43* Apical bracts of the peduncle > 9 cm long; basal primary bracts 7.2–16 cm long...46

44 Spikes densely imbricate, covering the inflorescence rachis (except at the extreme base), suberect; primary bracts suberect... *Wittmackia spinulosa*

44* Spikes lax, exposing the inflorescence rachis, divaricate; primary bracts divaricate to reclined...45

45 Leaf blades 2–6.4 cm wide in the middle; fertile portion of the inflorescence bearing 7–14 branches, rachis subflexuose; primary bracts serrate; petal appendages absent. Puerto Rico... *Wittmackia portoricensis*
45* Leaf blades (6.5-)7.9–13 cm wide in the middle; fertile portion of the inflorescence bearing (13-)30–65 branches, rachis straight; primary bracts entire; petal appendages absent. Cuba and Jamaica... *Wittmackia penduliflora*

46 Stipes > 19 mm... *Wittmackia sp. nov. aff negrilensis* [p.p]

46* Stipes < 17 mm...47

47 Fertile portion of the inflorescence 56–57 × 10.3–10.4 cm; basal primary bracts 1–1.2 cm wide; flowers 50 to 60 per spike, 10.4–12.5 mm long; petals white; epigynous tube 0.2 mm; ovary 1.9–2.4 mm long... *Wittmackia negrilensis*

47* Fertile portion of the inflorescence 26–55 × 7.2–10.2 cm; basal primary bracts 0.4–0.7 cm wide; flowers 15 to 45 per spike, 13.6–17.3 mm long; petals green; epigynous tube 1–1.2 mm; ovary 2.9–4 mm long...48

48 Leaf blades 14 cm wide at the base; stipes 3–5 mm long, 4–5 mm in diameter; spikes 2.2–2.7 cm wide; flowers 16–17.3 mm long; petals 12.5–13.4 × 2.4–3 mm; petal appendages detaching at 3.1–4.2 mm from the petal base... *Wittmackia mesoamericana*

48* Leaf blades 5–12.7 wide at the base; stipes 6–18 mm long, 2–3 mm in diameter; spikes 1.2–2 cm wide; flowers 13.5 mm; petals 8.3–9.3 × 1.2 mm; petal appendages detaching at 1.7 mm from the petal base... *Wittmackia caymanensis*

2.4.4.2 Synopsis

Habitats: humid limestone forests in exposed or shaded areas.

Distribution area: endemic to the Cockpit Country in central Jamaica at 275-840 m elevation.

Representative specimens examined: Jamaica: Aguirre-Santoro 1812 (IJ, NY, US).

2. Wittmackia altocaririensis (Leme & L. Kollmann) Aguirre-Santoro, comb. nov. = Aechmea altocaririensis Leme & L. Kollmann, Phytotaxa 16: 6, figs. 2A-B, 3l-M. 2011.—TYPE: Brazil, Minas Gerais, proximo a divisa com a Bahia, Santa Maria do Salto, distrito de Talismã, Parque Estadual do Alto Cariri, fazenda de Flozino Teixeira, 16°23.6’ S, 40°02.24’ W, 910 m, 24 March 2010, E.M.C. Leme, 8217 (holotype, RB [web]!; isotype, HB [n.v.]).

Habitats: understory of humid montane forest.

Distribution area: Atlantic Forest in the southern state limits of Minas Gerais and Bahia in Brazil at 900 m elevation.

Representative specimens examined: Brazil: Leme 8237 (RB).


Habitats: understory of humid montane forest.

Distribution area: endemic to southeastern Bahia, Brazil at 100-400 m elevation.

Representative specimens examined: Brazil: Monteiro 479 (RB).
Notes: Wittmackia amorimii normally exhibits simple inflorescences, but some individuals in cultivation can develop short, basal branches; however, this species differs from other short-branched, paniculate species of Wittmackia by its distinctively long flowers and green sepals (vs. short flowers and orange or yellow sepals).


Habitats: understory of humid, montane forest.

Distribution area: endemic to the Atlantic Forest of Southern Bahia, near Wenceslau Guimarães, Brazil at ca. 800 m elevation.

Representative specimens examined: Brazil: Monteiro 487 (RB).


Habitats: limestone forests on karst hills.

Distribution area: Puerto Rico and probably Grand Camanoe Island (British Virgin Islands) at 0-840 m elevation.

Representative specimens examined: Puerto Rico: Aguirre-Santoro 1823 (NY, UPR).


Habitats: understory of humid montane forest.

Distribution area: endemic to the Atlantic Forest of southern Bahia in Brazil at 400–600 m elevation.

Representative specimens examined: Brazil: Monteiro 483 (RB).

Notes: Smith & Downs (1979) mentioned that the actual type locality of W. bicolor was located in Santa Catarina state, Brazil; however, this commentary was only a confusion discussed and resolved by Leme (1997), which confirmed that this is a species endemic to southern Bahia state. Most specimens of Brazilian Wittmackia with simple inflorescences are commonly misidentified in herbaria as W. bicolor. This is due to the fact that most species of Wittmackia were recently described, and that the actual diversity of this genus in Brazil still needs further study.


*Habitats*: understory of humid lowland or montane forest.

*Distribution area*: endemic to the Atlantic Forest of southeastern Bahia in Brazil at 200-700 m elevation.

*Representative specimens examined*: Brazil: Monteiro 473 (RB).


*Habitats*: humid montane forests.

*Distribution area*: endemic to the Atlantic Forest in the southeastern corner of Minas Gerais, near the state limits with Bahia and Espírito Santo, Brazil at about 300–400 m elevation.

*Representative specimens examined*: U.S.A. (cultivated plant): DeLeon s.n. (SEL).

*Habitats:* understory of humid montane forest.

*Distribution area:* endemic to the Atlantic Forest of southeastern Bahia in Brazil at 500–800 m elevation.

*Representative specimens examined:* Brazil: *Monteiro 480* (RB, NY).

*Notes:* this species is very distinctive within *Wittmackia* by its channeled leaf blades, narrowed towards the base.


*Habitats:* understory of humid montane forests.

*Distribution area:* endemic to the Atlantic Forest of southeastern Bahia in Brazil at ca. 100 m elevation.

*Representative specimens examined:* Brazil: *Monteiro 488* (RB).

*Habitats:* shaded limestone forests.

*Distribution area:* Grand Cayman (Cayman Islands) and Providencia Island (Colombia) at 0–20 m elevation.

*Representative specimens examined:* Cayman Islands: *Proctor 31031* (IJ); Colombia: *Aguirre-Santoro 1949* (COL).


≡ *Hohenbergia brittoniana* L.B. Sm., **syn. nov.**, Contr. Gray Herb. 98: 8. pl. 1, figs. 12–14. 1932.—TYPE: Jamaica, Hanover Parish, Dolphin Head and vicinity, 400 m, 18–20 March 1908, *N.L. Britton 2313* (holotype, NY!).

*Habitats:* humid limestone forests in shaded or exposed areas.

*Distribution area:* endemic to western Jamaica, near Dolphin Head mountains at 15–550 m elevation.


*Notes:* *Hohenbergia brittoniana* is synonymized here because its type specimen corresponds to a fruiting individual of *Wittmackia distans* rather than a different species with unusually long spikes. The examination of specimens of *W. distans* in the herbarium and in the
field revealed that the spikes elongate up to 1.5 times their original size in the transition from flower to fruit. Moreover, the type specimen of *H. brittoniana* was collected in the type locality of *W. distans*.


**Habitats:** forest edges or understory of humid cloud forests.

**Distribution area:** endemic to the Blue and John Crow Mountains in eastern Jamaica at 300–1250 m elevation.

**Representative specimens examined:** Jamaica: *Aguirre-Santoro 1801* (IJ, NY, US).


**Habitats:** forest edges or understory of humid cloud forests.

**Distribution area:** endemic to the Blue Mountains in eastern Jamaica at 1000–1400 m elevation.

**Representative specimens examined:** Jamaica: *Aguirre-Santoro 1803* (IJ, NY, US).
15. Wittmackia frosii (L.B. Sm.) Aguirre-Santoro, comb. nov. ≡ Aechmea frosii (L.B. Sm.)
frosii L.B. Sm., Smithsonian Misc. Collect. 126(1): 15. 1955.—TYPE: Brazil, Bahia, Colônia
Itatinga to Bom Gosto, November 1942, R. De L. Frões 19970 (holotype, NY!).

Habitats: understory of humid lowland forests.

Distribution area: endemic to the Atlantic Forest from Pernambuco to southern Bahia
states in Brazil at 0-500 m elevation.

Representative specimens examined: Brazil: Monteiro 447 (RB).

Notes: Wittmackia frosii is part of a morphologically variable species complex that also
includes W. lingulata, W. lingulatoides, and W. patentissima. The most typical individuals of W.
frosii can be recognized by their fewer inflorescence branches (ca. 5-8 vs. more than 7
branches), terminal spikes nearly as long or longer than the inflorescence rachis (vs. generally
shorter), pink to lilac sepals (vs. green to cream), longer than 6 mm (vs. 2-5 mm long), and short
sepal mucros (vs. strongly mucronate). Nevertheless, specimens exhibiting intermediate
morphology have been identified in several herbaria as W. frosii, especially those occurring
from Alagoas to Pernambuco states. It is possible that these specimens correspond to different
species; however, the characters preserved in the herbarium samples do not provide sufficient
information for their correct placement. It is necessary a more thorough study of the populations
in the field in order to take further taxonomic decisions.

16. Wittmackia gregaria (Leme & L. Kollmann) Aguirre-Santoro, comb. nov. ≡ Aechmea
gregaria Leme & L. Kollmann, Phytotaxa 177(2): 66, figs. 2, 3E-I. 2014.—TYPE: Brazil, Bahia,
Nilo Peçanha near the border with Ituberá, APA Pratigi, Faz. Barra dos Carvalhos, 13°41'49" S,
30°59'20" W (coordinates inaccurate), 8 m, 7 June 2013, E.M.C. Leme, L. Kollmann & P. Lima 8761 (holotype, RB [web]!; isotype, HB [n.v.]).

Habitats: shaded understory of Restinga forests, near coastal areas.

Distribution area: only known from the type locality on the coast of southeastern Bahia, near Ituberá and Nilo Peçanha, Brazil at 0–10 m elevation.

Conservation status: critically endangered (CR), according to Leme et al. (2014).

17. Wittmackia incompta (Leme & H. Luther) Aguirre-Santoro, comb. nov. ≡ Aechmea incompta Leme & H. Luther, Selbyana 19(2): 186, fig. 3. 1998.—TYPE: Brazil, Bahia, Porto Seguro, fl. cult., May 1994, E.M.C. Leme 904 (holotype, HB [as seen in high resolution photo]!; isotype, SEL!).

Habitats: understory of humid lowland forests.

Distribution area: endemic to the Atlantic Forest of southern Bahia in Brazil, near Porto Seguro.

Representative specimens examined: U.S.A. (cultivated plant): Luther s.n. (SEL).


Habitats: humid limestone forests in shaded or exposed areas.

Distribution area: endemic to the Cockpit Country in central Jamaica at 100-670 m elevation.
Representative specimens examined: Jamaica: Aguirre-Santoro 1808 (IJ, NY).


*Habitats:* shaded understory of Restinga forests, near coastal areas

*Distribution area:* endemic to Restinga on the coast of southeastern Bahia, near Ituberá and Nilo Peçanha, Brazil at 0–10 m elevation.

*Representative specimens examined:* Brazil: Wendt 458 (RFA).

20. **Wittmackia jamaicana** (L.B. Sm. & Proctor) Aguirre-Santoro, **comb. nov.** ≡ *Hohenbergia jamaicana* L.B. Sm. & Proctor, Phytologia 7: 251, tab. 1, figs. 3-4. 1960.—TYPE: Jamaica, St. James Parish, 1.5 miles N of Catadupa, 381 m, 5 April 1952, G.R. Proctor 6543 (holotype, IJ!; isotype, US [fragment]!).

*Habitats:* shaded and humid limestone forests.

*Distribution area:* endemic to the Cockpit Country in central Jamaica at 300 m elevation.

*Representative specimens examined:* Jamaica: Aguirre-Santoro 1810 (IJ, NY).

21. **Wittmackia laesslei** (L.B. Sm.) Aguirre-Santoro, **comb. nov.** ≡ *Hohenbergia laesslei* L.B. Sm., Bull. Bromeliad Soc. 6: 52, fig. 1956.—TYPE: Jamaica, St. James Parish, Cockpit Country near Sweet Water, 570 m, 16 August 1952, *A. Laessle s.n.* (holotype, IJ!; isotype, US [fragment]!).
Habitats: humid limestone forests in shaded or exposed areas.

Distribution area: endemic to the Cockpit Country in central Jamaica at 550-750 m elevation.

Representative specimens examined: Jamaica: Aguirre-Santoro 1809 (IJ, NY, US).


Habitats: understory of humid montane forests.

Distribution area: endemic to the Atlantic Forest of southeastern Bahia, near Ibicuí and Nova Canaã, Brazil at 500–600 m elevation.


Habitats: understory of marshy lowland forest.

Distribution area: only known from the type locality in the Atlantic Forest of southeastern Bahia, near Ituberá, Brazil at 0-50 m elevation.


1955.—LECTOTYPE: Plate 170 of the Boerhaave set of Plumier illustrations at the library of Rijksuniversiteit, Groningen, designated by Cedeño-Maldonado (in Acevedo-Rodríguez & Strong (2005)).


= Lamprococcus ramosus Beer, Fam. Brom. 106. 1856. = Aechmea surinamensis Van Houtte Hortus ex Beer, Bromel. 106. 1857 [nom. nud.].—TYPE: No location, no date, C. Plumier s.n. (holotype, P [n.v.]).


Habitats: Shaded or open areas of dry coastal forest.

Distribution area: Bahamas, Lesser Antilles, Caribbean coast of Mexico and Panama, and Atlantic coast of South America from Venezuela to Pará state in Brazil.

Representative specimens examined: Tortola (British Virgin Islands): D’Arcy 819 (GH); Saint-Martin: Howard 20735 (GH); Antigua: Smith 10474 (GH); Dominica: Ernst 1568 (GH); Martinique: Howard 11733 (GH); St. Lucia: Slane 566 (GH); St. Vincent: Morton 4732 (GH); The Grenadines: Howard 10851 (GH); Trinidad and Tobago: Britton 1962 (GH); Panama: DeLeon s.n. (SEL); Venezuela: Johnston 293 (GH); Guyana: Hitchcock 17631 (GH); Brazil: Pires 50294 (NY).
Notes: *Wittmackia lingulata* is the first described species of the morphologically variable species complex that also includes *W. froesii, W. lingulatoides*, and *W. patentissima*. The most typical individuals of *W. lingulata* can be recognized by their fewer and ascending inflorescence branches (vs. many branches generally divaricate to reclined), floral bract mucros longer than their laminar bases (vs. shorter to equaling), and pink-tipped petals (vs. white). Like in *W. froesii*, the ovaries are ovoid, as opposed to cylindrical-clavate in the other two species. The specimens occurring in the Caribbean and northern South America always exhibit these characteristic morphology; however, there are many individuals from south of Ceará state in Brazil exhibiting intermediate phenotypes that require further study.

25. *Wittmackia lingulatoides* (Leme & H. Luther) Aguirre-Santoro, **comb. nov.** = *Aechmea lingulatoides* Leme & H. Luther, Selbyana 19(2): 187. 1998.—TYPE: Brazil, Bahia, without exact locality from caatinga vegetation, originally collected by Roberto Burle Marx s.n., fl. cult., E.M.C. Leme, s.n. (holotype, HB [as seen in high resolution photo]!; isotype, SEL!).

*Habitats*: cliffs or understory of dry forests in Caatinga and Campos Rupestres.

*Distribution area*: endemic to eastern Brazil from Ceará to Bahia at 0-900 m elevation.

*Representative specimens examined*: Brazil: Monteiro 495 (RB, NY).

*Notes*: this species also belongs to the morphologically variable species complex that includes *W. froesii, W. lingulata*, and *W. patentissima*. Although several individuals are difficult to differentiate from large specimens of *W. patentissima*, *W. lingulatoides* can be recognized by its rupicolous habit (vs. generally epiphytic), presence of stolons (vs. absence), stout and black teeth on the blade margins (vs. generally slender and green), and generally longer, suberect to ascending spikes (vs. shorter and divaricate to reclined spikes).

*Habitats*: understory of humid montane forests.

*Distribution area*: endemic to the Atlantic Forest of southeastern Bahia in Brazil at 100-750 m elevation.

*Representative specimens examined*: Brazil: Monteiro 478 (RB).

27. **Wittmackia maranguapensis** (Leme & Scharf) Aguirre-Santoro, **comb. nov.** ≡ *Aechmea maranguapensis* Leme & Scharf, Bromelie 2011(2): 59, figs. 2011.—TYPE: Brazil, Ceará, Maranguape, Serra de Maranguape, 500 m, 3 August 1997, *E.M.C. Leme, J.M. Braga 3914* (holotype, RB [web]!).

*Habitats*: understory of humid, montane, secondary forests.

*Distribution area*: endemic to areas of fragmented Atlantic Forest in Serra de Maranguape, Ceará, Brazil at 500 m elevation.

*Representative specimens examined*: Brazil: Martinelli 15071 (RB).

carretera federal 307 Reforma Agraria-Puerto Juárez, tramo Tulum - Playa del Carmen, 0 m, 20°32'3''N, 87°9'50''W, 10 March 2008, *W. Cetzal Ix* 20 (holotype, CICY [web]!; isotype, MO!).

*Habitats:* shaded and humid limestone forests.

*Distribution area:* only known from the type locality on the coast of the Yucatan peninsula in Mexico at 0-10 m elevation.

*Representative specimens examined:* Mexico: Ramirez 1666 (SEL).

*Conservation status:* critically endangered (CR), according to (2010).


*Habitats:* forests or open areas on limestone formations.

*Distribution area:* endemic to western Jamaica at 0-50 m elevation.

*Representative specimens examined:* Jamaica: Proctor 11109 (IJ).


*Habitats:* understory of humid, montane, primary forest.

*Distribution area:* only known from the type locality in the Atlantic Forest of southeastern Bahia, near Wenceslau Guimarães, Brazil at about 800 m elevation.


**TYPE:** Brazil, Bahia, Almada, no date. *C.F.P. Von Martius s.n.* (holotype, M [web]!).


**Habitats:** shaded to open forested areas.

**Distribution area:** endemic to the Atlantic Forest in eastern Brazil from Ceará to Rio de Janeiro at 50-900 m elevation.

**Representative specimens examined:** Brazil: Monterio 459 (RB)

**Notes:** this species is part of the morphologically variable species complex that also includes *W. froesii*, *W. lingulata*, and *W. lingulatoides*. In general, it can be recognized by its cylindrical-clavate ovaries and very short sepals. These two characters are also typical for *W. lingulatoides*; however, *W. patentissima* roughly differs from the latter by its epiphytic habit (vs. rupicolous), cespitose disposition (vs. stoloniferous), slender and green teeth on the blade margins (vs. generally stout and black), and generally shorter, divaricate to reclined spikes (vs. longer and suberect to ascending spikes). There are also several specimens with intermediate phenotypes between *W. lingulata* and *W. patentissima* that require further study.


*Habitats*: shaded and humid limestone forests to cloud forests in mountainous regions.

*Distribution area*: Cuba and Jamaica at 0–1200 m elevation.

*Representative specimens examined*: Cuba: *Britton 5823* (NY); Jamaica: *Aguirre-Santoro 1802* (JJ, NY).


*Habitats*: understory of humid lowland forests.

*Distribution area*: endemic to the Atlantic Forest of southeastern Bahia in Brazil at 200–300 m elevation.
34. **Wittmackia pernambucentris** (J.A. Siqueira & Leme) Aguirre-Santoro, **comb. nov.** $\equiv$

*Aechmea pernambucentris* J.A. Siqueira & Leme, Fragm. Atlantic Forest N. E. Brazil 227, figs. 2007.—TYPE: Brazil, Pernambuco, Taquaritinga do Norte, subida para a Torre de Microondas da TV Pernambuco, 1060 m, 7°54′13″S, 36°2′30″W, 21 September 1998, *G.S. Baracho, J.A. Siqueira-Filho* 761/838 (holotype, UFP [as seen in high resolution photo]!).

*Habitats:* montane humid forests of medium-high altitude known as "Brejos de altitude."

*Distribution area:* endemic to fragments of Atlantic Forests in Ceará, Pernambuco, and Alagoas, Brazil at about 1000 m elevation.

35. **Wittmackia polycephala** (Baker) Aguirre-Santoro, **comb. nov.** $\equiv$ *Aechmea polycephala* Baker, J. Bot. 17: 164. 1879. $\equiv$ *Hohenbergia polycephala* (Baker) Mez, Monogr. Phan. 9: 133. 1896.—TYPE: Jamaica, no locality, no date, *Wright s.n.* (holotype, BM!).


$\equiv$ *Hohenbergia gnetacea* Mez, **syn. nov.** Fl. Bras. 3(3): 272, t. 60, fig. 1. 1891.—TYPE: no locality, no date, *Morren Hortus s.n.* (holotype, G [as seen in high resolution photo]!).

*Habitats:* shaded and humid limestone forests to cloud forests in mountainous regions.

*Distribution area:* endemic to Jamaica, distributed across the island at 70–1000 m elevation.

Notes: *Hohenbergia gnetacea* is synonymized here into *Wittmackia polycephala* because the type of the former exhibits the following diagnostic characters for *W. polycephala*: sessile, subglobose spikes surpassed by the primary bracts, and floral bracts covered with brown-tomentose-lepidote indument. Smith (1960) had already suggested that the type specimen of *H. gnetacea* was doubtfully different from *W. polycephala* but did not propose its synonymy because this specimen lacks leaves, the inflorescence is exceptionally lax, and does not have locality information. The study of intraspecific variation in *W. polycephala* in the present work revealed that lax inflorescences are common in *W. polycephala*, thus discarding this character as diagnostic for *H. gnetacea*. Moreover, the leaf architecture among the species of Caribbean *Wittmackia* is rarely used to differentiate species within the group; for this reason, it is safe to suggest that the lack of this character may not have a large impact in the proposal of the present synonymy. Although it is impossible to know the original locality of the type specimen of *H. gnetacea*, its strobiliform spikes and unappendaged ovules allow its placement within Caribbean *Wittmackia*.

36. *Wittmackia portoricensis* (Mez) Aguirre-Santoro, **comb. nov.** = *Hohenbergia portoricensis* Mez, Monogr. Phan. 9: 136. 1896.—**TYPE:** Puerto Rico, Naguabo, Sierra de Naguabo, ad arbor. in sylv. prim. montis Piedra pelada, 26 April 1885, *P. Sintenis 1321* (holotype, B!).

= *Hohenbergia attenuata* Britton, Sci. Surv. Porto Rico & Virgin Islands 5: 134. 1923.—**TYPE:** Puerto Rico, Naguabo, Sierra de Naguabo, Río Icaco and adjacent hills, 465–720 m, 30 July to 5 August 1914, *J.A. Shafer 3567* (holotype, NY!, isotype, GH [fragment; web]!).

**Habitats:** understory and edges of humid forests.
Distribution area: endemic to Puerto Rico, distributed across the island at 200-970 m elevation.

Representative specimens examined: Puerto Rico: Aguirre-Santoro 1817 (NY, UPR).


Habitats: understory of humid montane forests.

Distribution area: endemic to the Atlantic Forest of southeastern Bahia in Brazil at 200-700 m elevation.

Representative specimens examined: Brazil: Fiaschi 1764 (NY).

38. *Wittmackia spinulosa* (Mez) Aguirre-Santoro, **comb. nov.** ≡ *Hohenbergia spinulosa* Mez, Symb. Antill. 2(2): 253. 1900.—TYPE: Jamaica, Manchester Parish, New Green, 610 m, 30 April 1896, W.H. Harris 6433 (holotype, B!).

Habitats: shaded and humid limestone forests.

Distribution area: endemic to southwestern and central Jamaica at 100-975 m elevation.

Representative specimens examined: Jamaica: Aguirre-Santoro 1805 (IJ, NY, US).

39. *Wittmackia sulbahianensis* (Leme, Amorim & J.A. Siqueira) Aguirre-Santoro, **comb. nov.** ≡ *Aechmea sulbahianensis* Leme, Amorim & J.A. Siqueira, Fragm. Atlantic Forest N. E. Brazil 392, fig. 2007.—TYPE: Brazil, Bahia, Uruçuca (Água Preta), road from Uruçuca to Serra
Grande, secondary road on the right to Fazenda São José, 130 m, 14°31'19.3 S, 39°9'23.7 W, 22 September 2005, E.M.C. Leme, J.L. Paixão 6720 (holotype, HB [as seen in high resolution photo]!; isotype, CEPEC!).

_Habitats_: lowland to montane humid forests, rarely in open areas.

_Distribution area_: endemic to the Atlantic Forest of southeastern Bahia to northern Espirito Santo states in Brazil at 0–600 m elevation.

_Representative specimens examined_: Brazil: Monteiro 470 (RB).

### 40. *Wittmackia tentaculifera* (Leme, Amorim & J.A. Siqueira) Aguirre-Santoro, **comb. nov.** ≡ *Aechmea tentaculifera* Leme, Amorim & J.A. Siqueira, Fragm. Atlantic Forest N. E. Brazil 391 fig. 2007.—_TYPE_: Brazil, Bahia, Camacã, RPPN Serra Bonita, 9.6km NNW of Camacã on road to Jacareci and Jussari, then 6km up road to Serra Bonita, 820 m, 15°23'29 S, 39°33'55 W, 21 September 2004, W.W. Thomas, A.M. Amorim, J.L. Paixão & S. Sant'Ana 14218 (holotype, CEPEC!; isotype, NY!).

_Habitats_: understory or canopy of humid montane forests.

_Distribution area_: endemic to the Atlantic Forest of southeastern Bahia in Brazil at 700–1000 m elevation. Only known from two localities: Serra Bonita and Serra de Jacareci, near Camacã and Santa Terezinha, respectively.

_Representative specimens examined_: Brazil: Monteiro 463 (RB).

_Notes_: this species is very distinctive within *Wittmackia* by its long branches and bright red rachis, ovaries and sepals.
41. Wittmackia turbinocalyx (Mez) Aguirre-Santoro, **comb. nov.** = Aechmea turbinocalyx Mez, Fl. Bras. 3(3): 359. 1892. = Macrochordion turbinocalyx (Mez) L.B. Sm. & W.J. Kress, Phytologia 66(1): 77. 1989.—TYPE: Brazil, Bahia, no date, Blanchet s.n. (holotype, G [n.v.]).

= Streptocalyx curranii L.B. Sm. Contr. Gray Herb. 95: 44. 1931. **syn. nov.** = Aechmea curranii (L.B. Sm.) L.B. Sm. & M.A. Spencer, Phytologia 72(2): 97. 1992.—TYPE: Brazil, Bahia, Rio Gongogi, 100–500 m, 30 November to 01 October 1915, H.M. Curran 143 (holotype, US [web]).

*Habitats:* understory of humid forests.

*Distribution area:* endemic to the Atlantic Forest of southeastern Bahia and Minas Gerais in Brazil at 50-700 m elevation.

*Representative specimens examined:* Brazil: Monteiro 449 (RB).

*Notes:* This species is distinguished within *Wittmackia* by its turbinate calyx. Faria & Wendt (2004) discussed how *Aechmea curranii* is hard to separate from *W. turbinocalyx* by showing the morphological overlapping between their type specimens and several specimens collected in southeastern Bahia. They emphasized that there are many intermediate individuals exhibiting entire and serrate leaves and simple to 1-divided inflorescences bearing 1 to 7 branches, characters considered diagnostic to separate the species. The only definite character that can help separate *W. turbinocalyx* from *A. curranii* would be the presence or absence of petal appendages; however, it is unknown if the type of *W. turbinocalyx* exhibit these structures. Given the lack of unambiguous diagnostic characters to separate these species and their overlapping geographic distribution, *A. curranii* is here synonymized into *W. turbinocalyx.*

≡ *Hohenbergia proctorii* L.B. Sm., Phytologia 7: 252, tab. 1, fig. 5, 6. 1960. **syn. nov.** —

TYPE: Jamaica, St. Elizabeth Parish, 1 mile north of Four Paths, along road to Ginger Hill, 229 m, 6 April 1952, *G.R. Proctor 6567* (holotype, US!; isotype, IJ!).

_Habitats:_ humid limestone forests in shaded or open areas.

_Distribution area:_ endemic to central Jamaica at 100–950 m elevation.

_Representative specimens examined:_ Jamaica: *Aguirre-Santoro 1804* (IJ, NY, US).

_Notes:_ *Hohenbergia proctorii* is synonymized here to *W. urbaniana* based on the remarkable similarity of its type collection with fructifying individuals of *W. urbaniana* and the overlap in the diagnostic characters of these two species. The main diagnostic character used to separate *H. proctorii* from *W. urbaniana* is the acuminate and inconspicuous wing of the posterior sepals in the former (vs. obtuse); however, this ambiguous character was found to be variable in flowering and fructifying specimens of *W. urbaniana*, and it is not particularly distinctive in the type of *H. proctorii*. Another justification for this synonymization is that the type locality of *H. proctorii* overlaps with the distribution range of *W. urbaniana*.


_Habitats:_ understory of humid montane forests.
Distribution area: endemic to the Atlantic Forest of southeastern Bahia in Brazil at 400–600 m elevation.

Representative specimens examined: Brazil: Monteiro 464 (RB)

44. *Wittmackia sp. nov. aff negrilensis*

Habitats: shaded and humid limestone forests.

Distribution area: endemic to western Jamaica, near Dolphin Head mountains at 20-370 m elevation.

Representative specimens examined: Aguirre-Santoro 1813 (IJ, NY, US).

Notes: robust plant similar to *W. negrilensis* but exhibiting longer stipes and longer floral mucros. This species is awaiting publication.
Chapter 3

3 Taxonomic revision of the Caribbean-endemic species of

Wittmackia (Bromeliaceae)³

3.1 Abstract

A taxonomic revision of the seventeen Caribbean-endemic species of Wittmackia (Bromeliaceae) is presented. This group is a monophyletic lineage previously circumscribed as Hohenbergia subgenus Wittmackiopsis but later transferred to Wittmackia based on phylogenetic and morphological evidence. This taxonomic treatment includes a complete overview of the morphological variation of the species, their geographical distribution and habitat, and notes on their ecology and conservation. A taxonomic key for the identification of the species is provided. Finally, complete descriptions with comments on the taxonomy, geographic distribution and habitat of the species are presented.

3.2 Introduction

The genus Wittmackia Mez (1891: 274) (Bromeliaceae, Bromelioideae) was recently resurrected and recircumscribed by Aguirre-Santoro (in preparation; see chapter 2) based on phylogenetic and morphological evidence. This genus is characterized for its relatively small flowers, corolla tubes apically spreading, white (occasionally green or light purple) petals, and unappendaged ovules (Aguirre-Santoro in preparation; see chapter 1). Wittmackia includes 44

³ Manuscript follows the guidelines of Phytotaxa.
species, 17 of which form a robust monophyletic clade composed by species endemic to the Caribbean (Aguirre-Santoro in preparation; see chapter 1). This Caribbean Clade of *Wittmackia* (Bromeliaceae) includes all the species formerly placed in *Hohenbergia* subgenus *Wittmackiopsis* and it is the subject of the present taxonomic revision.

*Hohenbergia* subgenus *Wittmackiopsis* was first proposed by Mez (1896) as a placeholder for the seven Caribbean-endemic species of *Hohenbergia* Schult. f. in Schultes & Schultes (1830: LXXI), and to separate them from their congeneric South American relatives. Mez (1896) justified the separation of *Hohenbergia* subgenus *Wittmackiopsis* from other *Hohenbergia* based on the lack of independent foliar schlerenchyma fascicles and the presence of unappendaged ovules in the former. These diagnostic characters, however, were not sufficient in his view to propose a new genus because the presence of strobiliform spikes and lack of petal appendages were considered as unambiguous diagnostic characters for *Hohenbergia*. This taxonomic revision was later updated by Mez (1934), who maintained the circumscription of *Hohenbergia* subgenus *Wittmackiopsis* and increased the number of species from seven to 13. Smith (1960) published a synopsis of *Hohenbergia* subgenus *Wittmackiopsis* in order to add six recently described species from Jamaica and the Cayman Islands, and highlight the taxonomic affinities among the species already described in the group. Since the publication of this study, the taxonomy of the group has been revisited two additional times, first by Read (1972), which provided a synopsis of *Hohenbergia* subgenus *Wittmackiopsis* in its main center of diversity: Jamaica; and second by Smith & Downs (1979), which presented the most comprehensive revision of the group to date. These contributions established the current knowledge of *Hohenbergia* subgenus *Wittmackiopsis*, although they did not add major taxonomic changes or new taxa to the group. After the revision of Smith & Downs (1979) the taxonomy of the group
has only been partially revised for Puerto Rican species by Cedeño-Maldonado in Acevedo-Rodríguez & Strong (2005) or mentioned in floristic treatments and taxonomic publications (e.g. Ramírez-Morillo et al. 2010; Acevedo-Rodríguez and Strong 2012).

Although recent advances in phylogenetics pointed out the widespread taxonomic problems in Bromeliaceae (Faria et al. 2004; Schulte et al. 2009; Sass and Specht 2010), they also provided a framework from which the taxonomy of several groups can be revisited. This is important for groups that require urgent study because of their potential to understand conservation and evolutionary issues. In this context, the present taxonomic revision of Caribbean Wittmackia is based on the results of Aguirre-Santoro (in preparation; see chapter 1) and Aguirre-Santoro (in preparation; see chapter 2), which proposed that Hohenbergia subgenus Wittmackiopsis is in reality a monophyletic lineage nested within the genus Wittmackia rather than a group related to other species of Hohenbergia. This complete update on the taxonomic, morphological, and geographical knowledge of the group provides valuable information that can be used by systematists, evolutionary biologists, and conservationists interested in understanding the diversity of this Caribbean-endemic lineage. Compared to the last taxonomic revision of Hohenbergia subgenus Wittmackiopsis by Smith & Downs (1979), the present study is a significant update because 1) the placement of the species in Wittmackia and their phylogenetic relationships are considered; 2) it includes a better understanding of the intraspecific morphological variation in the group because of the examination of more than twice the number of specimens and the study of the species in the field; 3) it presents recent taxonomic novelties and more detailed morphological information for the identification of the species; and 4) it contains a more detailed overview of the geographic distribution and habitat of the species.
3.3 Materials and Methods

Fieldwork was conducted in Jamaica, Puerto Rico and Providencia Island in Colombia between 2012 and 2014. During these expeditions 15 out of the 17 species of Caribbean *Wittmackia* were observed in their natural habitat, photographed, collected, and preserved for further study. Flowers and fruits were preserved in ethanol 70% and deposited in the spirit collection of the New York Botanical Garden. Additional geographical, ecological and morphological information for the descriptions was taken from the examination of a total of 318 collections from the herbaria B, BM, CAYM, CICY, COL, F, FTG, G, GH, HAJB, IJ, K, LE, MICH, MO, NY, P, S, SEL, UCSI, UPR, and US (abbreviations follow Thiers (2015)). The concept used here to delimit each species follows the phylogenetic species concept of Nixon & Wheeler (1990), which states that species are “the smallest aggregation of populations (...) diagnosable by a unique combination of character states in comparable individuals.”

Large structures such as leaves, inflorescences and branches were measured with a standard metric ruler, whereas smaller structures such as floral bracts and floral parts were measured using a *Bausch & Lomb SteroZomm*-4 stereoscope with a calibrated scale. When possible, all structures were measured from all available specimens; however, petals, stamens, styles, and ovaries were only measured from liquid collections or rehydrated flowers from one to three representative specimens per species. All morphological descriptions follow the same format and are parallel to each other. Most terminology is conserved from Smith & Downs (1979); however, the term “teeth” was used instead of “spine” to refer to the serration of the blades; “peduncle” was used instead of “scape” for the stalk that supports the fertile part of the inflorescence; and “1-divided” and “2-divided” were used instead of “pinnate” and “bipinnate”
to indicate the degree of ramification of the inflorescence. This change in terminology reflects the trend of recent taxonomic treatments in Bromeliaceae to be more consistent with the general botanical lexicon. The measurements of length and width of laminar structures do not include spinescent projections like mucros or teeth; these structures were measured separately. Samples for scanning electronic microscopy were dried using the HMDS method (Chissoe et al. 1994), mounted on aluminum stubs, coated for 2–3 min with gold-palladium in a Hummer 6.2 sputter coater (Anatech, Springfield, VA), and examined and photographed in a Jeol JSM-5410 LV scanning electron microscope operated at 10 kV. Images from liquid samples were generated in a Nikon SMZ1500 stereoscope connected to a Nikon DS-U3 digital camera.

3.4 Results

3.4.1 Morphology

_Habit and general plant structure._ All the species of the Caribbean _Wittmackia_ are facultative epiphytes, growing on the basal branches of robust trees; sometimes they grow in terrestrial and rupicolous habitats when the availability of robust trees to support them is scarce. All the species form small to large populations in the understory or forest edges, where the individuals grow near each other or form cespitose clumps of clonal plants. Some exceptions include _W. abbreviata, W. fawcettii, W. penduliflora_ and _W. polycephala_, which have been occasionally observed as solitary plants in open areas. All the species are acaulescent and range from 0.5 to 1.5 m tall, including the inflorescence. The leaf sheaths loosely overlap in order to form a broad tank rosette, where water and debris accumulate; this tank-forming arrangement of the rosette is also known as phytotelmata (Benzing 2000). Species such as _W. antillana, W._
penduliflora, *W. negrilensis*, *Wittmackia rohan-estyi*, and *W. urbaniana* exhibit the largest rosettes, whereas *W. portoricensis* has the smallest ones.

*Leaves*. The leaves in the species of Caribbean *Wittmackia* are clearly differentiated in two parts: sheath and blade. The sheaths are always broader than blades, oblong to elliptical, and non-photosynthetic in the most part, which gives them their characteristic white, pale brown or dark castaneous colors. The sheaths are determinant structures for water and nutrient absorption of the plants; their shape and size determine the capacity of rosettes to form phytotelmata while their dense aggregation of absorptive lepidote scales on both surfaces allows them to efficiently capture water and nutrients. *Wittmackia portoricensis* and *W. abbreviata* have the smallest sheaths, whereas *W. antillana* and *W. negrilensis* have the largest ones. Most species exhibit small teeth (0.5–1 mm) on the margins of the distal part of the sheaths; however, it is common to find entire margins within the same species.

Blades are always lingulate and strongly coriaceous; in some cases, like in *Wittmackia antillana* and *W. negrilensis*, the blades are almost succulent. Species such as *W. antillana* and *W. inermis* exhibit the largest blades (up to 120 cm long), whereas *W. abbreviata*, *W. portoricensis* and *W. spinulosa* have the smallest ones (from 39 cm long). The blade width is variable, although the very narrow blade of *W. portoricensis* can be used as a good diagnostic character for this species (2.5–4.5 cm wide). In all species the blades are green, but in *W. caymanensis*, *W. jamaicensis* and *Wittmackia rohan-estyi* it is common to find maculate blades with irregular areas of darker green. The adaxial surface is normally glabrescent, although some species exhibit sparse lepidote scales. The abaxial surface is densely covered with white-lepidote absorptive scales; in *W. eriostachya*, *W. polycephala* and *W. portoricensis* these scales are abundant and give the abaxial surface of the blade a green-cinereous color. All species have
serrate leaves; however, specimens with entire blades have been collected in *W. abbreviata*, *W. inermis* and *W. jamaicana*. The teeth range from 0.2 to 3 mm long and are erect to antorose; only *W. caymanensis* occasionally exhibits retrorse teeth. All the species have obtuse, round or retuse apices ended in a stout mucro; however, rosettes exhibiting both acuminate and round leaf apices are common in *W. mesoamericana* and *W. portoricensis*.

*Inflorescence.* All the species of Caribbean *Wittmackia* are monocarpic, meaning that the inflorescences are produced in the center of the rosette only once during the life of the plant. In anthesis, most species have erect to inclined inflorescences; however, inflorescences are always pendulous in *W. abbreviata*, *W. distans* and *W. portoricensis*. In many cases, the inflorescences turn pendulous when the plants grow in an inclined position, are obstructed by other plants, or when the inflorescences reach their senescence and can no longer remain erect. All species exhibit a long peduncle, which is the sterile portion of the primary inflorescence axis that holds the fertile portion of the inflorescence (also called scape in the earlier taxonomic literature of Bromeliaceae). Species such as *W. jamaicana* and *Wittmackia rohan-estyi* have robust peduncles with diameters up to 14 mm, whereas species such as *W. portoricensis* exhibit a slender peduncle of only 2.5–6 mm in diameter. The peduncle is green to dull-purple and covered with floccose indument. This indument consists of an irregular aggregation of tufts formed by detached absorptive scales. This indument is lost in many species during the senescence of the inflorescence. Marcescent bracts of variable in size and shape protect the peduncle. These bracts are normally erect and longer than their internodes; however, bracts shorter than their internodes have been observed in *W. abbreviata*, *W. distans*, *W. fawcettii*, *W. inermis*, *W. laesslei* and *W. penduliflora*. The bracts of the peduncle are green, light green, or cream, rarely dull-purple, and exhibit acuminate to attenuate apices. Their margins can be entire or serrate, a character that is
intraspécifically variable in species such as *W. jamaicana*, *Wittmackia rohan-estyi*, *W. spinulosa*, *W. negrilensis* and *W. penduliflora* but can be diagnostic for the other species in the group.

The fertile portion of the inflorescence is a conical to subcylindrical panicle, normally 1-divided, although specimens with 2-divided panicles have been collected for *W. caymanensis*, *W. fawcettii*, *W. jamaicana*, *W. inermis*, *W. penduliflora* and *Wittmackia rohan-estyi*. The panicles of *W. antillana* and *W. urbaniana* produce the lowest number of first-level branches (as few as 6 branches) whereas *Wittmackia rohan-estyi* produces up to 83 first-level branches per panicle. These branches are polystichously oriented and separated from each other along the rachis of the inflorescence about 1–3 cm; several specimens of *W. polycephala* and *W. spinulosa* exhibit an exceptionally dense aggregation of branches along the rachis. The inflorescence rachis is straight but some specimens of *W. portoricensis* exhibit a slightly flexuous rachis. The rachis is also white-floccose in most species but glabrous in *W. jamaicana*.

**Primary bracts.** The primary bracts always subtend the first-level branches of the inflorescence. These bracts can be shorter or much longer than the branches. This is a very useful character to separate several species of Caribbean *Wittmackia* such as *W. abbreviata*, *W. eriostachya* and *W. negrilensis*, among others; however, this character is intraspecifically variable in species such as *W. penduliflora*, *W. portoricensis* and *W. urbaniana*. The primary bracts are oriented 45° to 145° with respect to the inflorescence rachis and gradually diminish in size towards the apex of the inflorescence. The basal primary bracts are linear to lanceolate. They can be as short as 2.5 cm in *W. polycephala* and *W. eriostachya* and reach longitudes up to 16 cm in *W. mesoamericana*, *W. negrilensis* and *Wittmackia rohan-estyi*. All bracts are marcescent; cream, green, pale brown, rarely dull-purple; and floccose on both surfaces or only abaxially. The margins can be entire or serrulate, a character useful to recognize species such as
W. antillana, W. caymanensis and W. portoricensis, although intraspecifically variable in other species. The apices of the primary bracts are always attenuate to acuminate.

Branches. The branches of the inflorescence are composed of two parts: stipe and spike. Stipe is defined here as the sterile portion of the primary branch and spike as the undivided, fertile portion of the branch that bears the floral bracts and flowers. Spikes that resulted from a secondary ramification are always sessile. The stipe is highly variable and very characteristic of the Caribbean Wittmackia. In fact, the length of the stipes in relation to the spikes has long been considered as a definitive character to separate species of Caribbean Wittmackia (Mez 1934; Smith 1960; Read 1972; Smith and Downs 1979). They range from 0 mm long in W. polycephala to 133 mm long in W. distans and always exceed the spike length in W. abbreviata, W. distans and W. laesslei. The stipe length is highly variable within species and should be used as diagnostic only in combination with other characters. Moreover, it is possible that stipes keep elongating in the transition from flower to fruit. Spikes are globose, ovoidal or cylindrical, and frequently elongate twice its length in the transition from flower to fruit, like in W. distans, W. eriostachya, Wittmackia rohan-estyi and W. urbaniana. Spikes range from 0.9 cm long in W. polycephala to 17 cm long in W. urbaniana. The latter also has the widest spikes among the species of Caribbean Wittmackia. The spike rachis is always concealed because of the dense imbrication of flowers and floral bracts in the spikes.

Floral bracts. Floral bracts are always imbricate and polystichously distributed along the spike. In most species, they form an angle from 30º to 45º with the spike rachis. Exceptions to this case are W. inermis and W. urbaniana, which have floral bracts tightly appressed to the rachis in anthesis but gradually diverging from the rachis in fruit. Floral bracts are always concave and vary in their level of concavity. The most concave floral bracts can be found in W.
eriochanta, and *W. polycephala*, whereas the flattest are present in *W. caymanensis*. Floral bracts partially cover the flowers; however, they can enlarge to completely cover the flowers, permitting only the exposure of the corolla, as in *W. urbaniana*. Previous taxonomic revisions considered this relative size of the floral bracts compared to floral parts as an important diagnostic character to recognize species such as *W. eriochanta*, *W. fawcetii*, *W. jamaicana* and *W. polycephala*. Although they were correct in many cases, species like *W. eriochanta* and *W. polycephala* are highly variable for this character. The smallest floral bracts can be found in *Wittmackia rohan-estyi* and *W. spinulosa* (from 3.2 mm long), whereas *W. antillana* and *W. urbaniana* exhibit the largest ones (up to 26 mm long). Floral bracts are orbicular to ovate; green, cream, yellow, orange, or pale brown; and glabrous, white-lepidote floccose, or brown-tomentose-lepidote, the latter only present in *W. eriochanta* and *W. polycephala*. Most species exhibit floral bracts with entire margins but species like *W. antillana* and *W. caymanensis*, among others, have minutely serrulate margins. In many cases this serrulation can only be observed with a stereoscope. The apices of the floral bracts vary from acuminate to truncate and have been frequently used as diagnostic characters. Species that typically exhibit acuminate to acute apices include *W. caymanensis*, *W. mesoamericana* and *W. portoricensis*, among others, whereas species with round to truncate apices are represented by *W. eriochanta*, *W. fawcetii* and *W. polycephala*. Species like *W. distans*, *W. jamaicana* and *W. urbaniana* show both acute to round floral bract apices, adding ambiguity to the diagnostic power of this character. Finally, the floral bracts of all species exhibit an apical mucro of variable size, a structure probably useful for protection against undesired floral visitors. The smallest mucros are found in *W. fawcetii* (from 0.2 mm long), whereas *W. portoricensis* and *W. spinulosa* have the longest mucros (up to 8.8 mm long).
**Flowers.** The flowers in all the species of Caribbean *Wittmackia* are always polystichous and densely distributed along the spike. This disposition of the flowers gives the spikes a strobililate appearance, a character until now used to justify the placement of the species in the genus *Hohenbergia*. However, recent phylogenetic analyses suggested that strobililate spikes appeared multiple times during the evolution of Bromelioideae and do not longer support the diagnosis of *Hohenbergia* (Faria et al. 2004; Sass and Specht 2010). The flowers form an angle with the spike rachis from 10º in *W. urbaniana* to 45º in *W. caymanensis* and *Wittmackia rohan-estyi*. The number of flowers ranges from eight in *W. polycephala* to 70 in *W. urbaniana* and *W. negrilensis*. All species have sessile flowers.

**Calyx.** The aestivation of the sepals of the Caribbean species of *Wittmackia* is contorted. The calyx is dorsiventrally compressed, where the two posterior sepals develop a keel and the anterior sepal remains ecarinate. The degree of calyx compression is variable among the species and permits the dense imbrication of the flowers in the spike. The least compressed calyx can be observed in *W. abbreviata* and *W. distans* whereas and the most compressed one is present in *W. eriostachya*, *W. polycephala* and *W. urbaniana*. The more compressed the calyx, the more pronounced the posterior sepal keels. The sepals of all species are basally connate, strongly coriaceous, triangular, and asymmetrical. The asymmetry is defined by the wing-like prolongation of the overlapping side of the sepal. The sepal wing is variable in width across all the species and its widest part can be located either in the middle of the sepal like in *W. urbaniana* or towards the apical region like in *W. distans*. Sepals can be green, yellow or cream, and glabrous to sparsely floccose. The margins are normally entire, although some specimens of *W. antillana* have minutely serrulate sepals. The apex is acute and ends in a short to very
prolonged mucro. The size of the sepal mucro is useful to recognize species such as *W. fawcettii* or *W. spinulosa*.

**Corolla.** The corolla of all species forms a tube of variable length, spreading at the apex of the corolla. The basal portion of the corolla tube is tightly covered by the calyx. The distal part of the corolla tube extends several millimeters beyond the calyx, conserving its diameter throughout its length. The petals are free, membranaceous, oblong to subspatulate, glabrous, and entire. Most species have white petals, except for *W. caymanensis* and *W. mesoamericana* with green petals. Occasional green petals have also been recorded in some individuals of *W. penduliflora* and *W. spinulosa*. The apices are acuminate to acute, except for one individual of *W. penduliflora* with obtuse petals.

The adaxial surface of the petals always contains two longitudinal callosities that extend parallel to each other from the petal base to its medial portion. Some species also exhibit two petal appendages derived from the same tissue that constitutes the callosities. These petal appendages partially detach from the petal surface at least 1.5 mm above the petal base and exhibit irregular apical lobes. The presence or absence of petal appendages has traditionally been used as a character to diagnose genera in Bromelioideae; however, recent studies showed that the taxonomic value of this character must be reassessed (Brown and Terry 1992). In the case of Caribbean *Wittmackia*, this is a good character to separate individual species.

**Stamens.** The stamens are always included. The filaments of the antepetalous stamens are partially adnate to the petals and are laterally flanked by the petal longitudinal callosities. The filaments are flattened and white. The anthers are dorsifixed, introse, rectangular to lanceolate, and white to cream. The connective extends forming a mucro or apicule at the apex of the anthers.
Epigynous tube. The epigynous tube is a cavity that separates the ovary from the three external whorls of the flower. In the species of Caribbean *Wittmackia* the size of this structure is variable across the species but does not provide diagnostic information.

Gynoecium. The ovary is tricarpelar, subovoid, dorsiventrally flattened, green, white, or yellow, and bears three septal nectaries. The placentation in all the species is apically-axile and each flower produces a large number of ovules of about 50 to 100 per ovary. The ovules are orthothropous, round, and do not exhibit chalazal appendages. The style is always longer than the stamens, cylindrical, and white to green. The stigma is trilobate, conduplicate-spiral, and papillose.

Fruits and seeds. The fruits are globose to subovoid berries, and conserve the dorsiventral compression of the ovaries. In species with large floral bracts, like *W. urbaniana* and *W. inermis*, the fruits remain concealed within the spikes and do not develop a significant change of color. In species were the fruits are less protected by the floral bracts, like *W. portorcensis* and *W. penduliflora*, the fruits exhibit yellow or bluish pigmentation. In other species, like *W. caymanensis* and *Wittmackia rohan-estyi*, the fruits remain green or light green. Fruits are glabrous to sparsely floccose. The sepals are persistent in the fruits and in some cases become partially fleshy at their bases, like in *W. urbaniana* and *W. polycephala*. Each fruit produces about 10 to 20 seeds per fruit. The seeds are club-shaped, angulate, gray, stramineous or reddish-brown.

3.4.2 Phylogeny and biogeographic trends

The phylogenetic analysis of Aguirre-Santoro (in preparation; see chapter 1) suggested that Caribbean *Wittmackia* is a robust monophyletic clade nested within a grade of mostly
Brazilian-endemic species (Fig. 3.1). In this study, the sister group of the Caribbean *Wittmackia* is *W. bicolor* (L.B. Sm. (1956a: 12)) Aguirre-Santoro (pending publication), a species endemic to Southeastern Brazil; however, this relationship received a medium support value (Posterior Probability = 0.98). The details on how the Brazilian and Caribbean centers of species distribution of *Wittmackia* became disjunct are still unknown. Within the Caribbean Clade of *Wittmackia*, the earliest-diverging lineage includes three species: the Puerto Rican-endemic *W. antillana*, and the Jamaican-endemic *W. eriostachya* and *W. polycephala*. This relationship indicates at least one event of migration or vicariance between Jamaica and Puerto Rico. The remaining species are grouped in a robust but poorly resolved clade. The bulk of this clade is formed by Jamaican-endemic species, but it also includes the Puerto Rican-endemic *W. portoricensis*; the Yucatan Peninsula-endemic *W. mesoamericana*; *W. caymanensis* from the small western Caribbean islands; and *W. penduliflora*, which occurs both in Cuba and Jamaica. These relationships illustrate how Jamaica is an important center of diversity for the group, but the details on the routes of dispersal within the group still need to be studied using a biogeographic approach.
3.4.3 Geographic distribution, habitat and conservation

The Caribbean species of Wittmackia are distributed from 13° to 24° of longitude north and 65° to 82° of latitude west (Fig. 3.2). Most species grow in lowlands between 0 and 800 m elevation. Some species occupy large altitudinal gradients between 0 and 1200 m elevation like Wittmackia bicolor.
W. antillana, W. penduliflora, W. spinulosa and W. urbaniana, whereas species like W. eriostachya, W. fawcettii, and W. portoricensis are restricted to medium-high elevations between 500 and 1300 m. Thirteen species occur in Jamaica, twelve of which are endemic to the island, and one, W. penduliflora, also occurs in Cuba. Two species are endemic to Puerto Rico: W. antillana and W. portoricensis. It is possible that W. antillana also occurs in the Great Camanoe Island (British Virgin Islands), but the locality information of the only collection in this island is imprecise (Proctor 44881). The remaining two species occur in the western Caribbean: W. caymanensis inhabits Grand Cayman and the island of Providencia in Colombia, whereas W. mesoamericana is endemic to the coast of the Yucatan Peninsula in Mexico. Surprisingly, no species occur in Hispaniola. The absence of Wittmackia species on this major island may not be related to lack of collecting because extensive botanical expeditions have been conducted here and the species of this genus are normally conspicuous and abundant locally. This island contains similar environmental conditions and habitats compared to other major islands such as Jamaica and Puerto Rico; for these reasons, it is possible that extinction, strong competition, lack of pollinators, or lack of opportunity for arrival to the island explains the absence of Wittmackia species in Hispaniola.

In Jamaica, the species exhibit marked patterns of geographical distribution. Only W. penduliflora and W. polycephala are widely distributed in the island, growing at low to medium-high altitudes. Wittmackia eriostachya and W. fawcettii are endemic to the medium-high altitudes of the Blue and John Crow Mountains, east of Jamaica, where they grow as epiphytes on large trees in forested areas. These mountains are characterized by their complex geology and steep altitudinal gradient that permitted the formation of cloud forests on the island with robust host trees for the establishment of epiphytes (Tanner 1986; James 2005). Despite the protected status
of this region, invasive species are rapidly spreading in the area, and extensive human activities related to tourism and expansion of crops pose serious threats for the integrity of the species’ habitats (WWF and IUCN 1997). Six species are mainly restricted to the Cockpit Country and surrounding areas in central Jamaica: *W. abbreviata, W. inermis, W. jamaicana, W. laesslei, W. spinulosa* and *W. urbaniana*. This protected area contains forests on mesic limestone dominated by a heterogeneous topography of valleys, caves, and karst hills. These geographic attributes created a wide variety of microhabitats and barriers that explain the rich endemism of plants in the region (Acevedo-Rodríguez and Strong 2008). Although the Cockpit Country is a largely isolated Forest Reserve, there is presence of invasive species, farming, illegal logging, and construction of roads in the area, which represent imminent threats for this biodiversity reservoir (Eyre 1995; WWF and IUCN 1997). The remaining three species endemic to Jamaica are restricted to forested limestone formations in western Jamaica. *Wittmackia negrilensis* occurs in lowlands near the coastline, whereas *W. distans* and *Wittmackia rohan-estyi* are mostly restricted to the Dolphin Head Mountains and surrounding areas. The latter is a steep system of karst hills containing limestone forest that is sufficiently isolated and rich in microhabitats to be a species refuge with its own endemics (Buskirk 1985; Kelly 1985). Unfortunately, this is probably the most endangered species refuge in Jamaica as rapidly growing urban areas surround these mountains. In response to this threat, the Dolphin Head Mountains region was established as a Forest Reserve and has been proposed as a National Park (NRCA/NEPA 2001).

The two species endemic to Puerto Rico occur widespread in forested areas of the island. While *W. antillana* is more commonly found in the understory of rocky limestone hills at low elevations (0–300 m elevation), *W. portoricensis* inhabits cloud forests above 500 m. *Wittmackia caymanensis* and *W. penduliflora* are the only species of Caribbean *Wittmackia* that
simultaneously inhabit two islands in the Caribbean. In the first case, *Wittmackia caymanensis* occurs on Grand Cayman and Providencia Island in Colombia, growing on rocky limestone formations as rupicolous or epiphytes in exposed areas, or in the understory. The small size of these islands (50 km$^2$ and 190 km$^2$, respectively) combined with their growing human populations and touristic industry makes *W. caymanensis* a highly endangered species. A contrasting situation can be observed with *W. penduliflora*. This species occurs both in Cuba and Jamaica, growing as a widespread in different biomes. Although this species prefers humid, forested areas, its ability to colonize different types of habitats makes it less vulnerable than *W. caymanensis*. Finally, *W. mesoamericana* is the only species of Caribbean *Wittmackia* distributed in continental Central America. According to Ramírez-Morillo et al. (2010), this species occurs only in one locality in the coast of the Yucatan Peninsula in Mexico characterized by its highly vulnerable dry forest on limestone formations. This study categorized *W. mesoamericana* as Critically Endangered (CR) because of the current habitat destruction of the only known population of this species.
3.4.4 Ecology and reproductive biology

Most ecological studies including species of Caribbean *Wittmackia* correspond to inventories of the fauna that inhabits their phytotelmata (e.g. Laessle 1961; Hartnoll 1964; Wambold et al. 2011; Foissner and Stoeck 2013). These studies reported up to 15 species of invertebrates living in one individual rosette, including diptera (mosquitoes, midges, ceratopogonids, tanypodid midges), copepods (canthocamptids, ostracods, hapacticoids), tubellarians, aquatic beetles, oligochaetes, ciliophores, and fresh water grapsid crabs. Moreover, vertebrate species, such as the Jamaican laughing frog (*Osteopilus brunneus*) and the Jamaican blackbird (*Nesopsar nigerrimus*) have been found associated with *W. urbaniana* (Cruz 1978; Hedges 1987) as predators of fauna inhabiting its phytotelmata. No studies on the pollination of Caribbean *Wittmackia* were found. Nevertheless, during the fieldwork of the present study, it was possible to observe hummingbirds visiting the flowers of *W. fawcettii* and *W. portoricensis* in Jamaica and Puerto Rico, respectively. There is scarce literature describing seed dispersal and herbivory in Caribbean *Wittmackia*. In one example, Taboada & Pine (1969) reported consumption of fruits and seeds of *W. penduliflora* in bats of the genus *Brachyphylla* and the Phyllonycterinae in Cuba. Moreover, Jamaican orioles (*Icterus leucopteryx*) were observed consuming the fruits of *W. urbaniana* (pers. obs.). In the case of herbivory, Lygaeids (heteroptera) were reported as highly restricted to the inflorescences of *W. penduliflora*, *W. polycephala* and *W. urbaniana* in Jamaica (Slater and Baranowski 1978). During the fieldwork of the present study, mites were observed in the flowers of *W. laesslei*, *W. penduliflora* and *Wittmackia rohan-estyi*, whereas mechanically damaged flowers were detected for *W. eriostachya*, *W. laesslei*, *W. penduliflora* and *W. urbaniana*. Ants of the genus *Crematogaster*
were frequently found on the inflorescences of Caribbean species of *Wittmackia*; however, it is unknown whether they are random visitors, provide protection to the plant, serve as seed dispersers, or act as herbivores.

### 3.4.5 Taxonomy of the Caribbean Clade of Wittmackia

**Diagnosis.** Inflorescence central, completely exposed out of the rosette; bracts of the peduncle green, cream, pale brown, rarely dull purple; fertile portion of the inflorescence paniculate, 1-divided, occasionally 2-divided, rachis exposed, occasionally concealed by the imbricate spikes. Spikes globose to cylindrical. Floral bracts partially enclosing the ovaries. Flowers polystichous and densely aggregated along the spike rachis, sessile. Calyx strongly compressed; sepals strongly asymmetrical, forming a lateral wing, the posterior sepals carinate, the anterior sepal ecarinate, mucronate. Corolla tubular, apically spreading; petals free, white, occasionally green, apex acute, occasionally obtuse; petal appendages absent or present, two, arising more than 1.5 mm above the petal base, flanking the filaments of the stamens, apically lobate. Stamens included, the antepetalous partially adnate to the petals; anthers dorsifixed. Epigynous tube short, subcompressed. Ovary dorsiventrally flattened, placentation apically-axile. Ovules more than 30 per ovary, round, unappendaged. Fruits berries. Seeds more than 20 per fruit, club-shaped.

**Taxonomic comments and affinities:**—Most species of Caribbean *Wittmackia* are easily diagnosable even when petals, stamens, and stigmas are not available for examination. Previous taxonomic keys for the species in the group are very useful and work well most times; however, the interpretation of a few diagnostic characters in these keys is ambiguous and tried to be avoided in the taxonomic key presented in this taxonomic treatment. For instance, a broadly
acute floral apex can be interpreted as an intermediate state between acute and obtuse. This character can be problematic in the case of *W. distans* and *Wittmackia rohan-estyi*, where floral apices can vary from acute to obtuse within the same individual. Other ambiguities in diagnostic characters that tried to be avoided here include spike shape and length, conspicuousness of floral bract venation, sepal position with respect to floral bracts, and relative size of sepal mucro with respect to sepal length.

### 3.4.5.1 Key to the identification of the Caribbean species of *Wittmackia*

1. Stipes of the basal branches longer or equaling the length of the spikes...2
2* Stipes of the basal branches shorter than the length of the spikes...5

2. Inflorescence erect to inclined at anthesis; primary bracts surpassing the basal branches...3
2* Inflorescence pendulous at anthesis; primary bracts shorter than the basal branches...4

3. Medial bracts of the peduncle shorter than the internodes, peduncle diameter 6–8 mm; stipes of the basal branches 40–42 mm long, spikes bearing 12–18 flowers...9. *W. laesslei*
3* Medial bracts of the peduncle longer than the internodes, peduncle diameter 9–14 mm; stipes of the basal branches 17–39 mm long, spikes bearing 25 to 35 flowers...15. *Wittmackia rohan-estyi* [p.p.]

4. Fertile portion of the inflorescence 36–51 × 9.4–20 cm; primary bracts 4.7–7.4 cm long; stipes 51–63 mm long, spikes bearing 9–25 flowers; floral bracts green to cream at anthesis, 3.8–4.9 mm long; petal appendages arising at 2–2.5 mm from the petal base...1. *W. abbreviata*
4* Fertile portion of the inflorescence 52–91 × 23–36 cm; primary bracts 7.5–9 cm long; stipes 85–133 mm long, spikes bearing 26–50 flowers; floral bracts yellow at anthesis, 6.5–11 mm long; petal appendages arising at 4 mm from the petal base...4. *W. distans*
5 Sepals $\geq$ 7 mm long, long-triangular, the winged side enlarged towards the medial region of the sepal...6

5* Sepals < 7 mm long, short-triangular, the winged side enlarged towards apical region of the sepal...8

6 Stipes 24–49 mm, 1.8–3.2 mm in diameter...7. *W. inermis*

6* Stipes 4–20 mm, 4–10 mm in diameter...7

7 Bracts of the peduncle and basal primary bracts serrate; floral bracts floccose to sparsely floccose, green, serrulate; petals 11–13.8 cm long, petal appendages absent. Puerto Rico and British Virgin Islands...2. *W. antillana*

7* Bracts of the peduncle and basal primary bracts entire; floral bracts glabrous, bright yellow to orange at anthesis, entire; petals 14.5–18 cm long, petal appendages present. Jamaica...17. *W. urbaniana*

8 Floral bracts, ovaries and sepals brown-tomentose-lepidote...9

8* Floral bracts, ovaries and sepals glabrous to white-floccose-lepidote...10

9 Leaf teeth < 1mm long; primary bracts longer than the spikes; spikes sessile...13. *W. polycephala*

9* Leaf teeth > 1mm long; primary bracts shorter than the spikes; spikes stipitate...5. *W. eriostachya*

10 Floral bracts obtuse to truncate; sepal mucro 0.2–0.8 mm long...11

10* Floral bracts acuminate to acute; sepal mucro 1–5 mm long...12

11 Peduncle 10–12 mm in diameter; bracts of the peduncle serrulate; fertile portion of the inflorescence 15–25 cm wide, rachis glabrous; spikes 5.8–7.8 cm long, bearing 40–50 flowers; floral bracts glabrous, mucro 1.7–4.7 mm long; sepals 3–4.5 mm long...8. *W. jamaicana*
11* Peduncle 4–9 mm in diameter; bracts of the peduncle entire; fertile portion of the inflorescence 7.8–12.8 cm wide, rachis sparsely floccose; spikes 2.9–4.7 cm long, bearing 18 to 35 flowers; floral bracts sparsely floccose, mucro 0.2–0.9 mm long; sepals 5.8–7 mm long. \( W.\) fawcettii

12 Apical bracts of the peduncle < 8.2 cm long; basal primary bracts 3–7.1 cm long. \( \text{13} \)

12* Apical bracts of the peduncle > 9 cm long; basal primary bracts 7.2–16 cm long. \( \text{15} \)

13 Spikes densely imbricate, covering the inflorescence rachis (except at the extreme base), suberect; primary bracts suberect. \( \text{16. } W.\) spinulosa

13* Spikes lax, exposing the inflorescence rachis, divaricate; primary bracts divaricate to reclined. \( \text{14} \)

14 Leaf blades 2–6.4 cm wide in the middle; fertile portion of the inflorescence bearing 7–14 branches, rachis subflexuose; primary bracts serrate; petal appendages absent. Puerto Rico. \( \text{14. } W.\) portoricensis

14* Leaf blades (6.5-)7.9–13 cm wide in the middle; fertile portion of the inflorescence bearing (13-)30–65 branches, rachis straight; primary bracts entire; petal appendages absent. Cuba and Jamaica. \( \text{12. } W.\) penduliflora

15 Stipes > 19 mm. \( \text{15. } Wittmackia rohan-estyi [p.p.] \)

15* Stipes < 17 mm. \( \text{16} \)

16 Fertile portion of the inflorescence 56–57 × 10.3–10.4 cm; basal primary bracts 1–1.2 cm wide; flowers 50 to 60 per spike, 10.4–12.5 mm long; petals white; epigynous tube 0.2 mm; ovary 1.9–2.4 mm long. \( \text{11. } W.\) negrilensis
16* Fertile portion of the inflorescence 26–55 × 7.2–10.2 cm; basal primary bracts 0.4–0.7 cm wide; flowers 15 to 45 per spike, 13.6–17.3 mm long; petals green; epigynous tube 1–1.2 mm; ovary 2.9–4 mm long...17

17 Leaf blades 14 cm wide at the base; stipes 3–5 mm long, 4–5 mm in diameter; spikes 2.2–2.7 cm wide; flowers 16–17.3 mm long; petals 12.5–13.4 × 2.4–3 mm; petal appendages detaching at 3.1–4.2 mm from the petal base...10. *W. mesoamericana*

17* Leaf blades 5–12.7 wide at the base; stipes 6–18 mm long, 2–3 mm in diameter; spikes 1.2–2 cm wide; flowers 13.5 mm; petals 8.3–9.3 × 1.2 mm; petal appendages detaching at 1.7 mm from the petal base....3. *W. caymanensis*

3.4.5.2 **Taxonomic treatment**


Basionym: *Hohenbergia abbreviata* L.B. Sm. & Proctor in (1960: 253). TYPE:—JAMAICA.

Trelawny Parish: vicinity of Ramgoat Cave, Cockpit Country, 457 m, 22 October 1955, *G.R. Proctor* 11048 (holotype US!, isotype IJ!).

**Plant** epiphytic or rupicolous, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** 56–87.5 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong to elliptical, 14–22.5 × 10–12 cm, pale brown, lepidote on both surfaces, entire; blade lingulate, 41–75 cm long, 8.5–9.5 cm wide at the base, 8.2–8.9 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, serrulate, occasionally entire, the teeth evenly distributed along the margins, triangular to hook-shaped, erect to antrorse, green, 0.2–0.8 mm long, apex rounded, mucronate. **Inflorescence** central, strongly inclined to pendulous; peduncle almost completely exposed out of the rosette, stout, rigid, 72–
89.8 cm long, 4.5–10 mm in diameter, green, floccose, internodes between the medial bracts 3.2–7 cm, internodes between the apical bracts 2.5–3.8 cm; bracts of the peduncle shorter to longer than the internodes, marcescent, chartaceous, nervous, green to pale brown, the medial bracts erect, imbricate to lax, lanceolate, 4.5–9 × 1.1–1.8 cm, sparsely floccose, entire, apex acuminate, the apical bracts erect, imbricate to lax, lanceolate, 4.8–8.2 × 0.3–0.9 cm, sparsely floccose, entire, apex acuminate; fertile portion of the inflorescence paniculate, conical, 36–50.7 cm long, 9.4–20 cm wide in the middle, 1-divided, branches 30 to 46(-65) per spike, polystichous, rachis straight, green, 33–54 cm long, 3–6 mm in diameter, floccose to sparsely floccose. Primary bracts similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, divaricate, marcescent, chartaceous, nervous, shorter than the branches, the basal bracts linear-lanceolate, 4.7–7.4 × 0.4–0.6 cm, pale brown, sparsely floccose to glabrescent, entire, apex attenuate; the apical bracts lanceolate, 1.3 × 0.2 cm, pale brown, glabrescent, entire, apex attenuate. Spikes globose to cylindrical, 1.3–4.1 cm long, 1–1.5(-1.8) cm wide in the middle; stipe exposed, 51–63 mm long, 1–2 mm in diameter, terete, sparsely floccose; rachis of the spike 1.3–4.1 cm long. Floral bracts partially enclosing the ovaries, imbricate, ascending to diverging from the rachis, subconcave, strongly coriaceous, ovate, 3.8–4.9 × 3.4–7 mm, light green, nervous, ecarinate, sparsely floccose to glabrescent, entire to minutely serrulate, apex acute to obtuse, mucronate, mucro 0.9–1.8 mm long. Flowers 9 to 25 per spike, polystichous, suberect to ascending, 3.8–4.9 mm long, sessile. Calyx dorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 3.4–4.8 mm long, 1.6–4.2 mm wide at the base, the unwinged side 0.6–1.3 mm wide, the winged side 2.1–2.5 mm wide, light green, nervous, the posterior sepals carinate, the anterior sepal ecarinate, sparsely floccose to glabrescent, entire, apex acute, mucronate, mucro 0.5–1.2 mm long. Corolla tubular,
apically spreading; petals free, chartaceous, oblong-lanceolate, 9.7 × 2.4 mm, white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 2.1 mm from the petal base. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 6.8 mm long, 0.3 mm in diameter, white; anthers dorsifixed, lanceolate, 2.6 × 0.6 mm, cream, mucronate. **Epigynous tube** 0.2–0.5 mm long. **Ovary** subovoid, dorsiventrally compressed, 2.4–2.9 mm long, 4.1 mm in diameter, light green, sparsely floccose to glabrescent, placentation apically-axile. **Style** longer than the stamens, 9 mm long; stigma conduplicate-spiral, 1.4 mm long. **Ovules** more than 30 per ovary, round, unappendaged. **Fruit** subovoid, dorsiventrally compressed, 5.5–8.9 mm long, 2.7–5.7 mm in diameter, white, glabrous; sepals persistent in fruit, not fleshy (Fig. 3.3).

**Etymology:**—The specific epithet of this species likely refers to its short spikes.

**Distribution, habitat, and phenology:**—**Wittmackia abbreviata** is endemic and highly restricted to the central region of the Cockpit Country in central Jamaica at 275–840 m elevation (Fig. 3.2F). It grows on wooded limestone hills, either in exposed or shaded areas. **Wittmackia abbreviata** grows sympatrically with **W. polycephala**. Collected in flower in July.

**Conservation status:**— Although the extent of occurrence of **Wittmackia abbreviata** does not exceed the 200 km², this species is categorized here as Vulnerable (VU, B1a; IUCN 2001) because it has been collected in nearly 6 to 8 locations and inhabits the central Cockpit Country of Jamaica, an area of well-established forests with potential threats derived mainly from sporadic deforestation.

**Taxonomic comments and affinities:**—**Wittmackia abbreviata** is one of the four species that exhibit stipes many times longer than the spikes. It can be confounded with specimens of **W. distans** with short spikes because of its pendulous inflorescence and exceptionally long stipes;
however, *W. abbreviata* has a shorter and narrower inflorescence (36–51 × 9.4–10 cm vs. 52–91 × 23–36 cm); generally shorter basal primary bracts (4.7–7.5 cm vs. 7.5–9 cm long); shorter stipes (51–63 mm vs. 85–133 mm long); and shorter floral bracts (3.8–4.9 mm vs. 6.5–11 mm long). In the protologue *W. abbreviata* is also compared with *W. laesslei* but differs from this species by its pendulous inflorescence in anthesis, peduncular bracts surpassing the internodes, and basal primary bracts longer than the basal branches.

**ADDITIONAL SPECIMENS EXAMINED. JAMAICA.** St. Ann Parish: 1.5 miles due south of Gibraltar P.O., 609 m, 14 July 1956, *Proctor 15522* (IJ, NY [photo], US). Trelawny Parish: Cockpit Country, unpaved road between Burnt Hills and Ramgoat Cave. About 6 km from Warsop, 545 m, 18°18'52.5"N, 77°33'27.8"W, 26 June 2012, *Aguirre-Santoro et al. 1812* (IJ, NY, US); Barbecue Bottom, 395 m, 23 June 1970, *duQuesnay 376* (UCWI); just north of Burnt Hill crossroads, 550–580 m, 15 August 1965, *Hespenheide 1257* (MICH); vicinity of Ramgoat Cave, Cockpit Country, 460 m, 4 July 1955, *Howard et al. 14435* (IJ, US); Alps district, 1.5 miles N.N.E. of Ulster Spring, 460 m, 22 August 1956, *Proctor 15661* (IJ); Cockpit Country along track between Windsor and Tyer, north of Troy, 490–520 m, 28 August 1956, *Proctor 15768* (IJ); Island View Hill, Wilson Valley district, 1.5 miles north of Warsop, 610–670 m, 26 June 1960, *Proctor 21335* (IJ); 10 April 1961, *Proctor 22190* (IJ); along track to Dry River below Sawyers, Ulster Spring main road, 275 m, 17 November 1968, *Proctor 29382* (IJ); hills overlooking Broadleaf Water, 1.5 miles northwest of Litchfield, 840 m, 5 July 1974, *Proctor 34112* (IJ); vicinity of Mango Tree Hill, Cockpit Country, 550–600 m, 9 December 2001, *Proctor 52040* (IJ); vicinity of Berlin Estate, c. 4.5 km due east of Ulster Spring, 450–600 m, 9 February 2007, *Proctor 52591* (IJ); along the donkey trail at top of ridge on right-hand side, 1 mile north of Burnt Hill Intersection, 400–550 m, 22 January 1967, *Read 1751* (US).

**Plant** rupicolous, terrestrial, or epiphytic, cespitose or solitary, 100–130 cm tall, acaulescent; rosette broad, forming phytotelmata. **Leaves** 80–153 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong to elliptical, 20–23 × 8.5–13 cm, pale brown, lepidote on both surfaces, serrate; blade lingulate, 98–120 cm long, 8.5–11.9 cm wide at the base, 8–11.5 cm wide in the middle, green, occasionally maculate, surface smooth, lepidote on both surfaces, more densely on the abaxial side, serrate, the teeth evenly distributed along the margins, hook-shaped, antrorse, green, 1.3–2 × 1–2 mm, apex rounded, mucronate.

**Inflorescence** central, erect to inclined; peduncle partially concealed by the rosette, stout, rigid, 26–36.5 cm long, 7–13 mm in diameter, green, floccose, internodes between the medial bracts 3.5–6.4 cm, internodes between the apical bracts 2–3.5 cm; bracts of the peduncle longer than the internodes, marcescent, coriaceous, nervose, green to pale brown, occasionally dull purple, the medial bracts erect, imbricate, lanceolate to elliptical, 8.9–13.2 × 1.3–2.5 cm, floccose abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, 0.2–1.5 mm, apex acuminate, the apical bracts suberect, imbricate, lanceolate, 7.5–11.5 × 0.6–2.4 cm, floccose abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, 0.2–1.5 mm, apex acuminate; fertile portion of the inflorescence paniculate, conical, 16–27 cm long, 8.7–12.8 cm wide in the middle, 1-divided, branches 6 to 12(-20) in number, polystichous, rachis straight, green, (8-)9.5–25 cm long, (3-)11–12 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, ascending to diverging from the rachis, marcescent, chartaceous, nervose, shorter...
or longer than the branches; the basal bracts lanceolate, 6–9.9 × 1.1–1.9 cm, green to pale brown, occasionally dull purple, floccose abaxially, glabrescent adaxially, serrulate, the teeth irregularly distributed along the margins, apex acuminate to attenuate; the apical bracts lanceolate, 2–4.2 × 0.6–1.4 cm, green to pale brown, occasionally dull purple, sparsely to densely floccose abaxially, glabrescent adaxially, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate. **Spikes** ovoidal to subcylindrical, 4.5–7.2 cm long, 2.4–4.2 cm wide in the middle; stipe partially covered by the primary bracts, 10–23 mm long, 3–9 mm in diameter, terete, floccose; rachis of the spike 4.5–7.2 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the ovaries, imbricate, suberect, subconcave, strongly coriaceous, ovate, 13–20 × 10–16 mm, green, nervose, ecarinate to carinate, floccose abaxially, glabrescent adaxially, minutely serrulate, occasionally entire, apex acute, mucronate, mucro 3–4.5 mm long. **Flowers** 17 to 30 per spike, polystichous, suberect, 13–20 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, long-triangular, asymmetrical, forming a lateral wing, 7.7–12 mm long, 1–4 mm wide at the base, the unwinged side 0.5–1.8 mm wide, the winged side 1.2–3.1 mm wide, green, nervose, the posterior sepals carinate, the anterior sepal ecarinate, floccose, entire, occasionally minutely serrulate, acuminate, mucronate, mucro 1.4–2 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, 11–13.8 × 1.7–1.8 mm, white, glabrous, entire, apex acute; petal appendages absent. **Stamens** included; filaments 12.5 mm long, 0.2 mm in diameter, white; anthers dorsifixed, 2.7 × 0.4 mm, white. **Epigynous tube** 0.8–2.4 mm long. **Ovary** subovoid, dorsiventrally compressed, 3.9–5 mm long, 7.7–8.2 mm in diameter, light green, floccose, placentation apically-axile. **Style** 15.7 mm long, white; stigma, conduplicate-spiral, 1.6 mm long. **Ovules** more than 100 per ovary, round, unappendaged. **Fruit** subovoid, dorsiventrally
compressed, 15 mm long, 8–10.2 mm in diameter, light green, floccose; sepal persistent in fruit, not fleshy. Seeds more than 20 per fruit, club-shaped, 2.5 mm × 0.5 mm (Fig. 3.4).

**Etymology:**—The specific epithet refers to the geographic distribution of this species in the Antilles.

**Distribution, habitat, and phenology:**—*Wittmackia antillana* occurs in Puerto Rico and most probably the British Virgin Islands at 0–275(-840) m elevation (Fig. 3.2B). The only collection of *W. antillana* in the British Virgin Islands (Proctor 44881), however, has imprecise locality information. It grows on wooded limestone hills forming large, but highly localized populations. *Wittmackia antillana* grows sympatrically with *W. portoricensis*. Collected in flower in July.

**Conservation status:**— *Wittmackia antillana* is categorized here as Endangered (EN, B1a; IUCN 2001) because it has an extent of occurrence of about 2,000 km² and grows strictly in karst hills near developing urban areas.

**Taxonomic comments and affinities:**—*Wittmackia antillana* is very distinctive and hard to confound with other species of *Wittmackia* because of its robust inflorescence with green, large floral bracts, covered with white floccose indument. This species and *W. portoricensis* are the only two species of *Wittmackia* that occur in Puerto Rico; however, they are distant relatives (Aguirre-Santoro in preparation; see chapter 1) and do not share overlapping diagnostic characteristics. In Jamaica, only *W. urbaniana* has comparable diagnostic characters with *W. antillana*. Both species have robust inflorescences, spikes broader than 1.8 cm, and floral bracts longer than 12 mm; however, *W. antillana* is different by its serrate bracts of the peduncle and basal primary bracts (vs. entire); floral bracts floccose to sparsely floccose (vs. glabrous), green
(vs. yellow), and serrulate (vs. entire); longer petals (11–13.8 cm vs. 14.5–18 cm long), and petal appendages absent (vs. present).

Proctor & Cedeño-Maldonado (1999) described *Hohenbergia tetaensis* based on a collection of *W. antillana* that occurred in the peaks of Salinas (also known as Las Tetas de Cayey), an isolated mountainous area in Southern Puerto Rico. Cedeño-Maldonado in Acevedo-Rodriguez (2005) later synonymized this species into *H. antillana* (= *W. antillana*) based on the observation of populations with intermediate morphology between *W. antillana* and *H. tetaensis* occurring in the type locality of the latter. This synonymization is confirmed in this taxonomic revision based on the comprehensive revision of specimens of *W. antillana* and a recent visit by the author to the peaks of Salinas.

ADDITIONAL SPECIMENS EXAMINED. BRITISH VIRGIN ISLANDS. Guana Island: said to have been collected as a wild plant on Great Camanoe Island, E. of Guana, by Mary Randall, 8 July 1988, *Proctor 44881* (IJ, NY). PUERTO RICO. Arecibo: 5 km S of Biáfara, 60 m, 18°24′08″N, 66°39′53″W, 25 June 2001, *Acevedo-Rodriguez et al. 11646* (US); 0.5 km of Biáfara, 60 m, 18°24′08″N, 66°39′53″W, 10 July 2001, *Acevedo-Rodriguez et al. 11700* (US); Between Arecibo and Utuado, 4 March 1914, *Britton et al. 2041* (NY, US); barrio Miraflores, Sector Biáfara, Finca Dentón, Road 637, between Roads 656 and 638. About 1 km South, though a private paved road, mogote peak on the west side, about 100 m before the house, 240 m, 18°23′984″N, 066°39′857″W, 14 September 2003, *Trejo et al. 2393* (UPR); Bo. Dominguito, Mata de Plátano Natural Reserve, S corner, border with El Tallonal Private Reserve, 195 m, 18°24′54.7″N, 66°43.743″W, 3 October 2003, *Trejo et al. 2425* (UPR); 178 m, 18°24′53.8″N, 66°43.755″W, 20 February 2005, *Trejo 2864* (NY, UPR). Bayamón: near Bayamón, 150 m, 21 September 1963, *Liogier 10261* (GH, NY); 9 January 1960, *Woodbury s.n.* (UPR).


**Plant** epiphytic, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** 15 to 30 in number, 69–95 cm long, coriaceous; sheath conspicuously differentiated from the blade, oblong, 12–21 × 9–12 cm, pale brown, lepidote on both surfaces, serrulate, occasionally entire; blade lingulate, 60–83 cm long, 5–12.7 cm wide at the base, 5.1–10.8 cm wide in the middle,
light green to dark green, occasionally maculate, surface smooth, lepidote abaxially, glabrescent adaxially, serrulate, the teeth evenly distributed along the margins, hook-shaped or triangular, erect to extrorse, green, 0.4–0.6 mm long, apex obtuse to rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle almost completely exposed out of the rosette, stout, rigid, 68–77 cm long, 8–12 mm in diameter, green, sparsely floccose, internodes between the medial bracts 1.8–5.1 cm, internodes between the apical bracts 3.8–4.3 cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nervose, light-green, occasionally dull-red; the medial bracts erect, imbricate, linear-lanceolate, 10–11 × 1–1.2 cm, lepidote to floccose on both surfaces, serrulate, the teeth irregularly distributed along the margins, apex acuminate, the apical bracts suberect, imbricate, linear-lanceolate, 9.2–9.5 × 0.7–0.9 cm, lepidote to floccose on both surfaces, serrulate, the teeth irregularly distributed along the margins, apex acuminate; fertile portion of the inflorescence paniculate, conical, 28–55 cm long, 7.2–10.2 cm wide in the middle, 1-divided, occasionally 2-divided, branches (24-)40 to 65 in number, polystichous, rachis straight, green, 21–50 cm long, 5–7 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, diverging from the rachis to divaricate, marcescent, chartaceous, nervose, longer than the branches; the basal bracts linear-lanceolate, 7.2–9.8 × 0.5–0.7 cm, light-green, occasionally dull-red, lepidote, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate; the apical bracts lanceolate, 1.6–2.5 × 0.1–0.2 cm, light-green occasionally dull-red, floccose on both surfaces, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate. **Spikes** cylindrical, ovoidal, 2.6–3.7 cm long, 1.2–2 cm wide in the middle; stipe exposed, 6–18 mm long, 2–3 mm in diameter, terete, floccose; rachis of the spike straight, 2.6–3.7 cm long, green. **Floral bracts** gradually diminishing in size towards the
apex of the spike, partially enclosing the ovaries, imbricate, ascending, subconcave, chartaceous, ovate to lanceolate, 3.5–6.1 × 3.3–4.8 mm, green to pale brown, nervose, ecarinate, sparsely floccose, minutely serrulate, apex acuminate, mucronate, mucro 4.8–5.8 mm long. **Flowers** 18 to 30 per spike, polystichous, suberect, 3.5–6.1 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, asymmetrical, forming a lateral wing, 3.6–4 mm long, 2.2–3.2 mm wide at the base, the unwinged side 0.5–1.1 mm wide, the winged side 1.2–2.2 mm wide, green, the posterior sepals carinate, the anterior sepal ecarinate, sparsely floccose, entire, mucronate, mucro 1.9–5 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, oblong-lanceolate, 8.3–9.3 × 1.2 mm, green, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 1.7 mm from the petal base. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments 7.4–8.4 mm long, 0.2 mm in diameter; anthers dorsifixed, 2.2 × 0.6 mm. **Epigynous tube** 1.1 mm long. **Ovary** ovoidal, dorsiventrally subcompressed, 2.9 mm long, 3.9 mm in diameter, placentation apically-axile. **Style** 9 mm long; stigma conduplicate-spiral, 1.2 mm long. **Ovules** unappendaged. **Fruit** subglobose, 7.4–11.5 mm long, 4.3–7 mm in diameter, green, glabrescent to sparsely floccose; sepals persistent in fruit, not fleshy. **Seeds** more than 20 per fruit, club-shaped, 2.4 × 0.6 mm, stramineous to reddish-brown (Fig. 3.5).

**Etymology:**—The specific epithet refers to the Cayman Islands, where the type specimen was collected.

**Distribution, habitat, and phenology:**—*Wittmackia caymanensis* was thought to be endemic to Grand Cayman in the Cayman Islands at 0–20 m elevation. However, this species was recently found in the Colombian island of Providencia at 0–70 m elevation (Fig. 3.2A). It
forms large but highly localized populations in shaded areas of forested limestone formations. Collected in flower between November and March.

**Conservation status:**—According to Burton et al. (2014), *Wittmackia caymanensis* is categorized as Critically Endangered (CR, B1ab(i,ii,iii,iv,v) + 2ab(i,ii,iii,iv,v)), mainly because of its extremely reduced area of occupancy and imminent threats provided by the expansion of urban areas in George Town. The recent discovery of this species in Providencia island (Colombia) does not represent a significant decrease in the level of threat for this species for four main reasons: 1) the area of this island does not exceed 20 km²; 2) only two populations of the species are known to occur in the island; 3) the rapid growth of the tourism infrastructure in the island represents a serious threat for the species; and 4) the natural forests of the island are not protected by national environmental agencies.

**Taxonomic comments and affinities:**—*Wittmackia caymanensis* resembles *W. mesoamericana* and *Wittmackia rohan-estyi* by its floccose inflorescence rachis, primary bracts much longer than the inflorescence branches, clearly stipitate spikes, long floral bract mucros (4–5 mm long), and long sepal mucros (2–5 mm long). *Wittmackia caymanensis*, however, differs from *Wittmackia rohan-estyi* by its shorter stipes (6–18 mm vs. 19–39 mm long), green corollas (vs. white), and shorter and narrower petals (8–9.5 × 1.2 mm vs. 11.2 × 3 mm). In the second case, *W. caymanensis* can be separated from *W. mesoamericana* by its narrower leaf blades (5–12.7 cm vs. 14 cm wide at the base); longer (6–18 mm vs. 3–5 mm long) and more slender stipes (2–3 mm vs. 4–5 mm in diameter); narrower spikes (1.2–2 cm vs. 2.2–2.7 cm wide); shorter flowers (13.5 mm vs. 16–17.3 mm long); shorter and narrower petals (8.3–9.3 × 1.2 mm vs. 12.5–13.4 × 2.4–3 mm); and petal appendages detaching at 1.7 mm from the petal base (vs. 3.1–4.2 mm). In the protologue *W. caymanensis* is compared with *W. spinulosa* from which it differs.
for its divergent branches laxly distributed along the inflorescence rachis and much longer stipes (vs. subsessile).

ADDITIONAL SPECIMENS EXAMINED. CAYMAN ISLANDS. Grand Cayman: 1.5 miles southeast of Georgetown, 10–20 m, 6 September 1969, Proctor 31031 (IJ); George Town. Flowers subdivision near the High School on Carmen and Osie Godfrey land, 0–20 m, 14 December 1991, Roulstone 10 (CAYM). COLOMBIA. San Andrés y Providencia: Providencia, trocha entre playa suroeste y playa Manzanillo, aproximadamente a 500 m al noroccidente de playa Manzanillo, 70 m, 13°19'34.8''N, 81°23'06.7''W, 21 December 2013, Aguirre-Santoro 1949 (COL); Providencia, entre suroeste y Bahía Manzanillo, 5 m, 19 July 1990, Lowy et al. 146 (COL). UNITED STATES. Florida: Sarasota, field collected in Grand Cayman, and flowered in cultivation at the Marie Selby Botanical Gardens, 21 June 2011, Aguirre-Santoro 1509 (SEL).


*Hohenbergia brittoniana* L.B. Sm. (1932: 8). TYPE:—JAMAICA. Hanover Parish: Dolphin Head and vicinity, 400 m, 18–20 March 1908, *N.L. Britton 2313* (holotype NY!).

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Plant epiphytic or rupicolous, cespitose or solitary, 80–100 cm tall, acaulescent; rosette broad, forming phytotelmata. Leaves 70–90 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, elliptical, 19–24 × 8.5–12 cm, pale brown, lepidote on both surfaces, serrulate, occasionally entire; blade lingulate, 55–65 cm long, 7–9.5 cm wide at the base, 6.4–9.5 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, erect to antrorse, green, 0.2–1 mm long, apex rounded, mucronate. Inflorescence central, pendulous; peduncle almost completely exposed out of the rosette, stout, rigid, 60–78 cm long, 4–9 mm in diameter, green to dull purple, sparsely floccose, internodes between the medial bracts 2–6.5 cm, internodes between the apical bracts 1.8–3.5 cm; bracts of the peduncle shorter than the internodes, marcescent, chartaceous, nervose, green to dull purple, the medial bracts erect, lax, lanceolate, 7.3–9.3 × 1.2–1.8 cm, sparsely floccose, entire, apex acuminate, the apical bracts erect to suberect, lax, lanceolate, 8.7–10.7 × 0.5–0.9 cm, sparsely floccose, entire, apex acuminate to attenuate; fertile portion of the inflorescence paniculate, conical, 52–91 cm long, 23–36 cm wide in the middle, 1-divided, branches 19 to 38 in number, polystichous, rachis straight to slightly flexuous, green to dull purple, (45-)53.5–101 cm long, 3.3–6 mm in diameter, sparsely floccose. Primary bracts similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, divaricate to reclined, marcescent, chartaceous, nervose, shorter than the branches; the basal bracts lanceolate, 7.5–9 × 0.5–1 cm, green to dull purple, sparsely floccose, entire, apex attenuate; the apical bracts lanceolate, 1–2 × 0.3 cm, green to dull purple, sparsely floccose on both surfaces, entire, apex attenuate. Spikes cylindrical, 2.5–9.2 cm long, 1.2–2.1 cm wide in the middle; stipe exposed, 85–133 mm long, 1.3–1.8 mm in diameter, terete, sparsely floccose to glabrescent; rachis of the spike 2.5–9.2 cm long. Floral
bracts partially enclosing the ovaries, imbricate, suberect to ascending, subconcave, coriaceous, ovate, 6.5–11 × 6–7.8 mm, yellow, nervose, ecarinate, glabrous, entire, apex acute, mucronate, mucro 0.4–2.5 mm long. Flowers 26 to 50 per spike, polystichous, suberect, 6.5–11 mm long, sessile. Calyx dorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 4.4–5.3 mm long, 2.6–3 mm wide at the base, the unwinged side 0.9 mm wide, the winged side 2.2–3 mm wide, greenish yellow, surface smooth, the posterior sepals carinate, the anterior sepal ecarinate, glabrous, entire, apex acute, mucronate, mucro 0.4–1.2 mm long. Corolla tubular, apically spreading; petals free, membranaceous, oblong to oblanceolate, 9.3–13 × 1.4–2.7 mm, white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 4 mm from the petal base. Stamens included, the antepetalous stamens partially adnate to petals; filaments flattened, 8–8.1 mm long, 0.2–0.3 mm in diameter, white; anthers dorsifixed, rectangular to elliptical, 2.7–3.1 × 0.5–0.9 mm, white, apiculate. Epigynous tube 0.4–0.9 mm long. Ovary subovoid, dorsiventrally compressed, 2.2–3.3 mm long, 3.1–5.7 mm in diameter, yellow, glabrous, placentation apically-axile. Style longer than the stamens, flattened, 8.8–10.8 mm long, white; stigma conduplicate-spiral, white, 1.2 mm long. Ovules more than 30 per ovary, round, unappendaged. Fruit subovoid, dorsiventrally compressed, 7.8 mm long, 5.3–6.2 mm in diameter, white, glabrous; sepals persistent in fruit, partially fleshy (Fig. 3.6).

Etymology:—The specific epithet likely refers to the long distance between the spike and the inflorescence rachis.

Distribution, habitat, and phenology:—Wittmackia distans only occurs in fragmented forested areas in western Jamaica in the Parishes of Hanover and Westmoreland at 15–550 m elevation (Fig. 3.2F). Most collections of this species come from the Dolphin Head peaks in
Hanover Parish. It normally grows as epiphytic in moist limestone forests but can also be found as terrestrial on exposed limestone formations. *Wittmackia distans* grows sympatrically with *Wittmackia rohan-estyi*. Collected in flower from June to January.

**Conservation status:**—*Wittmackia distans* is categorized here as Critically Endangered (CR, B1a; IUCN 2001) because it has an extent of occurrence of less than 100 km² and only occurs in the Dolphin Head mountains, a protected area surrounded by rapidly growing urban development.

**Taxonomic comments and affinities:**—*Wittmackia distans* also belongs to the group of species with exceptionally long stipes, like *W. abbreviata, W. laesslei*, and *Wittmackia rohan-estyi*; in fact, this species exhibits the longest stipes in the group (up to 133 mm long). Besides this character, the most similar species of *W. distans* is *W. abbreviata* because of its pendulous inflorescence. However, *W. distans* has a longer and broader inflorescence (52–91 × 23–36 cm vs. 36–51 × 9.4–10 cm); generally longer basal primary bracts (7.5–9 cm vs. 4.7–7.5 cm long); longer stipes (85–133 mm vs. 51–63 mm long); and longer floral bracts (6.5–11 mm vs. 3.8–4.9 mm long).

**ADDITIONAL SPECIMENS EXAMINED. JAMAICA.** Hanover Parish: Dolphin Head Mountain, NE side of mountain; top of Dolphin Head mountain; on hillside, 544 m, 6 September 2011, *Acevedo-Rodriguez 11923* (IJ, NY, US); top of east side of the Dolphin Head mountains. Above Askenish, 542 m, 18°22′24.6″N, 78°9′18.5″W, 3 July 2012, *Aguirre-Santoro et al. 1814* (IJ, NY, US); road between Kingsvale and Retirement. Western slopes of Dolphin Head, 294 m, 18°22′32.7″N, 78°10′41.9″W, 4 July 2012, *Aguirre-Santoro et al. 1815* (IJ); Dolphin Head, 544 m, 9 June 2001, *Campbell s.n.* (IJ); 460–490 m, 24 May 1906, *Harris 9296* (GH, NY, UCWI); 490 m, 20 August 1952, *Proctor 7164* (IJ, US); interior summit slopes of Dolphin Head, 460–

*Hohenbergia eriostachya* Mez (1900: 255). TYPE:—JAMAICA. Portland Parish: between Lancaster and Moody's Gap, 700 m, 8 March 1895, *W.H. Harris 5566* (holotype B!, isotypes IJ!, NY [fragment attached to Britton 3419]!, UCWI!).

**Plant** epiphytic, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** 68.8–92 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, elliptical, 18–24 × 10–12.5 cm, green to pale brown, lepidote on both surfaces, serrulate, occasionally entire; blade lingulate, 48–72 cm long, 8.4–9.2 cm wide at the base, 7.2–9.3 cm wide in the middle, cinereous-green, surface smooth, lepidote on both surfaces, more densely on the abaxial side, serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, erect to antrorse, green to castaneous, 1.2–2.2 mm long, apex rounded, mucronate.

**Inflorescence** central, erect; peduncle partially concealed by the rosette, stout, rigid, 36.5–45 cm long, 4–9 mm in diameter, green, floccose, internodes between the medial bracts (1-)4.5–6.1 cm, internodes between the apical bracts 2.4–6.5 cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nervose, pale brown, the medial bracts erect, imbricate, lanceolate, 3.9–4.2 × 1–1.2 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate, the apical bracts erect, imbricate, lanceolate, 3–3.3 × 0.4–0.7 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate; fertile portion of the inflorescence paniculate, conical, 25.5–38.5 cm long, 6–9.6 cm wide in the middle, 1-divided, branches 20 to 50 in number, polystichous, rachis straight, green, 24.5–37.5 cm long, 4–4.2 mm in diameter, floccose.

**Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, ascending to diverging from the rachis, marcescent, chartaceous,
nervose, shorter than the branches; the basal bracts lanceolate, 2.5–3.2 × 0.4–0.5 cm, pale brown, floccose abaxially, glabrescent adaxially, entire, apex acuminate; the apical bracts triangular, 0.6–1.1 × 0.2–0.3 cm, pale brown, floccose on both surfaces, entire, apex acuminate. **Spikes** globose to cylindrical, 2.3–2.6 cm, 1–1.7 cm wide in the middle; stipe exposed, 17–27 mm long, 1.5–3 mm in diameter, terete, floccose; rachis of the spike 2.3–2.6 cm long. **Floral bracts** partially enclosing the ovaries, imbricate, suberect, concave, strongly coriaceous, orbicular to broadly ovate, 7.3–9.1 × 9.1–13 mm, dark castaneous, nervose, ecarinate, floccose-lepidote abaxially, glabrescent adaxially, entire, apex rounded to truncate, mucronate, mucro 0.8–1.4 mm long. **Flowers** 10 to 16 per spike, polystichous, suberect, 7.3–9.1 mm long, sessile. **Calyx** dorsiventrally compressed; sepals strongly coriaceous, asymmetrical, forming a lateral wing, 3.6–5.4 mm long, 2.2 mm wide at the base, the unwinged side 0.9 mm wide, the winged side 2.1 mm wide, stramineous, nervose, the posterior sepals carinate, the anterior sepal ecarinate, floccose, entire, mucronate, mucro 0.3–1 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, 9.5 × 1.3 mm, white, glabrous, entire, apex acute; petal appendages absent. **Stamens** included; filaments 6.7 mm long, 0.2 mm in diameter; anthers dorsifixed, 2.3 × 0.5 mm. **Epigynous tube** 0.2–0.8 mm long. **Ovary** subovoid, dorsiventrally compressed, 2.4–3.5 mm long, 5.4–5.7 mm in diameter, light green, floccose, placentaion apically-axile. **Style** 9 mm long; stigma conduplicate-spiral. **Ovules** unappendaged. **Fruit** subovoid, dorsiventrally compressed (Fig. 3.7).

**Etymology:**—The specific epithet comes from the Greek *erion* (=wool) and *stachys* (=spike). It probably refers to the characteristic brown-tomentose-lepidote indument present in floral bracts and flowers.
Distribution, habitat, and phenology:—*Wittmackia eriostachya* is endemic to the Blue and John Crow Mountains in eastern Jamaica at 300–1250 m elevation (Fig. 3.2F). It grows as epiphytic in moist montane forest, at the edges of forests. *Wittmackia eriostachya* occurs sympatrically with *W. penduliflora* and at the edge of the distribution of *W. fawcetii* and *W. polycephala*. Collected in flower in September.

Conservation status:—*Wittmackia eriostachya* is categorized here as Endangered (EN, B1a; IUCN 2001) because it has an extent of occurrence of about 600 km², has been collected in at least six localities, and grows strictly in medium-high elevations of the protected Blue and John Crow Mountains of Jamaica. Despite the protected status of this area, the expansion of crops and recent colonization of invasive species represent potential threats for *W. eriostachya*.

Taxonomic comments and affinities:—*Wittmackia eriostachya* is a very distinctive species that can be recognized from other Caribbean *Wittmackia* by its stipitate spikes bearing floral bracts and flowers covered with a characteristic brown-tomentose-lepidote indument. This type of indument is also present in *W. polycephala* but this species has always leaf teeth of 0.3–1 mm long (vs. 1.2–2.2 mm long); primary bracts longer than the spikes (vs. shorter), and sessile spikes.

ADDITIONAL SPECIMENS EXAMINED. JAMAICA. Portland Parish: Blue Mountains. Hardwar Gap, Hollywell Park. Shelter trail, 1231 m, 18°5′5.6″N, 76°43′30.1″W, 20 June 2012, Aguirre-Santoro et al. 1801 (IJ, NY, US); upper Swift River, study site of ecological survey, Blue Mt. Multipurpose project near Mossman's peak, 850 m, 28 September 1983, Bretting J-258 (IJ); vicinity of Cinchona. Slopes of John Crow peak, 2–10 September 1906, Britton 291 (NY); John Crow Mountains. Eastern slopes, 520 m, 9–11 March 1909, Britton 4142 (NY); Proctor's Pool, 730 m, duQuesnay 351 (UCWI); John Crow mountains, 1.5 miles.


**Plant** epiphytic, cespitose or solitary, acaulescent; rosette broad, forming phytotelmata. **Leaves** 79–91 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, elliptical, 13–26 × 8.7–14.8 cm, cream to pale brown, serrulate, occasionally entire; blade lingulate, 66–71 cm long, 6.7–8.2 cm wide at the base, 5.4–7.7 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, hook-shaped, antrorse, castaneous, 0.8–2.8 mm long, apex obtuse to rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle almost completely exposed out of the rosette, stout, rigid, 47–48 cm long, 4–9 mm in diameter, green, floccose, internodes between the medial bracts 3–4.8 cm, internodes between the apical bracts 1–4.3 cm; bracts of the peduncle shorter to longer than the internodes, deciduous, chartaceous, nervose, pale brown, the medial bracts erect, lax, lanceolate to ovate, (3-)7.5–8.4 × (0.7-)1.3–1.7 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate, the apical bracts erect to suberect, lax, lanceolate, (3.1-)3.8–4.7 × 0.7–1.2 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate; fertile portion of the inflorescence paniculate, conical, 18.8–46.5 cm long, 7.8–12.8 cm wide in the middle, 1-divided, occasionally 2-divided, branches 17 to 41 in number, polystichous, rachis straight, green, 15.5–41 cm long, 4–7 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, divaricate, marcescent, chartaceous, nervose, shorter than the branches; the basal bracts
lanceolate, (2.4-)3.8–7.4 × 0.6–1.4 cm, pale brown, floccose abaxially, glabrescent adaxially, entire, apex acuminate; the apical bracts triangular, 0.8–1.6 × 0.2–0.3 cm, pale brown, floccose on both surfaces, entire, apex acuminate. **Spikes** cylindrical, 2.9–4.7 cm, 1.2–1.5 cm wide in the middle; stipe exposed, 11–24 mm long, 2.5–3 mm in diameter, terete, sparsely floccose; rachis of the spike straight, 2.9–4.7 cm long. **Floral bracts** partially enclosing the ovaries, imbricate, suberect, concave, strongly coriaceous, orbicular to broadly ovate, 5.9–8.2 × 7–10 mm wide, stramineous, nervose, ecarinate, sparsely floccose to glabrescent, entire, apex obtuse to rounded, mucronate, mucro 0.2–0.9 mm long. **Flowers** 17 to 25 per spike, polystichous, suberect, 5.9–8.2 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, asymmetrical, forming a lateral wing, 5.8–7 mm long, 2.8–2.9 mm wide at the base, the unwinged side 1–1.5 mm wide, the winged side 2.6–2.7 mm wide, light green, surface smooth, the posterior sepals carinate, the anterior sepal ecarinate, glabrescent to floccose towards the apex, entire, apex acute, mucronate, mucro 0.2–0.5 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, 12–14 × 2.8 mm, white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens. **Stamens** included; filaments flattened, 9.7 mm long, 0.1–0.5 mm in diameter, white; anthers dorsifixed, rectangular, 2.6–3.3 × 0.4–0.6 mm, cream, mucronate. **Epigynous tube** 0.4–0.5 mm long. **Ovary** subovoid, dorsiventrally compressed, 3–3.5 mm long, 4.2–5.5 mm in diameter, light green, glabrous, placentation apically-axile. **Style** longer than the stamens, 13 mm long, white; stigma conduplicate-spiral, white, 1.2 mm long. **Ovules** round, unappendaged. Fruit subovoid, dorsiventrally compressed, 9.8 mm long, 4.7 mm in diameter, glabrous; sepals persistent, not fleshy. **Seeds** more than 10 per fruit, club-shaped, 2.1 × 0.8 mm, reddish-brown (Fig. 3.8).
Etymology:—Wittmackia fawcettii was named in honor to the British botanist William Fawcet.

Distribution, habitat, and phenology:—Wittmackia fawcettii is endemic to the Blue Mountains in eastern Jamaica at 1000–1400 m elevation (Fig. 3.2E). It grows as epiphytic in moist montane forest, at the edges of forests and near rivers. Wittmackia fawcettii grows sympatrically with W. penduliflora and W. polycephala. Collected in flower in June.

Conservation status:—Wittmackia fawcettii is categorized here as Endangered (EN, B1a; IUCN 2001) because it is only known from a restricted area within the Blue mountains characterized for the presence of agricultural activities and aggressively invasive species such as Pittosporum undulatum and Polygonum chinense. Nevertheless, this species still occurs within the protected area of the Blue and John Crow Mountains National Park.

Taxonomic comments and affinities:—Wittmackia fawcettii resembles W. jamaicana by its elongated spikes, obtuse floral bracts, and short sepal mucros; however, it differs from this species by its more slender peduncle (4–9 mm vs. 10–12 mm in diameter); bracts of the peduncle entire (vs. serrate); narrower inflorescence (7.8–12.8 cm vs. 15–25 cm wide), rachis sparsely floccose (vs. glabrous); shorter spikes (2.9–4.7 cm vs. 5.8–7.8 cm long), bearing less flowers (18 to 35 vs. 40 to 50 flowers per spike); floral bracts sparsely floccose (vs. glabrous), with a shorter mucro (0.2–0.9 mm vs. 1.7–4.7 mm long); and longer sepals (5.8–7 mm vs. 3–4.5 mm long). Moreover, W. jamaicana is endemic and highly restricted to the western side of Jamaica. In the protologue W. fawcettii is compared to W. polycephala but mainly differs from this species by its stipitate spikes (vs. sessile) and floral bracts sparsely white-floccose (vs. brown-tomentose-lepidote).

**Plant** epiphytic or rupicolous, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** 88–124 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, elliptical, 20–24 × 9.5–11.3 cm, pale brown, lepidote on both surfaces, entire; blade lingulate, 62–100 cm long, 4.3–8.9 cm wide at the base, 4–8 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, entire to serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, erect to antrorse, green, 0–1.1 × 0.6–0.8 mm, apex rounded, mucronate. **Inflorescence** central, erect to pendulous; peduncle almost completely exposed out of the rosette, stout, pliable, 57.5–73.2 cm long, 3.5–9 mm in diameter, green, floccose, internodes between the medial bracts 4.2–6.6 cm, internodes between the apical bracts 4.7–7 cm; bracts of the peduncle shorter to longer than the internodes, marcescent, chartaceous, nervous, green to dull purple, the medial bracts erect, imbricate to lax, lanceolate, 6–8.5(-10.2) × 1.3–1.8 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate, the apical bracts erect, imbricate, lanceolate, 5.2–7.8(-9.8) × 0.9–1.6 cm, sparsely floccose, entire, apex acuminate to attenuate; fertile portion of the inflorescence paniculate, conical, 21.5–39.5 cm long, 9.8–17.8 cm wide in the middle, 1-divided, occasionally 2-divided, branches 10 to 20 in number, polystichous, rachis straight, green to dull purple, (14-18–37 cm long, 2.8–5 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, diverging from the rachis, marcescent, chartaceous, nervous, shorter than the branches; the basal bracts linear-lanceolate, 4.8–6.3(-7.5) × 0.7–1 cm,
green to dull purple, sparsely floccose, entire, apex attenuate; the apical bracts lanceolate to triangular, 1.5–2.2 × 0.3–0.4 cm, green to dull purple, sparsely floccose on both surfaces, entire, apex attenuate. **Spikes** ovoidal to cylindrical, 2.2–6 cm long, 1.4–1.8(-2.4) cm wide in the middle; stipe exposed, 24–49 mm long, 1.8–3.2 mm in diameter, terete, sparsely floccose; rachis of the spike straight, 2.2–6 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the ovaries, imbricate, suberect, subconcave, coriaceous, ovate, 9.5–13 × 6–11 mm, cream to yellow, nervose, carinate, glabrous, occasionally sparsely floccose on both surfaces, entire, apex acute, mucronate, mucro 0.9–2.7 mm long. **Flowers** 8 to 20 per spike, polystichous, suberect, 9.5–13 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 7–8.2 mm long, 2.4–3.2 mm wide at the base, the unwinged side 0.7–1.7 mm wide, the winged side 1.7–2.5 mm wide, green to yellow, surface smooth, the posterior sepals carinate, the anterior sepal ecarinate, glabrous, entire, apex acute, mucronate, mucro 0.9–1.9 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, 9.8–15 × 1.4–2.6 mm, white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 4 mm from the petal base. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 8.3 mm long, 0.2 mm in diameter, white; anthers dorsifixed, rectangular, 2.9–3.2 × 0.6 mm, cream, mucronate. **Epigynous tube** 0.6 mm long. **Ovary** subovoid, dorsiventrally compressed, 1.5–5.4 mm long, 3.5–5.8 mm in diameter, greenish white, glabrous, placentation apically-axile. **Style** longer than the stamens, 10–12.5 mm long; stigma conduplicate-spiral, 0.9–1.4 mm long. **Ovules** more than 30 per ovary, round, unappendaged. **Fruit** 11.8 mm long, 7 mm in diameter (Fig. 3.9).
**Etymology:**—The specific epithet probably refers to the lack or scarcity of teeth on the leaf blades.

**Distribution, habitat, and phenology:**—*Wittmackia inermis* is endemic to the central and western regions of the Cockpit Country in Jamaica at 100–670 m elevation (Fig. 3.2E). It grows as epiphytic on wooded limestone hills or as terrestrial on exposed limestone banks. Collected in flower from August to November.

**Conservation status:**—*Wittmackia inermis* is categorized here as Vulnerable (VU, B1a; IUCN 2001) because its extent of occurrence of about 900 km$^2$ includes more than ten populations inhabiting well-preserved, but often fragmented, forests in central to western Jamaica, including the protected Cockpit Country.

**Taxonomic comments and affinities:**—The relatively large and yellow floral bracts at anthesis of *Wittmackia inermis* makes it similar to *W. urbaniana*. However, *W. inermis* is different because of its generally longer inflorescence rachis ((14-)18–37 cm vs. 7.3–16 cm long); longer (24–49 mm vs. 4–20 mm long) and more slender stipes (1.8–3.2 mm vs. 5–10 mm in diameter); shorter sepals (7–8.2 mm vs. 9.1–11.8 mm long); petal appendages detaching at 7.3 mm from the base (vs. 10–12 mm); and shorter filaments (8.3 mm vs. 10.3–13 mm long). In the protologue *W. inermis* is compared with *W. portoricensis* but mainly differs from this species by its broader inflorescence (10–18 cm vs. 4–9 cm wide); longer stipes (24–49 mm vs. 12–21 mm long); floral bracts longer (9.5–13 mm vs. 6.6–10.2 mm long), yellow in anthesis (vs. green), and obtuse (vs. acuminate to acute); longer sepals (7–8.2 mm vs. 3.8–5–8 mm long); and presence of petal appendages (vs. absence).

**ADDITIONAL SPECIMENS EXAMINED. JAMAICA. St. James Parish: Cockpit Country. Road between Niagara and Mocho. 3 km N of Niagara. Close to White Rock Hill, 612**
m, 18°15'58.2"N, 77°49'49.5"W, 25 June 2012, Aguirre-Santoro et al. 1808 (IJ, NY); 1 mile south of Sweet Water, 640 m, 23 May 1953, Proctor 7978 (IJ); Chatsworth district, 1.5 miles N.N.W. of Maroon Town, 488 m, 10 March 1955, Proctor 11751 (IJ); White Rock Hill, c. 1 mile south of Sweet Water, 610–670 m, 2 December 1962, Proctor 23001 (IJ, US). Trelawny Parish: about 4 miles WNW of Troy, on Crown Lands road. Cockpit Country, 549–610 m, 15 July 1963, Crosby et al. 756 (UCWI); Boothe district, c. 3 miles north of Troy, 488 m, 14 March 1955, Proctor 9959 (IJ); Windsor estate, 122–183 m, 27 August 1955, Proctor 10626 (IJ, US).

Westmoreland Parish: Newmarket and vicinity. Near Darliston, 13–22 September 1907, Britton 1468 (NY); Bluefields and vicinity. Bluefields mountain, 6–7 March 1908, Britton 1966 (NY); Copse Mountain 1–2 km Sw. of Rat Trap S. of Bethel Town, 366–549 m, February to March 1986, Kelly et al. 1725 (IJ); Kelly et al. 1726 (MO); 1 mile W.N.W. of Hopewell, 533 m, 21 November 1955, Proctor 11239 (IJ, US); vicinity of One-day Cave, c. 1 mile west of Rat Trap, 304–335 m, 23 October 1960, Proctor 21505 (IJ, US); between Struie and Copse near Darliston, 14 September 1966, Read 1706 (US). UNITED STATES. Florida: Sarasota, flowered in cultivation at the Marie Selby Botanical Gardens, BIC 396. Originated from Jamaica, 25 June 1991, Dexter s.n. (SEL); 13 July 1991, Dexter s.n. (SEL).


Basionym: *Hohenbergia jamaicana* L.B. Sm. & Proctor in Smith (1960: 251). TYPE:—

JAMAICA. St. James Parish: 1.5 miles N of Catadupa, 381 m, 5 April 1952, *G.R. Proctor 6543* (holotype IJ!, isotype US [fragment]!).

**Plant** epiphytic, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** 102–104 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong to elliptical, 18–27 × 10–11.5 cm, pale brown, lepidote on both surfaces, entire; blade lingulate, 75–80 cm long, 8–8.2 cm wide at the base, 6.5–8.2 cm wide in the middle, green, occasionally maculate, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, triangular, erect, dark castaneous, 1–1.2 × 0.7 mm, apex rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle almost completely exposed out of the rosette, stout, rigid, 35.2–73.5 cm long, 10–12 mm in diameter, green,
internodes between the medial bracts 3.2–4.2 cm, internodes between the apical bracts 1.6–2.1 cm; bracts of the peduncle all bracts longer than the internodes, marcescent, chartaceous, nervous, pale brown, the medial bracts erect, imbricate, linear-lanceolate, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate, the apical bracts ascending to diverging from the rachis, lax, linear-lanceolate, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate; fertile portion of the inflorescence paniculate, conical, 30–50.2 cm long, 15–25 cm wide in the middle, 1-divided, occasionally 2-divided, branches 32 to 50 in number, polystichous, rachis straight, green, 39–50 cm long, 5–7 mm in diameter, glabrescent. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, ascending to diverging from the rachis, marcescent, chartaceous, nervous, longer than the branches; the basal bracts linear-lanceolate, pale brown, entire, apex attenuate; the apical bracts lanceolate, pale brown, entire. **Spikes** cylindrical, 5.8–7.8 cm long, 1.6–1.8 cm wide in the middle; stipe exposed, 18–52 mm long, 3 mm in diameter, terete, glabrous; rachis of the spike straight, 5.8–7.8 cm long. **Floral bracts** partially enclosing the ovaries, imbricate, suberect to ascending, concave, coriaceous, broadly ovate, 6.1–9.2 × 6.3–8.6 mm, castaneous, nervous, ecarinate, glabrous, entire, apex obtuse, mucronate, mucro 1.1–4.7 mm long. Flowers 40 to 50 per spike, polystichous, ascending, 6.1–9.2 mm long, sessile. **Calyx** dorsiventrally compressed; sepals strongly coriaceous, asymmetrical, forming a lateral wing, 3–5.4 mm long, 2.6–4 mm wide at the base, the unwinged side 0.9 mm wide, the winged side 2.3 mm wide, green to castaneous, nervous, the posterior sepals carinate, the anterior sepal ecarinate, glabrous, entire, mucronate, mucro 0.5–0.8 mm long. Petals, stamens, and style unknown. **Epigynous tube** 0.6–7 mm long. **Ovary** dorsiventrally compressed, placentation apically-axile. **Fruit** subovoid, dorsiventrally compressed, 8.3–10 mm
long, 4.9–7.3 mm in diameter, light green, glabrous. **Seeds** club-shaped, 2.1 × 5 mm, reddish-brown (Fig. 3.10).

**Etymology:**—The specific epithet refers to the occurrence of this species in Jamaica.

**Distribution, habitat, and phenology:**—*Wittmackia jamaicana* is endemic to the western region of the Cockpit Country in the Parishes of Hanover and St. James of Jamaica at 300 m elevation (Fig. 3.2E). It grows as epiphytic at the edges of forests on limestone formations. The flowering phase of this species is unknown.

**Conservation status:**—*Wittmackia jamaicana* is categorized here as Critically Endangered (CR, B1a; IUCN 2001) because it is only know from three small populations located in the western edge of the Cockpit Country, in a region surrounded by urban areas and main roads. This area is beyond the limits of the Cockpit Country, thus its protection has not been considered prioritary.

**Taxonomic comments and affinities:**—The corollas of *Wittmackia jamaicana* are unknown; however, this species is easy to recognize by its glabrous, obtuse floral bracts bearing a long mucro, and sepals short-mucronate. *Wittmackia jamaicana* is similar to *W. fawcettii*, an endemic to the Blue Mountains in eastern Jamaica, but differs from this species by its stouter peduncle (10–12 mm vs. 4–9 mm in diameter); bracts of the peduncle serrate (vs. entire); broader inflorescence (15–25 cm vs. 7.8–12.8 cm wide), glabrous rachis (vs. sparsely floccose); longer spikes (5.8–7-8 cm vs. 2.9–4.7 cm long), bearing more flowers (40 to 50 vs. 18 to 35 flowers per spike); glabrous floral bracts (vs. sparsely floccose), with a longer mucro (1.7–4.7 mm vs. 0.2–0.9 mm long); and shorter sepals (3–4.5 mm vs. 5.8–7 mm long).

Country. Road between Marchmont and Bruce Hall, 205 m, 18°16'.22.2”N, 77°53'18.4”W, 25 June 2012, *Aguirre-Santoro et al. 1810* (IJ, NY, US); Mt. Carey district, 1 mile south of Anchovy, 200 m, 7 July 1957, *Proctor 16452* (IJ, NY [photo]).

![Wittmackia jamaicana](image)


9. *Wittmackia laesslei* (L.B. Sm.) Aguirre-Santoro, (pending publication). Basionym:

*Hohenbergia laesslei* L.B. Sm. (1956b: 52). TYPE:—JAMAICA. St. James Parish: Cockpit Country near Sweet Water, 570 m, 16 August 1952, *A. Laessle s.n.* (holotype IJ!, isotype US [fragment]!).
**Plant** epiphytic, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** 70–90 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong to elliptical, 17–23 × 9.8–12 cm, white to pale brown, lepidote on both surfaces, entire; blade lingulate, 55–73 cm long, 7.3–9 cm wide at the base, 7.3–8.3 cm wide in the middle, green, occasionally maculate, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, triangular, erect, castaneous, 0.3–0.7 mm long, apex rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle almost completely exposed out of the rosette, stout, rigid, 41–66.5 cm long, 6–8 mm in diameter, light green, floccose, internodes between the medial bracts 3.5–5 cm, internodes between the apical bracts 2–3.5 cm; bracts of the peduncle shorter than the internodes, marcescent, chartaceous, nerveose, light green to cream, the medial bracts erect, imbricate, lanceolate, 10.8–12.5 × 1.3–1.6 cm, floccose on both surfaces, entire, apex acuminate, the apical bracts erect, lax, linear-lanceolate, 10.7–12.5 × 0.7–0.9 cm, floccose on both surfaces, entire, apex attenuate; fertile portion of the inflorescence paniculate, conical, 37.5–39 cm long, 11.4–12.5 cm wide in the middle, 1-divided, branches 32 to 47 in number, polystichous; rachis straight, green, 29–35 cm long, 3–5 mm in diameter, densely floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, reclined, marcescent, chartaceous, nerveose, longer than the branches; the basal bracts linear-lanceolate, 10.2–10.7 × 0.9–1 cm, light green to cream, floccose on both surfaces, entire, apex attenuate; the apical bracts lanceolate, 1.2–1.4 × 0.2–0.3 cm, light green, floccose on both surfaces, entire, apex attenuate. **Spikes** subcylindrical to ovoidal, 2.3–3.3 cm long, 1.1–1.5 cm wide in the middle; stipe exposed, 40–42 mm long, 2.5–3 mm in diameter, terete, sparsely floccose; rachis of the spike straight, 2.3–3.3 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially
enclosing the ovaries, imbricate, suberect, subconcave, coriaceous, ovate, 5.8–10.2 × 7–9.8 mm, light green to cream, nerveose, ecarinate, sparsely floccose, minutely serrulate, occasionally entire, apex acute to acuminate, mucronate, mucro 1.8–4.5 mm long. **Flowers** 12 to 18 per spike, polystichous, suberect, 5.8–10.2 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, coriaceous, triangular, asymmetrical, forming a lateral wing, 4.2–5 mm long, 2.3–3.3 mm wide at the base, the unwinged side 0.5–0.8 mm wide, the winged side 1.9–2 mm wide, light green, nerveose, the posterior sepals carinate, the anterior sepal ecarinate, glabrous, entire, apex acute, mucronate, mucro 0.5–1.4 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, spatulate, 9–10.2 × 1.7–2.1 mm, white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 2.6 mm from the petal base. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 7.9 mm long, .4 mm in diameter, white; anthers dorsifixed, elliptical, 2.4 × 0.6 mm, cream, mucronate. **Epigynous tube** 0.2–0.3 mm long. **Ovary** subovoid, dorsiventrally compressed, 2.8–4.2 mm long, 4.4–6.3 mm in diameter, light green, sparsely floccose, placentation apically-axile. **Style** longer than the stamens, 11.8 mm long, white; stigma conduplicate-spiral, white, 0.8 mm long. **Ovules** more than 30 per ovary, round, unappendaged. **Fruit** unknown (Fig. 3.11).

**Etymology:**—This species was named in honor to Albert M. Laessle, collector of the type specimen.

**Distribution, habitat, and phenology:**—*Wittmackia laesslei* is endemic to the western region of the Cockpit Country in Jamaica at 550–750 m elevation (Fig. 3.2C). It grows as epiphytic or rupicolous on forested limestone hills. This species is only known from the type locality, where it forms large populations. Collected in flower from June to August.
**Conservation status:**—*Wittmackia laesslei* is categorized here as Critically Endangered (CR, B1a; IUCN 2001) because it is only known from two small populations growing in a restricted area of the central Cockpit Country.

**Taxonomic comments and affinities:**—*Wittmackia laesslei* is another species that can be easily recognized by its exceptionally long stipes, just like *W. abbreviata*, *W. distans* and *Wittmackia rohan-estyi*. It can be separated from *W. abbreviata* and *W. distans* by its erect to inclined inflorescence in anthesis (vs. pendulous) and primary bracts longer than the inflorescence branches (vs. shorter). *Wittmackia laesslei* differs from *Wittmackia rohan-estyi* by its medial bracts of the peduncle shorter than the internodes (vs. longer); longer stipes (40–42 mm vs. 19–39 mm long); lesser flowers per spike (12 to 18 vs. 18 to 35 flowers per spike); and broader floral bracts (7–9.8 mm vs. 3.6–6.5 mm wide). In the protologue *Wittmackia laesslei* is compared with *W. inermis* and *W. fawcettii* but mainly differs from both species by its much longer primary bracts, floral bracts light green to cream (vs. pale brown or yellow), and shorter sepals (4.2–5 mm vs. 5.8–8.2 mm long).

**ADDITIONAL SPECIMENS EXAMINED. JAMAICA.** St. James Parish: Cockpit Country. Road between Mocho and Catadupa. About 2.5 km W of Mocho, 642 m, 18°17′16.1″N, 77°50′40.8″W, 25 June 2012, Aguirre-Santoro et al. 1809 (IJ, NY, US); about 0.5 mile west northwest of Mocho Crossroads on road to Catadupa, 670–731 m, 23–24 August 1965, Hespenheide et al. 1585 (MO); Mocho District, 640 m, 30 July 1955, Proctor 10393 (IJ).

*Plant* terrestrial, cespitose, acaulescent, ca. 130 cm tall; rosette broad, forming phytotelmata. **Leaves** 66 (j) cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, subelliptical, 13–16 × 10.5–14 cm, green to black castaneous, lepidote on both surfaces, entire; blade lingulate, 120 cm long, 14 cm wide at the base, 11.2 cm wide in the middle, green, nervose, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, hook-shaped, mainly antrorse, castaneous, 1.5 mm long, apex acute to rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle almost completely exposed out of the rosette, stout, rigid, 54–71 cm long, 5–10 mm in diameter, green, densely floccose, internodes between the medial bracts 5–9 cm, internodes between the apical bracts 4.2 cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nervose, light green, the medial bracts erect, imbricate, linear-lanceolate, 9–16 × 0.5–1.3 cm, lepidote on both surfaces, serrulate, the teeth evenly distributed along the margins, apex attenuate, the apical bracts ascending, lax, linear, 9–15.5 × 0–5–0.9 cm, lepidote on both surfaces, serrulate, the teeth evenly distributed along the margins, apex attenuate; fertile portion of the inflorescence paniculate, conical, 29–48 cm long, 9.4 cm wide in the middle, 1-divided, branches 21 to 50 in number, polystichous, rachis straight, green, 24–43 cm long, 7 mm in diameter, densely floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in
size towards the apex of the inflorescence, diverging from the rachis, marcescent, chartaceous, nervose, longer than the branches; the basal bracts linear, 8.2–14.5 × 0.4–0.6 cm, light-green, floccose-lepidote on both surfaces, serrulate, the teeth irregularly distributed along the margins, apex attenuate-caudate; the apical bracts linear-lanceolate, 1.9 × 0.3 cm, light green, lepidote on both surfaces, entire, apex attenuate. **Spikes** cylindrical to long-ovoidal, 3.2–4.9 cm, 2–2.7 cm wide in the middle; stipe exposed, 3–6 mm long, 4–5 mm in diameter, terete, densely floccose; rachis of the spike straight, 4.5 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the ovaries, imbricate, suberect to ascending, subconcave, coriaceous, ovate, 5.7 × 5.6 mm wide, green, nervose, the posterior sepals carinate, the anterior sepal ecarinate, floccose-lepidote on both surfaces, minutely serrulate, occasionally entire, apex acuminate, mucronate, mucro 4.2 mm long. **Flowers** 15 to 45 per spike, polystichous, suberect to ascending, 16–17.3 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 5 mm long, 4–4.1 mm wide at the base, the unwinged side 1.8 mm wide, the winged side 2.2 mm wide, green, nervose, the posterior sepals carinate, the anterior sepal ecarinate, sparsely floccose, entire, apex acute, mucronate, mucro 2.6 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, oblong to subspatulate, 12.5–13.4 × 2.4–3 mm, green, basally white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 3.1–4.2 mm from the petal base. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 8.3–9 mm long, 0.2 mm in diameter, white; anthers parallel versatile, rectangular to lanceolate, 2.7–2.9 × 0.5–0.7 mm, cream, apiculate. **Epigynous tube** 1.2 mm long. **Ovary** ovoidal, 4.4 mm long, 5.7 mm in diameter, green, floccose-lepidote, placentation apically-axile. **Style** longer than the stamens, cylindrical, 11.2 mm long, green; **stigma**
conduplicate-spiral, green, 2 mm long. **Ovules** more than 30 per ovary, round, unappendaged.

**Fruit** unknown (Fig. 3.12).

**Etymology:**—The specific epithet indicates that this is the only species of the Caribbean *Wittmackia* that occurs in Mesoamerica.

**Distribution, habitat, and phenology:**—*Wittmackia mesoamericana* is only known from one population in the coastal region of the Yucatan peninsula in Mexico at 0 m elevation (Fig. 3.2A). It grows as epiphytic or terrestrial on forested limestone formations. Collected in flower from February to March.

**Conservation status:**—In the protologue, Ramírez-Morillo et al. (2010) highlighted the imminent threats to the habitat of *Wittmackia mesoamericana* and categorized the species as Critically Endangered (CR, D).

**Taxonomic comments and affinities:**—*Wittmackia mesoamericana* is similar to *W. caymanensis* because of its floccose inflorescence rachis, primary bracts much longer than the inflorescence branches, clearly stipitate spikes, long floral bract mucros (4–5 mm long), long sepal mucros (2–5 mm long), and green petals. However, *W. mesoamericana* is different from *W. caymanensis* by its broader leaf blades (14 cm vs. 5–12.7 cm wide at the base); shorter (3–5 mm vs. 6–18 mm long) and stouter stipes (4–5 mm vs. 2–3 mm in diameter); broader spikes (2.2–2.7 cm vs. 1.2–2 cm wide); longer flowers (16–17.3 mm vs. 13.5 mm long); longer and broader petals (12.5–13.4 × 2.4–3 mm vs. 8.3–9.3 × 1.2 mm); and petal appendages detaching at 3.1–4.2 mm from the petal base (vs. 1.7 mm). The affinity between *W. mesoamericana* and *W. caymanensis* is supported by the phylogenetic study of Aguirre-Santoro (in preparation; see chapter 1), which shows these species as sister taxa. In the protologue, *W. mesoamericana* is compared with *W. spinulosa* because of their similar inflorescence architecture but, more
importantly, because both species exhibit green petals. *Wittmackia mesoamericana*, however, mainly differs from *W. spinulosa* by its longer and broader leaf blades (120 × 14 cm vs. 41–58 × 9.6–11 cm long; longer peduncle (54–71 cm vs. 21.8–33–5 cm long); broader inflorescence (9.4 cm vs. 4.6–8.7 cm wide); inflorescence branches laxly distributed along the rachis (vs. congested) and divergent (vs. suberect); and broader spikes (2.2–2.7 cm vs. 0.8–1.5 cm wide).

**ADDITIONAL SPECIMENS EXAMINED.** MEXICO. Quintana Roo: Solidaridad, predio Punta Young, rancho Estrella del Sur, fracción B y rancho Estrella del Sur, fracción C, flexión derecha del km 266 + 200, de la carretera federal 307 Reforma Agraria-Puerto Juárez, tramo Tulum - Playa del Carmen. Florecida de la planta original colectada en 10 marzo, 2008, 0 m, 20º32'3"N, 87º9'50"W, 1 February 2011, Ramírez 1666 (CICY, SEL).

![Figure 3.12. *Wittmackia mesoamericana.* A. Inflorescence and part of the leaf blades. B. Calyx and corolla of rehydrated flower. D. Sepals E. Petal. F. Petal appendages. F. Apical portion of the stamen. G. Apical portion of the style and stigma. (A-G: Ramírez 1666. Photos of living specimens: I. Ramírez).](image)

Basionym: *Hohenbergia negrilensis* Britton ex L.B. Sm. (1935: 151). TYPE:—JAMAICA.


**Plant** epiphytic or rupicolous, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** strongly coriaceous; sheath conspicuously differentiated from the blade, oblong, pale brown, lepidote on both surfaces, serrulate, occasionally entire; blade lingulate, 13.2 cm wide at the base, 11.5–12.1 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, triangular, erect, green or castaneous, 0.2–0.4 mm long, apex rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle partially concealed by the rosette, stout, rigid, 6–7 mm in diameter, green, floccose, internodes between the medial bracts 2.4–5.4 cm, internodes between the apical bracts 2.2–2.3 cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nervose, light green, the medial bracts erect, imbricate, linear-lanceolate, 15–19 × 1.2–1.5 cm, lepidote on both surfaces, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate, the apical bracts suberect, lax, linear-lanceolate, 14–17 × 0.9–1.3 cm, lepidote on both surfaces, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate; fertile portion of the inflorescence paniculate, conical, 57 cm long, 10.3–10.4 cm wide in the middle, 1-divided, branches 47 to 50 in number, polystichous, rachis straight, green, 48 cm long, 7–8 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, ascending to diverging from the rachis, marcescent, chartaceous, nervose, longer than the branches; the basal bracts linear-
lanceolate, 14.5–14.8 × 1–1.2 cm, light-green, lepidote, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate; the apical bracts lanceolate, 1.2 × 0.2 cm, light green, lepidote on both surfaces, entire, apex attenuate. Spikes cylindrical, 3.8–5.8 cm long, 1.7–1.9 cm wide in the middle; stipe exposed, 2–8 mm long, 3–4 mm in diameter, terete, floccose; rachis of the spike straight, 3.8–5.8 cm long, green. Floral bracts partially enclosing the ovaries, imbricate, ascending to diverging from the rachis, subconcave, coriaceous, ovate, 3.7–5 × 4.4–5.2 mm, green, nervous, floccose-lepidote abaxially, glabrescent adaxially, entire to minutely serrulate, apex acute, mucronate, mucro 4–4.2 mm long. Flowers 50 to 60 per spike, polystichous, ascending, 10–12.5 mm long, sessile. Calyx dorsiventrally compressed; sepal strongly coriaceous, asymmetrical, forming a lateral wing, 2.9–3.7 mm long, 2.2–4 mm wide at the base, the unwinged side 0.6 mm wide, the winged side 2 mm wide, green, nervous, the posterior sepals carinate, the anterior sepal ecarinate, glabrescent to sparsely floccose, mucronate, mucro 1.8–2.1 mm long. Corolla tubular, apically spreading; petals membranaceous, 7.4–9 × 1.4–1.7 mm, white, apex; petal appendages two, originating at 1.6 mm from the petal base. Stamens included; filaments flattened, 5.2–6.9 mm long, 0.1–0.2 mm in diameter; anthers dorsifixed, rectangular, 2.4–2.7 × 0.4 mm, apiculate. Epigynous tube 0.2 mm long. Ovary subovoid, dorsiventrally compressed, 1.9–2.4 mm long, 3.1–4.9 mm in diameter, green, placentation apically-axile. Style longer than the stamens, 8.8 mm long; stigma conduplicate-spiral, 0.9 mm long. Ovules unappendaged. Fruit subovoid, dorsiventrally compressed, 7.3 mm long, 4.5 mm in diameter, cream, glabrous. Seeds club-shaped, 1.9 × 0.5 mm, brown (Fig. 3.13).

Etymology:—The specific epithet refers to the city of Negril in Jamaica, where the type specimen was collected.
Distribution, habitat, and phenology:—Wittmackia negrilensis is endemic to the coastal and adjacent regions of western Jamaica at 0–50 m elevation (Fig. 3.2C). It grows on forested limestone formations. Collected in flower in November.

Conservation status:—Wittmackia negrilensis is categorized here as Critically Endangered (CR, B1a; IUCN 2001) because its extent of occurrence is less than 100 km² and includes fragmented forested areas near the western coast of Jamaica.

Taxonomic comments and affinities:—Wittmackia negrilensis resembles Wittmackia rohan-estyi because of its robust inflorescences, primary bracts much longer than the branches, long floral bract mucros, and long sepal mucros. However, W. negrilensis is different by its longer apical bracts of the peduncle (15–19 cm vs. 8–12.5 cm long); longer basal primary bracts (14.5–14.8 cm vs. 9–13.7 cm long); much shorter stipes (2–8 mm vs. 19–39 mm long); more numerous (50 to 60 vs. 18 to 35 flowers per spike) and shorter flowers (10–12.5 mm vs. 14–15 mm long); shorter petals (7.4–9 mm vs. 11.2 mm long); and shorter ovaries (1.9–2.4 mm vs. 3.1 mm long). Specimens of W. negrilensis with short spikes are often confused with W. penduliflora; however, these species are easily separated because W. negrilensis has basal primary bracts at least twice as long as the branches, while these bracts are shorter to slightly longer than the branches in W. penduliflora.

ADDITIONAL SPECIMENS EXAMINED. JAMAICA. Hanover Parish: 6 January 1891, Hitchcock s.n. (US). Westmoreland Parish: 1 mile northwest of Savanna-La-Mar, 15 m, 17 November 1955, Proctor 11109 (IJ); 1/2 mile northwest of New Broughton, 8 m, 18 November 1955, Proctor 11147 (IJ); Spring Garden District, 45 m, 20 November 1955, Proctor 11209 (IJ); vicinity of Bloody Bay, 0 m, 4–6 October 1999, Proctor 51582 (IJ).


*Aechmea virens* Brongn. ex Baker (1889: 45). *Hohenbergia virens* (Brongn. ex Baker) Mez (1934: 163). TYPE:—FRENCH GUYANA. in Paris Hortus, 1848, *Quesnel s.n.* (holotype P!). Comment: this specimen was probably collected originally in the West Indies rather than French Guyana.

**Plant** epiphytic, rupicolous, cespitose, 100–130 cm tall, acaulescent; rosette broad, forming phytotelmata. **Leaves** 77–103 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong, 18–21 × 10–15.2 cm, pale brown, lepidote on both surfaces, serrate, the teeth 0.7–1(-2) mm long; blade lingulate, 82–100 cm long, (6.5-)8.5–12 cm wide at the base, (6.5-)7.9–13 cm wide in the middle, green, surface smooth, lepidote on both surfaces, more densely on the abaxial side, serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, erect to antrorse, green, 0.5–2 × 0–7-0.9 mm, apex obtuse to rounded, mucronate. **Inflorescence** central, erect to pendulous; peduncle almost completely exposed out of the rosette, stout, pliable, 32–73 cm long, 3–10 mm in diameter, green, floccose, internodes between the medial bracts 4–10.2 cm, internodes between the apical bracts (0.5-)2.2–5 cm; bracts of the peduncle shorter to longer than the internodes, marcescent, chartaceous, nervose, green, occasionally dull purple, the medial bracts erect, imbricate, lanceolate, 5.7–8.5 × 0.8–3 cm, floccose-lepidote on both surfaces, entire, occasionally serrulate, the teeth irregularly distributed along the margins, apex acuminate, the apical bracts suberect, imbricate, lanceolate, 4.5–8.2 × 0.4–1.5 cm, floccose on both surfaces, entire, apex acuminate to attenuate; fertile portion of the inflorescence paniculate, conical to cylindrical, 14–63 cm long, 5.2–10.8 cm wide in the middle, 1-divided, occasionally 2-divided, branches (13-)30 to 65 in number, polystichous, rachis straight, green, (13.5-)18–46(-62) cm long, 3–4(-7) mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the
inflorescence, diverging from the rachis to divaricate, marcescent, chartaceous, nervose, shorter to longer than the branches; the basal bracts lanceolate, 3.3–4.6(-6) × 0.4–1.2 cm, green, occasionally dull purple, floccose-lepidote abaxially, glabrous adaxially, entire, apex acuminate to attenuate; the apical bracts lanceolate, 0.8–1.3(-1.7) × 0.2–0.3 cm, green, occasionally dull purple, floccose on both surfaces, entire, apex attenuate. **Spikes** ovoidal to cylindrical, 0.9–4.8 cm long, 1.2–2.4 cm wide in the middle; stipe partially covered by the primary bracts, 1.3–19 mm long, 2–3 mm in diameter, terete, floccose; rachis of the spike 0.9–4.8 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the ovaries, imbricate, ascending to diverging from the rachis, subconcave, coriaceous, ovate, 4–9 × 4.4–8 mm, green, nervose, ecarinate, floccose-lepidote abaxially, glabrescent adaxially, serrulate, occasionally entire, apex acute, mucronate, mucro 1.2–3.8 mm long. **Flowers** 10 to 20(-30) per spike, polystichous, ascending to diverging from the rachis, 4–9 mm long, sessile. **Calyx** dorsiventrally compressed; sepals strongly coriaceous, asymmetrical, forming a lateral wing, 3.5–6.2 mm long, 4.3 mm wide at the base, the unwinged side 1.5 mm wide, the winged side 3 mm wide, green, surface smooth, the posterior sepals carinate, the anterior sepal ecarinate, sparsely floccose to glabrescent, mucronate, mucro 1–2.5 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, 10.8–18 × 1.3–4 mm, white, occasionally green, glabrous, entire, apex acute to obtuse; petal appendages two, flanking the antepetalous stamens, originating at 6.5 mm from the petal base. **Stamens** included; filaments flattened, 7.8–11 mm long, 0.1–0.7 mm in diameter, white; anthers dorsifixed, rectangular, 2.1–4 × 0.3–0.8 mm, white to cream, apiculate. **Epigynous tube** 0.4–1.2 mm long. **Ovary** subovoid, dorsiventrally compressed, 3–4.9 mm long, 3.7–7.6 mm in diameter, green, glabrescent to sparsely floccose, placentation apically-axile. **Style** longer than the stamens, cylindrical, 7.3–18 mm long, white to
green; stigma conduplicate-spiral, papillose, white to light green, 0.7–1.8 mm long. **Ovules** more than 30 per ovary, round, unappendaged. **Fruit** subovoid, dorsiventrally compressed, 9.2–18 mm long, 4.7–6.7 mm in diameter, bluish, floccose; sepals persistent in fruit, fleshy. **Seeds** club-shaped, 1.9 × 0.6 mm, grey to reddish-brown (Fig. 3.14).

**Etymology:**—The specific epithet refers to the pendulous inflorescence of the type specimen.

**Distribution, habitat, and phenology:**—**Wittmackia penduliflora** is a widespread species in Cuba and Jamaica at 0–1200 m elevation (Fig. 3.2A). It grows on diverse ecosystems including coastal and in-land forested limestone formations, and montane moist forests of more complex geology such as the Blue and John Crow Mountains in Jamaica and Sierra Maestra in Cuba. Collected in flower from May to December.

**Conservation status:**—**Wittmackia penduliflora** is categorized here as Near Threatened (NT; IUCN 2001) because it is restricted to Jamaica and Cuba, but its distribution is widespread within the forested areas of both islands.

**Taxonomic comments and affinities:**—**Wittmackia penduliflora** is a phenotypically variable species characterized by its short to medium stipitate, subglobose spikes, acuminate to acute floral bracts, and relatively long flowers (13–20 mm long). These characteristics makes it similar to *W. portoricensis* but differs from this species by its longer and broader leaves (82–100 × (6.5-)7.9–1 cm vs. 39–71 × 2–5.1(-6.4) cm); stouter stipes (2–3 mm vs. 1.5–2 mm in diameter); entire primary bracts (vs. serrate); longer petals (10.8–18 mm vs. 8.8–10.7 mm long); presence of petal appendages (vs. absence); and longer filaments (7.8–11 mm vs. 6.2–7.7 mm long).
ADDITIONAL SPECIMENS EXAMINED. CUBA. Camaguey: vicinity of La Gloria, 8 February 1909, Shafer 334 (NY); Hills S.E. end, Cayo Guajaba, 7–8 November 1909, Shafer 2834 (NY, US); basal valley of Río Miel, Oriente, 17 March 1910, Shafer 4335 (NY).

Cienfuegos: Guajimico, 23 March 1910, Britton et al. 5823 (NY); Cienaguita, 3 July 1895, Combs 466 (NY); Soledad, 9 February 1927, Jack 4681 (NY). Granma: Sierra Maestra, in hills at Rio Bayamo near Corojo, Oriente, 6 May 1916, Ekman 7300 (NY [photo], S). Guantanamo: Imias, Los Calderos, 14 August 1995, Herbario del Jardín Botánico Nacional de Cuba et al. 27430 (HAJB); Yamuri through Mata to Baracoa, Oriente, 15 December 1910, Shafer 7955 (NY). Havana: Cojimar, 5 February 1916, Britton et al. 13982 (NY); 11 October 1904, Van Herman 191 (NY). Holguin: Alto Cedro to Paso Estancia, Oriente, 28 April 1909, Shafer 1629 (NY); Moa Bay, East of Río Moa, Oriente, 2–3 January 1911, Shafer 8319 (NY); Alto Cedro, March 1903, Underwood et al. 1631 (NY). Isle of Pines: Cerro San Juan del Mar, Columbia, 20 February 1916, Britton et al. 14662 (NY). Matanzas: Canimar River, 19 March 1903, Britton et al. 490 (NY). Pinar del Rio: San Diego De Los Baños, 31 August to 3 September 1910, Britton et al. 6666 (NY); Baños San Vicente, 12–16 September 1910, Britton et al. 7473 (NY); Corrientes Bay, 10–12 March 1911, Britton et al. 9922 (NY); Sierra Mendoza, 25 December 1911, Shafer 11158 (NY); vicinity of Los Palacios, 3–4 January 1912, Shafer 11673 (NY); vicinity of Sumidero, 2–4 August 1912, Shafer 13490 (NY); along Camino Aguacate from Bahia Honda to Baños Aguacate, 11–12 December 1910, Wilson 9208 (NY). Villa Clara: Trinidad Mountains, Santa Clara. Habanilla Falls, 1 March 1910, Britton et al. 4861 (NY); Sta. Clara, 28 August 1922, Leon 11386 (NY). Farallón de la Perla, Oriente, 14 February 1911, Shafer 8775 (NY). JAMAICA. Hanover Parish: Rockingham, 305 m, 4 September 1970, Adams 13201 (UCWI). Portland Parish: Blue Mountains. Road between Hardwar Gap and Section. 0.5 miles
south of Section, 1096 m, 18°5'17.7"N, 76°42'28.6"W, 20 June 2012, Aguirre-Santoro et al. 1802 (IJ, NY); near Port Antonio, 6 July 1897, Fredholm 3125 (US); Shotover Hill, 3 miles W.S.W. of Port Antonio, 305 m, 25 May 1952, Proctor 6708 (IJ); 1/2 mile west of Silver Hill Gap, 1070 m, 22 June 1952, Proctor 6850 (IJ); ridge southwest of Haycock Mountain, above Badarres P. O., 650–840 m, 11 June 1953, Proctor 8061 (IJ); side to one mile W of Section along the road to Newcastle, 970 m,, Till 9165 (WU). St. Ann Parish: 1 mile west of Discovery Bay, 30 m, 17 April 1960, Adams 6871 (UCWI); Moneague, 310–320 m, 17 September 1965, Adams 12717 (UCWI); Mt. Diablo, 425 m, 25 October 1970, Lack s.n. (UCWI); vicinity of Mosely Hall cave, near Blackstonedge, 610 m, 15 July 1952, Proctor 6936 (IJ); 24 August 1952, Proctor 7208 (US); along Queen's Highway, 2 miles east of Rio Bueno, 8 m, 23 August 1955, Proctor 10559 (IJ); Tobolski district, 3 miles southwest of Browns Town, 490 m, 28 March 1956, Proctor 11909 (IJ); Unity Valley district, along road between Moneague & Mt. Diablo, 460 m, 2 July 1965, Proctor 26484 (IJ). St. Catherine Parish: 1/2 mile southeast of Guys Hill, 490 m, 3 May 1952, Proctor 6659 (IJ, US). St. James Parish: Orange River valley, 1/2 mile southeast of Sign, 75 m, 15 September 1957, Proctor 16630 (IJ). St. Thomas Parish: Port Morant, 20 December 1890, Hitchcock s.n. (US); along trail between Whitehall and Big Hill, 305–915 m, 12 February 1953, Proctor 7664 (IJ); Big Level district, southeast end of the John Crow Mountains, 460–610 m, 16 March 1956, Proctor 11791 (IJ). Trelawny Parish: Windsor estate, 120 m, 23 August 1956, Proctor 15666 (IJ); Arawak Cave 2 miles W of Rio Bueno, about 10 m above sea level, 10–10 m, 20 August 1992, Till 9009 (SEL). Westmoreland Parish: near Revival, 75 m, 20 December 1960, Adams 8555 (UCWI); Kentucky Hill, Bluefields Mts, 610–760 m, 3 July 1908, Harris 10205 (UCWI). UNITED STATES. Florida: Sarasota, flowered in cultivation at the Marie Selby Botanical Gardens, November 1990, Berg s.n. (SEL); Miami,

**TYPE:**—JAMAICA. No locality, no date, *Wright s.n.* (holotype BM!).


*Hohenbergia pycnantha* (Baker) Mez (1891: 274). **TYPE:**—Morren illustration deposited at the herbarium of the Royal Botanical Gardens (K). (Lectotype designated by L.B. Smith (in Smith and Downs 1979)).

*Hohenbergia gnetacea* Mez (1891: 272). **TYPE:**—No locality, no date, *Morren Hortus* (holotype G!).

**Plant** epiphytic or rupicolous, cespitose or solitary, acaulescent; rosette broad, forming phytotelmata. **Leaves** 60–99 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong to elliptical, 18–22 × 10–12 cm, pale brown, lepidote on both surfaces, entire; blade lingulate, 42–78 cm long, 6.2–10.5 cm wide at the base, 6–10.3 cm wide in the middle, green, surface smooth, lepidote on both surfaces, more densely on the abaxial side, serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, erect to antrorse, green, 0.3–1 mm long, apex rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle partially concealed by the rosette, stout, rigid, 30–57 cm long, 5–12 mm in diameter, green, floccose, internodes between the medial bracts 2.1–2.7 cm, internodes between the apical bracts 0.5–2.5 cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nervose, pale brown, the medial bracts erect, imbricate, lanceolate, 4.5–10.2 × 1–1.5 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate, the apical bracts suberect, imbricate, lanceolate, 3.6–5.4 × 0.6–1.2 cm, sparsely floccose, entire, apex acuminate; fertile
portion of the inflorescence paniculate, cylindrical, 14–23 cm long, 4–10.8 cm wide in the middle, 1-divided, occasionally 2-divided, branches

35 to 60 in number, polystichous, rachis straight, green, (7.2–)10.8–28 cm long, 7–12 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, ascending, marcescent, chartaceous, nervose, longer than the branches, occasionally shorter than the branches; the basal bracts lanceolate, 2.4–7.5 × 0.6–1.4 cm, stramineous to castaneous, floccose abaxially on both sides, entire, apex attenuate; the apical bracts ovate, 0.6–2.2 × 0.5–1.3 cm, stramineous to castaneous, floccose on both surfaces, entire, apex attenuate. **Spikes** globose to cylindrical, 1.9–5.5 cm long, 1.4–1.8 cm wide in the middle, sessile; rachis of the spike 1.9–5.5 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the ovaries, imbricate, erect, concave, strongly coriaceous, orbicular, 7–10 × 7.2–11 mm, stramineous to castaneous, surface smooth, ecarinate, brown floccose, entire, apex obtuse to rounded, mucronate, mucro 0.3–1.2 mm long. **Flowers** 8 to 18 per spike, polystichous, erect, 7–10 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 4.4–8 mm long, 1.8–4 mm wide at the base, the unwinged side 0.6–1.4 mm wide, the winged side 1.7 mm wide, stramineous to castaneous, surface smooth, the posterior sepals carinate, the anterior sepal ecarinate, brown floccose, entire, apex acute, mucronate, mucro 0.5–0.9 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, 8.5–12.3 × 1.2–2.5 mm, white, glabrous, occasionally sparsely floccose, entire, apex acute; petal appendages absent. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 7–8.9 mm long, 0.1–0.2 mm in diameter, white; anthers dorsifixed, rectangular, 2.4–2.5 × 0.5 mm, cream, apiculate. **Epigynous tube** 0.3 mm long.
Ovary subovoid, dorsiventrally compressed, 2–3.2 mm long, 4.8–5.9 mm in diameter, white, glabrous, placentation apically-axile. Style longer than the stamens, 8.4–11.3 mm long, white; stigma conduplicate-spiral, 1.1–1.3 mm long. Ovules round, unappendaged. Fruit subovoid, dorsiventrally compressed, 9.5–12 mm long, 5.4–5.6 mm in diameter, densely brown-floccose; sepals persistent, partially fleshy (Fig. 3.15).

Etymology:—The specific epithet refers to the capituliform aspect of the spikes in anthesis.

Distribution, habitat, and phenology:—Wittmackia polycephala is endemic to Jamaica occurring widely in the island at 70–1000 m elevation (Fig. 3.2C). It grows on diverse forested or open limestone formations, and montane moist forests on soils of volcanic and metamorphic origin such as the Blue and John Crow Mountains. Collected in flower from February to December.

Conservation status:—Wittmackia polycephala is categorized here as Vulnerable (VU, B1a; IUCN 2001) because its area of extent is about 3,000 km² and includes both well-preserved forests in protected areas and highly fragmented forests near urbanized and agricultural regions of Jamaica.

Taxonomic comments and affinities:—Wittmackia polycephala, like W. eriostachya, is easy to recognize because of the characteristic brown-tomentose-lepidote indument that covers the floral bracts and flowers. However, W. polycephala differs from W. eriostachya by its shorter leaf teeth (0.3–1 mm long vs. 1.2–2.2 mm long); primary bracts much longer than the spikes (vs. shorter), and sessile spikes (vs. stipitate).

ADDITIONAL SPECIMENS EXAMINED. JAMAICA. Clarendon Parish: Peckham Woods, 760 m, 25 November 1953, Proctor 8223 (IJ); Mason River Savanna, 2.75–3 miles due
northwest of Kellits, 700 m, 14 October 1967, *Proctor 16727* (IJ); Broom Hall hills, 1.2 miles
due southwest of Cave Valley square, 550–610 m, 16 December 1977, *Proctor 37500* (IJ).
Parish: between Lancaster & Moody's Gap, 700 m, 8 March 1895, *Harris 5569* (s.n.). St. Andrew
Parish: Port Royal Mountains. Roadside between Red Light and Hardware Gap. One mile NE of
Red Light. On river valley, 892 m, 18°4'13.3” N, 76°43'2.7” W, 20 June 2012, *Aguirre-Santoro
et al. 1800* (IJ, NY, US); vicinity of Moody's Gap, 10 September 1908, *Britton 3421* (NY);
Hermitage road, Stony Hill, 520 m, 20 July 1967, *Page s.n.* (UCWI); 25 July 1967, *Page s.n.*
(UCWI); Hermitage Dam, 530–539 m, 21 February 1952, *Proctor 6253* (IJ); 3/4 mile E.S.E. of
near Moneague. St. Ann's Bay road, 3 April 1908, *Britton 2684* (NY); Broom Hall woods, 2
miles SW of Cave Valley Square, 540–550 m, 6 February 1980, *Gentry 28453* (IJ, MO); Lydford
Post Office, 455 m, 20–31 December 1953, *Howard et al. 13392* (IJ); vicinity of Mosely Hall
Cave, near Blackstonedge, 610 m, 24 August 1952, *Proctor 7207* (IJ, US); Forest Preserve, Mt.
Diablo, above picnic area, along trail, 12 January 1967, *Read 1746* (US). St. Catherine Parish:
between Ewarton and Worthy Park, 380 m, 31 March 1970, *Adams 13189* (UCWI); Hollymount,
790 m, 23 September 1962, *Adams 24191* (UCWI); vicinity of Bog Walk. Bowers mood road, 2
April 1908, *Britton 2620* (NY); Bog Walk, 17 December 1890, *Hitchcock s.n.* (F, US);
Hollymount, 19–20 September 1906, *Marble 737* (NY); Riverhead, 2 miles southwest of
Ewarton, 305 m, 14 January 1952, *Proctor 6137* (IJ); Juan de Bolas District, west of Point Hill.,
18 July 1952, *Proctor 6968* (IJ, US); along road between Bog Walk and Giblatore, 76–305 m, 15
November 1953, *Proctor 8187* (IJ, US); 2 miles southwest of Riversdale, 140 m, 24 April 1955,
*Proctor 10155* (IJ); vicinity of Hollymount, Mt. Diablo, 850–950 m, 4–5 April 2005, *Proctor
52354 (IJ); 4 miles SW of Ewarton along the road to Lluidas Vale, 480 m, 21 August 1992, Till 9022 (SEL). St. James Parish: Montego Bay, 22 March 1908, Britton et al. 2367 (NY); White Rock Hill, c. 1 mile south of Sweet Water, 610–670 m, 2 December 1962, Proctor 22997 (IJ). Trelawny Parish: woods along road from Barbecue Bottom to Ramgoat Cave: Cockpit country, 500 m, 25 January 1984, Bretting J-347 (IJ, MO); Mango Tree Hill, 540–540 m, 22 January 1967, Henry s.n. (UCWI); Ramgoat Cave District, Cockpit Country, 4 July 1955, Howard et al. 14436 (IJ); Alps district, 1.5 miles N.N.E. of Ulster Spring, 455 m, 22 August 1956, Proctor 16662 (IJ); vicinity of Mango Tree Hill, Cockpit Country, 550–610 m, 9 December 2001, Proctor 50041 (IJ); Island View Hill, 3 mi. N of Warsop on the main road to Albert Town, 750–750 m, 18°17.222' N, 77°34.556' W, 11 August 2006, Raz et al. 674 (NY); Mango Tree Hill, between Burnt Hill Intersection and Spring Garden, 9 November 1966, Read 1730 (US); Mango Tree Hill (Carambi Hill) half way between Burnt Hill Intersection and Spring Garden, 5 April 1967, Read 1858 (US). UNITED STATES. Florida: Sarasota, flowered in cultivation at the Marie Selby Botanical Gardens, 12 July 1993, Luther et al. s.n. (SEL).


*Hohenbergia portoricensis* Mez (1896: 136). TYPE:—PUERTO RICO. Naguabo: Sierra de Naguabo ad arbor. in sylv. prim. montis Piedra pelada, 26 April 1885, *P. Sintenis 1321* (holotype B!). Comment: Cedeño-Maldonado (in Acevedo-Rodríguez and Strong 2005) indicated that the holotype was destroyed; however, this information is erroneous.

**Plant** epiphytic, cespitose, solitary, acaulescent; rosette semierect, forming phytotelmata. **Leaves** 58–88 cm long, coriaceous; sheath conspicuously differentiated from the blade, oblong, 9–18.8 × 3.8–7.7 cm, pale brown, lepidote on both surfaces, serrulate; blade lingulate, 39–71 cm long, 2.5–4.1(-5.5) cm wide at the base, 2–5.1(-6.4) cm wide in the middle, green to cinereous-green, surface smooth, lepidote on both surfaces, more densely on the abaxial side, median canalicule present, serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, perpendicular to antorose, green, 0.6–0.9 mm long, apex acuminate to rounded, mucronate. **Inflorescence** central, pendulous; peduncle almost completely exposed out of the rosette, stout, pliable, 31–35 cm long, 2.5–6 mm in diameter, green, floccose, internodes between the medial bracts 3.6–5.8 cm, internodes between the apical bracts 3.2–7.4 cm; bracts of the peduncle shorter to equaling the internodes, apical bracts surpassing the internodes, marcescent, chartaceous, nervose, green, the medial bracts erect, lax, lanceolate, 3.4–6 × 0.6–0.8 cm, floccose abaxially, glabrescent adaxially, serrulate, the teeth irregularly distributed along the margins, apex acuminate, the apical bracts ascending, lax, lanceolate, 3.5–5.5 × 0.5–0.8 cm, floccose on both surfaces, serrulate, the teeth irregularly distributed along the margins, apex attenuate; fertile portion of the inflorescence paniculate, subcylindrical, 18–35.5 cm long, 4.3–8.8 cm wide in the middle, 1-divided, branches 7 to 14 in number, polystichous, rachis slightly flexuous, green, 7.2–31 cm long, 2.5–3.5 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, diverging from the rachis, marcescent, chartaceous, nervose, shorter to longer than the branches; the basal bracts lanceolate, 4–6.5 × 0.5–0.6 cm, green, floccose on both surfaces, serrulate, the teeth irregularly distributed along the margins, apex attenuate; the apical bracts lanceolate to ovate, 1.7–2.1 × 0.4–0.6 cm, green, floccose on both surfaces, serrulate, the teeth irregularly distributed along the
margins, apex acuminate to attenuate. **Spikes** ovoidal to cylindrical, 1.8–3.4 cm long, 2.2–2.6 cm wide in the middle; stipe exposed, 12–21 mm long, 1.5–2 mm in diameter, terete, floccose; rachis of the spike straight, 1.8–3.4 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the ovaries, imbricate, diverging from the rachis, subconcave, coriaceous, ovate, 6.6–10.2 × 4.7–9 mm, green, nervose, ecarinate, floccose on both surfaces, minutely serrulate, apex acuminate, mucronate, mucro 3.5–8.8 mm long. **Flowers** 10 to 15 per spike, polystichous, diverging from the rachis, 6.6–10.2 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 3.8–5.8 mm long, 2.4–4 mm wide at the base, the unwinged side 0.8–1.3 mm wide, the winged side 0.8–2.8 mm wide, green, nervose, the posterior sepals carinate, the anterior sepal ecarinate, sparsely floccose, entire, apex acute, mucronate, mucro 1.7–2.7 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, oblongue to subspatulate, 8.8–10.7 × 1.2–1.5 mm, white, glabrous, entire, apex acute; petal appendages absent. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 6.2–7.7 mm long, 0.1–0.5 mm in diameter, white; anthers dorsifixed, elliptical, 1.8–2.5 × 0.4–0.6 mm, white, apiculate. **Epigynous tube** 0.4–1.4 mm long. **Ovary** subovoid, dorsiventrally compressed, 2.8–5.5 mm long, 4–5.8 mm in diameter, green, sparsely floccose, placentation apically-axile. **Style** longer than the stamens, 8.5–10.2 mm long, white; stigma conduplicate-spiral, white, 0.9–1.3 mm long. **Ovules** more than 30 per ovary, round, unappendaged. **Fruit** globose, 10–12.5 mm long, 5.2–8.6 mm in diameter, bluish, sparsely floccose; sepals persistent, partially fleshy. **Seeds** more than 20 per fruit, club-shaped, 2.1–2.2 × 0.5 mm, reddish (Fig. 3.16).

**Etymology:**—The specific epithet refers to the occurrence of this species in Puerto Rico.
Distribution, habitat, and phenology:—*Wittmackia portoricensis* is endemic to Puerto Rico occurring widely in the island at 200–970 m elevation (Fig. 3.2B). It grows as epiphytic in the understory and edges of moist forests. This species occurs sympatrically with *W. antillana*. Collected in flower from November to March.

Conservation status:—*Wittmackia portoricensis* is categorized here as Vulnerable (VU, B1a; IUCN 2001) because it mostly occurs in medium elevation, moist forests within protected state forests and national parks in Puerto Rico. The populations outside these protected areas are more vulnerable as they inhabit isolated mountains that are prone to human activities, such as construction and agriculture.

Taxonomic comments and affinities:—*Wittmackia portoricensis* is similar to *W. penduliflora* but differs from this species in its shorter and narrower leaves (39–71 × 2–5.1(-6.4) cm vs. 82–100 × (6.5-)7.9–1 cm); more slender stipes (1.5–2 mm vs. 2–3 mm in diameter); serrate primary bracts (vs. entire); shorter petals (8.8–10.7 mm vs. 10.8–18 mm long); absence of petal appendages (vs. presence); and shorter filaments (6.2–7.7 mm vs. 7.8–11 mm long). The synonymization of *Hohenbergia attenuata* into *W. portoricensis* by Cedeño-Maldonado in Acevedo-Rodríguez (2005) is supported here as it was observed that acuminate and obtuse leaves occur even within the same individual.

Forest, 500 m, 2 March 1982, Liogier et al. 32812 (UPR); Las Tetas, 820 m, 10 March 1983, Liogier et al. 34031 (NY, UPR); barrio Cercadillo: SE. side, summit ridge of Cerro Avispa, 835–
850 m, 5 November 1986, Proctor 42436 (UPR). Ciales: Bo. Toro Negro E slope of Los Tres Pichachos along ridge above upper jeep road through old coffee plantation from Rt 149 km 35.5, 700 m, 29 July 1993, Axelrod et al. 6700 (US). Cidra: Cerro de las Pinas, near Las Cruces, 600–
720 m, 29 March 1922, Britton et al. 6879 (NY). Luquillo: Catalina-Yunque Trail, Luquillo Mountains, 600 m, 23–26 February 1923, Britton 7576 (NY); southern slope of El Toro.
Luquillo Mts, 600 m, 21 March 1964, Liogier 10739 (NY); along El Toro Trail, Luquillo Mts, 650–700 m, 28 March 1979, Liogier et al. 28530 (UPR); El Verde, Luquillo Mts, 500 m, 14
January 1987, Liogier 36212 (UPR). Maricao: Maricao State Forest. Trail on an abandoned
vacational center just in front of cabins Monte del Estado, 845 m, 18°8'27.7"N, 66°58'30.1"W, 15
November 2012, Aguirre-Santoro et al. 1822 (NY, UPR); Maricao State Forest, 800 m, 30
March 1964, Liogier 10769 (NY). Naguabo: Maizales, Sierra de Naguabo, Barrio de Maizales, 600 m, 7 March 1914, Britton et al. 2141 (F, NY, US); Pico del Este, Luquillo National Forest, 1–6 April 1963, Howard et al. 15619 (GH); forest of lee side of East Peak, Luquillo Mts, 4
February 1969, Howard 17250 (GH); Sierra de Naguabo, 5 March 1914, Johnston 1577 (UPR);
Luquillo National Forest, La Mina recreation area to summit of El Yunque on trails and service roads, 30 March 1969, Pfeifer et al. 2867 (SEL); Loma La Mina, Sierra de Naguabo, Summit of Loma la Mina, 945 m, 20 July 1914, Shafer 3336 (NY, US); Sierra de Naguabo, Loma Icaco, 210–675 m, 24 July 1914, Shafer 3401 (NY). Orocovis: Toro Negro State Forest. Cerro El Bolo. Trail close to the Park administrative station on road 143, 966 m, 18°10'3.3"N, 66°29'6.7"W, 14
November 2012, Aguirre-Santoro et al. 1820 (NY, UPR); Toro Negro Forest Reserve, Camino
El Bolo, 860–970 m, 18°10.18' N, 66°29.23' W, 16 April 2011, Santiago et al. 4611 (US).

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**Plant** epiphytic, cespitose, 150 cm tall, acaulescent; rosette broad, forming phytotelmata.

**Leaves** 93–121 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong to elliptical, 15–26 × 8.5–17 cm, white to pale brown, lepidote on both surfaces, serrulate; blade lingulate, 73–94 cm long, 8.5–13.5 cm wide at the base, 8–11.5 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, hook-shaped, irregularly oriented, green to castaneous, 6.3–11 mm long, apex obtuse to rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle almost completely exposed out of the rosette, stout, rigid, 33–75 cm long, 7–14 mm in diameter, green, floccose, internodes between the medial bracts 2.3–4 cm, internodes between the apical bracts 1.5–2.2 cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nerveose, light green, the medial bracts erect, imbricate, lanceolate, 8–12.5 × 1–1.8 cm, sparsely floccose, entire, occasionally serrulate, apex acuminate, the apical bracts suberect, imbricate, lanceolate, 9.5–14 × 0.8–1.6 cm, sparsely floccose, entire, occasionally serrulate, apex attenuate; fertile portion of the inflorescence paniculate, conical, 39–78 cm long, 8–17.5 cm wide in the middle, 1-divided, occasionally 2-divided, branches 43 to 52(-83) in number, polystichous, rachis straight, green, 35–64 cm long, 4–8 mm in diameter, floccose to sparsely floccose.

**Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, reclined to descending, marcescent, chartaceous, nerveose, longer than
the branches; the basal bracts lanceolate, 9–13.7(-16) × 0.8–1(-1.7) cm, light green to cream, floccose to glabrescent, entire, apex attenuate; the apical bracts lanceolate, 1.1–2.4 × 2.8–3 cm, light green to cream, floccose to glabrescent, entire, apex attenuate. **Spikes** ovoidal to cylindrical, 2.1–5.8 cm long, 1–1.8 cm wide in the middle; stipe exposed, 19–39 mm long, 1.8–3 mm in diameter, terete, floccose to glabrescent; rachis of the spike 2.1–5.8 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the ovaries, imbricate, suberect to ascending, subconcave, coriaceous, ovate, 3.2–8 × 3.6–6.5 mm, green to cream, nervous, ecarinate, sparsely floccose, minutely serrulate, occasionally entire, apex acute to obuse, mucronate, mucro 1.5–5.8 mm long. **Flowers** 18 to 35 per spike, polystichous, ascending, 3.2–8 mm long, sessile. **Calyx** dorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 3.5–4.7 mm long, 2.6–3.6 mm wide at the base, the unwinged side 0.6–1.1 mm wide, the winged side 1.8–2.7 mm wide, green, yellow, or cream, surface smooth, the posterior sepals carinate, the anterior sepal ecarinate, floccose to glabrescent, entire, apex acute, mucronate, mucro 1.1–2.2 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, spatulate, 11.2 × 3 mm, white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 2.5 mm from the petal base. Stamens included, the antepetalous stamens partially adnate to petals; filaments flattened, 7.3 mm long, 0.3 mm in diameter, white; anthers dorsifixed, rectangular, 3.1 × 0.7 mm, white, mucronate. **Epigynous tube** 0.3 mm long. **Ovary** subovoid, dorsiventrally compressed, 3.1 mm long, 4.5 mm in diameter, green, glabrescent to sparsely floccose, placentation apically-axile. **Style** longer than the stamens, cylindrical, 11.6 mm long, white; stigma conduplicate-spiral, white, 1.3 mm long. **Ovules** more than 30 per ovary, round, unappendaged. **Fruit** subovoid, dorsiventrally compressed, 9.4–9.8 mm long, 4.8–6 mm
in diameter, cream, glabrous; sepals persistent, not fleshy. **Seeds** club-shaped, 2.1 × 0.7 mm, reddish (Fig. 3.17).

**Etymology:**—This species was named in honor to Rohan Esty, who made part of the team that collected the type specimen.

**Distribution, habitat, and phenology:**—*Wittmackia rohan-estyi* is endemic to western Jamaica at 20–370 m elevation (Fig. 3.2D). It grows in moist forests on limestone formations, especially in the region of the Dolphin Head Mountains. Collected in flower from July to November.

**Conservation status:**—*Wittmackia rohan-estyi* is categorized here as Critically Endangered (CR, B1a; IUCN 2001) because it has an extent of occurrence of less than 100 km² and only occurs in the Dolphin Head mountains, a protected area surrounded by rapidly growing urban development.

**Taxonomic comments and affinities:**—*Wittmackia rohan-estyi* is similar to *W. caymanensis*, *W. laesslei* and *W. negrilensis* because of its sublax inflorescence; basal primary bracts much longer than the branches; acuminate to broadly acute and long-mucronate floral bracts; and long-mucronate sepals. It can be easily separated from *W. negrilensis* by its much longer stipes (19–39 mm vs. 2–8 mm long) and less numerous flowers per spike (18 to 35 vs. 50 to 60 flowers per spike). *Wittmackia rohan-estyi* mainly differs from *W. caymanensis* by its longer stipes (19–39 vs. 6–18 mm long), green corollas (vs. white), and longer and broader petals (11.2 × 3 mm vs. 8–9.5 × 1.2 mm). Finally, *Wittmackia rohan-estyi* differs from *W. laesslei* by its medial bracts of the peduncle longer than the internodes (vs. shorter); shorter stipes (19–39 mm vs. 40–42 mm long); more numerous flowers per spike (18 to 35 vs. 12 to 18 flowers per spike); and narrower floral bracts (3.6–6.5 mm vs. 7–9.8 mm wide). This species was labeled as
Wittmackia sp. nov. aff negrilensis in the synopsis of Wittmackia (Aguirre-Santoro in preparation; see chapter 2).

ADDITIONAL SPECIMENS EXAMINED. JAMAICA. Hanover Parish: road between Kingsvale and Retirement. Western slopes of Dolphin Head, 294 m, 18°22'32.7" N, 78°10'41.9" W, 4 July 2012, Aguirre-Santoro et al. 1816 (IJ, NY, US); Below Cabarita River bridge, 0.3 miles north of Flower Hill P.A, 182–213 m, 8 August 1965, Proctor 26595 (IJ); Retirement Mountain area of Dolphin Head Forest Reserve, 183–366 m, 30 January to 27 February 2001, Proctor 51773 (IJ); slopes E. of Dolphin Head above Askenish, 275–335 m, 8 December 2001, Proctor 52037 (IJ); Retirement Mountain area, W. side of Dolphin Head Forest Reserve, 183–305 m, 12 November 2006, Proctor 52581 (IJ); Retirement Mountain area of Dolphin Head Forest Reserve, 183–305 m, 10 January 2007, Proctor 52588 (IJ). Westmoreland Parish: 1 mile northwest of Frome, 23 m, 19 November 1955, Proctor 11157 (IJ, US).

*Hohenbergia spinulosa* Mez (1900: 253). TYPE:—JAMAICA. Manchester Parish: New Green, 610 m, 30 April 1896, *W.H. Harris 6433* (holotype B!).

**Plant** epiphytic, cespitose, acaulescent; rosette broad, forming phytotelmata. **Leaves** 66–74.8 cm long, strongly coriaceous; sheath conspicuously differentiated from the blade, oblong to elliptical, 16–26 × 11.8–14 cm, white to pale brown, lepidote on both surfaces, entire; blade lingulate, 41–58 cm long, 9.6–11 cm wide at the base, 9.4–10.7 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, erect to retrorse, dark castaneous, 1–1.2 mm long, apex rounded, mucronate. **Inflorescence** central, erect to inclined; peduncle completely concealed by the rosette, stout, rigid, 21.8–33.5 cm long, 1.3–9 mm in diameter, green, sparsely floccose to glabrescent, internodes between the medial bracts 2–5.3 cm, internodes between the apical bracts 2.2–3(-3.8) cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nervous, cream to pale brown, the medial bracts erect, imbricate, linear-lanceolate, 4.5–7.5(-14.2) × 0.7–0.9(-1.8) cm, floccose on both surfaces, serrulate, occasionally entire, the teeth irregularly distributed along the margins, apex attenuate, the apical bracts ascending, lax, linear-lanceolate, 4.5 × 0.6 cm, floccose on both surfaces, serrulate, occasionally entire, the teeth evenly distributed along the margins, apex attenuate; fertile portion of the inflorescence paniculate, conical, 16–39.3 cm long, 4.6–8.7 cm wide in the middle, 1-divided, branches (20-50) to 80 in number, polystichous, rachis straight, green, 11–23.5(-39) cm long, 6–8(-12) mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, ascending, marcescent, chartaceous, nervous,
longer than the branches; the basal bracts linear-lanceolate, 4.5–7.1(-11.8) × 0.6–0.8(-1.2) cm, cream to pale brown, floccose-lepidote on both surfaces, entire, occasionally serrulate, the teeth irregularly distributed along the margins, apex attenuate; the apical bracts lanceolate, 1.5–1.8(-2) × 0.2–0.3 cm, cream to pale brown, sparsely floccose on both surfaces, entire, apex attenuate.

**Spikes** cylindrical, 1.9–3.5 cm long, 0.8–1.5 cm wide in the middle; stipe covered by the adjacent spikes, 1–3 mm long, 1.5–3 mm in diameter, terete, sparsely floccose; rachis of the spike straight, 1.9–3.5 cm long, green. **Floral bracts** partially enclosing the ovaries, imbricate, ascending, subconcave, coriaceous, ovate, 3.5–8.3 × 3–6.4 mm, green, nervose, sparsely floccose, minutely serrulate, occasionally entire, apex, acute to acuminate, mucronate, mucro 4.7–7.9 mm long. **Flowers** 12 to 18(-30) per spike, polystichous, suberect, 3.5–8.3 mm long, sessile. **Calyx** subdorsiventrally compressed; sepals basally connate, strongly coriaceous, triangular, asymmetrical, forming a lateral wing, 3.9–5 mm long, 2–3.1 mm wide at the base, the unwinged side 0.6–1.4 mm wide, the winged side 2.1–2.5 mm wide, green, nervose, the posterior sepals carinate, the anterior sepal ecarinate, glabrous, entire, apex acute, mucronate, mucro 1.7–3.7 mm long. **Corolla** tubular, apically spreading; petals membranaceous, 13.8–14.5 × 1.4–1.6 mm, white, occasionally green and basally white, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 4.7 mm from the petal base. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 9.3 mm long, 0.2 mm in diameter, white; anthers dorsifixed, rectangular, 2.7 × 0.4 mm, cream, mucronate. **Epigynous tube** 0.6–0.7 mm long. **Ovary** subovoid, dorsiventrally compressed, 2.1–4 mm long, 3–5.3 mm in diameter, green, sparsely floccose, placentation apically-axile. **Style** longer than the stamens, flattened, 13 mm long; stigma conduplicate-spiral, 1.6 mm long. **Ovules** more than 30 per ovary,
round, unappendaged. **Fruit** subovoid, dorsiventrally compressed, 8.1 mm long, 3.4 mm in diameter, green; sepals persistent, not fleshy (Fig. 3.18).

**Etymology:**—The specific epithet probably refers to the long mucros of the floral bracts and sepals.

**Distribution, habitat, and phenology:**—*Wittmackia spinulosa* is endemic to central-southern Jamaica at 100–975 m elevation (Fig. 3.2D). It grows as epiphytic in moist forests on limestone formations. This species grows sympatrically with *W. urbaniana*. Collected in flower in September.

**Conservation status:**—*Wittmackia spinulosa* is categorized here as Vulnerable (VU, B1a; IUCN 2001) because its extent of occurrence of about 1300 km² includes more than ten populations inhabiting well-preserved, but often fragmented, forests in central to southwestern Jamaica, including the southern edge of the Cockpit Country.

**Taxonomic comments and affinities:**—*Wittmackia spinulosa* is very distinctive among Caribbean *Wittmackia* because of its relatively short peduncle; densely congested inflorescence with numerous subsessile branches suberect and densely imbricated along inflorescence rachis; basal primary bracts much longer than the branches; and floral bracts and sepals long-mucronate. In general, *W. spinulosa* can also be recognized by its short and narrow inflorescences; however, the specimen by *Bullis s.n.* (SEL) has an exceptionally long inflorescence compared to other collections. This specimen was collected from a cultivated individual, which may explain the occurrence of this oversized inflorescence.

*Wittmackia spinulosa* somehow resembles *W. caymanensis* because of its long-mucronate floral bracts and sepals, and occasionally green petals: however, *W. spinulosa* has shorter leaf blades (41–58 cm vs. 60–83 cm long); shorter peduncle (21.8–33.5 cm vs. 68–77 cm long);
shorter bracts of the peduncle (4.5–7.5 cm vs. 9.2–11 cm long); shorter stipes (1–3 mm vs. 6–18 mm long); longer petals (13.8–14.5 mm vs. 8.3–9.3 mm long); and petal appendages arising at 4.7 mm (vs. 1.7 mm).

ADDITIONAL SPECIMENS EXAMINED. JAMAICA. Clarendon Parish: Glenwood Springs, along road between Balcarres & Sunbury, 945–975 m, 4 January 1974, Proctor 33696 (IJ). Manchester Parish: Marshalls Pen NW of Mandeville, 654 m, 18°3'33.1” N, 77°31'53.4”W, 23 June 2012, Aguirre-Santoro et al. 1805 (IJ, NY, US); Fairfield, 3–7 September 1908, Britton 3149 (NY); Lyndhurst, 21–23 September 1908, Britton 3771 (NY); Wales, 1 mile east of Newport, 685 m, 9 December 1951, Proctor 6064 (IJ); 2 miles northwest of Devon P.O., 610 m, 4 March 1952, Proctor 6306 (IJ); 1/4 mile due north of Retford Pen, northwest of Mandeville, 730 m, 25 February 1956, Proctor 11581 (IJ); along road between Fairfield & Huntley, 790–915 m, 9 January 1957, Proctor 16104 (IJ); Green Pond, 395 m, 9 January to 6 February 2001, Proctor et al. 51657 (IJ). St. Elizabeth Parish: 1 mile north of Four paths, 210 m, 13 April 1970, Adams 13225 (UCWI); Woodlands estate, 2 miles north east of Spur Trees, 760 m, 20 January 1956, Howard et al. 14173 (IJ); Hampton School, near Malvern, 640–700 m, 14 March 1953, Proctor 7732 (IJ); Retirement near Malvern, 700 m, 12 August 1954, Proctor 9271 (IJ); Mt. Charles state, 1 mile due S.S.W. of Giddy Hall P.O., 230–305 m, 9 March 1953, Proctor 11693 (IJ); 1 mile due north of Redgate, 150 m, 10 March 1956, Proctor 11725 (IJ); 1.5 miles due north of Redgate, 120 m, 10 March 1956, Proctor 11730 (IJ); Springfield, 460–530 m, 22 March 1964, Proctor 24729 (IJ). UNITED STATES. Florida: Sarasota, field collected in Jamaica, vic. Mandeville, and flowered in cultivation at the Marie Selby Botanical Gardens, Sarasota, Fl, USA, 21 June 2011, Aguirre-Santoro 1506 (SEL); Miami, flowered in cultivation in Miami. Originated from Jamaica, March 1989, Bullis s.n. (SEL).
17. *Wittmackia urbaniana* (Mez) Aguirre-Santoro, (pending publication). Basionym:


*Hohenbergia proctorii* L.B. Sm. (1960: 252). TYPE:—JAMAICA. St. Elizabeth Parish: 1 mile north of Four Paths, along road to Ginger Hill, 229 m, 6 April 1952, *G.R. Proctor 6567* (holotype US!, isotype IJ!).

*Plant* epiphytic, cespitose, 120–140 cm tall, acaulescent; rosette broad, forming phytotelmata. *Leaves* 71–123 cm long, strongly coriaceous; sheath conspicuously differentiated
from the blade, oblong to elliptical, 18.5–22 × 12–14 cm, white to pale brown, lepidote on both surfaces, serrulate, occasionally entire; blade lingulate, 48–100 cm long, 7.5–9.9 cm wide at the base, 6.2–8.2 cm wide in the middle, green, surface smooth, lepidote abaxially, glabrescent adaxially, serrate, the teeth evenly distributed along the margins, triangular to hook-shaped, erect, antorose to retrorse, green or castaneous, 0.2–1.2 mm long, apex rounded, mucronate.

**Inflorescence** central, erect, inclined, or pendulous; peduncle almost completely exposed out of the rosette, stout, rigid, 52–58 cm long, 7–10 mm in diameter, green, floccose, internodes between the medial bracts 4.5–5.9 cm, internodes between the apical bracts 4.2–5 cm; bracts of the peduncle longer than the internodes, marcescent, chartaceous, nervose, green to dull purple, the medial bracts erect, imbricate, lanceolate to elliptical, 7.3–7.8 × 1.6–2 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate, the apical bracts erect, imbricate, lanceolate, 5.5–6.5 × 1–1.9 cm, floccose abaxially, glabrescent adaxially, entire, apex acuminate; fertile portion of the inflorescence paniculate, conical to cylindrical, 12.8–26 cm long, 8.8–19 cm wide in the middle, 1-divided, branches 6 to 14 in number, polystichous, rachis straight, green, 7.3–16 cm long, 5–9 mm in diameter, floccose. **Primary bracts** similar to the bracts of the peduncle, gradually diminishing in size towards the apex of the inflorescence, diverging from the rachis, marcescent, chartaceous, nervose, shorter than the branches, occasionally surpassing the basal branches; the basal bracts lanceolate, 5.1–6.5 × 0.7–1.8 cm, green, floccose-lepidote abaxially, glabrous adaxially, entire, apex acuminate to attenuate; the apical bracts lanceolate, 2.8–4.4 × 0.8–1.4 cm, green, floccose-lepidote abaxially, glabrous adaxially, entire, apex attenuate. **Spikes** prolate to cylindrical, 4.1–16.5 cm long, 1.8–3.7 cm wide in the middle; stipe exposed, 4–20 mm long, 5–10 mm in diameter, terete, floccose to glabrescent; rachis of the spike 4.1–16.5 cm long. **Floral bracts** gradually diminishing in size towards the apex of the spike, partially enclosing the
ovaries, imbricate, erect to suberect, subconcave, strongly coriaceous, ovate, 12–26 × 10–17 mm, yellow to orange, occasionally greenish, nervose, ecarinate or carinate, glabrous, entire, apex acute to obtuse, mucronate, muro 1.1–3 mm long. **Flowers** 18 to 70 per spike, polystichous, erect, 12–26 mm long, sessile. **Calyx** dorsiventrally compressed; sepals strongly coriaceous, long-triangular, asymmetrical, forming a lateral wing, 9.1–11.8 mm long, 2.8–4.5 mm wide at the base, the unwinged side 0.7–1.5 mm wide, the winged side 1.3–2.5 mm wide, greenish yellow, surface smooth, the posterior sepals carinate, the anterior sepal ecarinate, glabrous, entire, apex acute to acuminate, mucronate, muro 1–2.2 mm long. **Corolla** tubular, apically spreading; petals free, membranaceous, oblong, 14.5–18 × 2–2.8 mm, white, glabrous, entire, apex acute; petal appendages two, flanking the antepetalous stamens, originating at 7.3–9 mm from the petal base. **Stamens** included, the antepetalous stamens partially adnate to petals; filaments flattened, 10.3–13 mm long, 0.3–0.4 mm in diameter, white; anthers dorsifixed, elliptical, 2.9–4 × 0.4–0.9 mm, white, mucronate. **Epigynous tube** 0.4–0.9 mm long. **Ovary** subovoid, dorsiventrally compressed, 3.2–4.5 mm long, 5.3–9 mm in diameter, white, glabrous, placentation apically-axile. **Style** longer than the stamens, 14.5–18 mm long, white; stigma conduplicate-spiral, white, 0.7–1.7 mm long. **Ovules** more than 30 per ovary, round, unappendaged. **Fruit** subovoid, dorsiventrally compressed, 12.2–14 mm long, 7.8 mm in diameter, green to yellow, glabrous; sepals persistent, fleshy. **Seeds** more than 10 per fruit, club-shaped, 2 × 0.5 mm (Fig. 3.19).

**Etymology:**—This species is named in honor to the German botanist Ignatz Urban.

**Distribution, habitat, and phenology:**—**Wittmackia urbaniana** is endemic to central and central-southern Jamaica at 100–950 m elevation (Fig. 3.2D). It grows as epiphytic in moist
forests on limestone formations. This species grows sympatrically with *W. spinulosa*. Collected in flower from July to September.

**Conservation status:**—*Wittmackia urbaniana* is categorized here as Vunerable (VU, B1a; IUCN 2001) because its extent of occurrence of about 1300 km² includes more than ten populations inhabiting well-preserved, but often fragmented, forests in central to southwestern Jamaica, including the southern edge of the Cockpit Country.

**Taxonomic comments and affinities:**—*Wittmackia urbaniana* is one of the most distinctive species of Caribbean *Wittmackia* because of its wide spikes bearing large (>12 mm long), highly imbricate, and mostly yellow to orange floral bracts that conceal the flowers, except the corolla. The most similar species to *W. urbaniana* is *W. inermis*, but differs from it by its generally shorter inflorescence rachis (7.3–16 cm vs. (14-)18–37 cm long); shorter (4–20 mm vs. 24–49 mm long) and stouter stipes (5–10 mm vs. 1.8–3.2 mm in diameter); longer sepals (9.1–11.8 mm vs. 7–8.2 mm long); petal appendages detaching at 10–12 mm from the base (vs. 7.3 mm); and longer filaments (10.3–13 mm vs. 8.3 mm long).

**ADDITIONAL SPECIMENS EXAMINED. JAMAICA.** Clarendon Parish: October 1972, *Adams 13281* (UCWI); Aenon Town to McKoy, 12 November 1972, *duQuesnay s.n.* (UCWI); Middlesex, Mocho Mountains, 1.5 miles southeast of Thompson Town, 610 m, 4 April 1952, *Proctor 6515* (IJ); 2 miles southeast of Crooked River P.O., 215 m, 10 June 1952, *Proctor 6768* (IJ); 2 miles southeast of Crooked River P.O., 215 m, 10 June 1952, *Proctor 6769* (IJ); 0.5 miles southeast of Suttons, 200 m, 11 April 1953, *Proctor 7876* (IJ); 0.5 miles southeast of Suttons, 200 m, 11 April 1953, *Proctor 7877* (IJ); Alcoa Teak Pen mining area, between Pits H-9 & H-7, 395–455 m, 31 December 1963, *Proctor 24362* (IJ); Middlesex, 1 mile E of Spaldings along the road to White Shop, 730 m, 9 September 1992, *Till 9143* (SEL); Middlesex, Balcarces
1 mile S of Ritchies along the road to Cumberland, 860 m, 9 September 1992, Till 9144 (SEL, WU). Manchester Parish: Bath to Somerset, 640 m, 23 December 1968, Adams 13112 (UCWI); Bellefield to Banana Ground, 790 m., Adams 24192 (UCWI); Marshalls Pen NW of Mandeville, 654 m, 18º3'33.1” N, 77º31'53.4” W, 23 June 2012, Aguirre-Santoro et al. 1804 (IJ, NY, US); road between Somerset and Bath. Roadside banks of limestone, 722 m, 18º6'18.9” N, 77º34'1.3” W, 23 June 2012, Aguirre-Santoro et al. 1806 (IJ); Aguirre-Santoro et al. 1807 (IJ); Mandeville and vicinity, 24–25 September 1907, Britton 1673 (NY); Mandeville to Brown's Tower, 3–7 September 1908, Britton 3117 (NY); Britton 3251 (NY); Britton 3252 (NY); Spaldings, Knox College, 610 m, 15 July 1949, Dignum s.n. (IJ, US); Rio Minho Valley, 365 m, 3 March 1910, Harris 10884 (NY, UCWI); Top Hill, 840 m, 22 September 1965, Morley 267 (UCWI); Morley 268 (UCWI); 0.5 miles S. Rose Hill Village, 760 m, 23 October 1965, Morley 279 (UCWI); no date, Morley s.n. (UCWI); summit of Herons Hill, 915–944 m, 3 March 1952, Proctor 6278 (IJ); 0.5 miles due north of Retford Pen, northwest of Mandeville, 730 m, 25 February 1956, Proctor 11582 (IJ); Marshalls Pen, 2.25 miles due northwest of Mandeville, 700 m, 12 September 1963, Proctor 24007 (IJ, US); near Rudds Corner, 790 m, 12 September 1963, Proctor 24008 (IJ); Marshalls Pen c. 2.25 miles due northwest of Mandeville, 640 m, 31 August 1979, Proctor 32287 (IJ); Walderston, 16 September 1966, Read 1707 (IJ, US); between Marshall's Pen & Somerset, 16 April 1959, Robertson 4129 (UCWI); Marshalls Pen, 455 m, 7 December 1958, Robertson 5402 (UCWI); east of Williamsfield, 427–457 m, 23 January 1958, Yuncker 18051 (NY). St. Elizabeth Parish: 1. mile N of Redgate, on the road to Ipswich, 145 m, 18º09'91” N, 77º49'67” W, 19 July 1997, Acevedo-Rodriguez 9518 (US); 1 m. N. of Four Paths, 215 m, 13 April 1970, Adams 13226 (UCWI); 1.5 m. N. of Four Paths, 200 m, 13 April 1970, Adams 13228 (UCWI); road between Ginger hill and Four Paths. Roadside banks of limestone, 355 m,
Aguirre-Santoro et al. 1811 (IJ); 1 mile south of Accompong, 365 m, 22 May 1953, Anderson s.n. (IJ, NY [photo]); along road between Four Paths & Ginger Hill, 230 m, 11 September 1963, Proctor 24000 (IJ); Bideford district, 1.5 miles due south of Malvern, 610 m, 25 January 1964, Proctor 24512 (IJ); between mileposts 4 & 5, Redgate to Ipswich road, 5 May 1977, Proctor 36827 (IJ). St. Elizabeth Parish: About 1/2 mile SSW of Ipswich along the road to Redgate, 110 m, 2 September 1992, Till 9125 (SEL, WU). St. James Parish: Glencoe district, 1 mile southeast of Stonehenge, 425–625 m, 21 March 1964, Proctor 24701 (IJ). Westmoreland Parish: Lenox District, 1 mile north of Hopeton, 365 m, 9 March 1956, Proctor 11716 (IJ). UNITED STATES. Florida: Sarasota, flowered in cultivation at the Marie Selby Botanical Gardens, 12 July 1993, Luther s.n. (SEL).
Chapter 4

4  The geographically disjunct evolution of the Ronnbergia Alliance (Bromeliaceae) reveals different evolutionary dynamics across three Neotropical biodiversity hotspots

4.1 Abstract

The Ronnbergia Alliance is part of the adaptive radiation that gave rise to the tank-epiphytic clade of berry-fruited bromeliads, also called the Core Bromelioidae. The ca. 70 species that compose the Ronnbergia Alliance are grouped in two main lineages, Ronnbergia and Wittmackia, which diversified within three centers of distribution of major conservation relevance: 1) the Tumbes-Chocó-Magdalena and adjacent forests (here called Pacific Forest), 2) the Atlantic Forest, and 3) the Caribbean. In this study, modern methods in biogeography and macroevolution were used to reconstruct the most plausible scenarios that explain the disjunct evolution of the Ronnbergia Alliance in these three centers of diversity and to compare the evolutionary rate dynamics of speciation and floral evolution of its lineages. The results suggest that since the early divergence of Ronnbergia and Wittmackia, ca. 3.6 mya, these lineages experienced contrasting patterns of evolution and geographic expansion. Ronnbergia diversified in the Pacific Forest, where its rates of speciation and floral evolution remained constant with a tendency to slow down over time while conserving a large amount of floral variation.

4  Manuscript follows the guidelines of Journal of Biogeography.
Conversely, the diversification of *Wittmackia* was more heterogeneous, as this lineage experienced multiple subsequent radiations within the Atlantic Forest and one radiation in the Caribbean after a long-distance dispersal event with origin in the Atlantic Forest. During the diversification in the Atlantic Forest, the speciation rates of *Wittmackia* faced a significant acceleration at its most derived nodes, coinciding with the climatic fluctuations of the Pleistocene glaciations. During the radiation in the Caribbean, the speciation rates further increased and coincided with a significant rate shift acceleration in the evolution of floral traits likely related to antiherbivory strategies. Although this study only explored a limited set of evolutionary processes, it demonstrates how species-level phylogenetic studies combined with ecological, geographic and morphological data can help understand fine-scale processes shaping the evolution of biodiversity within the most important biodiversity hotspots of the Neotropics.

### 4.2 Introduction

The Neotropics is the most biodiverse region on earth and includes more than one-third of the world’s species of seed plants (Govaerts 2001). This astonishing diversity is heterogeneously distributed across this region and is frequently concentrated in particular centers of diversity (Gentry 1982; Antonelli and Sanmartín 2011). Each of these centers of diversity offers unique biotic and abiotic conditions that promote the establishment and evolution of plant species and lineages (Antonelli and Sanmartín 2011). Unfortunately, many of these areas are highly endangered and classified as hotspots of biodiversity for conservation purposes because they contain high levels of plant endemism combined with a rapid loss of primary vegetation (WWF and IUCN 1997). For this reason, it is necessary to understand the evolutionary
mechanisms that originate and maintain biodiversity in these areas in order to propose informed actions to protect them. In this context, this study explores the geographic range evolution, species diversification and phenotypic evolution of a lineage of bromeliads that mainly diversified in three of the most important hotspots of biodiversity of the Neotropics: the Caribbean, the Atlantic Forest and the Tumbes-Chocó-Magdalena region.

The family Bromeliaceae (ca. 3500 spp.) is an excellent model with which to study evolutionary patterns in the Neotropics because it has diversified in almost every terrestrial biome of this region, producing a high number of endemic species and exhibiting a strong signal of adaptive diversification within its main lineages (Givnish et al. 2014; Bouchenak-Khelladi et al. 2015). Within the family, recent studies have focused on studying the evolution of the tank-epiphytic clade of berry fruited bromeliads, also called Core Bromelioideae (Schulte et al. 2009; Sass and Specht 2010; Givnish et al. 2014; Silvestro et al. 2014). These studies suggested that the diversification of this clade represents the most rapid event of adaptive radiation within Bromeliaceae, triggered by the acquisition of two key innovations—the epiphytic habit and the development of tank-forming rosettes—and made possible by the ancient acquisition of the CAM photosynthetic path, avian pollination and entangling seeds (Givnish et al. 2014; Silvestro et al. 2014). Moreover, this radiation extended across the low to medium elevation areas of the Neotropics forming clades highly restricted to specific biogeographic regions (Sass and Specht 2010). Although these studies revealed important mechanisms for the overall evolution of this lineage, there is little information about the evolutionary processes at the species level because of the widespread taxonomic problems that characterize this group and the lack of well-established monophyletic genera. In order to overcome this limitation, the present study represents a first approach to understand evolutionary mechanisms at the species level by targeting the study of a
recently described lineage within the Core Bromelioidae, called the *Ronnbergia* Alliance (Aguirre-Santoro in preparation; see chapter 1).

The *Ronnbergia* Alliance is one of the two main lineages of the Core Bromelioidae and contains about 70 species recently relocated in the genera *Ronnbergia* and *Wittmackia* (Aguirre-Santoro in preparation; see chapter 2). One of the remarkable features of this lineage is that its main subclades have a very strong geographical structure, as their species are highly restricted to three main centers of diversity. The first clade, represented by the genus *Ronnbergia*, comprises species mostly restricted to the area of influence of the Tumbes-Chocó-Magdalena biodiversity hotspot and adjacent forests. The second clade, represented by the genus *Wittmackia*, is composed by a grade of species endemic to the Atlantic Forest in eastern Brazil, the widespread species *Wittmackia lingulata*, and a nested monophyletic clade formed by species endemic to the northern portion of Caribbean, called the Caribbean Clade (Fig. 4.1). This highly restricted geographic separation of the lineages in the *Ronnbergia* Alliance provides an excellent case to understand biogeographic mechanisms that interconnect the three centers of plant diversity that the species inhabit and explore how this geographic isolation affected the evolutionary dynamics within the lineages. Therefore, in this paper the phylogenetic study of the *Ronnbergia* Alliance is revisited in order to tests hypotheses in biogeography and evolutionary dynamics in this group.
Figure 4.1. Phylogeny of the *Ronnbergia* Alliance showing its two main clades—*Ronnbergia* and *Wittmackia*—and the main radiations within *Wittmackia* (Source: Aguirre-Santoro (in preparation; see chapter 1)). Images in front of the phylogeny correspond to representative species within the main radiations. Top row from left to right (Caribbean Clade): *Wittmackia distans, W. penduliflora, W. urbaniana* and *W. portoricensis*. Middle row from left to right (Brazilian radiation): *W. laevigata, W. bicolor* and *W. lingulatoides*. Bottom row from left to right (*Ronnbergia*): *Ronnbergia maidifolia, R. nidularioides, R. drakeana* and *R. fraseri*. (All photos by J. Aguirre-Santoro, except for *W. laevigata, W. bicolor, W. drakeana, W. fraseri* (courtesy of the Marie Selby Botanical Gardens) and *R. maidifolia* (photo by J. Betancur)).
Given that each of the three centers of diversity offered different times and biotic and abiotic conditions for the diversification of lineages of the *Ronnbergia* Alliance, it is expected that the evolutionary dynamics among these areas also occurred in a unique fashion. However, it is possible that random evolution, extinction, or niche conservatism make evolutionary dynamics among clades undistinguishable (Kozak and Wiens 2006; Smith et al. 2011; Mahler et al. 2013). Detecting differences in evolutionary dynamics among clades is now possible with the development of new methods on macroevolution that provide a statistical framework for hypothesis testing (Harmon et al. 2003; Alfaro et al. 2009; FitzJohn 2012; Revell et al. 2012; Ingram and Mahler 2013; Rabosky et al. 2013, 2014a; Rabosky 2014). Here, the overall rates of speciation of the lineages among centers of diversity are estimated and compared in order to identify possible mechanisms that affected the rates of speciation after the geographic isolation of the lineages.

Besides the predicted disparities in speciation rates, differences in the tempo and mode of evolution of adaptive traits among centers of diversity are also expected as a response to differential ecological opportunity. Because the *Ronnbergia* Alliance is part the large adaptive radiation of the Core Bromelioideae, it has been suggested that its diversification is likely driven by the ability of the plants to colonize epiphytic habits, form tank rosettes and use the CAM photosynthetic pathway (Crayn 2004; Quezada and Gianoli 2011; Givnish et al. 2014; Silvestro et al. 2014; Crayn et al. 2015). However, characters that modulate the radiation in response to pollinators, herbivores or seed dispersers also played an important role in the diversification of lineages within the Bromeliaceae (Benzing 2000; Givnish et al. 2014). For instance, the combination of color and size of floral bracts and petals, organ armature, floral compression and the development of petal appendages may act synergistically to protect the flowers from
predators and attract potential pollinators (Benzing 2000). The function of these traits in the adaptive radiation of the Core Bromelioideae, however, has never been studied in a phylogenetic context. For this reason, the heterogeneous floral variation observed in the *Ronnbergia* Alliance was measured (Fig. 4.1) and its evolutionary rate dynamics were quantified and compared among lineages as an indirect way to explore the potential impact of pollinators and floral predators in the radiation of the group.

This paper seeks to present the diversification of the *Ronnbergia* Alliance as an empirical case that shows how evolutionary dynamics can be different but interconnected among the Caribbean, the Atlantic Forest and the Tumbes-Chocó-Magdalena biodiversity hotspots. A biogeographic analysis was conducted to provide a hypothesis of ancestral geographical range evolution and a comparison of evolutionary rate dynamics among lineages was carried out in order to contrast the influence of geographic isolation in the evolution of the *Ronnbergia* Alliance. The results of this study are expected to be part of a holistic view that helps understanding the complex origin and preservation of Neotropical biodiversity hotspots and providing the basis to understand the outstanding adaptive radiation of the Core Bromelioideae across tropical America.

4.3 Methods

4.3.1 Time-calibrated phylogeny

Divergence times were estimated in the phylogeny of the *Ronnbergia* Alliance using *BEAST v. 2.1.3* (Bouckaert et al. 2014) through the CIPRES Science Getaway platform (Miller et al. 2011). The DNA sequence data and initial taxon sampling used for this analysis corresponds
to the six-gene dataset from Aguirre-Santoro (in preparation; see chapter 1). In addition, the
topology for the BEAST analysis was fixed using the best Maximum Likelihood tree from the
same study (see chapter 1, Fig. 1.10) in order to avoid topological conflicts and achieve rapid
convergence while still integrating over uncertainty in the estimation of branch lengths and
divergence times. Because there are no known fossils of bromeliads that can be used to infer the
absolute ages of clades, two calibration points were specified using the indirect calibrations from
Givnish et. al. (2014). First, a normally distributed prior age of 9.4 mya (standard deviation (SD):
0.5) was determined for the crown of the subfamily Bromeliioideae at the root of our tree as
specified in Givnish et al. (2014). Second, a uniform prior of 5.5 mya (SD: 0.5) was used for the
crown age of the tank-epiphytic clade sister to Acanthostachys (also known as Core
Bromeliioideae; Givnish et al 2014). The BEAST analysis were conducted on the partitioned
DNA sequence dataset using the same models of evolution specified by Aguirre-Santoro (in
preparation; see chapter 1) and divergence times were estimated under a Yule tree prior and
unlinked lognormal relaxed clock models. Two independent MCMC runs of 100 million
generations each were performed, sampling every 30,000 generations and discarding the samples
from the first 25 million generations as burn-in. Convergence and appropriate parameter mixing
of the MCMC runs were inspected in Tracer v. 1.6 (Rambaut and Drummond 2003). Finally, the
postburn-in set of trees of the two runs were combined in a single file using LogCombiner
(Bouckaert et al. 2014) and, subsequently, a time-calibrated Maximum Credibility Tree (MCC)
was generated in TreeAnnotator (Bouckaert et al. 2014) setting the branch lengths as the mean
node ages across all trees.

In order to have a time-calibrated tree that only includes species of the Ronnbergia
Alliance, all outgroups were pruned while conserving the original branch lengths using the R
packages *ape* and *geiger* (Paradis et al. 2004; Harmon et al. 2007; R Development Core Team 2015). Additionally, duplicate accessions of the same species within the *Ronnbergia* Alliance were pruned in order to include only one representative per species. For this selection, accessions represented by type specimens or wild-collected specimens identified by the first author were preferred (Table 4.1). This subsampled dataset includes 56 species, representing nearly 80% of the total number of species described in the *Ronnbergia* Alliance (Aguirre-Santoro in preparation; see chapter 2).

**4.3.2 Biogeography**

To infer the most likely biogeographic scenario that explains the disjunct distribution within the *Ronnbergia* Alliance, seven areas of endemism were defined based on the marked geographic structure observed in the clades of the phylogeny. The first area, here named “Pacific Forest,” corresponds to the continuous range encompassed by the Tumbes-Chocó-Magdalena biodiversity hotspot, including its adjacent forests of southern Costa Rica and Panama and the Inter-Andean and eastern slopes of the Andes of Ecuador to Central Peru. The second area, here called “Atlantic Forest”, includes the Atlantic Forest, including its adjacent semi-deciduous forests and gallery forests from Ceará to Rio de Janeiro states in Brazil. Except for the widespread *Wittmackia lingulata*, the remaining area occupied by the species of the *Ronnbergia* Alliance is restricted to the Caribbean, which was separated in four areas: Puerto Rico, Jamaica, Cuba, and Western Caribbean. The latter encompasses Grand Cayman, Providencia Island (Colombia) and the Yucatán Peninsula of Mexico. Finally, one area that unites the northern Atlantic coast of South America and the Lesser Antilles was defined in order to accommodate the range of *W. lingulata* that does not overlap with the remaining six areas.
Based on these areas of endemism, the evolution of geographical ranges was inferred in the time-calibrated MCC tree of the *Ronnbergia* Alliance using the R package *BioGeoBears* (Matzke 2013; R Development Core Team 2015). This package allows estimating ancestral areas across six different models of range evolution in a likelihood framework and chooses the best fitting model through statistical comparisons. The three main models used in *BioGeoBears* correspond to the dispersal-extinction-cladogenesis model (DEC; Ree and Smith 2008); a probabilistic implementation of the dispersal-vicariance model (DIVA-like; Ronquist 1997); and a likelihood variation of the BayArea model (BAYAREA-like; Landis et al. 2013). The remaining three models are nested within each of the first three models and include an additional parameter that represents a founder-event speciation (+ J; Matzke 2014). Independent biogeographic analyses were conducted under each model without specifying any constraints in direction or time for dispersal and their fit was assessed using the Akaike Information Criterion with correction for sampling size (AICc). The best biogeographic reconstruction was selected as the one inferred using the model with the lowest AICc value. Finally, the marginal probabilities of the inferred ancestral areas were plotted on the time-calibrated MCC tree for further interpretation.

4.3.3 Speciation rate dynamics

In order to compare if the overall speciation rates were different among specific clades in the *Ronnbergia* Alliance, a Bayesian analysis of macroevolutionary mixtures was conducted on the time-calibrated MCC tree (Rabosky et al. 2013; BAMM; Rabosky 2014). This method uses reversible-jump MCMC to explore simple to complex models that differ in the number of diversification regimes and select those models that improve the posterior probability over time.
At the end of the analysis, BAMM provides a posterior distribution of rate regime scenarios that best fit the diversification dynamics of the *Ronnbergia* Alliance, including an estimation of the speciation rates at any point of any branch across all samples of the posterior distribution. For this analysis, appropriate priors on rate parameters were chosen for our phylogenetic tree using the function “setBAMMpriors” from the *R* package *BAMMtools* (Rabosky et al. 2014b; R Development Core Team 2015). The effect of missing taxa was also accounted for by specifying that the taxonomic sampling represents 80% of the known diversity of the *Ronnbergia* Alliance. Subsequently, two MCMC runs analyses were performed in *BAMM* v. 2.2.0 (Rabosky 2014) for 5 million generations each, using a sampling frequency of 1000. Convergence of the MCMC and appropriate effective sampling size of the log-likelihoods and number of shift events was assessed with the *R* package *coda* (Plummer et al. 2006; R Development Core Team 2015).

All analyses explained below were conducted on the output of the BAMM analysis using different functions of the *R* package *BAMMtools* (Rabosky et al. 2014b; R Development Core Team 2015). Overall speciation rate dynamics were compared among clades in three ways. First, Lineage Through Time (LTT) and density plots of the mean marginal speciation rate were constructed for the clades that diversified after the first geographical split of the *Ronnbergia* Alliance: *Ronnbergia* and *Wittmackia*. Similarly, density plots of the mean marginal speciation rate were generated for the radiation of the Caribbean Clade and compared against the overall speciation rates of the background lineages. Second, rate through time plots (RTT plots) were generated for each of the above-described lineages in order to compare and visualize if speciation rates changed overtime within each radiation. Third, because the first two comparisons only permit contrasting the overall magnitude and direction of speciation rates among clades, a macroevolutionary cohort analysis was used to make pairwise comparisons of
the probability that species (or clades) share similar evolutionary dynamics across the phylogeny (Rabosky et al. 2014b). Finally, BAMM was used to automatically quantify and localize significant rate shifts along the phylogeny without \textit{a priori} specifications in order to describe the possible causes that led to changes in diversification regimes. To achieve this objective, the posterior distribution of the number of rate shifts was summarized in order to detect what rate shift count model has the higher posterior probability. Subsequently, the 95\% credible set of shift configurations and their frequencies sampled during the MCMC were explored in order to detect the most likely locations of the rate shifts along the phylogenetic history of the \textit{Ronnbergia} Alliance. The general information on the location and magnitude of the rate shift was summarized in a phylorate plot, which displays the mean of the marginal posterior density of speciation rates along the branches of the phylogeny in a gradient of colors.

\subsection*{4.3.4 Flora evolutionary dynamics}

To study the rate of evolution of floral traits along the phylogeny of the \textit{Ronnbergia} Alliance, total flower length and twelve floral substructures were measured as they may confer plasticity to the overall shape of the flower in response to pollinators, herbivores and/or seed dispersers (Table 4.1). Only one well-preserved individual flower per species was measured because corollas are frequently absent or poorly conserved in herbarium specimens of bromeliads. This strategy assures to record only actual proportions observed in the species rather than unbalanced averages of the substructures. Raw measurements were log-transformed prior to all analyses. Because the petals and ovaries of \textit{Ronnbergia sp. nov.} and \textit{Wittmackia jamaicana} are unknown, measurements on these structures were inferred using the function \textquote{anc.ML} of the \textit{R} package \textit{phytools} (Revell 2012; R Development Core Team 2015). This method uses
maximum likelihood ancestral character reconstructions under a Brownian motion model to calculate tip states for a continuous character with missing data. Finally, the effect of flower size on the log-transformed measurements of all floral substructures was corrected using the phylogenetic size correction function “phyl.resid” of the R package phytools (Revell 2012; R Development Core Team 2015) and their residual values were conserved for subsequent analyses.

To determine whether variation in flower length and in size-corrected floral substructures can be attributed to the phylogenetic relationships of the species, phylogenetic signal was tested on each trait using Blomberg’s $K$ (Blomberg et al. 2003) and Pagel’s $\lambda$ (Pagel 1999) as implemented in the function “phylosig” of phytools (Revell 2012; Table 2; R Development Core Team 2015). Subsequently, a phylogenetic principal component analysis (pPCA) was conducted on the residuals of the floral substructures using the function “phyl.pca” of phytools to reduce the number of floral variables into a smaller number of components. The PC scores for each species were obtained and only the first two principal components (PC1 and PC2) were conserved, as they explain 66% of the total variance of floral shape (Table 4.2). In summary, the final morphological dataset for the evolutionary rate analyses consisted of three floral axes: the log-transformed measurements of flower length and the scores of the first two principal components representing floral shape (Table 4.1).

To analyze the evolutionary rate dynamics of flower length and shape, the variation of these phenotypic axes was visualized in a morphospace plot, which allows for the identification of general trends in floral evolution across the species of the Ronbergia Alliance. Then, the rates of phenotypic evolution for each floral axis were quantified and distinct rate shifts across the phylogeny were explored as explained above for the speciation rate dynamics analysis in
BAMM. For each analysis of floral evolutionary dynamics, two parallel BAMM runs were conducted for 5 million generations with a sampling frequency of 1000, using appropriate priors from the “setBAMMpriors” function of BAMMtools, and checking MCMC convergence and effective sample size. As in the analysis of speciation rates, comparisons of the overall rate of phenotypic evolution were performed between Ronnbergia and Wittmackia, and between the Caribbean Clade and its background lineages using density plots and RTT plots. A macroevolutionary cohort analysis was also carried out to compare the probabilities that two lineages share the same phenotypic rate regime. Significant rate shifts in floral evolution were summarized and displayed by generating phylorate plots and analyzing the posterior probabilities of distinct rate shift counts and configurations.

4.4 Results

4.4.1 Divergence time and biogeography

The MCC tree of the BEAST analysis shows the origin of the Ronnbergia Alliance in the early Pliocene, around 3.6 mya (95% Highest Posterior Density interval (HPD): 1.8-5.5 mya); at this point Ronnbergia and Wittmackia diverged from each other. The diversification of Ronnbergia started around 2.9 mya (95% HPD: 1.1-3.7 mya), whereas the cladogenesis of Wittmackia began later, around 2.3 (95% HPD: 1.1-3.7 mya). The diversification of the Caribbean Clade started in the early Pleistocene within Wittmackia, exhibiting a crown age of 0.8 mya (95% HPD: 0.4-1.4 mya).

The AICc comparisons of log-likelihood values obtained under different biogeographic models in BioGeoBears suggest that the DIVA-like + J model is the best fit for the dataset (Table
4.3). The second best fitting model, DEC + J, produced an almost identical ancestral area estimation for the dataset. The biogeographic history inferred under the DIVA-like + J model shows that the origin of the Ronnbergia Alliance, and simultaneous split between Ronnbergia and Wittmackia, occurred in South America and resulted in a vicariant event that separated the Pacific Forest and the Atlantic Forest (Fig. 4.2). The whole radiation of Ronnbergia was restricted to the Pacific Forest, while the radiation of Wittmackia started in the Atlantic Forests and was followed by multiple consecutive radiations in this area (labeled as the Brazilian radiation in Figs. 4.1–4.3 and 4.5–4.6) and two independent dispersals outside this region. One of these dispersal events with origin in the Atlantic Forest corresponds to the recent migration of W. lingulata to northern South America, the Lesser Antilles and the Pacific Forest. On the other hand, the most significant dispersal event corresponds to the long-distance range shift, around 1.2 mya, between the Atlantic Forest and Jamaica, which subsequently gave origin to the Caribbean Clade. Jamaica was reconstructed as the main center for the radiation of the Caribbean Clade, from where two independent dispersals to Puerto Rico, one dispersal to Cuba, and one dispersal to the Western Caribbean (Grand Cayman + Providencia + the Yucatán Peninsula) occurred. Although each of these independent dispersals from Jamaica resulted in the rise of new species (except in Cuba), only the Western Caribbean was center of a secondary in situ diversification event that produced two species.
Figure 4.2. Ancestral area reconstruction of the *Ronnbergia* Alliance under the DIVALIKE + J model of *BioGeoBears*. Red arrows represent the location of the major geographic splits in the phylogenetic history of the group. The maps to the right summarize the main biogeographic events. Points in the map correspond to the current geographic distribution of the species; their colors match the color of the clade that they belong to (except for *W. lingulata*, which is labeled in red). Bottom: early vicariance of *Ronnbergia* and *Wittmackia*. Middle: long distance dispersal from the Atlantic Forest to Jamaica (thick arrow) and dispersal of *W. lingulata* to northern South America and the Lesser Antilles (narrow arrow). Top: dispersal events in the Caribbean Clade with center in Jamaica.
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Table 4.1. Vouchers and morphological measurements. The last three columns correspond to the values of three floral axes used in the evolutionary rate analyses.
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**PERCENT EXPLAINED**  
39% 27%

Table 4.2. Columns 1-4: Phylogenetic signal using Blomberg’s $K$ and Pagel’s $\lambda$, including their corresponding p-values. Columns 5-6: loadings of the first two principal components of the pPCA analysis and the percent of variation explained by these components. Values in bold represent the traits that explain the variation on each principal component.

<table>
<thead>
<tr>
<th>Model</th>
<th>Ln likelihood</th>
<th>Degrees of freedom</th>
<th>p-value of Likelihood Ratio Test</th>
<th>AICc</th>
<th>d</th>
<th>e</th>
<th>j</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEC+J</td>
<td>-45.08</td>
<td>3</td>
<td>0.0007</td>
<td>96.16</td>
<td>0.01016</td>
<td>0.00000</td>
<td>0.00627</td>
</tr>
<tr>
<td>DEC</td>
<td>-50.88</td>
<td>2</td>
<td>Null model</td>
<td>105.8</td>
<td>0.02008</td>
<td>0.00000</td>
<td>0.00000</td>
</tr>
<tr>
<td>DIVALIKE+J</td>
<td>-44.08</td>
<td>3</td>
<td>0.0015</td>
<td>94.16</td>
<td>0.01072</td>
<td>0.00000</td>
<td>0.00591</td>
</tr>
<tr>
<td>DIVALIKE</td>
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<td>2</td>
<td>Null model</td>
<td>102.2</td>
<td>0.02151</td>
<td>0.00000</td>
<td>0.00000</td>
</tr>
<tr>
<td>BAYAREALIKE+J</td>
<td>-48.13</td>
<td>3</td>
<td>1.70E-10</td>
<td>102.3</td>
<td>0.00922</td>
<td>0.00000</td>
<td>0.00840</td>
</tr>
<tr>
<td>BAYAREALIKE</td>
<td>-68.52</td>
<td>2</td>
<td>Null model</td>
<td>141</td>
<td>0.02307</td>
<td>0.11632</td>
<td>0.00000</td>
</tr>
</tbody>
</table>

Table 4.3. Comparison of the fit of six biogeographic models in *BioGeoBears* using our empirical dataset. Row highlighted in grey corresponds to the best-fit model with the lowest AICc value in bold. d: estimated rate of dispersal; e: estimated rate of extinction; j: estimated rate of founder events.
4.4.2 Floral morphology

The first principal component of the pPCA analysis (PC1) explains 39% of the variation of the floral substructures, whereas PC2 explains 27% of the variation. PC1 summarizes the variation in width of the floral bracts, flowers and petals, in addition to the variation in length of the sepals and their mucros (Table 4.2). Species with wide floral bracts, flat and wide flowers, wide petals, and short sepal mucros, like *Ronnbergia veitchii* and *Wittmackia urbaniana*, have negative values in the PC1 axis, while species with narrow floral bracts, terete and narrow flowers, narrow petals, and long sepal mucros, like *R. weberbaueri* and *R. petersii*, have positive values in the same axis. PC2 mainly accounts for the variation in width and length of the floral bracts and the length of sepal mucros (Table 4.2). Species with small floral bracts and short sepal mucros, like *Ronnbergia drakeana* and *R. killipiana*, show positive values of PC2, whereas species with long floral bracts and long sepal mucros, like *R. deleonii* and *W. antillana*, show negative values. The morphospace plots show that the species of *Ronnbergia* exhibit the largest phenotypic variation both in floral shape (PC1 and PC2) and flower length compared to *Wittmackia* (Fig. 4.3). Moreover, *Ronnbergia* tends to exhibit longer flowers than *Wittmackia*, although there is overlap. Within *Wittmackia*, the species that diversified in the Atlantic Forest (Brazilian radiation) and the Caribbean form separate clusters along the floral shape axes but overlap around low values of flower length. These clusters describe that the species in the Caribbean Clade tend to exhibit wider and longer floral bracts, flatter and wider flowers, longer sepals, and wider petals than those species that diversified in the Atlantic Forest.
Figure 4.3. Morphospace plots for the three floral axes: Flower length, PC1 and PC2. Blue points represent values for *Ronnbergia* species. Green and orange points represent values for *Wittmackia* species. Green: Caribbean Clade; orange: Brazilian radiation.
4.4.3 Evolutionary rate dynamics

The BAMM analyses overwhelmingly favored models with more than one rate shift for speciation rates (posterior probability [PP]: 0.80) and phenotypic rates of PC1 (PP: 0.86) across the phylogeny of the *Ronnbergia* Alliance. In the case of flower length and PC2, a single rate model (no rate shifts) was the most frequently sampled with posterior probabilities of 0.49 and 0.5, respectively (Table 4.4).

Table 4.5 and Figure 4.4 summarize and compare the variation of the mean marginal evolutionary rates among the main clades of the *Ronnbergia* Alliance. The BAMM analyses suggest slightly faster overall rates of speciation and phenotypic evolution of PC1 for the radiation of *Wittmackia* compared to *Ronnbergia*, and much faster for the Caribbean Clade compared to the background lineages. The rate through time (RTT) plots show that the rates of speciation in *Ronnbergia* did not experience dramatic rate shifts and have a tendency to slow down over time, while the speciation rates of *Wittmackia* are more heterogeneous and have a tendency to increase over time. This is further confirmed with the lineage through time plot (Fig. 4.5), which shows a marked increase in lineage proliferation for *Wittmackia* around 1–1.3 mya compared to the constant pattern of *Ronnbergia*. In the case of the Caribbean Clade, it can be observed that the background lineages exhibit a constant decrease over time in the speciation rate, while the significantly faster Caribbean radiation experienced an initial rate increase followed by a slight decrease after reaching a maximum rate threshold (Fig. 4.4).
### Table 4.4

<table>
<thead>
<tr>
<th>Number of rate shifts</th>
<th>Speciation rates</th>
<th>Flower length</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.2</td>
<td>0.49</td>
<td>0.14</td>
<td>0.5</td>
</tr>
<tr>
<td>1</td>
<td>0.49</td>
<td>0.3</td>
<td>0.42</td>
<td>0.3</td>
</tr>
<tr>
<td>2</td>
<td>0.22</td>
<td>0.14</td>
<td>0.28</td>
<td>0.14</td>
</tr>
<tr>
<td>3</td>
<td>0.062</td>
<td>0.052</td>
<td>0.11</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Mean marginal rate 1.43 0.1 1.11 0.96

Table 4.4. Posterior probabilities of rate shift counts for speciation rate and phenotypic rates of the three floral axes.

Bottom row shows the estimated mean marginal rate for speciation rate and phenotypic rates of the three floral axes.

### Table 4.5

<table>
<thead>
<tr>
<th>Clade</th>
<th>Speciation rates</th>
<th>95% C.I.</th>
<th>Flower length</th>
<th>95% C.I.</th>
<th>PC1</th>
<th>95% C.I.</th>
<th>PC2</th>
<th>95% C.I.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ronnbergia Alliance</td>
<td>1.43</td>
<td>0.07-0.14</td>
<td>1.11</td>
<td>0.96</td>
<td>0.67-1.37</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ronnbergia</td>
<td>1.17</td>
<td>0.06-0.15</td>
<td>0.97</td>
<td>0.98</td>
<td>0.66-1.45</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wittmackia</td>
<td>1.69</td>
<td>0.07-0.14</td>
<td>1.24</td>
<td>0.95</td>
<td>0.67-1.33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribbean Clade</td>
<td>2.16</td>
<td>0.07-0.14</td>
<td>2.45</td>
<td>0.9</td>
<td>0.64-1.26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Background (non-Caribbean)</td>
<td>1.35</td>
<td>0.07-0.15</td>
<td>0.95</td>
<td>0.97</td>
<td>0.67-1.39</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4.5. Variation of the mean marginal evolutionary rates among the main clades of the Ronnbergia Alliance and their corresponding 95% confidence intervals.

The heterogeneity of the phenotypic rate dynamics of PC1 showed a different pattern compared to that of speciation rates (Fig. 4.4). In Ronnbergia the phenotypic rates of PC1 remained invariable and constant over time. Although these rates exhibit the same pattern at the beginning of the radiation of Wittmackia, they experienced a significant rapid increase from around 0.7 mya to the present day. The significantly faster phenotypic rates of PC1 in the Caribbean Clade compared to its background lineages are markedly heterogeneous and show a
pattern of initial massive rate increase overtime, followed by a plateau of fast phenotypic rate variation. On the other hand, the phenotypic rate of the background lineages remained invariable and constant over time. In the case of flower length and PC2, the overall phenotypic rates did not vary among the main clades of the *Ronnbergia* Alliance.
Figure 4.4. Density plots and Rate Through Time plots of the analysis on evolutionary rate dynamics.
Figure 4.5. Lineage Through Time plot comparing the diversification of *Ronnbergia* and *Wittmackia*.

Figure 4.6 shows the results of the macroevolutionary cohort analyses, which compare the probability of shared rate regimes among clades. In these analyses, hot colors (e.g. red) represent the highest probability of a shared regime between pairs of species, whereas the cold colors (e.g. blue) represent low probability of shared regimes. As expected from the previous comparisons of evolutionary rate variation in flower length and PC2, all the species and clades in the *Ronnbergia* Alliance share the same constant rate regime (Fig. 4.6, C-D). In the case of speciation rates, the cohort analysis shows that all the species within *Ronnbergia* share a similar rate regime (Fig. 4.6A; cohort A1); this is also the case for the Caribbean Clade (Fig. 4.6A; cohort A3). However, the comparison between *Ronnbergia* and the Caribbean Clade shows that
both clades differ drastically in rate regimes. The multiple lineages that originated in the Brazilian radiation exhibit different patterns of rate regimes. For instance, the earliest-diverging clade of *Wittmackia* shows a rate regime similar to that of *Ronnbergia* (Fig. 4.6A; cohort A1), but completely different from that of the Caribbean Clade. The rate regime of this clade also differs to a lesser extent from the regimes observed in the other lineages of the Brazilian radiation (Fig. 4.6A; cohort A2), except for the first branch of its sister clade. Two lineages at the core of the Brazilian radiation diversified with almost identical rate regimes (Fig. 4.6A; cohort A2). The first clade includes *Wittmackia brasiliensis* and its sister clade, whereas the second lineage is represented by *W. bicolor*. The rate regime of these two lineages is intermediate between the regimes of *Ronnbergia* and the Caribbean Clade, although tends to be more similar to the regime of the Caribbean Clade (Fig. 4.6A; cohort A3). Finally, the macroevolutionary cohort analysis of the phenotypic rates of PC1 shows that these rates in most of the Caribbean Clade are different than those of the background lineages (Fig. 4.6B; cohorts B2 and B3), which in turn, share the same rate regime (Fig. 4.6B; cohort B1). Within the Caribbean Clade, however, the phenotypic rate regime of earliest-diverging lineage has a tendency to be more similar to that of the non-Caribbean lineages (Fig. 4.6B; cohort B2).
Figure 4.6. Macroevolutionary cohort analyses of the evolutionary rate dynamics. Colors correspond to the probability that a pair of species share the same rate regime. Labeled boxes correspond to arbitrarily selected cohorts with similar evolutionary rate dynamics.
The analysis of speciation rates favored a two-rate regime model (one rate shift) with a posterior probability of 0.49 (Table 4.4). The inspection of the 95% credible set of rate shift configurations shows that a significant rate shift occurred at the core of the Brazilian radiation, two or three nodes above the beginning of the radiation in *Wittmackia* (PP: 0.23 and PP: 0.16, respectively). Other shift configurations with lower posterior probabilities suggest that the rate shift occurred at the beginning of the radiation in the Caribbean Clade or immediately after its first split (PP: 0.10 and PP: 0.06, respectively). The phylorate plot of Figure 4.7 suggests that speciation rates decreased during the radiation of *Ronnbergia* and the earliest-diverging clade of *Wittmackia*. On the other hand, there was a slight increase in speciation rate at the second node of *Wittmackia*, followed by a significant increase at the third node, where the most significant rate shift is located (Fig. 4.7). After this rate shift event, the lineages that continued diversifying in the Atlantic Forest exhibit a slight slow down over time, whereas the radiation of the Caribbean Clade shows acceleration in speciation rates. In the case of phenotypic rates in PC1, BAMM also supports a two-rate regime model (one rate shift) with a posterior probability of 0.42. The best rate shift configuration (PP: 0.37) and phylorate plot show that this rate shift is located at the core of the Caribbean Clade, immediately after the first split in the radiation (Fig. 4.7). The earliest-diverging clade of the Caribbean Clade, however, exhibits a slight acceleration compared to the background lineages. Finally, the phylorate plots of the phenotypic rates of flower length and PC2 show that there were no significant rate shifts and only one rate regime across the phylogeny of the *Ronnbergia* Alliance.
Figure 4.7. Phylorate plots of the evolutionary rate dynamics. Branch colors are proportional to the estimated mean marginal rate of speciation, PC1, flower length and PC2. Density plots at the bottom of each phylorate plot represent how these colors were assigned based on the frequency of rate values obtained during the BAMM analyses. Red circles represent the location of the most significant rate shift found in the BAMM analyses.

4.5 Discussion

4.5.1 1. The early major split: evolution in the “Pacific Forest” and the Atlantic Forest

According to Givnish et al. (2011, 2014), the adaptive radiation of the Core Bromelioidae likely started around 5.5 mya in the Brazilian shield, coinciding with the uplift of
the Serra do Mar and Serra da Matinqueira, and the consolidation of the rainy, high-moisture forests in the Atlantic Forest of eastern Brazil. Although the *Ronnbergia* Alliance is the earliest-diverging lineage of the Core Bromelioideae, the ancestral range reconstructions obtained in the present study do not entirely suggest its origin in the Brazilian Shield. Instead, they indicate an area of origin that unifies the Pacific Forest and Atlantic Forest, from where *Ronnbergia* and *Wittmackia* diverged in a vicariant event, about 3.6 mya (Fig. 4.2). Despite this result, the confidence on the reconstruction of this vicariant event is low because of the scale of this study. In this sense, the geographic range of the sister group of the *Ronnbergia* Alliance was not considered in the biogeographic analysis because its numerous species occupy a large number of areas across the entire Neotropics. For this reason, it is suggested that only a comprehensive biogeographic study across the whole Core Bromelioideae can bring clarity to the area of origin of the *Ronnbergia* Alliance. Regardless of whether *Ronnbergia* and *Wittmackia* were separated by a vicariant or a dispersal event, the most important pattern that emerges from this geographically disjunct diversification is that the radiations of both genera occurred within the most humid and species-rich regions of South America: the Pacific Forest and the Atlantic Forest.

Several studies have described the similarities of floras between the Atlantic Forest and the Andes; however, they mostly refer to high altitude and cold tolerant groups that migrated from the central Andes to the mountainous regions of the Atlantic Forest (Thorne 1972; DeForest Safford 1999; Fiaschi and Pirani 2009). Records of floristic similarities between northwestern South America and the Atlantic Forest in groups that inhabit medium to low elevation ranges, however, are scarce and normally include a transitional zone in the Amazon (Gentry 1982, 1992; Fiaschi and Pirani 2009; Hoorn et al. 2010; Antonelli and Sanmartín 2011). This is not
completely the case for the *Ronnbergia* Alliance, as *Ronnbergia* and *Wittmackia* occupy areas drastically disjunct without transitional zones in the Amazon. It must be noted, however, that two species of the early-diverging clade *Ronnbergia* inhabit the mountainous western extreme of the Amazon: *Ronnbergia drakeana* and *R. wuelfinghoffii*, suggesting that an ancient presence of the *Ronnbergia* Alliance in the Amazon rainforest cannot be discarded. In terms of precipitation, soil fertility and dissected topography, the Atlantic Forest and Pacific Forest are more similar to each other than to the Amazon rainforest, which has lower annual precipitation, less fertile soil types, and a less drastic topographic variation (Gentry 1982; Thomas and Britton 2008; Hoorn et al. 2010). This pattern may explain the absence of species of the *Ronnbergia* Alliance in the Amazon and suggests a tendency to climatic niche conservatism in its early diversification.

Moreover, the origin of the *Ronnbergia* Alliance, around 3.6 mya, and the start of the radiation of *Ronnbergia* about 2.9 mya, coincide with the final uplift of the northern Andes, a factor that probably contributed to the drastic isolation of this lineage in the forests of northwestern South America, near the Pacific coast, and subsequent migration through the Panama isthmus.

The results obtained here showed that the diversification of *Ronnbergia* took place in the Pacific Forest (Fig. 4.3). The definition used here for the Pacific Forest, however, is quite broad as it represents a continuous area of mostly medium to low elevation, superhumid forests with center in the Magdalena-Chocó-Tumbes biodiversity hotspot that expands to equally threatened areas in southern Costa Rica to northern Panama and the inter-Andean valleys and eastern Andean slopes of southern Ecuador and northern Peru. Although fine-scale ancestral range reconstructions were not performed for the lineages that inhabit the Pacific Forest, it can be inferred that species that occur in the southern distribution of the clade may have originated early in the radiation. This is not the case for the species that colonized Central America, as they
appeared later in separate parts of the phylogeny. This trend suggests a south to north pattern in
the radiation that coincides with the already consolidated Panama Isthmus (Montes et al. 2012;
Bacon et al. 2015).

According to the results the rates of speciation within Ronnbergia are relatively constant
and lower than those of Wittmackia, with a trend to a slow down over time (Fig. 4.4). Slowdowns in diversification after the start of an adaptive radiation are expected according to the
early-burst mode of evolution, where ecological opportunity is predicted to decrease as niches
become filled and interspecific competition becomes stronger over time (Rabosky and Lovette
2008; Burbrink and Pyron 2010; Glor 2010; Mahler et al. 2013; Wellborn and Langerhans 2015).
This pattern is observed in the phylorate plot of speciation rate (Fig. 4.7), which shows that
during the split of Ronnbergia and Wittmackia the speciation rates were slightly rapid but
subsequently decreased across the radiation of Ronnbergia and at the early stages of the
diversification of Wittmackia. Although slowdowns are also expected in the rates of phenotypic
evolution (Mahler et al. 2013), this pattern is not so evident in the evolution of floral structures
within Ronnbergia, where the phenotypic rates of the three floral axes remained constant and
invariable over time (Figs. 4.4-4.6).

Ronnbergia exhibits the largest floral variation within the Ronnbergia Alliance (Fig. 4.3). This is not surprising, as the species of this bird-pollinated lineage inhabit a region that
concentrates the largest diversity in hummingbirds in the world (McGuire et al. 2014) and co-
occur with hundreds of potential herbivores and seed dispersers (Rangel Ch 2004). Despite this
large floral diversity, the constant rate pattern in floral evolution indicates that niches in the
Pacific Forest were probably filled at a gradual manner and, in some cases, speciation may have
not responded directly to adaptation during the late stages of the radiation. In this case, the
influence of non-adaptive mechanisms, such as geographic divergence may have played an important role in the diversification of *Ronnbergia* (Givnish 2015). It is possible that high extinction rates also had an influence in the estimations of phenotypic rate; however, this effect was not directly assessed in this study.

The evolutionary rate comparisons showed that speciation rates and phenotypic rates of PC1 were more heterogeneous and faster in *Wittmackia* than in *Ronnbergia*, while flower length and PC2 remained invariable throughout the radiation of the *Ronnbergia* Alliance (Fig. 4.4 and 4.6C-D). The speciation rates were slow at the early stages of the radiation in *Wittmackia* and remained as such in its early-diverging lineages (Figs. 4.4-4.7; cohort A1). This pattern is consistent with the early-burst mode of evolution. However, the results showed that this pattern was disrupted during the Brazilian radiation at the most derived nodes of *Wittmackia*, where the speciation rates faced a rapid acceleration, around 1.5 mya (Figs. 4.4-4.7; cohort A2). This acceleration experienced a slight decrease in the lineages the continued diversifying in the Atlantic Forest but became greatly enhanced in the diversification of the Caribbean Clade, around 0.8 mya (Figs. 4.4 and 4.6). It is possible that the acceleration that occurred in the core lineages of the Brazilian radiation reflects the effect of the Pleistocene glaciations in the Atlantic Forest. For instance, recent studies showed that during the Pleistocene, the Atlantic Forest experienced repeated events of major area fluctuation, producing not only multiple opportunities for speciation, but also creating stable areas that became refuges for biodiversity (Carnaval et al. 2009). This pattern is consistent with the phylogeny of *Wittmackia* because of two characteristics: 1) the early-diverging lineage, which did not experience speciation rate shifts, only occurs in the highly stable forests of Southern Bahia, whereas 2) the core lineages involved in the speciation rate shift diversified in both the stable forests of southern Bahia and the unstable
northern-most extremes of the Atlantic Forest (e.g. breijos de altitude in Ceará state) or even the northern part of South America and the Lesser Antilles, in the case of *W. lingulata*.

Floral traits did not experience significant rate shifts during the radiation of lineages within the Atlantic Forest. The flowers in the Brazilian species of *Wittmackia* (including *W. lingulata*) are not as phenotypically diverse as the flowers in *Ronnbergia* (Fig. 4.3). Moreover, the petals of the Brazilian species do not show remarkable color variation and rarely produce petal appendages (Aguirre-Santoro in preparation; see chapter 1). This reduced morphological spectrum, combined with constant phenotypic rates, indicates a tendency to niche conservatism during the diversification of *Wittmackia* in the Atlantic Forest, where speciation may be driven by geographical and climatic shifts rather than rapid adaptation to pollinators and herbivores. Interestingly, this contrast between the large floral diversity in *Ronnbergia* and the reduced variation in *Wittmackia* coincides with the large diversity of hummingbirds in northwestern South America compared to their low diversity in the Atlantic Forest (McGuire et al. 2014). This possible correlation between hummingbird diversity and floral variation in the *Ronnbergia* Alliance, however, still needs to be assessed.

### 4.5.2 The second major split: dispersal from the Atlantic Forest to Jamaica and evolutionary dynamics in the Caribbean Clade

The second major shift in geographic range within the *Ronnbergia* Alliance was the long-distance dispersal from the Atlantic Forest to Jamaica, around 1.2 mya (Fig. 4.2). This type of dispersal is unusual and has rarely been recorded in the literature for other groups of organisms (Acevedo-Rodriguez and Strong 2008). The biogeographic reconstructions and BAMM analyses suggested that a founder event, followed by a remarkably rapid radiation with center in Jamaica,
gave rise to the 17 species that comprise the Caribbean Clade (Figs 4.2, 4.4 and 4.7). Although the overall rates of speciation and phenotypic rates of PC1 in the Caribbean are considerably faster than in its background lineages (Fig. 4.4), our results suggest that the major acceleration occurred during the second main split in the clade, which formed the here called “Core Caribbean” clade (Fig. 4.7). The Core Caribbean clade includes all the species endemic to the dissected limestone forests of Jamaica and other species that recently colonized similar environments in Cuba, the Western Caribbean, and Puerto Rico. In contrast, the relatively slow-evolving, early diverging lineage of the Caribbean Clade is represented by species mostly endemic to the Blue and John Crow Mountains of Jamaica and one species endemic to limestone formations in Puerto Rico. These contrasting geographic characteristics indicate that the colonization of limestone habitats in Jamaica had a stronger effect in the rates of speciation and the phenotypic rates of PC1 than mountainous habitats; however, this hypothesis still needs to be assessed using soil and climatic data.

The species of the Caribbean Clade occupy a restricted area in the morphospace of floral variation (Fig. 4.3). They have predominantly small flowers and form a cluster around the most negative values of the two PC floral axes. Moreover, they are morphologically very different from the other lineages of Ronnbergia Alliance because of their compact, strobilate spikes (Aguirre-Santoro in preparation; see chapter 3). This constrained morphological variation in the Caribbean Clade suggests a possible tendency of the flowers to evolve towards an optimum adaptive peak or, alternatively, the lack of sufficient time for the species to strongly diverge in morphology from each other. In the dataset, only the first floral shape axis (PC1) shows a significant rate shift that started with the radiation of the Core Caribbean clade (Figs. 4.4, 4.6–4.7; cohort A3). The values on this axis describe the variation in structures that may be related to
floral protection, such as long and wide floral bracts, wide and flattened flowers, and robust sepals. This pattern indicates that floral protection likely played an important role in the evolution of the Caribbean Clade, especially after the colonization of limestone habitats in Jamaica. Adaptations to floral protection not only increase the chances of successful pollination, but also may be related to strategies to deter undesired seed predators. Benzing (2000) mentioned that many berry-fruited bromeliads produce seeds that become unviable after consumption by animals; therefore, they developed strategies to only attract dispersers interested in consuming the fruits externally, without detaching them from the infructescence. These strategies may include fruit compression, sepal persistence with pungent apical mucros, fruit explosiveness (like in Ronnbergia), among others. Although fruits were not measured in this study, the signature of some of these strategies is present in traits quantified here, such as sepal mucros, floral compression, and sepal size. The dataset used here, however, serves only to infer mechanisms that still require extensive empirical study in the field.

The co-occurrence of rate acceleration in both speciation and PC1 within the Caribbean Clade suggests a possible correlation between them. If this were the case, the diversification of the Caribbean Clade would be a clear example of a nested adaptive radiation occurring within the Core Bromelioideae. Nevertheless, this correlation was not explicitly tested here because correlation tests, such as phylogenetic independent contrasts or phylogenetic generalized least squares, seem to provide misleading results (Rabosky et al. 2013).

4.6 Concluding remarks

There are several issues not addressed in this study that deserve the attention of future projects. First, phylogenetic uncertainty was not accounted in the analyses. This is important
because the phylogenetic relationships within the most recent lineages of the Brazilian radiation and the Caribbean Clade are still poorly supported. However, given that these are “shallow” clades, incorporating phylogenetic uncertainty would not drastically change the final results. Second, the dynamics of extinction rates in the evolution of the Ronnbergia Alliance were not measured; instead, the analyses were focused only in speciation and phenotypic rates. Obtaining accurate estimates of extinction is still a controversial issue and there are no robust methodologies to efficiently approach this problem (Rabosky 2010). Third, the evolutionary rate dynamics of other potentially adaptive reproductive and vegetative structures were not tested here. These characters include, for example, petal appendages, inflorescence branching, flower color, pseudopetioles, the CAM photosynthetic pathway, formation of tank rosettes and epiphytism. These characters may have played a role as important as the floral traits assessed in this study and have the potential to reveal differential effects of adaptation across lineages in the Ronnbergia Alliance.

The evolution of the Ronnbergia Alliance is only one episode within the much larger adaptive radiation of the Core Bromelioidae. This study demonstrates that species-level phylogenies help identify the fine-scale processes that modulated this diversification. More importantly, this study helped revealing how diversification occurs in situ among centers of biodiversity with conservation priority. In this case, it was revealed how the Caribbean, especially Jamaica, is a much more dynamic area of diversification compared to the Atlantic Forest and the Pacific Forest. In the latter two areas, evolution seems to have occurred at a more constant pace, although it could have been influenced by drastic climatic fluctuations, like in the lineages that diversified in the Atlantic Forest. The pattern of disjunct geographic range separation, followed by rapid in situ diversification, has occurred many times during the
evolution of the Core Bromelioideae; for this reason, new species-level phylogenetic studies are still necessary in order to reveal the tempo and mode of evolution of this adaptive radiation restricted to the Neotropics.
5 References


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