Systematics and Biogeography of Orthaea Kloztsch (Ericaceae: Vaccinieae)

Nelson Salinas

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SYSTEMATICS AND BIOGEOGRAPHY OF Orthaea Kloztsch (ERICACEAE: VACCINIEAE)

by

NELSON R. SALINAS

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

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Abstract

SYSTEMATICS AND BIOGEOGRAPHY OF *Orthaea* Klotzsch (ERICACEAE: VACCINIEAE)

by

Nelson R. Salinas

Adviser: Dr. Paola Pedraza-Peñalosa

In the first chapter a study of the distribution patterns of the neotropical Vaccinieae (Ericaceae) is presented. Five areas of endemism were recovered: Central America, northern Chocó, southern Chocó, eastern Ecuador, and Yungas. Divergence times estimations indicate that the Andean clade of Vaccinieae migrated to South America during the Late Oligocene or Early Miocene (28.9–17.84 MA), and most of the subsequent diversification took place during the Tertiary. The Yungas was the first Andean area to be colonized, and several dispersals towards the north expanded their distribution range. Both areas of endemism and dispersal events were influenced by geological processes, such as the raise of the Andes, the western Andean Portal, and the establishment of the Central America isthmus. The second chapter is a phylogenetic analysis of *Orthaea* Klotzsch (Vaccinieae: Ericaceae) based on molecular and morphological data. *Orthaea* is polyphyletic, with members evolving independently in several lineages within the tribe Vaccinieae. Currently accepted species of *Orthaea* s.l. were recovered within four clades: Guiana Shield, *Empedoclesia, Thibaudia* p.p., and *Cavendishia + Orthaea* p.p. clades. Most of the Andean species of *Orthaea* s.l. are closely related to *Cavendishia*, however, relationships
within this clade were not strongly supported. Combined analyses of molecular and morphological data only provided support and uncovered synapomorphies for the Guiana Shield and Empedoclesia clades. Although a core Orthaea s.s. clade was identified, no nomenclatural changes are here proposed for the remainder species of Orthaea s.l. (20 spp.), except for those previously classified in Empedoclesia, a genus that needs to be reinstated. The third chapter is a taxonomic monograph of Orthaea s.s., as delimited in the combined phylogenetic analysis mentioned above. Fifteen species were studied, including two new species (O. eteocles N. R. Salinas and O. fissiflora N. R. Salinas & Pedraza) and a new synonym (O. glandulifera Luteyn = O. oedipus Luteyn).
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Nomenclatural changes and new names proposed herein are not intended to constitute valid publication.
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Chapter 1

Historical biogeography of the tribe Vaccinieae (Ericaceae) in the tropical Andes and adjacent regions

Abstract

Distribution patterns of the neotropical Vaccinieae (Ericaceae) were studied. Areas of Endemism were estimated for the Andean Cordillera and adjacent regions. A time-calibrated phylogeny and a reconstruction of the range evolution were assessed. Five areas of endemism were recovered: Central America, northern Chocó, southern Chocó, eastern Ecuador, and Yungas. The Andean clade of Vaccinieae migrated to South America during the Late Oligocene or Early Miocene (28.9–17.84 MA), and most of the subsequent
diversification took place during the Tertiary. The Yungas was the first Andean area to be colonized, and several dispersals towards the north expanded their distribution range. Both areas of endemism and dispersal events were influenced by geological processes, such as the raise of the Andes, the western Andean Portal, and the establishment of the Central America isthmus.

1.1 Introduction

The tropical Andes harbors one of the most diverse, yet threatened, floras of the world (Myers et al. 2000). The plant family Ericaceae, and particularly the tribe Vaccinieae, are a prominent component of the Andean flora: they are diverse (28 genera and more than 600 species, almost all native) and can be found in most of the Andean ecosystems, sometimes among of the dominating taxa (Luteyn 2002). Most of the Vaccinieae diversity is concentrated in humid enclaves, such as the premontane forests of the western slope of Colombia and Ecuador, the montane forests of the eastern slopes of Peru and Bolivia (commonly known as Yungas), and the high altitude grasslands of Colombia, Ecuador and Venezuela (Páramos). Secondary centers of diversity of Vaccinieae lie in areas also close to the Andes, such as the premontane forest of Costa Rica and Panama (in Central America), the lowland rain forests of western Colombia and Ecuador (widely known as the Chocó biogeographic region), and the mesic savannas and isolated table-top mountains—tepuis—of eastern Venezuela (Guiana Shield). Several other plant groups have similar distribution patterns in the Andes, and mode and tempo of their diversification process
are topics of active research and debate (Hoorn et al. 2010, 2011; Rull 2011; Luebert and Weigend 2014). Although several details of that process remain still unknown, it is widely accepted that the Andean uplift played an important role in the diversification of several plant groups centered in the Andes, such as Vaccinieae (Antonelli et al. 2009; Luteyn 2002). As mountain ranges extended, new ecosystems were created, providing new niches to plants to diversify (Gentry 1982a).

There is a sole analytical account of historical processes behind the colonization of Vaccinieae in the Andes (Kron and Luteyn 2005). Their preliminary analyses show that Vaccinieae migrated from the north (probably North America) to South America, initially colonizing the uppermost regions of the Andes. In their reconstruction of ancestral ranges, vicariance took place at the most basal nodes while dispersion occurred more recently.

Despite the contributions of Kron and Luteyn (2005), several details of the Vaccinieae diversification in the Andes are still missing, such as a temporal framework and evaluation of alternative cladogenetic processes (e.g., founder event). Furthermore, an appropriate scheme of areas to test this kind of historical questions is also absent. The latter is of particular interest because distribution patterns of Vaccinieae overlap, making difficult to set areas for analyses with unambiguous boundaries.

Therefore, the main goals of this study is to infer the divergence times, ancestral distribution ranges of Vaccinieae in the tropical Andes and adjacent regions. Areas for historical analyses will be delimited according to an assessment of Areas of Endemism. Through
the ancestral area reconstruction it is expected to uncover the geographic dimension of
the evolution of the Andean Vaccinieae and explore its influence in the diversification
process. This will give also a basis to gauge the impact of specific geological processes
related to the uplift of the Andes with colonization history Vaccinieae in South America.

1.2 Methods

1.2.1 Phylogenetic inference

Phylogenetic inference was based on molecular sequence data of two plastid markers
(matK and ndhF) and a nuclear region (ITS). Sequences from 154 species of Ericaceae
(153 OTUs) were analyzed. Priority was given to the neotropical clade of Vaccinieae
(15 genera, 79 species, 80 OTUs), which is mostly composed by species from the Andes
and Central America (Kron et al. 2002b). Other tribes of Ericaceae were sampled, such
as Andromedeae (2 species), Bejariaeae (3 species), Empetreae (6 species), Ericae (3
species), Gaultherieae (16 spp.), Phyllodoceae (14 species), and Rhodoreae (6 species).
Phylogenetic analyses were rooted with Enkianthus campanulatus (Miq.) G. Nicholson
(Enkianthoideae), as phylogenetic analyses have indicated the genus is the most basal
lineage within Ericaceae (Kron et al. 2002a).

Four fossils were used to calibrate the phylogenies:
1. *Vaccinium creedensis* Axelrod (Late Oligocene, 26.2–26.8 MA) as crown age of the Vaccinieae (Axelrod 1987). This fossil belongs to the Creede formation (SW Colorado), previously dated through radiometric analysis (Steven et al. 1967). This fossil comprises several leaves with the typical vaccinioid acrodromous venation. Although the reproductive structures are unknown, leaf venation is very similar to that of extant species of *Vaccinium* from North America, such as *V. caespitosum*.

2. *Zenobia fasterholtensis* Friis (Langhian, Middle Miocene, 15–17 MA) as crown age of the Andromedeae (Friis 1985). Recent radiometric analyses based on strontium isotope decay dated this fossils to 17.4–15.3 MA (Eidvin et al. 2014).

3. Unnamed oldest pollen tetrad grains with viscin threads (Lutetian, Middle Eocene, 48.0–43.9 MA) as crown age of *Rhododendron* (Zetter and Hesse 1996). These fossils belong to the Geiseltalian, a formation recently dated through radiometry of the oldest (48.0–47.6 MA) and the newest (44.7–43.9 MA) strata (Franzen 2005). The combination of pollen tetrads, viscin threads, and club-like exine ornamentation confidently points at *Rhododendron* as the most likely classification of these fossils.

4. *Paleoenkianthus sayrevillensis* Nixon and Crepet (Late Cretaceous, 93.9–89.5 MA), from the South Amboy Fire Clay, Magothy Formation, as the crown age of the Ericaceae (Nixon and Crepet 1993). Although several fossils have been described from this stratigraphic unit, no radiometric analyses are available. Therefore, the age assumed here is the period assigned by the International Commission on Stratigraphy
for the Turonian (Cohen et al. 2013). *Paleoenkianthus sayrevillensis* is a well preserved fossil and nearly all flowering structure is known (Nixon and Crepet 1993). The classification of this fossil in the Ericaceae is supported by several floral characters, such as the inverted stamens with pseudoterminal awns and the presence of viscin threads in the pollen (Nixon and Crepet 1993).

Most DNA sequences were retrieved from GenBank and additional data was generated at The New York Botanical Garden from tissues collected in Colombia, Ecuador, and Peru (Appendix A). Genomic DNA extractions were done with the Qiagen DNeasy Plant Mini Kit (Qiagen 2006) or a custom protocol based on Alexander et al. (2007). Sequence alignments were conducted in Mafft (Katoh and Standley 2013) and additional matrix post-editing in Jalview (Waterhouse et al. 2009). Matrices were concatenated using 2matrix.pl (Salinas and Little 2014). Nucleotide substitution models were selected through the corrected Akaike Information Criterion, as implemented in the R package Phangorn (Schliep 2011).

Bayesian estimation of phylogenetic relationships and divergence times were done with BEAST v. 1.7.5. (Drummond et al. 2012). Two independent chains of $30 \times 10^6$ generations each were run, and parameters were sampled every 1000 generations. A Yule process was assumed as divergence prior (Yule 1924). Time calibration was achieved through the Uncorrelated Log-Normal model (Drummond et al. 2006). Bayesian MCMC convergence and parameter statistics were assessed with Tracer 1.5.0 (Rambaut et al. 2013). The first 6000 trees (20%) of the final tree file were discarded as burn-in. Tree topology and
parameters were summarized using the program Sumtrees v. 3.3.1 of the Python library DendroPy v. 3.12.0 (Sukumaran and Holder 2010).

Phylogenetic and divergence times inference under the Maximum Likelihood criterion was executed in RAxML (Stamatakis 2006) and treePL (Smith and O’Meara 2012), respectively. Heuristic search in RAxML was executed using the rapid bootstrap algorithm for 1000 replicates. Maximum Likelihood time calibration was conducted under the penalized likelihood approach, as implemented in treePL, using default settings (smoothing parameter=100).

1.2.2 Geographic distribution data

Distribution data for 108 species (17 putative genera) of neotropical Vaccinieae was retrieved from specialized literature (Luteyn 1983, 1996a; Luteyn and Sylva S. 1999; Salinas and Betancur 2005), the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/), and herbarium specimens deposited at COL, MO, NY, QCA, QCNE, and US. The correct identification of critical and rarely taxa was assessed with the collections were available at The William and Lynda Steere Herbarium of the New York Botanical Garden (NY). The quality of the coordinates of the records was assessed through comparison with public gazetteers [e.g., GeoNames (http://www.geonames.org/)]. Dubiously identified or georeferenced records were discarded. A total of 5915 records were kept, the majority of them (5648) corresponding to taxa of the Andean clade (according to Kron et al. 2002b).
1.2.3 Areas of Endemism (AE)

Geographic areas for historical reconstructions were mostly defined using two analytical approaches: Biotic Element Analysis (BEA Hausdorf and Hennig 2003) and Parsimony Analysis of Endemism (PAE Morrone 1994). Both analyses were executed using the same type of spatial units: grids of 0.5°, 1.0°, 2.0°, and 3.0° cells. Different offset values of grid delimitation were also explored in combination with grid size: 0.25° (0.5° grid), 0.5° (1° grid), 1° (2° and 3° grids), and 2° (3° grid).

The PAE was carried out on TNT (Goloboff et al. 2008), but data was manipulated through custom-made Perl scripts. Parsimony heuristic search strategy involved 200 ratchet and drift iterations on 10 initial Wagner trees. On the other hand, the BEA was ran on the R package PRABCLUS (Hennig and Hausdorf 2012), with the default search settings maintained throughout the analyses.

A set of biogeographic areas reflective of the distribution of Vaccinieae in Central and South America was developed upon the results from the analyses above described. In regions where AE were not detected, complementary areas were delimited using the biogeographic scheme for Latin America proposed by Morrone et al. (2002). Maps, shapefiles and geographic data in general were managed through the geographic information system QGIS (QGIS Development Team 2009).
1.2.4 Ancestral range inference

Ancestral geographic ranges were estimated with the R package BioGeoBEARS v. 0.23 (Matzke 2013). This package provides a flexible environment for ancestral area inference, including a various range evolution models, implementation of the “founder event” parameter, and hypothesis testing capabilities.

The following models of geographic range evolution were employed:

1. Dispersal Extinction Cladogenesis (DEC) model, a widely used model originally proposed by Ree and Smith (2008).

2. Dispersal Extinction Cladogenesis with founder event parameter (DEC + J). A founder event parameter (or long distance dispersal parameter) is included to raise the explanatory power of simpler biogeographic models (see Matzke 2014).

3. A Maximum Likelihood implementation of the Dispersal Vicariance (DIVA) model (Ronquist 1997). This model incorporates branch length information to estimate event probabilities (DIVA-like).

4. The DIVA model explained above with founder event parameter (DIVA-like + J).

Given that analyses with such complex models put a strain on computational resources, three was the maximum number of ancestral areas allowed per taxon. This meant that taxa present in more than three areas were eliminated from further analyses. Only taxa
represented in the molecular phylogeny were used in the ancestral range inference. The final matrix contained information of 67 species (Appendix B).

1.3 Results

1.3.1 Areas of Endemism

Four AE were unambiguously identified by both PAE and BEA (Tables 1.1 and 1.2): Central America, eastern Ecuador, northern Chocó, and southern Chocó; the last two were occasionally united into a single area, Chocó). Also, BEA retrieved two other AE: Yungas and a widespread element.

<table>
<thead>
<tr>
<th>Cell size</th>
<th>Offset</th>
<th>Areas recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>0</td>
<td>1: northern Chocó</td>
</tr>
<tr>
<td>0.5</td>
<td>0.25</td>
<td>1: northern Chocó</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>0.5</td>
<td>2: eastern Ecuador, northern Chocó</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>3: northern Chocó, southern Chocó (two nested areas)</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>5: eastern Ecuador, northern Chocó (two nested areas), southern Chocó (two nested areas)</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>3: Central America, Ecuador, Northern Chocó</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>2: Ecuador, northern Chocó</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>5: Central America, Chocó (three nested areas), southern Ecuador-northern Peru</td>
</tr>
</tbody>
</table>

Table 1.1: Parsimony Analysis of Endemicity results.

Analyses based on wide celled grids ($2^\circ$ and $3^\circ$) recovered more AE. Offset usage had an important effect in wide celled grids, usually increasing the number of AE retrieved when it was employed. In general terms, BEA was more sensitive and disclosed more areas per
### Table 1.2: Biotic Element Analysis results.

<table>
<thead>
<tr>
<th>Cell size</th>
<th>Offset</th>
<th>Areas recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>0</td>
<td>6: Central America, eastern Ecuador, northern Chocó, Widespread (two elements), Yungas</td>
</tr>
<tr>
<td>0.5</td>
<td>0.25</td>
<td>4: Central America, Widespread (three elements)</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>6: Central America, eastern Ecuador, northern Chocó, southern Chocó, Widespread, Yungas</td>
</tr>
<tr>
<td>1</td>
<td>0.5</td>
<td>6: Central America, eastern Ecuador, northern Chocó, southern Chocó, Widespread, Yungas</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>7: Central America, eastern Ecuador, northern Chocó, southern Chocó, Widespread (two elements), Yungas</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>10: Central America, Chocó, eastern Ecuador, northern Chocó, southern Chocó, western Ecuador, Widespread (two elements), Yungas</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>8: Central America, eastern Ecuador, northern Chocó, southern Chocó, western Ecuador, Widespread (two elements), Yungas</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>7: Central America, eastern Ecuador, northern Chocó, southern Chocó (two elements), Widespread, Yungas</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>9: Central America, Chocó, eastern Ecuador, northern Chocó, southern Chocó, Widespread (three elements), Yungas</td>
</tr>
</tbody>
</table>

execution, even under the same grid settings (mean area recovered per run: 2.44 by PAE vs. 7 by BEA).

Results from both assessments of Areas of Endemism were summarized into a single biogeographic scheme (Fig. 1.2). This scheme was later employed to code taxa distributions for the reconstruction of ancestral ranges. Areas were delimited by identifying sets of species frequently included in groups of homologous clusters.

#### 1.3.2 Phylogenetic analyses

Phylogenetic inference was in agreement with previous analyses of the Vaccinieae (Kron et al. 2002b; Pedraza-Peñalosa 2009; Powell and Kron 2003) and the major clades within
Figure 1.1: Areas of Endemism recovered by the Biotic Element Analysis (grid: 1 degree, offset: 0.5 degrees). Cell color intensity correlated with the percentage of members of the AE present in that cell (e.g., solid black=100%, white=0%). A: Central America, B: northern Chocó, C: southern Chocó, D: eastern Ecuador, E: Yungas, F: Widespread area.
the Neotropical Vaccinieae were all well supported (Fig. 1.3, Table 1.3). Both Maximum Likelihood and Bayesian inferences (not shown) agreed in their general topology. However, divergence times differed between both methods. TreePL estimates were usually younger than BEAST 95% posterior probability intervals (Table 1.4). Despite that, both pointed at late and middle Miocene as the most important period for diversification of the deep nodes of the Neotropical Vaccinieae (Fig. 1.3 and Table 1.4).
Figure 1.3: Maximum Likelihood topology of the Neotropical clade of Vaccinieae, branch lengths adjusted to median values from the bayesian stationary distribution (bars = 95% interval). Circled numbers indicate clades discussed in the text: Andean clade (1), *Thibaudia* p.p. clade (2), Heteroandrous clade (3), homoandrous and continuous pedicel clade (4), *Disterigma* s.s. (5), *Ceratostema* + *Macleania* + *Psammisia* clade (6), Mesoamerican clade (7). Q = Quaternary, MA = Millions years ago.
<table>
<thead>
<tr>
<th>Clade</th>
<th>Bootstrap</th>
<th>Posterior probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andean (1)</td>
<td>100</td>
<td>1</td>
</tr>
<tr>
<td><em>Thibaudia</em> p.p. (2)</td>
<td>99</td>
<td>1</td>
</tr>
<tr>
<td>Heteroandrous (3)</td>
<td>99</td>
<td>1</td>
</tr>
<tr>
<td>Homoandrous and continuous pedicel (4)</td>
<td>100</td>
<td>1</td>
</tr>
<tr>
<td><em>Disterigma</em> s.s. (5)</td>
<td>100</td>
<td>1</td>
</tr>
<tr>
<td><em>Ceratostema</em> + <em>Macleania</em> + <em>Psammisia</em> (6)</td>
<td>92</td>
<td>1</td>
</tr>
<tr>
<td>Mesoamerican (7)</td>
<td>100</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 1.3: Maximum Likelihood (bootstrap) and Bayesian (posterior probability) support of selected subclades within the Neotropical clade of Vaccinieae. Numbers in parentheses correspond to clades in Fig. 1.3.

<table>
<thead>
<tr>
<th>Clade</th>
<th>95% posterior distribution interval</th>
<th>ML estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andean (1)</td>
<td>28.90–17.84 MA</td>
<td>14.82 MA</td>
</tr>
<tr>
<td><em>Thibaudia</em> p.p. (2)</td>
<td>19.29–9.13 MA</td>
<td>8.81 MA</td>
</tr>
<tr>
<td>Heteroandrous (3)</td>
<td>20.28–11.69 MA</td>
<td>10.49 MA</td>
</tr>
<tr>
<td>Homoandrous and continuous pedicel (4)</td>
<td>19.95–10.75 MA</td>
<td>10.56 MA</td>
</tr>
<tr>
<td><em>Disterigma</em> s.s. (5)</td>
<td>17.27–5.58 MA</td>
<td>7.16 MA</td>
</tr>
<tr>
<td><em>Ceratostema</em> + <em>Macleania</em> + <em>Psammisia</em> (6)</td>
<td>22.46–11.97 MA</td>
<td>12.44 MA</td>
</tr>
<tr>
<td>Mesoamerican (7)</td>
<td>25.37–9.87 MA</td>
<td>12.81 MA</td>
</tr>
</tbody>
</table>

Table 1.4: Divergence times of selected subclades within the Neotropical clade of Vaccinieae. Numbers in parentheses correspond to clades in Fig. 1.3.

### 1.3.3 Ancestral range reconstruction

The corrected Akaike Information Criterion selected DEC + J as the most fitting model to describe the range evolution in the dataset (Table 1.5).

Ancestral range probabilities at each node of the phylogeny are shown in figure 1.4.
Figure 1.4: Ancestral ranges annotated on the most likely tree. C: Central America (red), R: Caribbean (dark blue), N: northern Chocó (pink), S: southern Chocó (yellow), A: northern Andes, E: eastern Ecuador (light blue), Y: Yungas (green), G: Guiana Shield (purple). Circled numbers indicate clades discussed in the text: Andean clade (1), Thibaudia p.p. clade (2), Heteroandroous clade (3), homoandroous and continuous pedicel clade (4), Disterigma s.s. (5), Ceratostema + Maclitaia + Psammisia clade (6), Mesoamerican clade (7).
Figure 1.5: Historical events. A: Dispersals from Yungas to Central America and southern Chocó. B: Dispersals between Central America and South America. C: Dispersals from Yungas or eastern Ecuador to northern Chocó. D: Dispersals from N and S Chocó to eastern Ecuador. Color codes: Central America (red), northern Chocó (pink), southern Chocó (yellow), northern Andes (brown), eastern Ecuador (blue), Yungas (green).
Table 1.5: Range evolution models likelihoods and AICc scores.

Reconstructions optimized Yungas as the most likely ancestral area in the basal node of the Andean clade (probability = 0.300405, Fig. 1.4, clade 1). From the Yungas the Vaccinieae dispersed northwards, principally to southern Chocó and Central America (Fig. 1.5A). Colonization of Central America was achieved by a series of migrations back and forth from South America (Fig. 1.5B). Migration to northern Chocó occurred more recently (posterior probability interval 6.83–2.14 MA), however it is not certain whether the Yungas or eastern Ecuador was the origin of such event (Fig. 1.5C). Three different lineages recently dispersed to eastern Ecuador, during the Pleistocene–Pliocene epochs (posterior probability interval 4.83–0.21 MA). These lineages emigrated from Chocó (both north and south) and Yungas (Fig. 1.5D).

1.4 Discussion

1.4.1 Areas of Endemism

Five Areas of Endemism were uncovered by the analyses: Central America, northern Chocó, southern Chocó, eastern Ecuador, and Yungas (Fig. 1.1). These analyses corroborated that Vaccinieae diversity is unevenly distributed across the tropical portion of
the Andean Cordillera, and largely follows the patterns previously proposed by Luteyn (cited as “centers of diversity”, 2002). Some important disagreements were also evident, nonetheless:

1. A páramo region was not detected as an Area of Endemism in this study. As conceived by Luteyn (2002), the páramo center of diversity is mainly defined by endemic species of Gaultheria L. and Plutarchia A. C. Sm. The former genus was not included in this study because it belongs to a different tribe, Gaultherieae, whereas the latter, unfortunately, is a taxon poorly represented in herbaria and public datasets, and no representative was included as well.

2. The present analyses discriminate between northern and southern Chocó. Traditionally, the Chocó floristic province has been conceived as the contiguous lowland forest west of the Andes between the southern tip of Panama and northern Ecuador (Gentry 1982b). This region also has a distinctive Vaccinieae flora and Luteyn (2002) recognized it as a center of diversity, in agreement with the aforementioned geographical limits. Phytogeographic subdivision of the Chocó region has not been previously proposed for Vaccinieae flora; however, this is not a novel pattern of neotropical flora as similar disjunctions have been reported for other groups, such as Aroids (Mora et al. 2006) and ferns (Lellinger 1975). Although the phytogeographic discontinuity here presented could be an analytical artifact given the lack of collections from the Departamento del Cauca, right on the border between northern and southern Chocó Areas of Endemism, the presence of the dry valley of the Patia
river represents an important ecological barrier for the Vaccinieae, a group particularly adapted to humid environments all year round. Recently, Morrone (2014), using data from several groups of plants and animals, has proposed a biogeographic scheme for the Neotropics that recognizes a division of the Chocó region in similar units to those reported here, northern and southern Chocó Areas of Endemism.

3. Both northern and southern Chocó Areas of Endemism have higher elevational limits (2000–2400 m), in contrast to the almost lowland-restricted Chocó province as traditionally framed. The classical delimitation of this floristic region proposed by Lellinger (1975) and Gentry (1982b, 1986) only included the lowland forests between the Pacific ocean and the Andes (up to 1000 m), from southern Panama to northern Ecuador. Based on biotic, edafic and climate data, Rangel-C. (2004) proposed a lower altitudinal limit at 800 m. This region was initially characterized because of its vegetation physiognomy, but it also has high levels of diversity and endemicity. Ericaceae workers have identified the Chocó lowland forests as one of the centers of diversity of neotropical Vaccinieae (Luteyn 2002; Smith 1946). The results of this study indicate that the Chocó Areas of Endemism extend to the west to include the western slope of the Andes. Previous phytogeographic studies (Salinas and Betancur 2005) have recognized that both montane and lowland Vaccinieae from western Colombia have overlapping distribution ranges, which makes necessary to include both in the Chocó region. Here their proposal is corroborated through PAE and BEA analyses.
4. The “northern Andean unit” was not detected in this study. According to Luteyn (2002), this unit comprises the Andes from Colombia, extending south to northern Ecuador (in the western slope) and northern Peru (in the eastern slope). In the analyses presented here, species distributed over the area that roughly corresponds to the “northern Andean unit” were clustered into the eastern Ecuador, northern Chocó, or southern Chocó Area of Endemism, or not clustered into any area.

These results are largely due to the expansion of the northern and southern Chocó AEs upwards in the western slope of the Andes. Several species from these AEs have been traditionally considered Andean elements instead of part of the Chocó flora. However, the analyses here presented showed that their geographic distributions are more congruent with spatial patterns from the Chocó region than those from the Andean one.

Although these results advance our understanding of the history of Vaccinieae in the Neotropics, they are not definitive. There are several gaps in the geographic distribution and phylogenetic data that need to be filled before a comprehensive biogeographic classification could be proposed. Specifically, more data from Venezuela and eastern Colombia is needed to infer Areas of Endemism in those regions. Also, putative lineages that are confined to specific regions (e.g., Plutarchia, mostly endemic to páramos from eastern Colombia) or widespread across the tropical Andes (e.g., Thibaudia s.l.), need to be better represented.
1.4.2 Historical processes

The estimated divergence times here provided constitute the first temporal framework of the Andean Vaccinieae evolution. Although node age credibility intervals were generally wide and fossils more close to the clade of interest were not available, this time-calibrated phylogeny support that the diversification of the Andean Vaccinieae occurred mostly during the terciary. Similarly, ancestral range reconstructions suggest dispersal was the most important biogeographic phenomenon behind the colonization of the tropical Andes, stressing the influence of geography in the evolution of Vaccinieae.

Previous biogeographic studies of the Vaccinieae also pointed at the Early Miocene as the beginning of Vaccinieae immigration into South America (Kron and Luteyn 2005). Ages of the basal clades within the Andean Vaccinieae are also in agreement with hypothesis of a diversification process shaped by paleogeographical events (Gentry 1982a; Luteyn 2002), as most of the diversification events occurred during the Miocene (Fig. 1.3).

Ancestral reconstruction pointed at the Yungas as the source of current Vaccinieae diversity in the tropical Andes, and successive dispersals northwards explain colonization of the rest of the areas (Figs. 1.4, 1.5A). Thus dispersals, instead of vicariant events, explain early diversification process of Vaccinieae along the tropical Andes. Contrary to this results, previous works have suggested the ancestor of the neotropical clade of Vaccinieae was widespread in the Antilles, Central America, and the Andes, and successive vicariant events led to further speciation in the Neotropics (Kron and Luteyn
Colonization of the tropical Andes from the Yungas via dispersal is a diversification pattern with geological basis nonetheless, as intense mountain building activity in the Central Andes (Peru–Bolivia massif) took place during the Paleogene (65 MA), before similar events started in the north during the late Oligocene (23 MA) (Hoorn et al. 2010). Therefore, the Central Andes could have provided the first montane environments for floristic elements migrating south from Central America.

Dispersals from the Yungas to the north started with two colonization events into southern Chocó and two more toward Central America, following the northern progression of Andean uplift during the Miocene (Fig. 1.5A). The Vaccinieae did not seem to have colonized two areas in the northern range during that time, eastern Ecuador and northern Chocó. Eastern Ecuador, as delimited here, corresponds to the Amotape-Huancabamba Zone (Weigend 2002), a geographic region that was subjected to an oceanic intrusion from the Eocene to Middle Miocene (Antonelli et al. 2009). This paleogeological phenomenon prevented any land colonization before the mountain uplift that ended that intrusion (ca. 13–11 MA). However, no dispersal toward northern Chocó during that time remains unexplained, as the western Cordillera of Colombia and Ecuador rose in a more or less synchronous fashion, and montane environments suitable for colonization in both Chocó areas should have been available more or less at the same time.

The geographic evolution of *Cavendishia* Lindl. and *Satyria* s.s. Klotzsch was shaped by successive migrations back and forth between Central–South America during the upper Miocene (13–6 MA, Fig. 1.5B). This reconstruction agrees with Kron and Luteyn (2005),
who also stated that diversification of these two genera in Central America was a recent event. The Panama Isthmus comprised a number of contiguous islands during that time (late Miocene, 11–6 MA), and an increase in biotic interchange have been reported for many organisms (Coates 1997). However, recent geological surveys claim that land connections between Central and South America could have been older, probably early Oocene–early Miocene (Farris et al. 2011). Although both theories on the emergency of a connection between Central and South America are geologically correct for the observed taxon distributions, the latter offers a simpler scenario for biotic interchange between Central and South America before the Pliocene. Other biogeographic studies have also found dispersal events between both continents to be older than the Pliocene, supporting a Oligocene–Miocene hypothesis of Panama Isthmus evolution (Bacon et al. 2013; Cody et al. 2010).

Analyses revealed that northern Chocó was colonized during the Pliocene or Late Miocene (6.83–2.14 MA). It is not clear where these lineages immigrated from, but it could have been from Yungas or eastern Ecuador (Figs. 1.4 and 1.5C). An improved representation of this poorly known region is necessary to overcome the uncertainty of both phylogenetic and biogeographic reconstructions to understand the mechanism behind the colonization of northern Chocó.

Two independent dispersals to eastern Ecuador from both north (north and south Chocó) and south (Yungas) in the Pliocene (4.8–2.8 MA) reveal the diverse origin of the flora from this region (Fig. 1.5D). Previous phytogeographical analyses of *Oxalis* L. (Oxalidaceae)
(Weigend 2002), as well as panbiogeographical analyses of Bomarea Mirb. (Alstroemeriaceae) (Alzate et al. 2008) indicated the convergence of both northern and southern elements into this region. Although the results then suggest a relatively recent establishment of Vaccinieae in this part of the Andean Cordillera, a Pliocene date seems late given that this part of the Andes probably raised during middle Miocene (13–11 MA, Antonelli et al. 2009). Unfortunately, details of this the geological processes that took place in eastern Ecuador are largely unknown (Gregory-Wodzicki 2000) and more historical information is still necessary to understand the origin of this rich and unique flora.

The alternative and less optimal models (DEC, DIVA-like and DIVA-like + J) produced similar reconstructions in general sense. Some differences where observed nonetheless, probably a consequence of the higher vicariance rates retrieved by those models. For example, the ancestral range of the Andean Clade ancestor (node 1 in Figure 1.4) involved a joint Southern Chocó–Yungas area, and the distribution of the descendant lineages was explained by vicariance. Another remarkable difference is the geographic evolution of the Cavendishia clade, uncovered as a succession of vicariant events involving Yungas, Central America, Southern Chocó, Northern Chocó and Northern Andes, instead of a series of Central–South American dispersions reconstructed by the DEC+J model.
1.5 Conclusions

The Vaccinieae are a diverse and important element of the tropical South American flora, particularly of the Andean cordillera, a massive mountain range whose geology and physical attributes have substantially shaped the distribution and history of this group of plants. However, although most of the Vaccinieae of Andean origin are restricted to the Andean Cordillera, this group is ecologically and geographically diverse, and they are also present in the lowland rain forests of the Neotropics, as well as in the premontane rainforests of Central America. Endemicity analyses corroborated the existence of some centers of diversity previously proposed for the Vaccinieae, such as Central America, eastern Ecuador, and Yungas. However, this study has also challenged current conceptions and limits of other centers of biodiversity, such as Chocó, which was found to be a composite area that also includes the western slope of the Andean cordillera.

Ancestral range reconstructions suggested that Vaccinieae began the colonization of the Andes in the Early Miocene through the Yungas. From this region they dispersed northwards in several occasions, mainly to southern Chocó and Central America. Paleogeological events probably were a major influence to the geographic evolution of the Vaccinieae, particularly the closure of the Panama Isthmus, the rise of the Andean Cordillera, and ancient oceanic intrusions into this mountain range.
Chapter 2

Phylogenetic relationships of *Orthaea* (Vaccinieae: Ericaceae), based on molecular and morphological data.

Abstract

The phylogenetic relationships of *Orthaea* (Vaccinieae: Ericaceae) were explored using molecular and morphological data. *Orthaea* is polyphyletic, with members evolving independently in several lineages within the tribe Vaccinieae. Currently accepted species of *Orthaea* s.l. were recovered within four clades: Guiana Shield, *Empedoclesia*, *Thibaudia* p.p., and *Cavendishia* + *Orthaea* p.p. clades. Most of the Andean species of *Orthaea* s.l. are closely related to *Cavendishia*, however, relationships within this clade were not...
strongly supported. Incongruence among molecular markers was assessed through simulations, revealing that topological differences were due to uncertainty in the phylogenetic estimation, not to strongly conflicting signals. Combined analyses of molecular and morphological data only provided support and uncovered synapomorphies for the Guiana Shield and Empedoclesia clades. Although a core Orthaea s.s. clade was identified, no nomenclatural changes are here proposed for the remainder species of Orthaea s.l. (20 spp.), except for those previously classified in Empedoclesia, a genus that needs to be reinstated.

2.1 Introduction

Ericaceae is a diverse plant family with more than 4100 species, mainly distributed in arctic, temperate, and montane tropical ecosystems (Stevens et al. 2004). In the neotropical region, this family is mostly represented by the tribe Vaccinieae, with 28 native genera and more than 600 species, most of them restricted to rain forest habitats (Luteyn 2002). One of such genera is Orthaea Klotzsch, which includes 37 currently accepted species. Traditionally, this genus has been delimited by the presence of conspicuously dimorphic stamens with filaments of alternating lengths and equal-sized anthers. Although most Orthaea are found in the Andean Cordillera (Colombia to Bolivia), some are found in the Guiana Shield (Venezuela and Guyana) and Central America (S Mexico–Panama), usually in montane and premontane ecosystems (1000–3000 m).
Since its inception by Klotzsch (1851), several taxa have been transferred to Orthaea, gradually increasing its morphological and geographic range. The first important change was the inclusion of Findlaya Hook. f., a genus of Vaccinieae endemic to the Guiana Shield (Smith 1932). Although Findlaya differed from Orthaea because of its few-flowered fascicles and truncate calyces (vs. many-flowered racemes and lobed calyces in Orthaea), Smith (1932) merged them both due to their similar staminal morphology. Furthermore, Luteyn (1987) synonymized Empedoclesia Sleumer and Lysiclesia A. C. Sm. under Orthaea, two Central American genera of Vaccinieae, under Orthaea because of their similar dimorphic stamens. Therefore, current circumscription of Orthaea includes all neotropical Vaccinieae with dimorphic filaments and isomorphic anthers, ranging from southern Mexico to central Bolivia and east to Guyana.

Cavendishia Lindl. (ca. 130 spp) and Satyria Klotzsch (ca. 30 spp), two other putative genera of Vaccinieae native to the Neotropics, have always been though to be closely related to Orthaea (Klotzsch 1851; Luteyn 1987; Smith 1932). These three genera have dimorphic stamens, an uncommon feature among Vaccinieae. Because taxonomic classifications are heavily influenced by staminal morphology, taxonomists have always suggested they form an isolated group within Vaccinieae (Luteyn 1983; Smith 1932). A preliminary phylogenetic analysis of neotropical Vaccinieae partially supported that hypothesis (Kron et al. 2002b). Although therein most of the sampled species of Cavendishia, Orthaea and Satyria made up a clade, some Satyria and Orthaea were resolved somewhere else outside that group. Later phylogenetic analyses have found that Orthaea and Satyria are actually polyphyletic (Pedraza-Péñalosa et al. 2013; Powell and Kron 2003). The reduced
sampling of *Orthaea* and *Cavendishia* in such studies was still too limited to uncover the exact phylogenetic relationships of the taxa with dimorphic stamens, and most specially of *Orthaea*.

Thus, the main goal of this analysis was to test the monophyly of *Orthaea* s.l. and uncover its position within Vaccinieae, using a much richer sampling. Analyses included data of 18 species (48% of *Orthaea* s.l.) in the molecular dataset and 36 species (99%) in the combined matrix. In addition to nuclear and plastid molecular markers, morphological characters were also scored and analyzed, to both test current morphological limits and reveal putative synapomorphies.

2.2 Methods

2.2.1 Taxon sampling

Two datasets were assembled for phylogenetic inference: one containing exclusively molecular data and another with both morphological and molecular characters.

The molecular dataset (116 OTUs, 113 species, 22 genera) represented all major lineages of Vaccinieae, but focused in *Orthaea* s.l. (20 OTUs, 18 species) and its putative sister groups: *Cavendishia* (20 OTUs, 19 species) and *Satyria* s.l. (14 OTUs, 14 species). Old World Vaccinieae were also represented because phylogenetic analyses have suggested they might be related to some members of *Orthaea* s.l. from the Guiana Shield (Kron et al.
This large scale molecular analysis was directed to establish the relationships of *Orthaea* s.l. to other Vaccinieae.

The combined dataset comprised almost all currently recognized species of *Orthaea* s.l. (37 OTUs, 36 species) and its sister linages (12 OTUs, 12 species), as recovered from the previous large scale analysis. This matrix included two undescribed species of *Orthaea* (2 OTUs) and 12 species (13 OTUs) exclusively represented by morphological data. Analyses of the combined dataset were aimed to uncover the relationships between the major clades of *Orthaea* s.l., their putative morphological synapomorphies, and lastly, the evolutionary affinities of those taxa for which DNA sequences were not available.

Tissues for molecular work were retrieved from the New York Botanical Garden DNA collection or collected directly from the wild through field work in Ecuador and Colombia. The molecular sequences generated for this study were complemented with sequences previously submitted to GenBank (Appendix C). Because of their basal position respect to the ingroups (Kron et al. 2002a,b), *Zenobia pulverulenta* (W. Bartram ex Willd.) Pollard and *Vaccinium hirsutum* Buckley were selected as outgroups in the molecular and combined analyses, respectively.

### 2.2.2 DNA extraction and sequences

Genomic DNA was extracted using Qiagen DNeasy Plant Mini Kit (Qiagen 2006) and a silica-based method (Alexander et al. 2007). Sequences of internal transcribed
spacer (ITS), maturase K (matK), and the 5' end of the NADH dehydrogenase sub-
unit F (ndhF) were used for phylogenetic inference. Primers used to amplify ITS were
CCTTATCATTTAGAGGAAGGAG (18S, F), TATGCTTAAAYTCAGCGGGT (26S-25,
R), GCTACGTTCTTCATCGATGC (5.8S-32, R), and GCATCGATGAAGAAGCTAGC
(5.8S-32, F). Primers used to amplify matK were: ATCCAAATAAATTGGGG
(650, F), CCATTTATCATCAAAAGAAACG (1350, R), GCATTATGTTAGATATC-
GAGG (1295, F), and AACCTGCTCTCCCTCCG (1436, R). Primers used to amplify
ndhF were: ATGGAACAKACATATSATATGC (1, F), TCCCCTACACGATTAGT-
TACAA (536, R), CGAACATAATAATGCRGTTAATCC (1318, R), and ACAAG-
GCCTGTTGCAGCAAG (450, F). The PCR thermal profiles used are summarized in
Table 2.1; deviations mainly included “step-up” alterations, using 2°C below the opti-
mal annealing temperature during the first five cycles. Chromatograms were edited in
Sequencher 5.2.3 (Gene Codes Corporation 2013).

2.2.3 Molecular analyses

Multiple sequence alignments were done with MAFFT, using the global pair option (Ka-
toh and Standley 2013). Additional matrix editions were carried out with Jalview (Wa-
terhouse et al. 2009). Phylogenetic information of gaps was extracted from the alignments
using the simple indel coding method (Simmons and Ochoterena 2000), as implemented
in the Perl script 2matrix.pl (Salinas and Little 2014).
Table 2.1: Polymerase chain reaction thermal profiles.

<table>
<thead>
<tr>
<th>Marker</th>
<th>F primer</th>
<th>R primer</th>
<th>Thermal profile</th>
</tr>
</thead>
<tbody>
<tr>
<td>ITS</td>
<td>18S</td>
<td>26S-25</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 1:00 @ 48°, 1:00 @ 72°), 10:00 @ 72°</td>
</tr>
<tr>
<td>ITS</td>
<td>18S</td>
<td>26S-25</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 0:45 @ 50°, 1:30 @ 72°), 7:00 @ 72°</td>
</tr>
<tr>
<td>ITS</td>
<td>18S</td>
<td>5.8S-32</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 0:45 @ 48°, 0:35 @ 72°), 7:00 @ 72°</td>
</tr>
<tr>
<td>ITS</td>
<td>5.8S-32</td>
<td>26S-25</td>
<td>2:30 @ 94°, 5 × (0:30 @ 94°, 0:45 @ 45°, 0:35 @ 72°), 30 × (0:30 @ 94°, 0:45 @ 48°, 0:35 @ 72°), 10:00 @ 72°</td>
</tr>
<tr>
<td>matk</td>
<td>650</td>
<td>1350</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 1:00 @ 45°, 1:00 @ 72°), 10:00 @ 72°</td>
</tr>
<tr>
<td>matk</td>
<td>1295</td>
<td>1436</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 1:00 @ 48°, 1:00 @ 72°), 10:00 @ 72°</td>
</tr>
<tr>
<td>ndhf</td>
<td>1</td>
<td>536</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 1:00 @ 45°, 1:00 @ 72°), 10:00 @ 72°</td>
</tr>
<tr>
<td>ndhf</td>
<td>1</td>
<td>536</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 1:00 @ 48°, 1:05 @ 72°), 10:00 @ 72°</td>
</tr>
<tr>
<td>ndhf</td>
<td>450</td>
<td>1318</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 1:00 @ 48°, 1:05 @ 72°), 10:00 @ 72°</td>
</tr>
<tr>
<td>ndhf</td>
<td>450</td>
<td>1318</td>
<td>2:30 @ 94°, 35 × (0:30 @ 94°, 1:00 @ 51°, 1:05 @ 72°), 10:00 @ 72°</td>
</tr>
</tbody>
</table>

Parsimony analyses were carried out with TNT (Goloboff et al. 2008). Search strategy involved a combination of 200 ratchet and 200 tree drift iterations over ten starting random addition sequences. Clade support was assessed with 1000 Jackniffe replicates.

Maximum Likelihood (ML) estimates were done with RAxML (Stamatakis 2006), using the rapid bootstrap algorithm on 1000 replicates. Nucleotide substitutions models were selected with the corrected Akaike Information Criterion, as implemented in the R package phangorn (Schliep 2011). Likelihood function of candidate models was optimized on a neighbor joining tree based on Jukes Cantor distances. As result, GTR+G+I was selected as the most appropriate model for the three partitions.
Bayesian inference was done on MrBayes 3.2.2 (Ronquist et al. 2012). Eight Markov chains distributed in two coupled runs were executed during 20,000,000 generations. Phylogenetic trees and parameter estimates were reported every 1,000 generations. The first 8,000 trees (20%) were discarded as burn-in. Convergence and parameter values behaviour throughout analyses were assessed with Tracer 1.5.0 (Rambaut et al. 2013).

Incongruence among the molecular markers was investigated through the Approximate Unbiased Shimodaira-Hasegawa test (AU-SH test; Shimodaira 2002) and parametric bootstrapping (SOWH test; Swofford et al. 1996). Phylogenetic inference and site likelihood score estimation for both tests were carried out in RAxML. Critical values for the AU-SH test were estimated in Consel (Shimodaira 2001). Datasets for the SOWH test were simulated in Seq-Gen (Rambaut and Grass 1997). A custom Python script using the Python library Dendropy (Sukumaran and Holder 2010) was implemented to run all the phylogenetic estimations on simulated matrices. All p-values were adjusted using the method proposed by Benjamini and Hochberg (1995).

Topological tests on competing phylogenetic hypotheses were conducted to evaluate their support given the data. Two different approaches were followed: a frequentist implementation, the AU-SH test (Shimodaira 2002), and a bayesian alternative, posterior odds evaluation (Bergsten et al. 2013). The ML procedure required heuristic searches on the topological constraints, followed by optimization of model parameters. Both computations were carried out in RAxML.
2.2.4 Phylogenetic analyses of morphological and combined datasets

Morphological characters were scored from specimens held at the New York Botanical Garden herbarium (NY). Observations were complemented with the study of specimens from other Latin and North American herbaria (COL, CUVC, LPB, MO, QCA, QCNE, US). Observations were done on five collections per species. A morphological matrix of 77 characters was assembled; nine were continuous (Table 2.2) and 68 categorical (Table 2.3). Character state descriptions are presented in the Appendix D. Continuous characters were treated as such, employing the optimization algorithms proposed by Goloboff et al. (2006). Continuous measurements were transformed to z-scores (Spatz 2010). Discrete characters were treated as non-ordered, except character 41 (bracteole position along the pedicel). Implied weighting was used to explore different regimes as follows: all characters equally weighted or with implied weights (concavity constant $k$ set to 3, 10, 30, or 100). Artificial weight increase in characters with missing data can occur under implied weights (Goloboff 2014). To correct for this problem, homoplasy in missing entries was scaled 0.5 times the homoplasy of observed entries. Most parsimonious trees (MPTs) were retrieved after TBR on 1000 random addition sequences. Support was assessed with 1000 jackknife replicates. Characters were optimized upon the MPT using the Deltran algorithm implemented in TNT (Goloboff et al. 2008).

Phylogenetic independent contrasts (Felsenstein 1985) were used to estimate the correlation among continuous characters. Some of these characters were expected to be correlated to some degree given that they are measurements of nested floral structures
(e.g., stamen and anther sizes). This test was carried out on a subset of 44 species representing different lineages of Vaccinieae. Although the model was not a good fit for three of the putative correlations considered (long stamen: corolla ratio vs. corolla length, short stamen: corolla ratio vs. corolla length, and anther: corolla ratio vs. corolla length), it was significant for 1) calyx total length vs. calyx lobes length and 2) anther length vs. stamen length. However, in the latter two cases, the correlation coefficients were low (0.2259 and 0.644), indicating that a substantial part of the variation was not explained by the interaction between measurements. Thus, the use of these continuous characters in phylogenetic inference was deemed non-problematic.

The combined dataset of morphology and molecular data contained a significant proportion of missing data, as molecular data could not been retrieved for 29 species (49% of the terminals). Although molecular work was intended to produce sequence data of all species of *Orthaea* s.l., several circumstances prevented such a positive outcome. Lack of funding or collection permits made not possible to collect several species endemic to Bolivia, Mexico, Peru, and Venezuela. Despite field work carried out in Colombia and Ecuador, several species could not been sampled for a number of reasons (i.e., type localities underwent intense deforestation). Finally, molecular work on several samples stored at the NYBG tissue collection consistently failed in spite of trying several extraction and PCR protocols.

Therefore, several species of *Orthaea* were represented exclusively by morphology in the
combined analyses, as there is not another way to establish their phylogenetic relationships. Moreover, phylogenetic estimation was also conducted on all available data (morphological and molecular) following the total evidence principle of inductive reasoning: the degree of confirmation of a given hypothesis can only estimated if all available data at a that time is considered (Hempel 1965). When applied to phylogenetic estimation (Kluge 1989), the total evidence principle recommends the simultaneous analysis of all sources of data that the researcher has at hand because the explanatory power of the resulting phylogenies will be maximized, reducing the necessity of auxiliary *ad hoc* hypotheses (Farris 1983).
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Char. 0</th>
<th>Char. 1</th>
<th>Char. 2</th>
<th>Char. 3</th>
<th>Char. 4</th>
<th>Char. 5</th>
<th>Char. 6</th>
<th>Char. 7</th>
<th>Char. 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cavendishia grandifolia</td>
<td>2.542–3.210</td>
<td>0.800–1.199</td>
<td>0.154–0.309</td>
<td>2.134–3.032</td>
<td>0.312–0.624</td>
<td>0.109–0.119</td>
<td>3.414–3.855</td>
<td>4.618–6.717</td>
<td>4.806–4.806</td>
</tr>
<tr>
<td>C. isernii</td>
<td>0.361–1.204</td>
<td>0.267–0.720</td>
<td>0.154–0.540</td>
<td>0.786–1.235</td>
<td>0.000–0.000</td>
<td>0.097–0.116</td>
<td>2.919–3.745</td>
<td>0.892–1.732</td>
<td>3.184–3.400</td>
</tr>
<tr>
<td>C. martii</td>
<td>1.070–4.013</td>
<td>0.267–0.400</td>
<td>0.185–0.309</td>
<td>0.786–1.123</td>
<td>0.624–0.780</td>
<td>0.105–0.110</td>
<td>3.249–3.469</td>
<td>1.679–1.732</td>
<td>3.261–3.416</td>
</tr>
<tr>
<td>C. aff. martii (Pedraza 1551)</td>
<td>1.338–1.605</td>
<td>0.267–0.400</td>
<td>0.232–0.417</td>
<td>1.123–1.348</td>
<td>0.624–1.248</td>
<td>0.058–0.064</td>
<td>1.487–1.707</td>
<td>1.102–1.233</td>
<td>1.509–1.715</td>
</tr>
<tr>
<td>C. micayensis</td>
<td>0.602–1.338</td>
<td>1.066–1.866</td>
<td>0.463–1.235</td>
<td>2.246–4.155</td>
<td>0.000–0.000</td>
<td>0.059–0.072</td>
<td>1.652–2.313</td>
<td>1.863–2.388</td>
<td>1.113–1.844</td>
</tr>
<tr>
<td>C. quereme</td>
<td>0.401–0.736</td>
<td>0.000–0.200</td>
<td>0.077–0.154</td>
<td>1.067–1.202</td>
<td>0.125–0.749</td>
<td>0.088–0.098</td>
<td>2.919–3.745</td>
<td>1.049–1.312</td>
<td>2.581–2.736</td>
</tr>
<tr>
<td>C. tarapotana</td>
<td>0.134–1.806</td>
<td>0.666–0.800</td>
<td>0.154–0.154</td>
<td>0.337–0.483</td>
<td>0.312–0.624</td>
<td>0.069–0.105</td>
<td>1.762–3.249</td>
<td>4.093–5.405</td>
<td>2.287–2.571</td>
</tr>
<tr>
<td>Notopora schomburgkii</td>
<td>0.000–0.000</td>
<td>0.733–1.066</td>
<td>0.077–0.386</td>
<td>1.460–1.572</td>
<td>0.000–0.000</td>
<td>0.077–0.096</td>
<td>2.258–3.084</td>
<td>0.682–0.892</td>
<td>1.236–1.417</td>
</tr>
<tr>
<td>Orthaea abbreviata</td>
<td>0.027–0.214</td>
<td>0.160–0.466</td>
<td>0.015–0.123</td>
<td>3.369–4.492</td>
<td>0.936–1.092</td>
<td>0.105–0.027</td>
<td>0.220–0.661</td>
<td>0.315–0.341</td>
<td>0.000–0.098</td>
</tr>
<tr>
<td>O. apophysata</td>
<td>0.000–0.000</td>
<td>0.227–0.373</td>
<td>0.000–0.015</td>
<td>1.909–2.471</td>
<td>0.000–0.000</td>
<td>0.029–0.045</td>
<td>0.385–1.212</td>
<td>0.630–0.682</td>
<td>0.587–0.804</td>
</tr>
<tr>
<td>O. boliviensis*</td>
<td>0.187–0.535</td>
<td>0.200–0.400</td>
<td>0.046–0.154</td>
<td>2.021–3.706</td>
<td>0.624–0.936</td>
<td>0.030–0.043</td>
<td>0.551–1.267</td>
<td>0.367–0.446</td>
<td>0.134–0.453</td>
</tr>
<tr>
<td>O. brachysiphon*</td>
<td>2.675–4.013</td>
<td>0.800–1.133</td>
<td>0.386–0.463</td>
<td>2.358–3.144</td>
<td>0.000–0.000</td>
<td>0.030–0.033</td>
<td>0.220–0.275</td>
<td>0.498–0.630</td>
<td>0.350–0.464</td>
</tr>
<tr>
<td>O. breviflora*</td>
<td>0.067–0.107</td>
<td>0.147–0.293</td>
<td>0.077–0.123</td>
<td>1.101–1.101</td>
<td>0.156–0.187</td>
<td>0.034–0.035</td>
<td>0.661–0.936</td>
<td>0.000–0.079</td>
<td>0.386–0.546</td>
</tr>
</tbody>
</table>

Table 2.2: Matrix of continuous characters for neotropical Vaccinieae. Measurements are given in z-scores (Spatz 2010). Taxa without molecular data are indicate with a *.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Char. 0</th>
<th>Char. 1</th>
<th>Char. 2</th>
<th>Char. 3</th>
<th>Char. 4</th>
<th>Char. 5</th>
<th>Char. 6</th>
<th>Char. 7</th>
<th>Char. 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. bullata</td>
<td>0.268–0.602</td>
<td>0.107–0.267</td>
<td>0.062–0.154</td>
<td>1.011–1.235</td>
<td>0.624–0.936</td>
<td>0.039–0.045</td>
<td>0.936–1.322</td>
<td>0.157–0.420</td>
<td>0.799–1.056</td>
</tr>
<tr>
<td>O. carnosiflora*</td>
<td>0.268–0.736</td>
<td>0.133–1.066</td>
<td>0.247–0.463</td>
<td>2.246–2.808</td>
<td>0.936–1.248</td>
<td>0.042–0.063</td>
<td>1.046–1.872</td>
<td>0.945–1.469</td>
<td>0.943–1.097</td>
</tr>
<tr>
<td>O. caudata*</td>
<td>0.762–0.762</td>
<td>3.465–3.731</td>
<td>3.395–3.704</td>
<td>3.481–3.481</td>
<td>0.000–0.000</td>
<td>0.025–0.026</td>
<td>0.220–0.330</td>
<td>0.892–1.023</td>
<td>0.448–0.531</td>
</tr>
<tr>
<td>O. cavendishioides*</td>
<td>0.201–0.482</td>
<td>0.373–0.493</td>
<td>0.093–0.139</td>
<td>3.257–4.043</td>
<td>0.000–0.000</td>
<td>0.034–0.035</td>
<td>0.936–1.322</td>
<td>1.338–1.469</td>
<td>0.654–0.809</td>
</tr>
<tr>
<td>O. constans*</td>
<td>0.375–0.722</td>
<td>0.200–0.360</td>
<td>0.015–0.046</td>
<td>1.348–1.572</td>
<td>0.312–0.468</td>
<td>0.041–0.054</td>
<td>1.267–1.322</td>
<td>0.446–0.892</td>
<td>0.984–1.417</td>
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<tr>
<td>O. cordata</td>
<td>1.739–3.344</td>
<td>0.400–0.746</td>
<td>0.340–0.818</td>
<td>2.695–3.257</td>
<td>0.936–1.716</td>
<td>0.022–0.024</td>
<td>0.110–0.165</td>
<td>0.472–0.630</td>
<td>0.340–0.407</td>
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<tr>
<td>O. coriacea*</td>
<td>0.254–0.428</td>
<td>0.426–0.520</td>
<td>0.123–0.201</td>
<td>1.460–1.797</td>
<td>0.156–0.218</td>
<td>0.037–0.039</td>
<td>0.716–0.936</td>
<td>0.210–0.262</td>
<td>0.428–0.525</td>
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<td>O. crinita*</td>
<td>0.000–0.000</td>
<td>0.200–0.400</td>
<td>0.046–0.062</td>
<td>0.955–1.404</td>
<td>0.000–0.000</td>
<td>0.076–0.080</td>
<td>2.864–3.029</td>
<td>0.682–0.761</td>
<td>1.427–2.076</td>
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<tr>
<td>O. ecuadorensis</td>
<td>0.388–0.535</td>
<td>0.267–0.600</td>
<td>0.093–0.154</td>
<td>3.481–3.594</td>
<td>0.936–1.248</td>
<td>0.031–0.041</td>
<td>0.385–1.156</td>
<td>0.735–1.076</td>
<td>0.350–0.536</td>
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<td>O. ferreyrae*</td>
<td>0.241–0.508</td>
<td>0.453–0.600</td>
<td>0.062–0.123</td>
<td>2.021–2.358</td>
<td>2.185–2.497</td>
<td>0.047–0.051</td>
<td>1.212–1.322</td>
<td>0.708–0.892</td>
<td>0.824–0.829</td>
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<td>O. fimbriata</td>
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<td>0.267–0.400</td>
<td>0.062–0.108</td>
<td>2.134–2.695</td>
<td>0.624–0.999</td>
<td>0.052–0.046</td>
<td>1.322–1.377</td>
<td>0.577–0.787</td>
<td>0.598–0.628</td>
</tr>
<tr>
<td>O. glandulifera</td>
<td>0.334–0.562</td>
<td>0.267–0.533</td>
<td>0.772–0.170</td>
<td>3.257–3.594</td>
<td>0.312–0.624</td>
<td>0.026–0.037</td>
<td>0.165–0.661</td>
<td>0.157–0.315</td>
<td>0.005–0.072</td>
</tr>
<tr>
<td>O. hispida*</td>
<td>0.000–0.000</td>
<td>0.333–0.800</td>
<td>0.015–0.031</td>
<td>2.246–2.808</td>
<td>0.000–0.000</td>
<td>0.031–0.034</td>
<td>0.496–0.606</td>
<td>0.761–0.892</td>
<td>0.644–0.762</td>
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<tr>
<td>O. madidiensis</td>
<td>0.201–0.602</td>
<td>0.800–0.933</td>
<td>0.077–0.309</td>
<td>0.898–1.685</td>
<td>0.936–1.248</td>
<td>0.048–0.068</td>
<td>1.487–1.927</td>
<td>0.997–1.574</td>
<td>2.195–3.003</td>
</tr>
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<td>O. medusula</td>
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<td>0.267–0.360</td>
<td>0.170–0.232</td>
<td>0.674–1.011</td>
<td>0.125–0.312</td>
<td>0.068–0.072</td>
<td>2.093–2.203</td>
<td>0.236–0.446</td>
<td>1.427–1.628</td>
</tr>
<tr>
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<td>0.133–0.600</td>
<td>0.015–0.031</td>
<td>2.134–2.471</td>
<td>0.000–0.000</td>
<td>0.030–0.031</td>
<td>0.330–0.441</td>
<td>0.551–0.708</td>
<td>0.603–0.613</td>
</tr>
</tbody>
</table>

Table 2.2: Matrix of continuous characters for neotropical Vacciniaceae. Measurements are given in z-scores (Spatz 2010). Taxa without molecular data are indicated with a *.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Char. 0</th>
<th>Char. 1</th>
<th>Char. 2</th>
<th>Char. 3</th>
<th>Char. 4</th>
<th>Char. 5</th>
<th>Char. 6</th>
<th>Char. 7</th>
<th>Char. 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. minor</td>
<td>0.174–0.482</td>
<td>2.799–5.064</td>
<td>2.778–4.785</td>
<td>2.695–3.144</td>
<td>0.000–0.000</td>
<td>0.037–0.043</td>
<td>0.881–1.101</td>
<td>0.656–0.971</td>
<td>0.531–0.737</td>
</tr>
<tr>
<td>O. oedipus</td>
<td>0.348–0.642</td>
<td>0.400–0.666</td>
<td>0.077–0.108</td>
<td>3.818–3.818</td>
<td>0.156–0.312</td>
<td>0.038–0.041</td>
<td>0.661–0.881</td>
<td>0.315–0.420</td>
<td>0.046–0.108</td>
</tr>
<tr>
<td>O. ornitens</td>
<td>0.428–0.722</td>
<td>0.227–0.426</td>
<td>0.062–0.154</td>
<td>3.257–3.369</td>
<td>0.156–0.312</td>
<td>0.026–0.037</td>
<td>0.496–0.716</td>
<td>0.525–0.761</td>
<td>0.258–0.392</td>
</tr>
<tr>
<td>O. panamensis</td>
<td>0.094–0.736</td>
<td>4.398–5.997</td>
<td>4.322–5.711</td>
<td>2.471–3.818</td>
<td>0.000–0.000</td>
<td>0.029–0.038</td>
<td>0.220–0.771</td>
<td>0.787–1.233</td>
<td>0.577–0.685</td>
</tr>
<tr>
<td>O. paniculata*</td>
<td>0.696–1.030</td>
<td>0.533–0.666</td>
<td>0.154–0.232</td>
<td>1.909–2.134</td>
<td>0.312–0.936</td>
<td>0.048–0.054</td>
<td>1.267–1.487</td>
<td>0.525–0.551</td>
<td>0.603–0.685</td>
</tr>
<tr>
<td>O. peregrina*</td>
<td>0.401–0.629</td>
<td>1.066–1.466</td>
<td>0.463–0.772</td>
<td>1.685–2.134</td>
<td>0.312–0.624</td>
<td>0.033–0.037</td>
<td>0.881–0.936</td>
<td>0.446–0.577</td>
<td>0.628–0.716</td>
</tr>
<tr>
<td>O. pinnatinervia*</td>
<td>0.134–0.268</td>
<td>0.280–0.320</td>
<td>0.062–0.093</td>
<td>1.460–1.797</td>
<td>1.997–2.653</td>
<td>0.041–0.045</td>
<td>1.046–1.212</td>
<td>0.787–0.892</td>
<td>1.200–1.396</td>
</tr>
<tr>
<td>O. rusby*</td>
<td>0.736–1.137</td>
<td>0.133–0.267</td>
<td>0.031–0.108</td>
<td>2.695–3.257</td>
<td>0.312–0.936</td>
<td>0.043–0.047</td>
<td>0.936–1.156</td>
<td>0.787–0.840</td>
<td>0.469–0.598</td>
</tr>
<tr>
<td>O. secundiflora*</td>
<td>0.334–0.669</td>
<td>0.133–0.400</td>
<td>0.077–0.154</td>
<td>2.021–3.594</td>
<td>0.250–0.312</td>
<td>0.025–0.034</td>
<td>0.220–0.496</td>
<td>0.289–0.420</td>
<td>0.134–0.366</td>
</tr>
<tr>
<td>(Ecuador)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. secundiflora</td>
<td>0.468–0.642</td>
<td>0.187–0.453</td>
<td>0.062–0.108</td>
<td>2.583–3.594</td>
<td>0.468–0.468</td>
<td>0.022–0.031</td>
<td>0.000–0.496</td>
<td>0.315–0.656</td>
<td>0.237–0.278</td>
</tr>
<tr>
<td>(Peru)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. stipitata</td>
<td>2.943–4.414</td>
<td>0.800–1.066</td>
<td>0.262–0.417</td>
<td>2.695–3.369</td>
<td>0.000–0.000</td>
<td>0.039–0.041</td>
<td>0.606–0.771</td>
<td>1.154–1.364</td>
<td>0.788–0.896</td>
</tr>
<tr>
<td>O. thibaudioides*</td>
<td>0.000–0.000</td>
<td>0.160–0.400</td>
<td>0.015–0.046</td>
<td>1.797–2.246</td>
<td>0.000–0.000</td>
<td>0.054–0.058</td>
<td>1.487–1.597</td>
<td>1.207–1.312</td>
<td>1.303–1.587</td>
</tr>
<tr>
<td>O. venamensis</td>
<td>0.000–0.000</td>
<td>0.200–0.333</td>
<td>0.015–0.031</td>
<td>2.134–3.144</td>
<td>0.000–0.000</td>
<td>0.038–0.045</td>
<td>0.991–1.101</td>
<td>0.945–1.076</td>
<td>0.665–1.010</td>
</tr>
<tr>
<td>O. weberbauerii</td>
<td>0.348–0.829</td>
<td>0.200–0.333</td>
<td>0.077–0.232</td>
<td>1.909–2.021</td>
<td>0.312–0.624</td>
<td>0.030–0.035</td>
<td>0.661–0.826</td>
<td>0.394–0.420</td>
<td>0.510–0.531</td>
</tr>
</tbody>
</table>

Table 2.2: Matrix of continuous characters for neotropical Vaccinieae. Measurements are given in z-scores (Spatz 2010). Taxa without molecular data are indicated with a *.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Char. 0</th>
<th>Char. 1</th>
<th>Char. 2</th>
<th>Char. 3</th>
<th>Char. 4</th>
<th>Char. 5</th>
<th>Char. 6</th>
<th>Char. 7</th>
<th>Char. 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. sp. nov. 1</td>
<td>0.495–0.869</td>
<td>0.466–0.560</td>
<td>0.154–0.309</td>
<td>2.021–2.695</td>
<td>0.936–4.681</td>
<td>0.033–0.043</td>
<td>0.716–1.101</td>
<td>0.630–0.735</td>
<td>0.556–0.742</td>
</tr>
<tr>
<td>O. sp. nov. 2</td>
<td>0.107–0.321</td>
<td>0.200–0.400</td>
<td>0.031–0.077</td>
<td>2.808–2.920</td>
<td>1.872–2.809</td>
<td>0.039–0.047</td>
<td>0.936–1.322</td>
<td>0.630–0.813</td>
<td>0.438–0.546</td>
</tr>
<tr>
<td><em>Satyria polyantha</em></td>
<td>0.134–0.508</td>
<td>0.000–0.107</td>
<td>0.046–0.077</td>
<td>0.517–0.651</td>
<td>0.062–0.156</td>
<td>0.085–0.107</td>
<td>2.423–3.359</td>
<td>0.341–0.472</td>
<td>2.493–2.674</td>
</tr>
<tr>
<td><em>Thibaudia densiflora</em></td>
<td>0.067–0.308</td>
<td>0.533–0.933</td>
<td>0.154–0.386</td>
<td>1.235–1.628</td>
<td>0.312–0.624</td>
<td>0.075–0.086</td>
<td>1.983–2.478</td>
<td>1.181–1.312</td>
<td>1.927–2.416</td>
</tr>
<tr>
<td><em>Vaccinium crenatum</em></td>
<td>0.080–0.201</td>
<td>0.133–0.400</td>
<td>0.154–0.232</td>
<td>0.730–0.865</td>
<td>0.000–0.000</td>
<td>0.076–0.085</td>
<td>2.203–2.588</td>
<td>0.262–0.394</td>
<td>1.556–1.592</td>
</tr>
<tr>
<td><em>V. hirsutum</em></td>
<td>0.120–0.294</td>
<td>0.133–0.267</td>
<td>0.201–0.262</td>
<td>0.898–1.123</td>
<td>0.000–0.000</td>
<td>0.094–9.948</td>
<td>3.029–3.194</td>
<td>0.682–0.892</td>
<td>2.128–2.231</td>
</tr>
</tbody>
</table>

**Table 2.2:** Matrix of continuous characters for neotropical Vacciniaceae. Measurements are given in z-scores (*Spatz 2010*). Taxa without molecular data are indicated with an asterisk (*).
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Characters 9–76</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cavendishia quereme</td>
<td>1[01]11011111000100000100010101000000-11100-1102101101110110-120110[02]</td>
</tr>
<tr>
<td>Cavendishia tarapotana</td>
<td>111100101000010000101011100-1100010011101110100100-10000000</td>
</tr>
<tr>
<td>Notopora schomburgkii</td>
<td>01000000-0010-0110—001100100110-21000-0103010101101111033000[21]</td>
</tr>
<tr>
<td>Orthaea abbreviata</td>
<td>1111011010000100001011000100010100-1110[10]00111[01]01101110110100-0110001</td>
</tr>
<tr>
<td>Orthaea apophysata</td>
<td>21110010-0[01]11100110—1110001110011021100-01111011110010110000011[21]</td>
</tr>
<tr>
<td>Orthaea breviflora*</td>
<td>001101????000100000?0111????010100-11101001[10]??0011110110100-0110001</td>
</tr>
<tr>
<td>Orthaea carnosiflora*</td>
<td>0001111010000100000101[10]1?????110001011100-01111001111101100-0200101</td>
</tr>
<tr>
<td>Orthaea caudata*</td>
<td>00010010?00010000011[10]11101102020-01110-010??1000110010010-0110001</td>
</tr>
<tr>
<td>Orthaea cavendishioides*</td>
<td>11110111100001000001010001100100111100-01111111111101[10]100-0000[01]01</td>
</tr>
</tbody>
</table>

**Table 2.3:** Morphological matrix of discrete characters for neotropical Vaccinieae. Polymorphisms are annotated between square brackets, missing data with question marks, and inapplicable characters with hyphens. Taxa without molecular data are indicate with a *.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Characters 9–76</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orthaea constans*</td>
<td>0001011010000100000001111011010100–11100-011111011110110100-0110001</td>
</tr>
<tr>
<td>Orthaea cordata</td>
<td>110001001000011000010011010101000011111001001101100101100100-0110001</td>
</tr>
<tr>
<td>Orthaea coriacea*</td>
<td>111101100-000100000101110011000000–11100-011111011110110100-0110001</td>
</tr>
<tr>
<td>Orthaea ecuadorensis</td>
<td>10110110100001[10]00000011111010100100–01101011101110100-0110001</td>
</tr>
<tr>
<td>Orthaea ferreyrae*</td>
<td>000000010100001000010[01]111101001000110111010011111011110100-020[10]101</td>
</tr>
<tr>
<td>Orthaea sp. nov. 2</td>
<td>0001011011000[01]000001011111101100100101100-01100-01111101111110100-0201101</td>
</tr>
<tr>
<td>Orthaea glandulifera</td>
<td>1011011?100011000010111100111101101101101101010101010101010011001</td>
</tr>
<tr>
<td>Orthaea hispida*</td>
<td>01000001110000-[01]10–??1001001000–201010011[10]101110010111110200[?11</td>
</tr>
<tr>
<td>Orthaea madidiensis</td>
<td>01010110–001000001010010100010[01]0–11100-0111100110101[01]01[01]10-[01]22001</td>
</tr>
<tr>
<td>Orthaea merumensis*</td>
<td>211100????[01][01]01010—????001100-21100-011101011110010100200111</td>
</tr>
<tr>
<td>Orthaea oedipus</td>
<td>11110111100001100001111111101100110001010011001[01]100110011110-0110001</td>
</tr>
<tr>
<td>Orthaea panamensis</td>
<td>00000010100001100001111010010100100110100100-0110001</td>
</tr>
</tbody>
</table>

Table 2.3: Morphological matrix of discrete characters for neotropical Vaccinieae. Polymorphisms are annotated between square brackets, missing data with question marks, and inapplicable characters with hyphens. Taxa without molecular data are indicate with a *.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Characters 9–76</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orthaea paniculata*</td>
<td>10110010?1001100111111????1110?011011100-110110011111101100-0200101</td>
</tr>
<tr>
<td>Orthaea medusula</td>
<td>00110011?10011001111111010110000-0110100101000111001111110-0200101</td>
</tr>
<tr>
<td>Orthaea peregrina*</td>
<td>101100111000110000011111111010110000-1[10]100-10000101110011010100-020101</td>
</tr>
<tr>
<td>Orthaea secundiflora* (Peru)</td>
<td>110101??1000010000[10]010111010010000-01100-011??1001111010100-0110001</td>
</tr>
<tr>
<td>Orthaea thibaudioides*</td>
<td>21[10]10010-0000-[01]110—1111011001100-21100-01111010111001010110200110</td>
</tr>
<tr>
<td>Orthaea venamensis</td>
<td>2[10][10]10010-0010-1010—-????001100-11100-011101011110010100-0200111</td>
</tr>
<tr>
<td>Orthaea weberbauerii</td>
<td>1011011110000100000001101011011100-11[00]110111110110100-0201101</td>
</tr>
<tr>
<td>Vaccinium crenatum</td>
<td>000100[10]0-0100-00001010011010100[12][10]00-11100-01010101111000000-000000</td>
</tr>
</tbody>
</table>

Table 2.3: Morphological matrix of discrete characters for neotropical Vaccinieae. Polymorphisms are annotated between square brackets, missing data with question marks, and inapplicable characters with hyphens. Taxa without molecular data are indicate with a *.
2.3 Results

2.3.1 Incongruence among molecular partitions

An initial congruence assessment assumed the best tree from the concatenated molecular matrix (ITS + \textit{matK} + \textit{ndhF}) as the null hypothesis. Under this assumption, SOWH test did not reject the null hypothesis, but the AU test did, further suggesting that the best tree from the \textit{matK} dataset could be a plausible explanation to the concatenated dataset (Tables 2.4 and 2.5). Therefore, due to the differences between the preliminary tests, a more rigorous congruence assessment was carried out simulating the most likely tree for each molecular marker in the other two, then performing the SOWH test.

<table>
<thead>
<tr>
<th>Partition</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ITS</td>
<td>$2 \times 10^{-7}$</td>
</tr>
<tr>
<td>\textit{matK}</td>
<td>0.214</td>
</tr>
<tr>
<td>\textit{ndhF}</td>
<td>0.063</td>
</tr>
</tbody>
</table>

\textbf{Table 2.4: Congruence AU test}

<table>
<thead>
<tr>
<th>Partition</th>
<th>Observed likelihood difference</th>
<th>0.05 critical value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ITS</td>
<td>169.0599</td>
<td>400.7979</td>
<td>0.9993429</td>
</tr>
<tr>
<td>\textit{matK}</td>
<td>55.9673</td>
<td>148.8263</td>
<td>0.9990673</td>
</tr>
<tr>
<td>\textit{ndhF}</td>
<td>9.01578</td>
<td>78.49874</td>
<td>0.9001384</td>
</tr>
</tbody>
</table>

\textbf{Table 2.5: Congruence SOWH test, concatenated result used as null hypothesis}

The SOWH test did not rejected the null hypothesis in any of the pairwise simulations (Table 2.6), suggesting that topological differences among partitions fall within the expected
inference error interval, given the data and assumptions of the phylogenetic method. Overall, incongruence tests suggest that conflicting phylogenetic signal is generated by the uncertainty associated to the phylogenetic estimation, rather than incompatibility among the different partitions. Therefore, the subsequent phylogenetic analyses and discussion are based upon the concatenated dataset.

<table>
<thead>
<tr>
<th>Null hypothesis</th>
<th>Alternative hypothesis</th>
<th>Likelihood difference</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ITS</td>
<td>matK</td>
<td>419.9017</td>
<td>0.9999859</td>
</tr>
<tr>
<td>ITS</td>
<td>ndhf</td>
<td>334.6385</td>
<td>0.9991822</td>
</tr>
<tr>
<td>matK</td>
<td>ITS</td>
<td>422.3165</td>
<td>0.9877797</td>
</tr>
<tr>
<td>matK</td>
<td>ndhf</td>
<td>107.9415</td>
<td>0.9980595</td>
</tr>
<tr>
<td>ndhF</td>
<td>ITS</td>
<td>833.3749</td>
<td>0.9999999</td>
</tr>
<tr>
<td>ndhF</td>
<td>matK</td>
<td>413.835</td>
<td>0.9999947</td>
</tr>
</tbody>
</table>

Table 2.6: Pairwise congruence SOWH test from simulations based on the the most likely tree from each partition.

### 2.3.2 Molecular phylogeny

The parsimony analysis retrieved 2484 MPTs (L: 1923). Bayesian analyses reached convergence after $20 \times 10^6$ generations, and the estimated sample size (ESS) of all parameters were 450 or greater. The same optimal topology was retrieved regardless the optimality criterion employed. The most likely tree is presented in Figure 2.1 (log likelihood = -20374.239630) and will be used for the following discussion.

As currently circumscribed, *Orthaea* s.l. is polyphyletic, with several independent origins throughout the Vaccinieae, within the neotropical clade and outside of it (Fig. 2.1). *Orthaea* s.l. of extra-neotropical origin comprises two species from the Guiana Shield,
Figure 2.1: Best ML tree of Vaccinieae based on ITS, *matK*, and *ndhF* data (113 species). Highlighted clades are discussed in the text; their topology and detailed support are in figures 2.2–2.4. *Orthaea* s.l is in red.
*O. apophysata* (Griseb.) A. C. Sm. and *O. venamensis* Maguire, Steyerm. & Luteyn, and another from Southern Mexico to Honduras, *O. stipitata* (Luteyn) Luteyn. These three species are nested in a clade with well supported internal topology (95–100% ML bootstrap, 93–100% parsimony jackknife, and 1.0 bayesian posterior probabilities, Figs. 2.1 and 2.2). All the sampled taxa endemic to the Guiana Shield are monophyletic (*Notoporta schomburgkii* Hook. f., *O. apophysata*, and *O. venamensis*), whereas *O. stipitata*, a cloud forest species of subgenus *Empedoclesia*, is sister to *Vaccinium crenatum* (G. Don) Sleumer, a species native to the high elevation páramos and punas (shrub- and grass-dominated neotropical vegetation) of Venezuela–Peru (Fig. 2.2). Together, they are sister to taxa from south-east Asia and nested in a clade previously called the East Malesian clade (Kron et al. 2002b).

**Figure 2.2:** Detail of the Guiana Shield + East Malesian clade, along with bootstrap (above nodes, boldface), jackknife (below nodes, regular), and posterior probability values (left to nodes, italics). Its position relative to other Vaccinieae (Fig. 2.1) is shown in the inset to the left.

Within the Vaccinieae of Andean origin, *Orthaea madidiensis* Pedraza & Luteyn (Peru) was recovered within the *Thibaudia* Ruiz & Pav. ex J. St.-Hil. p.p. clade (100% ML bootstrap, 98% parsimony jackknife, 1 posterior probability; Fig. 2.3), along with other Vaccinieae from the same general region (Peru and Bolivia), such as *Polyclita turbinata*
(Kuntze) A. C. Sm., *Semiramisia speciosa* (Benth.) Klotzsch, some *Thibaudia* s.l., and three species segregated from *Satyria* s.s. and The closest relative of *Orthaea madidiensis* was *Satyria vargasii* A. C. Sm.

All the species of *Cavendishia* (18 spp.), the remaining species of *Orthaea* (14 spp.), all the species of *Satyria* from Central America and northern South America (11 spp.), and *Thibaudia costaricensis* Hoerold constituted the heteroandrous clade (98% ML bootstrap, 98% parsimony jackknife, 1 posterior probability, Fig. 2.4). This monophyletic group has notoriously dimorphic stamens, with the single exception of *T. costaricensis*. Within the heteroandrous clade, *Cavendishia* and *Orthaea* form a clade (98% ML bootstrap, 97% parsimony jackknife, 1 posterior probability); however, these two components were not reciprocally monophyletic: although the majority of *Orthaea* form a clade (68% ML bootstrap, 67% parsimony jackknife, 1 posterior probability), four species are found within *Cavendishia*.

**Figure 2.3:** ML topology of the *Thibaudia* clade, along with bootstrap (above nodes, boldface), jackknife (below nodes, regular style), and posterior probability values (left to nodes, italics). Its phylogenetic position relative to the Vaccinieae topology is shown in the inset to the left.
Figure 2.4: ML topology of the Heteroandrous clade, along with bootstrap (above nodes, boldface), jackknife (below nodes, regular style), and posterior probability values (left to nodes, italics). Its phylogenetic position relative to the Vaccinieae topology is shown in the inset in the bottom-left corner. A: *Cavendishia* + *Orthaea* p.p. clade.
The majority of the relationships within the *Cavendishia* + *Orthaea* p.p. are not well supported (Fig. 2.4). Among the most basal nodes, the only well supported clade (96% ML bootstrap, 94% parsimony jackknife, 1 posterior probability) is that of *O. minor* (A. C. S.) Luteyn + *O. panamensis* (Luteyn & Wilbur) Luteyn + *Cavendishia* p.p., with the species of *Orthaea* as sister taxa (100% ML bootstrap, 100% parsimony jackknife, 1 posterior probability, Fig. 2.4).

The other sampled species of the *Orthaea* of Andean origin (12 OTUs, 10 species) were recovered within a clade with moderate support (*Orthaea* s.s. clade hereafter, 68% ML bootstrap, 67% jackknife, 1 posterior probability). Only four subclades within *Orthaea* s.s. have bootstrap values ≥ 80%: 1) *O*. sp. nov. 1 + *O*. sp. nov. 2 + *O. weberbauerii* Hoerold (94%), 2) *O. fimbriata* Luteyn + *O. oriens* Luteyn (87%), 3) *O. abbreviata* Drake + *O. ecuadorensis* Luteyn (98%), and 4) *O. glandulifera* Luteyn + *O. oedipus* Luteyn (80%).

### 2.3.3 Topological tests

Given that most of the relationships pertaining members of *Orthaea* s.l. were weakly supported, topological tests were conducted to explore the compatibility between the data and alternative circumscriptions of *Orthaea*. This evaluation was done through the AU-SH test and posterior odds comparisons. The topological constraints employed for heuristic searches (AU-SH test) and tree filtering (posterior odds) were:

1. Unconstrained best ML tree.
2. *Orthaea* s.s. + *O. bullata* + *O. cordata* + *O. minor* + *O. panamensis* are monophyletic.

3. *Orthaea* s.s. + *O. bullata* + *O. cordata* are monophyletic.

4. *Orthaea* s.s. + *O. cordata* are monophyletic.

5. *Orthaea* s.s. + *O. bullata* are monophyletic.

6. *Orthaea* s.s. + *O. bullata* + *O. cordata* + *O. madidiensis* + *O. minor* + *O. panamensis* are monophyletic.

7. *Orthaea* s.s. + *O. bullata* + *O. cordata* + *O. madidiensis* + *O. minor* + *O. panamensis* + *O. stipitata* are monophyletic.

8. *Orthaea* s.s. + *O. apophysata* + *O. bullata* + *O. cordata* + *O. madidiensis* + *O. minor* + *O. panamensis* + *O. venamensis* are monophyletic.

9. *Orthaea* s.l. is monophyletic.

The AU-SH test rejected all the hypotheses, but three (*Orthaea* s.s. + *O. bullata* + *O. cordata*) and 4 (*Orthaea* s.s. + *O. cordata*) as plausible explanations of the data. Comparison of posterior odds among the hypotheses similarly found very small or no support to all hypotheses but the most likely topology (Table 2.7).
### Table 2.7: Topological tests results. P-values (AU-SH test) and proportion of trees from the stationary distribution (posterior odds) are reported for every tested hypothesis.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>AU-test value</th>
<th>Posterior odds</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.739</td>
<td>0.999</td>
</tr>
<tr>
<td>2</td>
<td>0.016</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td><strong>0.370</strong></td>
<td><strong>3.125 \times 10^{-5}</strong></td>
</tr>
<tr>
<td>4</td>
<td><strong>0.449</strong></td>
<td>0.027</td>
</tr>
<tr>
<td>5</td>
<td>0.043</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>$1 \times 10^{-68}$</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>$2 \times 10^{-7}$</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>$5 \times 10^{-67}$</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>$2 \times 10^{-68}$</td>
<td>0</td>
</tr>
</tbody>
</table>

#### 2.3.4 Morphological analyses

A summary of the phylogenetic analyses on the morphological dataset is shown in Table 2.8. The MP topology changed through the different analytical settings and support values were low, generally below 80% (Figs. 2.5–2.9). Remarkable exceptions were the *Empedoclesia* (*Orthaea stipitata* + *O. brachysiphon*) and *Lysiclesia* clades (*O. caudata* + *O. minor* + *O. panamensis*), which were consistently recovered and supported by resampling values greater than 90%. Given the lack of support and topological consistency between the morphological analyses and both the molecular and combined analyses, the discussion will be based exclusively on the results from the molecular and combined analyses.
### Combined analyses

These analyses were based on a matrix of 49 OTUs, including 36 species of *Orthaea* s.l. (50% of them represented exclusively by morphological data) and 12 additional Vaccinieae from other genera (all represented by both molecular and morphological data).

Heuristic search using an equally weighted matrix resulted in a single MPT (L: 1000.535, Fig. 2.10), which was retrieved in 274 out of 10000 search replicates. Each analysis under implied weights also found a single tree (Table 2.9) and they were not affected by the concavity values employed.

Taken altogether, implied weighting analyses retrieved the same optimal topology, differing only from the results of the equally weighted analysis in the position of *Notopora schomburgkii* (Fig. 2.10). The discussion will be based on the equally weighted optimal topology.

Only some basal nodes were strongly supported (Fig. 2.10): Extra-neotropical clade (92%), Andean clade (95%), *Thibaudia* p.p. (99%), *Cavendishia + Orthaea* p.p. clade

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### Table 2.8: Summary parameters of morphological dataset analyses.

<table>
<thead>
<tr>
<th>Morphology weights</th>
<th>Concavity constant</th>
<th>MP tree score</th>
<th>MP tree hits</th>
<th>MP topologies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-</td>
<td>430.102</td>
<td>562</td>
<td>1</td>
</tr>
<tr>
<td>Implied</td>
<td>3</td>
<td>12.4583</td>
<td>647</td>
<td>1</td>
</tr>
<tr>
<td>Implied</td>
<td>10</td>
<td>11.71904</td>
<td>1121</td>
<td>4</td>
</tr>
<tr>
<td>Implied</td>
<td>30</td>
<td>7.11829</td>
<td>389</td>
<td>4</td>
</tr>
<tr>
<td>Implied</td>
<td>100</td>
<td>2.81377</td>
<td>369</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 2.9: Summary parameters of combined dataset analyses

(95%), and Notopora + Orthaea from the Guiana Shield (92%). These clades were also highly supported in the molecular analyses.

In the combined analyses (both equal and implied weights) Orthaea s.l. is consistently resolved in five well supported clades (Fig. 2.10):

1. Guiana Shield clade (Notopora schomburgkii + Orthaea p.p.).

   This clade is supported by the inflorescence rachis length (0 mm, Fig. 2.11), the inflorescence type (fascicle or solitary flowers, Fig. 2.18), and the stamen disintegration tissue (present, Fig. 2.18).

2. Empedoclesia clade (Orthaea brachysiphon + O. stipitata).

   This clade is supported by the inflorescence rachis length (20–33 cm, Fig. 2.11), calyx length (8–10.5 mm, Fig. 2.12), calyx lobes length (1.7–3 mm, Fig. 2.13), the corolla length (21–30 mm, Fig. 2.14), corolla: short stamens length ratio (0.23–0.31, Fig. 2.15), corolla: long stamens length ratio (0.25–0.35, Fig. 2.16), corolla: anthers length ratio (0.13–0.24, Fig. 2.17), glandular hairs on the prophyll margin (present, Fig. 2.18), dehiscence orientation of the outer staminal cycle (terminal, Fig. 2.18), and by having the theca longer than the tubules (Fig. 2.18).
3. *Thibaudia* p.p. clade (*Orthaea madidiensis* + *Satyria polyantha* + *Thibaudia densiflora*).

Synapomorphies of this clade are the prophylls aestivation (valvate, Fig. 2.18), staminal filaments fusion (connate, Fig. 2.18), indumentum of the filaments (absent, Fig. 2.18), and anther: corolla length ratio (0.44–0.59, Fig. 2.17).

4. *Lysiclesia* clade (*Orthaea caudata* + *O. minor* + *O. panamensis*).

Synapomorphies for this clade include the axillary buds shape (complanate, Fig. 2.18), prophylls aestivation (imbricate, Fig. 2.18), prophylls apex (acute, Fig. 2.18), glandular hairs on prophylls margin (absent, Fig. 2.18), glandular hairs on rachis (present, Fig. 2.18), calyx merosity (3-merous, Fig. 2.18), calyx limb appearance and thickness (membranose, Fig. 2.18), calyx length (23–47 mm, Fig. 2.12), and calyx lobes length (18–37 mm, Fig. 2.13).

5. *Cavendishia* p.p. (*C. grandifolia* + *C. isernii* + *C. micayensis* + *C. quereme* + *C. tarapotana*).

This clade is supported by the short stamens: corolla length ratio (0.45–0.91, Fig. 2.15), long stamens: corolla length ratio (0.51–0.91, Fig. 2.16), anther: corolla length ratio (0.51–1, Fig. 2.17), and theca: tubule relative length (theca smaller than the tubule, Fig. 2.18).

In addition to these clades common to all different results from the combined analyses, eight species of *Orthaea* s.l. were resolved in different positions along the heterandrous clade. Three of them form a grade at the most basal nodes of the heterandrous clade (*O.*
breviflora, O. constans, and O. coriacea), four form a clade closely related to Lysiclesia and Cavendishia p.p. (O. bullata, O. cordata, O. fimbriata, and O. rusby), and O. cavendishiodes is sister to Cavendishia p.p. Support values for these relationships were weak, nevertheless (20–60%, Fig. 2.10).
Figure 2.5: Single most parsimonious tree from the morphological analysis, all characters equally weighted. Jackknife values below nodes.
Figure 2.6: Single most parsimonious tree from the morphological analysis under implied weights, k=3. Jackknife values below nodes.
Figure 2.7: Strict consensus of MP trees from the morphological analysis under implied weights, k=10. Jackknife values below nodes.
Figure 2.8: Strict consensus of MP trees from the morphological analysis under implied weights, k=30. Jackknife values below nodes.
Figure 2.9: Single most parsimonious tree from the morphological analysis under implied weights, k=100. Jackknife values below nodes.
Figure 2.10: Most parsimonious tree from the combined analyses, all characters equally weighted. Jackknife values above nodes. Dashed red line shows the alternative position of Notopora schomburgkii when implied weights are used for all morphological characters. A: Extra-neotropical clade. B: Andean clade. C: Cavendishia + Orthaea p.p. clade.
Figure 2.11: Optimization character 0: Inflorescence main axis length during flower anthesis. Values given as z-scores.
Figure 2.12: Optimization character 1: Calyx length. Values given as z-scores.
Figure 2.13: Optimization character 2: Calyx lobes length. Values given as z-scores.
Figure 2.14: Optimization character 3: Corolla length. Values given as z-scores.
FIGURE 2.15: Optimization character 5: Small stamens cycle: corolla length ratio. Values given as z-scores.
Figure 2.16: Optimization character 6: Long stamens cycle: corolla length ratio. Values given as z-scores.
Figure 2.17. Optimization character 8: Anther: corolla length ratio. Values given as z-scores.


2.4 Discussion

2.4.1 Molecular partition incongruence

Signal incongruence among the different partitions is an important concern in phylogenetic inference. Although alternative ways to deal with it have been proposed, there is not a unified approach (Leigh et al. 2011; Planet 2006). The method here followed simply tests a fundamental assumption of partitioned phylogenetic analyses: Does signal among partitions differ enough to consider their incongruent outcome an issue? Results from the AU- and SOWH-tests suggested that the incongruence among the partitions here analyzed is not statistically significant; most likely differences are due to insufficient phylogenetic signal.

Studying the relationships of recently evolved and closely related taxa is a difficult task. This type of datasets usually contains few phylogenetic informative sites, producing results with high levels of uncertainty. There are only two previous studies on neotropical Vaccinieae of similar taxonomical scope: the phylogenetic relations of Disterigma (Klotzsch) Nied. s.l. (Pedraza-Penalosa 2009, 2010a) and Satyria s.l. (Powell and Kron 2003). Such analyses are also characterized by low support values at the most internal nodes. In the Satyria s.l. dataset only 4 out of 8 nodes of the targeted clade had bootstrap support values higher than 80%. In the Disterigma s.l. dataset it was even less supported: only 3 out of 31 possible nodes were strongly supported (> 80% jackknife
Figure 2.18: Deltran optimization of selected discrete characters. Numbers below state transformations (black circles) are character numbers, numbers above are states. See appendix D for character and state names.
value). Therefore the lack of informative datasets for species-level phylogenetics of Vaccinieae has been a permanent issue, and a solution does not seem to come from commonly used molecular markers. Even though the support of most of the internal nodes is weak (Fig. 2.1), some basal clades of the concatenated tree were certainly well supported, such as the Heteroandrous, *Thibaudia* p.p., and the Guiana Shield + East Malesian clades (Fig. 2.1). Furthermore, as the topological test showed, some phylogenetic hypotheses are statistically rejected (Table 2.7).

The following are the major groups in which *Orthaea* s.l. was split:

### 2.4.2 *Orthaea* s.s.

The combined analyses retrieved *Orthaea secundiflora*, the type species of the genus, within a clade exclusively composed of Andean species of *Orthaea*. The use of different weighting schemes in the combined analyses did not influence either the composition or structure of the clade. Despite its topological stability, the support was not high and no morphological synapomorphies were uncovered.

Nonetheless, a new circumscription of *Orthaea* s.s. can be outlined using the following combination of characters: inflorescence rachis without eglandular hairs, 5-merous calyx without eglandular hairs, bistratose corolla longer than 16 mm, and stamens of two different lengths in which the anthers are of similar length but the filaments are unequal. If the corolla is shorter than 16 mm then the inflorescence is paniculate or the stamens
from the long cycle latrorsely dehiscent, with the pores facing the pore of the adjacent long stamen.

2.4.3 *Orthaea* from the Guiana Shield

Both molecular and morphological data strongly support the exclusion of the Guiana Shield species from *Orthaea* s.s. Support values (Figs. 2.2 and 2.10) and topological tests (Table 2.7) both agree that their relationships are outside the neotropical clade and that they should be transferred out of *Orthaea*. These results agree with Kron et al. (2002b), who found similar topologies, although based exclusively on molecular data and a smaller taxon sampling of *Orthaea* s.l.

The Guiana Shield clade of *Orthaea* forms a cohesive group because of its particular morphology and biogeographic distribution. Most of these species are endemic to a single mountain (“tepui”), and although they reach mid elevations (up to 2200 m), they usually grow in savannas or caatingas (low forests with open understory on white sand soil, < 1000 m), contrasting this way with the cool and humid forests where *Orthaea* s.s. thrive in the Andes.

The morphology of the Guiana Shield clade is also peculiar and distinct from *Orthaea* s.s. The species of *Orthaea* s.s. have racemose inflorescences with a well developed main axis (an exception are some populations of *Orthaea glandulifera* Luteyn). All members of the Guiana Shield clade do not develop inflorescence axis, instead they have either fasciculate inflorescences or solitary flowers. This two characters describing inflorescence architecture
(rachis length during flower anthesis and dominant inflorescence type) were recovered as synapomorphies for this clade. The presence of disintegration tissue is perhaps the most distinctive character of the Guiana Shield clade. No other Vaccinieae from the neotropical clade has it, thus it is an uncontradicted synapomorphy for the Guiana Shield clade. The nature and function of this powdery tissue are unknown, but it stands as a useful taxonomic and phylogenetic character.

Although it was not recovered as a synapomorphy, the presence of glandular tissue on vegetative organs is a useful character to distinguish the Guiana Shield clade from *Orthaea* s.s. Nectaries and glands are rarely reported in Vaccinieae, and only recently, through an anatomical and morphological survey of Vaccinieae leaves, the frequency and diverse nature of this character was revealed (Pedraza-Penalosa et al. 2013). Furthermore, the gland morphology is also different between the Guiana Shield and the Andean clade. Guiana Shield taxa tend to develop glands of irregular shape in the base of the lamina, whereas Andean species usually have circular glands on the adaxial side of the leaf.

Hooker (1876) described the first species of *Orthaea* from the Guiana Shield in the genus *Findlaya*, based on the morphological differences indicated above (fasciculate inflorescences or solitary flowers, presence of disintegration tissue). However, the lack of distinctive staminal characters later encouraged Smith (1932) to merge both genera. Smith’s point of view is not validated by the results here presented. The six species of *Orthaea* endemic to the Guiana Shield clearly have a different origin from *Orthaea* s.s., and it is recommended to either transfer them to *Notopora* or to describe a new genus to classify them (*Findlaya* Hook. f. is not available as a generic name because it is a later homonym
of *Findlaya* S. Bowdich, Primulaceae). However, before a new taxon is erected, more studies are still necessary as other Vaccinieae from the Guiana Shield need to be sampled, including additional species of *Notopora*.

### 2.4.4 *Empedoclesia* clade

The members of *Orthaea* s.l. currently classified in the subgenus *Empedoclesia* (*O. brachysiphon* (Sleumer) Luteyn and *O. stipitata*) form a distinctive clade of extra-neotropical origin (99% jackniffe, Fig. 2.10), that is well supported by the combined dataset. *Empedoclesia* is geographically isolated from *Orthaea* s.s., being restricted to southern Mexico, Guatemala, Belize, and Honduras. In contrast, *Orthaea* s.s. can only be found south of Costa Rica.

Several apomorphies supporting this clade are continuous characters, however only rachis length and tubule:theca length proportion do not have reversions. Therefore, *Empedoclesia* can be circumscribed based on the rachises at least 20 cm long and tubules conspicuously smaller than thecae, whereas in the other lineages of *Orthaea* s.l. rachises are up to 8 cm long at most (the only exception is *O. cordata*, with 13–25 cm long rachises) and tubules are almost as long as the theca. This unusual morphology of *Empedoclesia* was first noted by Sleumer (1934), who considered that *Empedoclesia* was related to *Dispterigma* because both have bracteoles subtending the calyx. He also conceived affinities between *Empedoclesia* and *Macleania* Hook., as both have tubules shorter than the thecae (Sleumer 1934). Results of this study did not support the viewpoint of Sleumer (1934)
and pointed at *Vaccinium crenatum* as the closest sampled relative of *Empedoclesia*. This relationship was also supported by the topological tests (Table 2.7), which rejected their membership to *Orthaea* s.s.

Although the type species of *Empedoclesia* (*E. brachysiphon* = *O. brachysiphon*) was not sampled for molecular analyses, it was coded for morphology in the combined dataset and resolved as sister to *O. stititata* (99% jackknife, Fig. 2.10). Therefore, the reinstatement of *Empedoclesia* seems necessary and justified. As binomials for both species of *Empedoclesia* are already available, no new combinations are necessary.

### 2.4.5 *Orthaea madidiensis*

According to the molecular and combined analyses, the relationships of *Orthaea madidiensis* lay within the *Thibaudia* p.p. clade [100% bootstrap, 98% jackknife (molecular), 99% jackknife (combined), 1 posterior probability Figs. 2.3 and 2.10]. Combined analyses uncovered several synapomorphies supporting this clade, including the aestivation of prophylls (valvate), the anther: corolla length ratio (0.44–0.65), the indumentum of the staminal filaments (glabrous), and the filaments fusion (connate). Thus, this taxon is segregated from *Orthaea* s.s.

Although the *Thibaudia* p.p. clade has been recovered consistently in previous phylogenetic analyses of Vaccinieae (*Pedraza-Peña 2009*; *Powell and Kron 2003*), its taxonomical extent and morphological boundaries have not been established yet. Besides containing several species of *Thibaudia*, this clade also gathers some elements from other
genera, such as *Satyria* and *Semiramusia* Klotzsch, and the monotypic *Polyclita* A. C. Sm. (Powell and Kron 2003; Pedraza-Penalosa 2009).

### 2.4.6 Heteroandrous clade

The classification of the Vaccinieae have been mostly based upon staminal characters, encouraging systematists to associate *Cavendishia*, *Orthaea* and *Satyria* because of their dimorphic stamens (Smith 1932; Luteyn 1983). Preliminary molecular phylogenies of the Vaccinieae found that heterandrous Vaccinieae were indeed closely related (Kron et al. 2002b; Powell and Kron 2003). In this study, the sampling of these taxa was expanded, specially for *Orthaea* s.l., the least represented genus.

All the sampled *Cavendishia*, *Orthaea* and *Satyria* of Andean origin and with dimorphic stamens clustered in a well supported major clade, the heteroandrous clade. This clade is divided in two major subclades (Fig. 2.4), *Satyria* s.s. (100% bootstrap, 100% jackknife, 1 posterior probability) and *Cavendishia* + *Orthaea* p.p. (98% bootstrap, 97% jackknife, 1 posterior probability). Relationships within *Satyria* s.s. (Fig. 2.4) were not totally congruent with previous reports, despite that the sampling represented the main lineages reported by Powell and Kron (2003). This issue was one of the subjects of a recent study (Pedraza-Penalosa et al. 2014) and their findings are not going to be repeated here.

The *Cavendishia* + *Orthaea* p.p. clade was strongly supported in molecular and combined analyses, but most of the internal nodes were otherwise (Figs. 2.4 and 2.10). Branches in that section of the molecular tree are very short and their support values low. Although
the topological tests rejected several alternative circumscriptions of Orthaea (Table 2.7),
relationships among O. cordata, O. bullata, and Orthaea s.s. remain uncertain. As men-
tioned above, this is likely due to the uncertainty associated to phylogenetic inference
based on the selected markers. Therefore, future approaches should commit a consid-
erable effort in the implementation of more informative markers that could uncover the
relationships of Cavendishia, Orthaea s.s., and related taxa.

The Cavendishia + Orthaea p.p. was also well supported in the combined analyses (94%
jackknife), but this was due mostly to the contribution from the molecular data (16 out
of 20 synapomorphies were molecular). Morphological synapomorphies were exclusively
characters of the inflorescence, such as rachis length and duration of bracts and bracteoles
(early caducous), that are variable and have several instances of reversions in this clade.
Thus, despite that the Cavendishia + Orthaea p.p. clade was strongly supported, no
morphological characters were uncovered to produce a stable morphological delimitation.

2.4.7 Lysiclesia clade

Both molecular and combined analyses corroborated the monophyly of former genus Lysiclesia, with solid support values in every case [100% bootstrap, 100% jackknife (molec-
ular), 98% jackknife (combined), 1 posterior probability, Figs. 2.4 and 2.10]. Combined
analyses revealed several synapomorphies for the former genus Lysiclesia, including a 3-
merous calyx with long and membranose lobes, characters that historically have played
an important role in the classification of this group and set apart Lysiclesia from other
Vaccinieae, as most Vaccinieae have 4- or 5-merous calyces with small and coriaceous lobes (Smith 1932; Luteyn and Wilbur 1977). Calyx morphology apart, the rest of the floral characters are similar to those of Orthaea s.l., and this was the argument used by Luteyn (1987) to synonymize Lysiclesia with Orthaea.

The sister group of Lysiclesia clade is still uncertain; molecular and combined analyses retrieved different sister clades for Lysiclesia and support of those relationships was low (Figs. 2.4, 2.10). Nonetheless, topological tests of the molecular dataset supported its exclusion from Orthaea s.s. (Table 2.7).

2.4.8  *Insertae sedis*

The relationships of the remaining eight species of Orthaea s.l. (*O. breviflora*, *O. bullata*, *O. cavendishioides*, *O. constans*, *O. cordata*, *O. coriacea*, *O. fimbriata*, and *O. rusby*) are still uncertain. Although the support of their relationships is weak (< 58%), they are all resolved outside Orthaea s.s. and consequently they all are excluded from such clade. However, before any taxonomic combinations could be proposed for these taxa, their relationships need to be further assessed with additional data.

2.4.9  Conclusions

Although phylogenetic analyses uncovered the extent of polyphyletic nature of Orthaea and revealed the evolutionary affinities of its members, its relationships with Cavendishia
remain unclear. Species of *Orthaea* endemic to the Guiana Shield, along with former genus *Empedoclesia*, are closely related to extra neotropical Vaccinieae, and it is suggested here to segregate them from *Orthaea* s.s. *Orthaea madidiensis* belongs to *Thibaudia* p.p. clade, and should not be classified in *Orthaea* s.s. as well. The former genus *Lysiclesia* was recovered as a monophyletic clade, however its sister group could not be uncovered precluding its reinstatement. Eight additional species of *Orthaea* should be segregated from *Orthaea* s.s. too (*O. breviflora*, *O. bullata*, *O. cavendishioides*, *O. constans*, *O. cordata*, *O. coriacea*, *O. fimbriata*, and *O. rusby*), however their exact affinities to other heteroandrous taxa remain uncertain. Finally, although phylogenetic analyses and topological test helped to set a new circumscription of *Orthaea* s.s., support values were weak and the sister group relationships are not definitely known yet.
Chapter 3

Taxonomic revision of *Orthaea* s.s. Klotzsch (Vaccinieae: Ericaceae).

3.1 Introduction

Updated taxonomic revisions of the neotropical Vaccinieae account for less than an estimated 25% of the total neotropical Vaccinieae (Luteyn 1983, 1991; Luteyn and Ortiz 2008; Pedraza-Peñaíosa 2010b). In order to alleviate this situation and provide updated taxonomic reference for poorly studied neotropical Vaccinieae, a taxonomic revision of *Orthaea* s.s Klotzsch was carried out. This monograph is part of a broader systematic assessment of the group that involves a phylogenetic study of *Orthaea* s.l.
Orthaea s.s. was circumscribed according to a phylogenetic analyses of both molecular and morphological data (see Phylogenetics). In such analyses, Orthaea s.s. was defined as the largest clade exclusive of Orthaea species (15 spp as total). Besides the type species, O. secundiflora (Poepp. & Endl.) Klotzsch, Orthaea s.s also includes O. abbreviata Drake, O. boliviensis Fedtsch. & Basil., O. carnosiflora N. R. Salinas & Pedraza, O. ecuadorensis Luteyn, O. eteocles N. R. Salinas, O. ferreyrae A. C. Sm., O. fissiflora N. R. Salinas & Pedraza, O. glandulifera Luteyn, O. medusula Pedraza, O. oriens Luteyn, O. paniculata Luteyn, O. peregrina A. C. Sm., O. pinnatinervia Mansf., and O. weberbauerii Hoerold. That circumscription of Orthaea s.s. is here adopted, and species of Orthaea s.l. not listed above are not covered in this treatment (see Exclude taxa). Two new species are here described (O. eteocles and O. fissiflora), whereas one is proposed as a new synonym (O. oedipus, under O. glandulifera).

As no synopomorphies were found in the combined analysis (based on morphological and molecular data), Orthaea s.s. can only be identified by a combination of several characters: they all have inflorescence rachis without eglandular hairs, calyx 5-merous without eglandular hairs, dimorphic stamens, dimorphic filaments, isomorphic anthers, and corolla bistratose longer than 16 mm. If corolla is shorter than 16 mm then the inflorescence is paniculate or the stamens from the long cycle latrorsely dehiscent, with the pores facing the pore of the adjacent long stamen.

Specimens from the herbaria AAU, BM, CAS, COL, CUVC, E, F, G, GB, HUA, JAUM, K, L, MO, NY, LOJA, LPB, P, QCA, QCNE, U, UC, US, and W where examined. Additional collections were procured through fieldwork in Colombia and Ecuador. A
total of 301 collections of *Orthaea* s.s. were examined during this monographic work. Specimen and morphological data was manipulated through a MySQL database, and accessed through custom Perl-DBI scripts.

Species were delimited according a Population Aggregation Analysis (Davis and Nixon 1992), a method that implements the phylogenetic species concept (Nelson and Platnick 1981; Nixon and Wheeler 1990). This analysis were carried out using the Perl script PPA.pl (Little 2014).

### 3.2 Phylogenetics

Phylogenetic analyses have shown that *Orthaea* s.l., as delimited by Luteyn (1987), is not a monophyletic group, with members nested in various clades of Vaccinieae of neotropical and extra-neotropical origin [as defined by Kron et al. (2002b)]. Species of *Orthaea* s.l. from the Guiana Shield, along with those previously classified in the genus *Empedoclesia*, are of extra-neotropical origin, that is, they are more closely related to Asian lineages of Vaccinieae than to their neotropical counterparts (Figs. 3.1 & 3.2). The rest of the species of *Orthaea* s.l. are nested in several nodes within the Andean Clade. Most of the Andean species of *Orthaea* s.l. are closely related to *Cavendishia*. An important exception is *Orthaea madidiensis* Pedraza & Luteyn, which is more related to some species of *Thibaudia* and *Satyria* from southern Peru and Bolivia. Relationships between *Cavendishia* and the rest of Andean species of *Orthaea* are well supported, however resolution within this clade is very weak still.
Figure 3.1: Best tree of the Vaccinieae from a Maximum Likelihood analysis based on ITS, *matK*, and *ndhF* data (116 OTUs). *Orthaea* s.l. highlighted in red.
The delimitation of *Orthaea* s.s. here adopted is based on the results from a total evidence analysis including morphological and molecular data. In this analysis *O. secundiflora*, the type species, was recovered within a clade along with other 14 species of *Orthaea*, and this group is informally recognized as *Orthaea* s.s. Although it is acknowledged support for this clade is weak, this analysis represent the most complete effort to solve the phylogeny of this group. It is recommended to undertake a broader phylogenetic assessment of this group, including more molecular data from both *Cavendishia* and *Orthaea* s.l., in order to corroborated the delimitation here presented.

### 3.3 Nomenclatural and taxonomical history

Klotzsch (1851) described *Orthaea* in his taxonomic revision of the class Bicornes, based on its bilocular anthers, connate and unequal staminal filaments, and campanulate calyx. Its single species, *O. secundiflora* (Poepp. & Endl.) Klotzsch, was originally described as *Thibaudia secundiflora* Poepp. & Endl., based on a Peruvian collection (Poeppig and Endlicher 1835).

The genus was named after a minor and poorly known character from Greek mythology. *Orthaea*, along with her sisters Antheis, Aegleis, and Lytaea, are known as the Hyacinthides, daughters of Hyacinth of Athens. They were sacrificed in order to redeem Athens from a massive famine and pest, at the prelude of the war against Minos (Apollodorus 1921). As it will be explained below, Klotzsch introduced a spelling (Orthaca) that did not correspond to any of the known Romanizations of Orthaea.
Only a few Greek mythology studies mention Orthaea or any of the other Hyacinthides.

The Library of Apollodorus, originally published in the 16th century, is one of the first to document this myth (Apollodorus 1921, par. 3.15.8). Classical transliteration of Apollodorus’ spelling (‘Ορθαῖα) is Orthaean, but contemporary translations of his work have employed romanizations such as Orthaea or Orthaeam (Apollodorus 1921; Müller and
Müller 1841). Phanodemus, another ancient Greek chronicler, documented this mythological character as well (Müller and Müller 1841). Nonetheless, the Greek spelling used by Phanodemus is very different, ‘Ὀρείθυια, or Oreithnia in classical romanization. The Latin spelling that survived in modern translations was also different: Orithyia (Müller and Müller 1841). There are no other significant mention of Orthaea in antique mythography.

It is impossible to know the reasons behind Klotzsch’s preference of Orthaca over Orthaea, Orthaeam, or Oreithnia. It could even have been a typographic error. Nevertheless, there has been a consensus on the inadequacy of his spelling, and since Hooker (1876), botanists had unambiguously reckoned Orthaea the correct name of the genus.

Orthaea remained unnoticed for 25 years until Hooker’s treatment of Vaccinieae for Genera Plantarum (Hooker 1876). Therein, Hooker proposed Findlaya Hook. f. as a new genus morphologically close to Orthaea. They were differentiated by the truncate calyx and 1–2-flowered inflorescences of Findlaya, which contrasted with the lobed calyx and secund racemes of Orthaea. Although Hooker did not add more species to Orthaea, he mentioned Orthaea as having distinct filaments, contradicting the concept previously proposed by Klotzsch (1851).

Fifteen years later, Drude classified Orthaea as a subgenus of Thibaudia Ruiz & Pav. ex J. St.-Hil., but mantained Findlaya as a genus (Drude 1891). Shortly after Baillon (1892) reinstated Orthaea, although apparently still with reservations, as evidenced by a question mark placed next to the name. He also accepted Findlaya, and differentiated it
from *Orthaea* because of its obscure leaf venation, truncate calyx, and oblique staminal pores.

Hoerold (1909) considered *Orthaea* and *Findlaya* as well delimited but not closely related genera. His diagnosis of *Orthaea* has hitherto prevailed: ten alternately unequal stamens, differing only in the length of the filaments. On the other hand, *Findlaya* was recognized by controversial characters: 15 stamens in three cycles, with the inner cycle modified into a long staminal tube with rudimentary, sterile anthers. This diagnosis was very remarkable, as most of neotropical Vaccinieae have 5–10 stamens, all of them completely functional.

Smith (1932) revised *Orthaea* as part of his monograph of the American Thibaudieae, probably the most comprehensive contribution of its time to the systematics of this group. Smith proposed important taxonomical changes by synonymizing *Findlaya* and *Orthaea*. He also described *Lysiclesia* A. C. Sm. to group two species from north-western Colombia with *Orthaea*-like stamens (dimorphic filaments and isomorphic anthers), but with 3-merous calyx of large and membranose lobes. In his treatment, Smith recognized 11 species of *Orthaea* and 2 of *Lysiclesia*.

Not long after, Sleumer (1934) described *Empedoclesia* Sleumer, yet another genus with strong taxonomic affinities to *Orthaea*, native from Guatemala. Despite the staminal similarities, Sleumer suggested *Empedoclesia* was more related to *Macleania* because of its also reduced anther tubules (Sleumer 1934).
During the next 45 years, 14 new species of *Empedoclesia*, *Lysiclesia*, and *Orthaea* were published. However the relationships between these genera remained unaddressed and no other attempts the revise *Orthaea* were made. Thus, the badly outdated revision of Smith (1932) as the most comprehensive taxonomic reference, including only 13 of of the 34 currently accepted species of *Orthaea* s.l. This situation motivated the publication of a generic synopsis (Luteyn 1987), in which both *Empedoclesia* and *Lysiclesia* were synonymized under *Orthaea*. These changes were meant to solve the taxonomic ambiguities originated by the increasing morphological variability introduce in these genera (Luteyn 1987).

### 3.4 Morphology

**Habit.** Most of the collections of *Orthaea* s.s. are shrubs, although some collectors have reported them as trees (*O. ecuadorensis*). Their size varies greatly, between 0.3 m and 3–4 m tall. Species of *Orthaea* s.s. can be either epiphytic or terrestrial, a condition that seems to be dependant upon the environmental moisture: terrestrial plants are mostly collected in open, often disturbed areas, whereas epiphytic individuals usually grow in the understory of cloud forests. Mature branches are usually erect, glabrous, and without exfoliating rhytidome.

**Indument.** Hairs of *Orthaea* s.s. can cover vegetative organs, such as the leaf, petiole, and young stems; or reproductive structures, such as the inflorescence axis, bract,
bracteole, pedicel, calyx, corolla, staminal filament or anther.

Hairs are either glandular or eglandular. Eglandular hairs are unicellular and derived from the outer layer of epidermal cells. If looked through a microscope, they seem clear, almost translucent. Glandular hairs are multicellular, they originate underneath the epidermis and generally become dark with age. Glandular hairs are made of depressed cells, arranged in a single row. The main deviation to this pattern are the glandular hairs on the abaxial side of the corollas of *Orthaea medusula* and *O. peregrina*. In this species, glandular hairs comprise a globose tip and a thin stalk made of elongated cells arranged in multiple rows. Through most of the taxonomic literature of the Vaccinieae, glandular hairs have been called “fimbria” (e.g., Luteyn 1983, 1996a). Glandular indument is typically appressed, although in some species it is raised. Eglandular indument is usually pubescent or puberulent.

**Prophylls.** Axillary buds of *Orthaea* s.s. are globose or complanate in shape. They are subtended by a short stalk up to a couple of millimeters long and enclosed by a couple of opposing prophylls. Prophylls are ovate and of variable apical shape; their margin is usually entire and ciliate. Prophylls aestivation is either valvate or imbricate. Sometimes prophylls can have a carina on the abaxial surface.

**Leaves.** Leaves of *Orthaea* s.s. are simple and alternate, although sometimes internodes can be reduced to less than 5 mm—some specimens of *O. fissiflora* even have opposite leaves. Petioles are terete, semiterete, or canaliculate, and frequently glabrous. When
young, petioles are smooth, but as they age their surface becomes coarse and rugose. Foliar lamina is elliptic or ovate, cuneate to rounded at base and acute to acuminate at apex; the margin is entire and usually revolute in herbarium material.

Venation is usually acrodromous, with one or two lateral veins that intersect the midvein at the base or a couple of millimeters above (suprabasal). Secondary venation comprises one to five lateral veins per side, in a camptodromous or brochidodromous framework. Primary and secondary venation is impressed on the adaxial surface, but raised on the adaxial one. Occasionally, some Orthaea s.s. can have pinnate venation (e.g., Orthaea pinnatinervia).

**Inflorescence.** All Orthaea s.s. have racemose inflorescences, with the exceptions of some populations of *O. abbreviata* that have fascicles and others of *O. glandulifera* that bear solitary flowers. Inflorescences are single and mostly simple, either axillary or terminal. The main axis of the inflorescence is usually divided in two sections: the peduncle and the rachis. The peduncle is the proximal portion devoid of flowers, the rachis is the terminal section that bear the flowers. Although this definition is widely used in Angiosperm terminology, students of Ericaceae have used it inconsistently. In this treatment, descriptions will follow the standard concepts. In Orthaea s.s., the main axis can be strongly reduced (0.3 cm) or elongated up to 11 cm. Only *O. etecoles, O. medusula,* and *O. paniculata* have branched inflorescences, bearing 1–4 branches at the base of the rachis. Flowers are spirally arranged along the rachis; however, many species have the pedicels bent, becoming secund.
Bracts and bracteoles. Species of Orthaea s.s. have several inflorescence bracts spirally attached to the base of the inflorescence. They are usually small (< 3 mm long), ovate, apically acute to acuminate. In some species they persist throughout flower anthesis (e.g., O. abbreviata and O. secundiflora), but they are caducous in most of the species.

Each pedicel is subtended by a single floral bract. Some species have floral bracts which morphology is homogeneous along the rachis, but in others this is not the case. When the floral bracts are homogeneous, all the floral bracts are alike and similar to the inflorescence bracts. If they are heterogeneous, floral bracts in the apex of the rachis are larger and thinner than the bracts at the base of the rachis, and with their apex is obtuse or rounded (e.g., O. abbreviata). Floral bracts usually have entire or ciliate margin. Pedicels bear two bracteoles either attached to its base or close to the middle. They are ovate or lanceolate, apically acute, and marginally ciliate. These structures are morphologically homogeneous in Orthaea s.s. and only the presence of marginal hairs is of taxonomic importance. Bracteoles usually have ciliate margin.

Flower. Flowers of Orthaea s.s. are and 5-merous and actinomorphic.

Calyx. Species of Orthaea s.s. have synsepalous calyx of valvate aestivation. General calyx morphology of neotropical Vaccinieae has already described several times by previous students of the family (e.g., Luteyn 1983; Pedraza-Penaloza 2010b; Smith 1932). That specific terminology is followed here as well. The calyx is articulate with the pedicel.
In some species, this junction can stretch upon drying, exposing the inner tissue. If this is the case, the calyx is considered to be stipitate. The general shape is frequently cylindric, but obconic, campanulate, cupuliform and globose calyces also occur. The calyx tube is usually terete in cross-section, although some times can be angulate. The base of the calyx is rounded, truncate, or apophysiate. Basal apophysis can be either parallel or perpendicular to the pedicel, with entire or ridged margin. Limb texture varie from membranaceous to coriaceous, flaring or adpressed to the corolla (i.e., straight). Calyx lobes are ovate to deltoid and the apex acute to obtuse. Calyx sinuses are U-shaped or V-shaped. Several species develop glandular tissue along lobes margins in the form of a thin marginal gland or clumps of glandular hairs.

**Corolla.** Petals of *Orthaea* s.s. are fused into a cylindric or urceolate corolla tube. Corolla is fleshy, actinomorphic, terete, usually red or pink with white apex, and 7.5–39 mm long. It always have five petals, which are deltoid or ovate with acute apex. The aestivation is frequently valvate, occasionally quincunx. Both sides of the corolla are usually glabrous; however, a group of species from western Colombia and Ecuador (*O. eteocles, O. glandulifera, O. medusula, and O. peregrina*) are characterized by the glandular hairs on the the abaxial side. In some species from Bolivia and Peru (e.g., *O. fissiflora* and *O. weberbauerii*), the corolla has the tendency to split longitudinally after anthesis, and exposing the stamens.
**Androecium.** Flowers of *Orthaea* s.s. bear 10 stamens (only a handful individuals of *O. secundiflora* had 11). As compared to other Vaccinieae, they are short—smaller than half the size of the corolla length. All species of *Orthaea* s.s. have dimorphic stamens as they are arranged in two alternate cycles of different lengths. The stamen dimorphism is determined by the filament length difference between stamen cycles. Anthers, on the other hand, usually have all the same length. Sometimes anthers from different cycles differ in the orientation of the tubule (long stamens have divergent tubules, short stamens have parallel tubules) or pores (e.g., long stamens are latrorskely dehiscent, short stamens are introrskely dehiscent). Filaments can be distinct or fused into a short tube. Some specimens of *O. ferreyrae* have flowers with filaments fused in pairs, that is, a pair of contiguous long and short filaments have the margins in between fused, whereas they are free from the other neighbour stamens. Filaments are white *in vivo*, laminar, and oblong or triangular in outline. Filaments have eglandular hairs distally on both the margin and lamina. Anthers are dorsally attached to the filaments and do not have spurs or any other appendages besides the tubules. Thecae are papillate and sometimes prognathous (e.g., *O. secundiflora*) or with unicellular and eglandular hairs at the basal tip (e.g., *O. carnosiflora* and *O. ferreyrae*). Tubules are usually as long as thecae and somewhat thinner; their apical pores can be intorse, extrorse, latrorse, or perfectly terminal—acroscopic. Not always stamens within a single flower have the same pore orientation, it can vary among stamens cycles (e.g., *O weberbauerii* has intorskely dehiscent short stamens and latrorskely dehiscent long stamens).
**Gynoecium.** The ovary of the species of *Orthaea* s.s. is inferior, with five carpels arranged in five or six locules of axile placentation. There are several ovules per locule, usually between 30 and 50. A flat and glabrous nectary disk is always develop at the top of the ovary. There is style unbrached and its stigma is punctiform. In general terms, the gynoecium is a very conserved structure in *Orthaea* s.s.

**Fruits and seeds.** The ovary matures into a fleshy berry, usually of dark color, purple or black. Seeds are small, ellipsoid, and alveolate. Sometimes the testa is mucilaginous. The embryo is a chlorophyllous, that is, white in living material (this character was only recorded for *O. glandulifera*).

### 3.5 Geographic distribution

*Orthaea* s.s. is restricted to the tropical Andes, from Colombia to central Bolivia (Fig. 3.3). There, they prefer montane and premontane forests (900–3300 m) that are submitted to intense precipitation, such as the western slope of the Andes in Colombia or the eastern slope in southern Peru and Bolivia. In this kind of humid forests, species of *Orthaea* s.s. are usually epyphites, whereas terrestrial plants of *Orthaea* s.s. are more frequently observed in drier environments. They usually grow in the edges of well conserved vegetation, but some species have been collected in forest remnants of pastures and cultivated fields (e.g., *O. abbreviata* and *O. oriens*).
Regarding elevation, they prefer mid elevation places (1000–3000 m), however there is a trend to grow at higher elevations in southern latitudes. In Colombia and north western Ecuador they usually grow at 1000–2000 m, but in southern Peru and Bolivia they are mostly found at 2000–3000 m. It is also noteworthy that populations north of the Equator grow in the western slope of the Andes, whereas south of it they grow in the eastern slope.

Peru is the most diverse country for *Orthaea* s.s., with seven species (three endemic), followed by Ecuador (five species, three endemic), Colombia (four species, all endemic), and Bolivia (three species, one endemic). Peruvian species are mainly distributed in the southern region of the country, in Cuzco department alone there have been collected five species.

### 3.6 Taxonomic treatment


Terrestrial or epiphytic shrubs, occasionally trees. **Mature branchlets** mostly glabrous. **Axillary** buds globose or complanate, stipitate, occasionally sessile, stalk 0.20–2.00 mm long; prophylls imbricate or valvate, usually ovate, 0.5–40.0 mm long, margin entire and ciliate, abaxial side glabrous or occasionally puberulous. **Leaves** alternate, nodes 0.10–5.50 cm long; petiole semiterete, 1.0–11.0 mm long, rugose in dried material, glabrous;
lamina coriaceous or chartaceous, elliptic or ovate, 2.60–19.00 × 0.50–7.80 cm, margin entire, revolute, eciliate, apex acuminate or acute, adaxial side usually glabrous, abaxial side glabrous or strigose; laminar glands absent; venation acrodromous or occasionally pinnate, prominent lateral veins 1–5 per side. **Inflorescence** axillary or terminal, single, usually a raceme, occasionally a panicle; axis 3.0–116.0 mm long, usually glabrous,

**Figure 3.3:** Geographic distribution of *Orthaea* s.s.
smooth in dried material, peduncle 0.5–60.0 mm long, rachis 1.0–100.0 mm long; inflorescence bracts early caducous, chartaceous, usually ovate, 1.0–25.0 × 0.2–12.0 mm, smooth, margin entire, glabrous on both sides, glandular bodies absent; floral bracts 1 per pedicel, early caducous, generally ovate or elliptic, 1.4–30.0 × 0.2–11.0 mm, smooth, margin entire, apex acute, glabrous, glandular bodies absent; pedicel stout, 5.0–48.0 mm long, sometimes apically swollen, 0.04–1.50 mm diam. at base, 0.50–6.50 mm diam. at apex, generally glabrous, articulate with the calyx; bracteoles 2, early caducous or occasionally persistent, basal in the pedicel, usually ovate, 0.70–10.80 × 0.10–3.00 mm, margin entire, multicellular or occasionally unicellular, apex acute, glabrous on both sides, glandular bodies absent. **Flower** 5-merous, diplostemonous. **Calyx** aestivation valvate, usually campanulate, 2.0–15.0 mm long, terete, glabrous; tube cylindric, 1.00–7.00 mm long, 1.50–80 mm diam.; limb chartaceous, 0.50–9.00 mm long, lobes deltoid, 0.10–5.50 × 0.20–5.40 mm, sometimes with a marginal gland, apex obtuse. **Corolla** aestivation valvate, bistratose, tubular, actinomorphic, sometimes splitting longitudinally apically at anthesis, terete, 7.5–39.0 mm long, 2.0–12.0 mm diam., 1.5–8.0 mm diam. at throat, glabrous on both sides; lobes deltoid 0.30–7.00 × 0.50–5.00 mm. **Stamens** 10, 3.90–15.50 mm long; filaments alternately unequal, distinct or connate, rarely adherent to corolla, straight, 0.80–11.00 × 0.30–1.50 mm, apically puberulous, disintegration tissue absent; anthers 2.30–7.00 mm long; thecae 1.40–4.20 mm long, 0.40–1.00 mm wide, papillate; tubules 2, distinct, parallel or divergent, 0.70–3.40 mm long, 0.40–1.00 mm diam., smooth, dehiscing by terminal pores 0.10–1.40 mm long. **Ovary** 5-locular, placentation axile; nectary disk flat, glabrous; style 8.0–51.0 mm long, exerted or included, stigma truncate. **Berry**
black, red, or white, spherical, 5.0–12.0 mm long, 5.0–13.0 mm diam., lobes ascending, glabrous, pericarp thick; seeds numerous, ellipsoidal or prismatic, occasionally fusiform, isodiametric or luniform, 0.60–1.90 × 0.30–1.00 mm, testa alveolate, sometimes with a mucilaginous coat, embryo white.

**Distribution.** *Orthaea* s.s. is a neotropical clade of 15 species ranging from northwestern Colombia (Antioquia department) to central Bolivia (Cochabamba department), along the Andean Cordillera.

### 3.6.1 Identification key to the species of *Orthaea* s.s.

All measurements are based in dehydrated herbarium specimens except when indicated otherwise (e.g., *in vivo*).

1. Inflorescence a panicle ................................................................. 2

   1′. Inflorescence a raceme, rarely a fascicle or single flowers ...................... 4

2. Calyx and corolla glabrous. Endemic to Cauca (Colombia) ........11. *O. paniculata*

   2′. Calyx and/or corolla with glandular hairs. Valle del Cauca (Colombia) and Esmeraldas (Ecuador) ................................................................. 3

3. Axillary buds globose; inflorescence with less than 25 flowers; inflorescence main axis ≥ 77.0 mm long, hirsute; pedicel ≥ 21.0 mm long; calyx basally apophysiate; corolla ≥ 34.0 mm long ...................................................... 5. *O. eteocles*
3'. Axillary buds complanate; inflorescence with more than 35 flowers; inflorescence main axis \( \leq 63.0 \) mm long, glabrous; pedicel \( \leq 15.0 \) mm long; calyx basally rounded; corolla \( \leq 8.30 \) mm long ......................................................... 9. *O. medusula*

4. Calyx and/or corolla with glandular hairs. Restricted to the western slope of the Andes, from Antioquia (Colombia) to Esmeraldas (Ecuador) .............. 5

4'. Calyx and corolla glabrous or with eglandular hairs. Restricted to the eastern slope of the Andes, from Napo (Ecuador) to Cochabamba (Bolivia). .................. 7

5. Inflorescence main axis in anthesis \( \geq 77.0 \) mm, hirsute; corolla \( \geq 34.0 \) mm long; stamens 14.00–15.50 mm long; style \( > 35.0 \) mm ......................... 5. *O. eteocles*

5'. Inflorescence axis in anthesis \( \leq 60.0 \) mm (although reaching 108 mm long when fruiting), glabrous, puberulous or scabrous; corolla \( \leq 34.0 \) mm (but up to 35.0 mm long *in vivo*); stamens 5.50–10.30 mm long; style \( < 35.0 \) mm ....................... 6

6. Calyx 4.0–6.0 mm long (6.0–7.0 mm *in vivo*), lobes without marginal glands; corolla 25.0–33.0 mm long ..................................................... 8. *O. glandulifera*

6'. Calyx 10.0–15.0 mm long (15.0–17.0 mm *in vivo*), lobes with marginal glands; corolla 14.0–20.0 mm long ..................................................... 12. *O. peregrina*

7. Pedicel 3.0–4.0 mm diam. at apex (6.5 mm *in vivo*); bracteole 2.00–3.00 mm wide; calyx stipitate upon drying, corolla lobes 3.5–7.0 mm long; anthers 5.00–7.00 mm long. ................................................................. 3. *O. carnosiflora*
7'. Pedicel 0.5–2.5 mm diam. at apex (2.20–3.50 \textit{in vivo}); bracteole 0.10–1.60 mm wide; calyx sessile upon drying; corolla lobes 0.30–2.50 mm long; anthers 2.50–4.90 mm long

8. Stamens of both cycles dehiscing by acroscopic pores (sometimes pores in the short cycle are slightly extrose) .................................................9

8'. Stamens of the long cycle dehiscing by latrorse or introrse pores, stamens of the short cycle dehiscing by introrse pores .................................................13

9. Inflorescence axis with glandular hairs ........................................10. \textit{O. oriens}

9'. Inflorescence axis with eglandular hairs or glabrous .........................10

10. Calyx lobes margin eciliate ..................................................14. \textit{O. secundiflora}

10'. Calyx lobes margin ciliate ....................................................11

11. Calyx 4.5–6.0 mm long; anthers of the long stamen cycle 4.50–4.80 mm long; stamens of the short cycle 9.3–12.0 mm long .........................4. \textit{O. ecuadorensis}

11'. Calyx 2.5–4.0 mm long; anthers of the long stamen cycle 2.80–3.80 mm long; stamens of the short cycle 4.30–8.80 mm long .................................12

12. Axillary buds globose, prophylls apically obtuse-mucronate; inflorescence bracts persistent, 10.0–18.0 mm long; floral bracts 18.0–30.0 mm long; style 37.0–51.0 mm long .................................1. \textit{O. abbreviata}

12'. Axillary buds complanate, prophylls apically acute or acuminate; inflorescence bracts
early caducous, 1.5–2.0 mm long; floral bracts 6.0–10.0 mm long; style 18.0–36.0 mm long

13. Axillary buds globose ........................................ 15. O. weberbauerii
13'. Axillary buds complanate ........................................ 14

14'. Stamens of the long cycle 6.50–8.40 mm long .................. 15

15. Primary venation always acrodromous; calyx green; corolla green at base; stamens of the long cycle 7.40–8.40 mm long, stamens of the short cycle 6.30–7.10 mm long ........

15'. Primary venation acrodromous or pinnate; calyx red; corolla red at base; stamens of the long cycle 6.50–7.00 mm long, stamens of the short cycle 4.80–5.50 mm long ........

3.6.2 Species descriptions

1. Orthaea abbreviata  Drake, J. Bot. 3: 75. 1889. Type. Ecuador. Río de San Francisco [probably sector San Francisco, Parque Nacional Podocarpus, Zamora Province; see Renner (1993); Wurdack (1979)], 5 Jan 1882 (fl), Poortmann 314 (holotype P!).

(Fig. 3.4)

Terrestrial or epiphytic shrubs 1–3 m tall. **Young branchlets** ridged, 2.0–3.0 mm diam., smooth, glabrous or occasionally puberulous, the hairs eglandular and unicellular; mature branchlets glabrous or occasionally puberulous, the hairs eglandular and unicellular, bark not exfoliating. **Axillary** buds globose, sessile or stipitate, stalk 0.30–0.80 mm long; prophylls 2, valvate, ovate, 0.60–1.10 mm long, carinate, margin entire, ciliate, the hairs glandular and multicellular, apex obtuse-mucronate, abaxial side glabrous.

**Leaves** alternate, nodes 0.90–2.50 cm long; petiole canaliculate or semiterete, 2.0–4.0 mm long, rugose in dried material, glabrous or puberulous, the hairs eglandular and unicellular; lamina chartaceous, ovate, 4.40–12.60 × 1.30–4.90 cm, base obtuse, cuneate or rounded, margin entire, revolute or flat in dried material, eciliate, apex acute or acuminate, adaxial side glabrous or scarcely puberulent, the hairs glandular and multicellular, abaxial side scarcely puberulous, the hairs glandular and multicellular; venation acrodromous, suprabasal, imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 1–3, raised on abaxial side, impressed on adaxial side. **Inflorescence** terminal or axillary, raceme or occasionally fascicle; axis 3.0–11.0 mm long, elongating up to 6.0–7.0 mm when fruiting, red or pink, glabrous, peduncle 0.5–2.0 mm long, rachis 1.0–9.5 mm long; bracts of the inflorescence persistent, pink or red, chartaceous, ovate, elliptic or oblong, 10–18 × 7–12 mm, smooth,
margin entire, eciliate, apex rounded or obtuse, glabrous on both sides; floral bracts early caducous or persistent, red or pink, membranose or chartaceous, shape and size heterogeneous along the rachis, oblong, obovate or oblanceolate, 18.0–30.0 × 3.0–11.0 mm, smooth, margin entire, eciliate, apex rounded or obtuse, glabrous on both sides; pedicel red or pink, stout, 6.0–18.0 mm long, not markedly swollen at apex, 0.60–1.50 mm diam. at base (1.50–2.00 mm in vivo), 0.80–1.50 mm diam. at apex (2.20–3.50 mm in vivo), glabrous or occasionally puberulous, the hairs eglandular and unicellular; bracteoles early caducous, basal, opposite, pink or red, acicular or linear, 1.20–4.00 × 0.10–0.40 mm, margin entire, eciliate, apex acute, acuminate or praemorse, glabrous on both sides. Calyx aestivation valvate, pink or red, cupuliform (tubular or cupuliform in vivo), 2.50–4.00 mm long (4.00–6.00 mm in vivo), sessile, terete, truncate at base, glabrous; tube cylindric, 1.50–2.50 mm long (2.80–5.00 mm in vivo), 2.00–3.00 mm diam. (4.90–5.50 mm in vivo); limb flaring (straight in vivo), membranose, 0.70–1.80 mm long, lobes deltoid, 0.20–0.50 × 0.20–1.00 mm, margin ciliate, the hairs glandular and multicellular, marginal gland absent, apex acute or obtuse, sinuses flat or v-shaped. Corolla aestivation valvate, pink or red at base, red or white at apex, membranose, bistratose, tubular, terete, 21.0–33.0 mm long (32.0–35.0 mm in vivo), 3.0–9.0 mm diam. (6.5–9.0 mm in vivo), 2.5–5.0 mm diam. at throat (3.9–5.1 mm in vivo), glabrous on both sides; lobes deltoid, 0.60–1.40 × 1.50–2.00 mm. Stamens distinct, not adherent to corolla. Long stamens 9.50–10.70 mm long; filaments straight, 6.80–8.00 × 1.00–1.10 mm, apically puberulous, the hairs eglandular and unicellular; anthers 3.00–3.40 mm long; thecae nonprognathous, 1.80–2.00 mm long, 0.50–0.80 mm wide, glabrous, not appendiculate; tubules parallel, 1.00–1.60
mm long, 0.40–0.60 mm diam., dehiscing by acroscopic pores, pores 0.10–0.20 mm long, margin entire. Short stamens like those of the longer cycle except for 8.20–8.80 mm long, filaments 5.00–6.30 mm long, anthers 3.30–3.80 mm long, thecae 1.20–2.20 mm long, 0.60–0.80 mm wide, tubules 1.50–2.10 mm long. Nectary disk flat, glabrous; style pink or red, 37.0–51.0 mm long, exerted. **Berry** black, spherical, 5.0–7.0 mm long, 5.0–8.0 mm diam., lobes ascending, glabrous; seeds ellipsoidal, 0.70–1.30 × 0.50–0.70 mm.

**Figure 3.4: Orthaea abbreviata.** A: Reproductive branch. B. Inflorescence. C. Calyx lobes (scale = 0.5 mm). D. Stamens (scale = 1 mm).
**Distribution and ecology.** *Orthaea abbreviata* is found from Southern Ecuador (Zamora-Chinchipe) to northern Peru (San Martín), on the eastern slope of the Andes, between 900–3200 m (Fig. 3.5). Although *O. abbreviata* is a commonly collected species that tolerates moderately transformed environments, it is not locally dominant and only a few individuals are observed per locality. Flowering and fruiting throughout the year.


**Morona-Santiago/Zamora-Chinchipe:** Eastern slope of the cordillera, valley of the ríos Negro and Chupianza, Sevilla de Oro–Mendez trail, region of Tambo-Pilas, ca. mouth of Río Patos, 31 Oct 1944 (fl), W. H. Camp E-757 (NY, US). **Zamora-Chinchipe:** Area

PERU. Amazonas: Prov. Condorcanqui, Cordillera del Condor, puesto de vigilancia Alfonso Ugarte (PV 3), cabeceras del Río Comainas, tributaio al W del Río Cenepa, 3° 54′ S, 78° 25′ W, 1200–1500 m, 15 Jul 1994 (fl), H. Beltrán 811 (F); 16 Jul 1994 (fl), 842 (F). Serranía de Bagua, ca. 12–20 km E of La Peca, 5° 34′ S, 78° 25′ W, 1800–2020 m, 13 Aug
Etymology. The epithet *abbreviata* refers to the short inflorescence axis.

The glabrous habit, short rachis, and large and usually persistent flower bracts set *Orthaea abbreviata* apart from other Ecuadorian and Peruvian species of the genus. Flower colors change with the sun exposure. For example, if the plant grows in shaded places, the flowers are pink with the tip of the corolla white, but if the plant is subjected to intense sun light, the flowers are completely red.


Epiphytic or terrestrial shrubs 1 m tall. Young branchlets complanate or terete, 1.0–1.5 mm diam., smooth, glabrous; mature branchlets glabrous, bark not exfoliating. Axillary buds complanate, stipitate, stalk 0.30–0.70 mm long; prophylls 2, valvate, ovate, 0.50–1.50 mm long, carinate or ecarinate, ciliate, the hairs glandular and multicellular, apex acute or acuminate, abaxial side glabrous. Leaves alternate, nodes 0.50–2.10 cm long; petiole canaliculate or semiterete, 1.5–3.0 mm long, rugose in dried material, glabrous; lamina chartaceous, elliptic or lanceolate, 3.80–7.00 × 1.00–2.40 cm, base obtuse or cuneate, margin entire, flat or revolute in dried material, eciliate, apex acuminate, adaxial side glabrous, abaxial side scarcely strigose or glabrous, the hairs glandular
Figure 3.5: Geographic distribution of *Orthaea abbreviata*.

and multicellular; venation acrodromous, suprabasal or basal, perfect, midvein raised on abaxial side, impressed or raised on adaxial side, secondary venation brochidodromous or camptodromous, prominent lateral veins 1–2, raised on abaxial side, raised on adaxial side. **Inflorescence** axillary, a 7–12-flowered raceme; axis 8.0–34.0 mm long, elongating up to 24.0–32.0 mm when fruiting, glabrous, peduncle 0.5–3.0 mm long, rachis 5.0–33.5 mm long; bracts of the inflorescence early caducous, membranose, ovate, 1.50–2.00 ×
1.00–1.50 mm, smooth, margin erose or entire, ciliate, the hairs glandular and multicellular, apex obtuse, glabrous on both sides; floral bracts early caducous, membranose, shape and size heterogeneous along the rachis, oblong or ovate, 6.00–10.00 × 1.50–3.00 mm, smooth, margin entire, ciliate, the hairs glandular and multicellular, apex acute, glabrous on both sides; pedicel red or pink, stout or slender, 11.0–22.0 mm long, not markedly swollen at apex, 0.5–1.0 mm diam. at base, 0.5–1.0 mm diam. at apex, glabrous; bracteoles early caducous, basal, subopposite, lanceolate, 1.50–10.80 × 0.20–0.30 mm, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate, glabrous on both sides. **Calyx** aestivation valvate, red or pink, cupuliform, campanulate or cylindric, 2.5–4.0 mm long, sessile, terete, truncate or rounded at base, glabrous; tube cylindric, 1.0–2.5 mm long, 1.5–4.0 mm diam.; limb straight or flaring, membranose, 0.70–2.50 mm long, lobes deltoid, 0.10–1.00 × 0.50–2.00 mm, margin ciliate, the hairs glandular and multicellular, marginal gland absent, apex obtuse, sinuses u-shaped. **Corolla** aestivation valvate, pink at base, white at apex, membranose, bistratose, tubular, terete, 14.0–34.0 mm long, 3.0–6.0 mm diam., 2.0–4.0 mm diam. at throat, glabrous on both sides; lobes deltoid, 0.50–1.00 × 1.00–2.00 mm. **Stamens** distinct, not adherent to corolla or adherent by 2.5–3.0 mm. Long stamens 6.50–10.50 mm long; filaments straight, 3.80–7.50 × 0.50–0.60 mm, apically puberulous, the hairs eglandular and unicellular; anthers 2.80–3.80 mm long; thecae nonprognathous, 1.50–1.90 mm long, 0.50–0.70 mm wide, glabrous, not appendiculate; tubules parallel, 1.40–1.80 mm long, 0.40–0.50 mm diam., dehiscing by acroscopic pores, pores 0.10–0.40 mm long, margin entire. Short stamens like those of the longer cycle except for 4.30–8.40 mm long, filaments 2.20–7.00 × 0.50–1.10 mm, anthers
2.50–4.00 mm long, thecae 1.50–2.00 mm long, 0.40–0.70 mm wide, tubules 1.30–2.30 mm long, 0.40–0.60 mm diam., dehiscing by slightly extrorse pores. Nectary disk flat, glabrous; style 18.0–36.0 mm long, exerted. Berry purple or black, spherical, 7.0–10.0 mm long, 7.0–10.0 mm diam., lobes ascending, glabrous; seeds ellipsoidal, 1.00 × 0.50 mm.

**Distribution and ecology.** *Orthaea boliviensis* is found in humid montane and premontane forests of Peru and Bolivia, at 400–2400 m (Fig. 3.6). Flowering in May, June, September, October, and November. Fruiting in March, May, June, November and December.


m, 17 Jun 2004 (fl), L. Valenzuela G. 3897 (NY). La Convención, Camp 2, ca. 8 km walking distance NE from Hacienda Luisiana and the Apurímac river, 12° 30′ S, 73° 30′ W, 1330–1460 m, 27 Jun 1968 (fl), T. R. Dudley 10547 (F, L, NY).

**Etymology.** Species named after the country of origin.

*Orthaea boliviensis* can be easily set apart from sympatric *Orthaea* because of its thin leaves with the veins adaxially raised. *O. ecuadorensis* is the morphologically closest species and both are discussed under *O. ecuadorensis*.

![Figure 3.6: Geographic distribution of *Orthaea boliviensis.*](image-url)

Epiphytic or terrestrial shrubs 0.5–3 m tall. **Young branchlets** 3-ridged or slightly complanate, 1.0–4.0 mm diam., smooth, glabrous; mature branchlets glabrous, bark exfoliating. **Axillary** buds compressed, stipitate, stalk 0.50–2.00 mm long; prophylls 2, imbricate, ovate or deltoid, 1.00–4.00 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate or acute, abaxial side glabrous or puberulous, the hairs eglandular and unicellular. **Leaves** alternate, nodes 0.70–3.50 cm long; petiole semiterete or canaliculate, 3.0–7.0 mm long, smooth or rugose in dried material, glabrous or puberulous, the hairs glandular and multicellular; lamina chartaceous, elliptic or ovate, 4.00–13.00 × 1.80–4.30 cm, base cuneate or round and slightly decurrent, margin entire, revolute or flat in dried material, eciliate, apex acuminate, adaxial side glabrous, abaxial side strigose, the hairs glandular and multicellular; venation acrodromous, suprabasal, imperfect, midvein raised on abaxial side, raised on adaxial side, secondary venation camptodromous or brochidodromous, prominent lateral veins 2–4, raised on abaxial side, flat or impressed on adaxial side. **Inflorescence** terminal or axillary, a 4–16-flowered raceme; axis 20.0–55.0 mm long, elongating up to 20.0–55.0 mm when fruiting, reddish-green, glabrous, peduncle 3.0–15.0 mm long, rachis 5.0–52.0 mm long; bracts of the inflorescence early caducous; floral bracts early caducous; pedicel red, carnose, 15.0–32.0 mm long (15.0–35.0 mm *in vivo*), markedly swollen at apex, 1.0
mm diam. at base (2.30–2.80 mm \textit{in vivo}), 3.0–4.0 mm diam. at apex (6.50 mm \textit{in vivo}), glabrous; bracteoles early caducous, basal, subopposite, obovate, 5.0–7.0 × 2.0–3.0 mm, margin entire, ciliate, the hairs glandular and multicellular, apex obtuse or acute, glabrous on both sides. **Calyx** aestivation valvate, purple or red, campanulate or obconic (slightly campanulate or tubular \textit{in vivo}), 3.0–10.0 mm long (8.0–9.0 mm \textit{in vivo}), stipitate (sessile \textit{in vivo}), terete, apophysate at base, apophysis perpendicular, entire, glabrous; tube cylindric or obconic, 2.0–4.0 mm long (4.30–5.40 mm \textit{in vivo}), 5.0–7.0 mm diam. (10.0 mm \textit{in vivo}); limb flaring (straight \textit{in vivo}), coriaceous, 3.0–7.0 mm long, lobes deltoid, 1.60–3.00 × 4.00–5.40 mm, margin eciliate, marginal gland absent, apex acute, sinuses v-shaped or u-shaped. **Corolla** aestivation valvate, red at base, white at apex, carnose, bistratose, urceolate or tubular, terete, 20.0–25.0 mm long (25.0–30.0 mm \textit{in vivo}), 5.0–9.0 mm diam. (12.0–14.0 mm \textit{in vivo}), 3.0–5.0 mm diam. at throat (5.0–6.0 mm \textit{in vivo}), glabrous on both sides; lobes lanceolate, ovate or triangular, 3.5–7.0 × 3.0–5.0 mm. **Stamens** distinct, not adherent to corolla. Long stamens 10.0–11.0 mm long; filaments straight, 5.00–6.30 × 1.00–1.50 mm, apically puberulous, the hairs eglandular and unicellular; anthers 5.0–7.0 mm long; thecae slightly prognathous, 2.80–4.20 mm long, 0.70–1.00 mm wide, scarcely pubescent at base, the hairs eglandular and multicellular, not appendiculate; tubules parallel or slightly divergent, 1.80–2.30 mm long, 0.60–1.00 mm diam., dehiscing by slightly latrorse pores, pores 0.70–1.20 mm long, margin erose. Short stamens like those of the longer cycle except for 8.00–9.50 mm long, filaments 3.50–5.00 mm long, anthers thecae tubules slightly divergent or parallel, dehiscing by introrose pores. Nectary disk moderately raised, glabrous; style 18.0–25.0 mm long,
included. **Berry** violet or red, spherical, 8.0–12.0 mm long, 9.0–13.0 mm diam., lobes ascending or reflexed, glabrous; seeds fusiform or ellipsoidal, 1.30–1.90 × 0.60–1.00 mm, testa alveolate, mucilaginous coat possibly with muscilaginous coat.

**Distribution and ecology.** *Orthaea carnosiflora* is known from central and southern Peru (Huánuco, Cuzco, and Pasco), in humid and pluvial montane forests, at 2400–3500 m (Fig. 3.7). Flowering in February, March and November. Fruiting in February–August.


**Etymology.** The specific epithet refers to the notoriously fleshy corolla and calyx.

*Orthaea carnosiflora* is differentiated from other members of the genus by the unique combination of racemose inflorescences with a main axis (2–)3–5.5 cm long, free staminal filaments, anthers from the longer staminal cycle dehiscing by slightly latrorse pores, and
medium sized (20–25 mm long) and extremely fleshy perianth. *O. ferreyrae* is morphologically the closest species to *O. carnosiflora*, however, *O. carnosiflora* has obovate and 5–7 mm long bracteoles (vs. elliptic and < 3 mm in *O. ferreyrae*), eciliate calyx lobes (vs. usually with glandular hairs), longer corolla lobes (3.5–7 vs. 0.5–1 mm long), and its free staminal filaments (vs. connate).

![Figure 3.7: Geographic distribution of Orthaea carnosiflora.](image)

Epiphytic or terrestrial, shrubs or trees, 3–4 m tall. **Young branchlets** terete or complanate, 1.0–3.0 mm diam., smooth, glabrous; mature branchlets glabrous, bark not exfoliating. **Axillary** buds globose, stipitate, stalk 1 mm long; prophylls 2, valvate, ovate, 0.70–1.00 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex obtuse-mucronate or obtuse, abaxial side glabrous. **Leaves** alternate, nodes 0.70–2.40 cm long; petiole canaliculate or semiterete, 2.00–4.00 mm long, rugose in dried material, glabrous; lamina chartaceous, elliptic, 5.50–9.30 × 1.70–4.40 cm, base cuneate or obtuse, margin entire, slightly revolute or flat in dried material, eciliate, apex acuminate or cuspidate, adaxial side glabrous, abaxial side glabrous or scarcely strigose, the hairs glandular and multicellular; venation acrodromous, basal or suprabasal, imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation brochidodromous, prominent lateral veins 2, raised on abaxial side, impressed or raised on adaxial side. **Inflorescence** terminal or axillary, a 8–13-flowered raceme; axis 24.0–40.0 mm long, elongating up to 27.0–38.0 mm when fruiting, red, glabrous, peduncle 0.5–2.0 mm long, rachis 22.0–39.5 mm long; bracts of the inflorescence early caducous; floral bracts early caducous, pink; pedicel red, stout, 11.0–21.0 mm long, not markedly swollen at apex, 0.5–1.0 mm diam. at base, 1.0–1.5 mm diam. at apex, glabrous; bracteoles early caducous, medial or basal, subopposite. **Calyx** aestivation valvate, cupuliform or campanulate, 4.5–6.0 mm long, sessile, terete, truncate at base, glabrous; tube cylindric or campanulate, 2.5–5.0 mm long, 4.0–6.5 mm diam.; limb flaring, membranose, 1.5–3.0 mm long, lobes deltoid, 0.30–1.20 × 0.50–2.50 mm, margin ciliate, the hairs glandular and
multicellular, marginal gland absent, apex obtuse or acute, sinuses u-shaped. **Corolla** aesture red or pink at base, red or pink at apex, membranose, bistratose, tubular, terete, 25.0–39.0 mm long, 5.0–12.0 mm diam., 2.5–8.0 mm diam. at throat, glabrous on both sides; lobes ovate or deltoid, 0.5–2.5 × 1–3.5 mm. **Stamens** distinct, not adherent to corolla. Long stamens 10.50–14.50 mm long; filaments straight, 6.40–11.00 × 1.00–1.20 mm, apically puberulous, the hairs eglandular and unicellular; anthers 4.50–4.80 mm long; thecae nonprognathous, 2.20–2.50 mm long, 0.50–0.70 mm wide, glabrous, not appendiculate; tubules parallel, 2.10–2.50 mm long, 0.50–0.60 mm diam., dehiscing by acroscopic pores, pores 0.10–0.20 mm long, margin entire. Short stamens like those of the longer cycle except for 9.3–12.0 mm long, filaments 5.30–9.50 × 1.50 mm, anthers 3.70–4.50 mm long, thecae 2.00–2.20 mm long, tubules 2.10–2.40 mm long. Nectary disk flat, glabrous; style 37.0–47.0 mm long, exerted. **Berry** black, spherical, 9.0–10.0 mm long, 9.0–10.0 mm diam., lobes ascending, glabrous; seeds ellipsoidal, 0.80–1.50 × 0.40–0.70 mm.

**Distribution and ecology.** *Orthaea ecuadorensis* is endemic to Mera (Pastaza), Ecuador, in cloud forests at 900–1300 m (Fig. 3.8). Flowering specimens have been collected in April and October, fruiting in March and October.

**Specimens examined.** **ECUADOR. Pastaza:** Hacienda San Augustín, 3 km NW de Mera en la carretera Mera–Río Anzu, 1° 26′ S, 78° 5′ W, 900–1300 m, 14 Oct 1984 (fl, fr), *C. H. Dodson 15361* (GB, MO, NY, QCNE). Rd. to Río Pastaza, 8 km NE of Mera, 1° 26′ S, 78° 5′ W, 1300 m, 13 Mar 1985 (fr), *D. A. Neill 6100* (GB, MO, NY, QCNE).
**Etymology.** Species named after Ecuador, the country it is endemic to.

*Orthaea ecuadorensis* is morphologically close to *O. boliviensis*, but *O. ecuadorensis* has larger calyx (4.5–6 × 4–6.5 mm vs. 2.5–4 × 2–3.5 mm) and longer stamens (long cycle 10.5–14.5 mm vs. 6.5–10.3 mm, short cycle 9.3–12 mm vs 4.3–8.4 mm).

![Figure 3.8: Geographic distribution of *Orthaea ecuadorensis*.](image)
5. *Orthaea eteocles* N. R. Salinas, **sp. nov.** Type. Ecuador. Esmeraldas: Near Lita, 0° 55' N, 78° 34' W, 600 m, 19 May 1987 (fl), H. H. van der Werff 9497 (holotype QCNE!; isotypes AAU!, MO!, NY!).

*Orthaea eteocles* differs from *O. glandulifera* Luteyn by having glabrous young branchlets (vs. pubescent in *O. glandulifera*), fewer flowers per inflorescence (6–13 vs. 15–24), and longer inflorescence axis (77–116 mm vs. 1.7–5 mm), v-shaped calyx sinuses (vs. u-shaped), longer corollas (34–37 mm vs. 25–33 mm), longer stamens (14–15.5 vs 8–10.2), and longer anthers (4.3–6.6 mm vs 2.9–3.4 mm).

Epiphytic shrubs. **Young branchlets** terete or complanate, 1.5–2.0 mm diam., smooth, glabrous; mature branchlets glabrous, bark not exfoliating. **Axillary** buds globose, stipitate, stalk 0.50–1.00 mm long; prophylls 2, valvate, ovate or deltoid, 0.50–1.10 mm long, carinate or ecarinate, margin entire, eciliate, apex obtuse, abaxial side glabrous. **Leaves** alternate, nodes 1.00–2.90 cm long; petiole canaliculate, 3.0–5.0 mm long, rugose in dried material, glabrous; lamina chartaceous, elliptic, 6.10–11.50 × 2.00–4.80 cm, base rounded or obtuse, margin entire, revolute in dried material, eciliate, apex rostrate or caudate, glabrous on both sides; venation acrodromous, basal, perfect or imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 1–2, raised on abaxial side, impressed or raised on adaxial side. **Inflorescence** axillary or terminal, a 15–24-flowered raceme or panicle; axis 77.0–116.0 mm long, hirsute, hairs glandular and multicellular, peduncle 15.0–60.0 mm long, rachis 17.0–100.0 mm long; floral bracts early caducous; pedicel fleshy, 21.0–48.0 mm long, markedly
swollen at apex, 0.5–1.0 mm diam. at base, 5.0–6.0 mm diam. at apex, glabrous; bracteoles early caducous. Calyx aestivation valvate, pink, tubular, 7.0–8.0 mm long, sessile or stipitate, terete, apophyseate at base, apophysis perpendicular, entire, glabrous or apically hirsute, the hairs glandular and multicellular; tube cylindric, 3.0–6.0 mm long, 4.0–6.5 mm diam.; limb straight, chartaceous or membranose, 3.0–5.0 mm long, lobes deltoid or ovate, 0.80–2.00 × 2.40–3.50 mm, margin eciliate, marginal gland present, apex round and apiculate, sinuses v-shaped. Corolla aestivation valvate, white at base, white at apex, membranose, bistratose, tubular, terete, 34.0–37.0 mm long, 4.0–6.0 mm diam., 3.0–4.0 mm diam. at throat, abaxial side hirsute, the hairs glandular and multicellular, adaxial side glabrous; lobes deltoid, 0.50–0.70 × 0.70–0.90 mm. Stamens distinct, not adherent to corolla. Long stamens 15.00–15.50 mm long; filaments straight, 10.50–11.00 × 1.10–1.20 mm, apically puberulous, the hairs eglandular and unicellular; anthers 4.30–4.70 mm long; thecae nonprognathous, 2.40–2.90 mm long, 0.60–0.80 mm wide, glabrous, not appendiculate; tubules parallel, 2.80–3.00 mm long, 0.70 mm diam., dehiscing by latrorse pores, pores 0.50–1.20 mm long, margin entire. Short stamens like those of the longer cycle except for 14.0–15.0 mm long, filaments 7.00–7.50 × 1.00–1.40 mm, anthers 5.80–6.60 mm long, thecae 2.90–3.00 mm long, 0.80 mm wide, tubules 3.00–3.40 mm long, 0.60–0.70 mm diam., dehiscing by introrse pores. Nectary disk flat, glabrous; style 38.0 mm long, included. Berry not seen.

**Distribution and ecology.** Orthaea eteocles is endemic to Esmeraldas province, Ecuador, in rain forest at 600–900 m (Fig. 3.9). Flowering specimens have been collected in May and June, fruiting only in May.

Etymology. Name after Eteocles, a mythological Greek character. Eteocles was the son of Oedipus and succeeded him as king of Thebes. Several classic tragedies are based on the story of his fight against his brother Polynices, such as “Thebaid” (by Homer), “Oedipus at Colonus” (by Sophocles), and “Seven against Thebes” (by Aeschylus).

Orthaea eteocles is morphologically similar to several species of Orthaea s.s. from western Colombia, such as O. glandulifera, O. medusula, and O. peregrina. All these species develop glandular indumentum on their reproductive structures and usually have pedicels notoriously swollen at the apex. Their differences are summarized in Table 3.1.


Epiphytic or terrestrial shrubs 0.7–5 m tall. Young branchlets angular or ridged, 1.0–2.0 mm diam., smooth, puberulous or glabrous, the hairs eglandular and unicellular; mature branchlets glabrous, bark not exfoliating. Axillary buds complanate, stipitate,
<table>
<thead>
<tr>
<th>Character</th>
<th><em>O. glandulifera</em></th>
<th><em>O. eteocles</em></th>
<th><em>O. medusula</em></th>
<th><em>O. peregrina</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Inflorescence</td>
<td>raceme</td>
<td>raceme</td>
<td>panicle</td>
<td>raceme</td>
</tr>
<tr>
<td>Calyx lobe margin</td>
<td>ciliate or eciliate</td>
<td>eciliate</td>
<td>eciliate</td>
<td>eciliate</td>
</tr>
<tr>
<td>Calyx lobe marginal gland</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Corolla shape</td>
<td>tubular</td>
<td>tubular</td>
<td>urceolate</td>
<td>tubular</td>
</tr>
<tr>
<td>Corolla color</td>
<td>white</td>
<td>white</td>
<td>red</td>
<td>white or pink</td>
</tr>
<tr>
<td>Corolla size (in mm)</td>
<td>25–33</td>
<td>34–37</td>
<td>7.5–8.3</td>
<td>16–20</td>
</tr>
<tr>
<td>Staminal filaments</td>
<td>distinct</td>
<td>distinct</td>
<td>connate</td>
<td>distinct</td>
</tr>
<tr>
<td>Long stamens (in mm)</td>
<td>7.5–10.3</td>
<td>15–15.5</td>
<td>5–6.5</td>
<td>7.5–9.8</td>
</tr>
<tr>
<td>Short stamens (in mm)</td>
<td>6.5–8.2</td>
<td>14–15</td>
<td>3.9–4.2</td>
<td>5.5–8.4</td>
</tr>
</tbody>
</table>

Table 3.1: Morphological differences among *Orthaea eteocles* and other similar species.

stalk 0.50–0.80 mm long; prophylls 2, imbricate, triangular or lanceolate, 2.00–3.00 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate, abaxial side glabrous or puberulous, the hairs eglandular and unicellular. **Leaves** alternate, nodes 0.20–2.90 cm long; petiole canaliculate or semiterete, 2.0–5.0 mm long, rugose in dried material, glabrous; lamina chartaceous, ovate or elliptic, 4.80–9.00 × 1.10–3.10 cm, base cuneate, rounded or obtuse, margin entire, flat or revolute in dried material, eciliate, apex acuminate, adaxial side glabrous, abaxial side glabrous or scarcely strigose, the hairs glandular and multicellular; venation acrodromous, suprabasal, imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 2, raised on abaxial side, impressed, raised or flat on adaxial side. **Inflorescence** axillary or terminal, a 6–15-flowered raceme; axis 10.0–68.0 mm long, elongating up to 35.0–58.0 mm when fruiting, red or green, glabrous
or pubescent, hairs eglandular and unicellular, peduncle 1.0–10.0 mm long, rachis 9.0–67.0 mm long; bracts of the inflorescence early caducous, membranose, ovate or oblong, 4.0–7.0 × 3.0–4.0 mm, smooth, margin entire, eciliate, apex acute or obtuse, glabrous on both sides; floral bracts early caducous, membranose, shape and size homogeneous along the rachis, oblong or ovate, 4.0–7.0 × 3.0–4.0 mm, smooth, margin entire, eciliate, apex obtuse or acute, glabrous on both sides; pedicel red or pink, stout or slender, 11.0–24.0 mm long, markedly swollen or not markedly swollen at apex, 0.5–1.0 mm diam. at base,
1.0–2.5 mm diam. at apex, glabrous or puberulous, the hairs eglandular and unicellular; bracteoles early caducous or persistent, medial or basal, subopposite, red or pink, ovate, lanceolate or orbicular, 1.30–2.50 × 0.80–1.60 mm, margin entire, ciliate, the hairs glandular and multicellular, apex obtuse-apiculate, obtuse or acute, adaxial side pubescent or glabrous, the hairs eglandular and unicellular, abaxial side glabrous. **Calyx** aestivation valvate, red or pink, obconic (tubular *in vivo*), 4.0–8.0 mm long (6.0–8.0 mm *in vivo*), sessile, terete, apophysate at base, apophysis perpendicular, entire, glabrous or pubescent, the hairs eglandular and unicellular; tube cylindric, 1.8–7.0 mm long (3.0–4.0 mm *in vivo*), 2.0–8.0 mm diam. (4.0–6.0 mm *in vivo*); limb flaring or straight (straight *in vivo*), coriaceous, 3.0–4.5 mm long, lobes ovate or deltoid, 0.50–0.80 × 0.50–3.00 mm, margin eciliate or scarcely ciliate, the hairs glandular and multicellular, marginal gland absent, apex obtuse-apiculate or acute, sinuses v-shaped or u-shaped. **Corolla** aestivation valvate, pink or red at base, white at apex, carnose, bistratose, tubular, terete, 15.0–22.0 mm long (20.0–23.0 mm *in vivo*), 5.0–10.0 mm diam. (8.5–9.0 mm *in vivo*), 2.5–8.0 mm diam. at throat (7.0–7.5 mm *in vivo*), abaxial side glabrous or pubescent, the hairs eglandular and unicellular, adaxial side glabrous; lobes deltoid, 0.50 × 1.00 mm. **Stamens** connate in pairs or fully connate in the basal 2.0–4.5 mm, not adherent to corolla. Long stamens 9.50–10.80 mm long; filaments straight, 6.50–7.70 × 1.20–1.50 mm, apically puberulous, the hairs eglandular and unicellular; anthers 4.20–4.50 mm long; thecae nonprognathous, 2.00–2.70 mm long, 0.60–0.70 mm wide, glabrous or pubescent at base, the hairs eglandular and unicellular, not appendiculate; tubules parallel or divergent, 1.40–2.00 mm long, 0.50 mm diam., dehiscing by latrorse or introrse pores, pores 0.80–1.20 mm long, margin
entire. Short stamens like those of the longer cycle except for 7.00–9.00 mm long, filaments 4.50–6.00 × 1.20–1.40 mm, anthers 4.20–4.80 mm long, thecae 2.00–3.00 mm long, 0.70–0.80 mm wide, tubules parallel, 1.40–2.40 mm long, dehiscing by introrse pores. Nectary disk flat, pubescent, the hairs eglandular and unicellular; style red or pink, 15.0–17.0 mm long, included. Berry greenish pink, red or reddish brown, obconic, 6.0–10.0 mm long, 6.0–8.0 mm diam., lobes ascending, glabrous; seeds ellipsoidal, 0.70–1.40 × 0.50–1.00 mm.

**Distribution and ecology.** *Orthaea ferreyrae* is found in the eastern slope of Peruvian Andes, in Cuzco, Huánuco, Junín, Pasco, and Ucayali, in premontane and montane humid forests at 1500–3500 m (Fig. 3.10). Flowering in January–May and October–November. Fruiting in January–July and September.


**Etymology.** Species named after Ramón Alejandro Ferreyra Huerta, Peruvian botanist that collected the type specimen.

Orthaea carnosiflora is the most similar species to O. ferreyrae. They are both discussed under the former.

7. **Orthaea fissiflora**  N. R. Salinas & Pedraza, sp. nov. Type. Bolivia. La Paz: Murillo, Yungas, valle del Río Zongo, 24.2 km al N de la cumbre, 16° 7′ S, 68° 7′ W, 2900 m, 11 Apr 1987 (fl, fr), J. C. Solomon 16538 (holotype LPB!; isotypes G!, MO!, NY!).

Orthaea fissiflora differs from O. pinnatinervia because its basally green corolla that usually splits longitudinally after anthesis (vs. red and without tears in O. pinnatinervia), connate staminal filaments (vs. distinct), and longer stamens (long cycle 7.4–8.4 mm vs. 6.5–7.0 mm; short cycle 6.3–7.0 mm vs. 4.8–5.5 mm).
Terrestrial or epiphytic shrubs 1–2 m tall. Young branchlets ridged or terete, 1.0–4.0 mm diam., smooth or striate, glabrous; mature branchlets glabrous, bark not exfoliating. Axillary buds complanate, stipitate, stalk 0.20–0.80 mm long; prophylls 2, imbricate, ovate or lanceolate, 1.00–2.60 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate, abaxial side glabrous. Leaves alternate, subopposite or opposite, nodes 0.10–1.40 cm long; petiole semiterete, 1.0–3.0 mm long, rugose in dried material, glabrous; lamina chartaceous or coriaceous, elliptic, ovate or
lanceolate, 2.60–6.60 × 0.50–2.00 cm, base rounded, obtuse or cuneate, margin entire, revolute, flat or revolute in dried material, eciliate, apex acuminate, adaxial side glabrous, abaxial side glabrous or strigose, the hairs glandular and multicellular; venation acrodromous, suprabasal, imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous or brochidodromous, prominent lateral veins 1–2, raised or flat on abaxial side, impressed on adaxial side. **Inflorescence** axillary or terminal, a 6–15-flowered raceme; axis 10.0–20.0 mm long, glabrous, peduncle 0.5–3.0 mm long, rachis 7.0–19.5 mm long; bracts of the inflorescence early caducous, chartaceous, ovate or deltoid, 1.00–1.50 × 1.00–1.40 mm, smooth, margin entire, ciliate or eciliate, the hairs glandular and multicellular, apex acute, obtuse or obtuse-mucronate, glabrous on both sides; floral bracts early caducous, chartaceous, shape and size homogeneous along the rachis, ovate, 2.50–4.50 × 1.40–2.00 mm, smooth, margin erose or entire, eciliate or ciliate, the hairs glandular and multicellular, apex acute or obtuse-mucronate, glabrous on both sides; pedicel stout, 7.0–13.0 mm long, not markedly swollen at apex, 0.5–1.0 mm diam. at base, 1.0–1.5 mm diam. at apex, glabrous; bracteoles early caducous, basal or medial, subopposite, ovate or lanceolate, 1.00–2.00 × 0.60–1.00 mm, margin entire, eciliate, apex acuminate or acute, glabrous on both sides. **Calyx** aestivation valvate, green, campanulate (tubular *in vivo*), 3.0–5.0 mm long (5.20–6.50 mm *in vivo*), sessile, terete, apophysate or truncate at base, apophysis perpendicular, entire, glabrous; tube cylindric, 1.50–2.80 mm long (3.00–4.00 mm *in vivo*), 2.0–3.0 mm diam. (4.0–5.5 mm *in vivo*); limb flaring (straight *in vivo*), chartaceous, 2.0–3.0 mm long, lobes deltoid, 0.30–0.50 × 0.30–1.00 mm, margin eciliate, marginal gland absent, apex acute, sinuses u-shaped. **Corolla**
aestivation valvate, green at base, green or white at apex, membranose, tubular, terete, 14.0–18.0 mm long (17.0–21.0 mm in vivo), 3.00–7.00 mm diam. (6.30–6.50 mm in vivo), 2.50–4.50 mm diam. at throat (5.20 mm in vivo), glabrous on both sides; lobes deltoid, 1 × 1 mm. **Stamens** distinct, not adherent to corolla. Long stamens 7.40–8.40 mm long; filaments straight, 3.90–4.40 × 0.60–0.80 mm, apically puberulous, the hairs eglandular and unicellular; anthers 4.50–4.80 mm long; thecae nonprognathous, 2.70–3.10 mm long, 0.50–0.70 mm wide, glabrous, not appendiculate; tubules divergent, 1.50–2.00 mm long, 0.50–0.70 mm diam., dehiscing by latrorse pores, pores 0.90–1.20 mm long, margin entire. Short stamens like those of the longer cycle except for 6.30–7.10 mm long, filaments 2.50–3.00 × 0.80–1.00 mm, anthers 4.50–4.90 mm long, thecae 2.00–2.50 mm long, 0.60–0.70 mm wide, tubules parallel, 1.80–2.50 mm long, 0.60–0.80 mm diam., dehiscing by introrse pores. Nectary disk flat, glabrous; style 18.0–21.0 mm long, included. **Berry** subconic or spherical, 6.0–9.0 mm long, 8.0 mm diam., lobes reflexed, glabrous; seeds ellipsoidal or isodiametric, 0.80–1.40 × 0.40–0.90 mm.

**Distribution and ecology.** *Orthaea fissiflora* is restricted to La Paz department, Bolivia, in humid montane forests at 2100–3400 m (Fig. 3.11). Flowering in March–May. Fruiting in January, March, April, May, July, September, and November.

**Specimens examined.** **BOLIVIA. La Paz:** Murillo, Valle del Río Zongo, 18–24 km N La Cumbre, 16° 7′ – 10′ S, 68° 4′ – 10′ W, 2150–2950 m, 10 May 1990 (fl, fr), J. L. Luteyn 13618 (NY); 2 Mar 2000 (fl), 15439 (NY); 14 Apr 2005 (fl), 15634 (NY). 18 Mar 1987 (fl, fr), J. C. Solomon 16371 (G, MO, NY). Yungas, 24.5 km N of the pass at the head of the Zongo Valley, 16° 19′ S, 68° 7′ W, 3100 m, 16 Sep 1984 (fr), J. C. Solomon
12311 (MO, NY, U). Sur Yungas, old town of Unduavi, 16° 19' S, 67° 54' W, 3139 m, 19 May 1990 (fr), J. L. Luteyn 13758 (NY). Inquisivi, Cuchiwas, bajando Pabellonani, 7 km NE de Choquetanga, 16° 48' S, 67° 16' W, 3300 m, 19 Jan 1994 (fr), N. Salinas 2144 (NY). Comunidad Choquetanga, serranías de Lulini, a 13.5 Km de Choquetanga, 16° 43' S, 67° 19' W, 3310 m, 3 Mar 1994 (fl, fr), N. Salinas 2542 (NY). Desvío Unduavi–Sud Yungas, 16° 16' S, 67° 50' W, 3100 m, 20 Jul 2001 (fr), C. Antezana 1548 (NY). La Paz–Coroico rd., Unduavi, at junction with rd. to Chulumani, 16° 16'−18' S, 67° 51'−54' W, 3170−3292 m, 4 Mar 2000 (fl), J. L. Luteyn 15445 (NY); 4 Mar 2000 (fr), 15449 (NY); 15 Apr 2005 (fl), 15603 (NY); 15 Apr 2005 (fl, fr), 15609 (NY); 15 Apr 2005 (fl), 15610 (NY); 15 Apr 2005 (fl), 15611 (NY). La Paz–Coroico rd., 0.5 km NW of Chuspipata, 16° 16' S, 67° 46' W, 3050 m, 16 Mar 2000 (fl), J. L. Luteyn 15468 (NY). Nor Yungas, 3.5 Km W de Chuspipata, 1.5 Km E de Cotapata, camino a Unduavi, 16° 18' S, 67° 50' W, 3300 m, 5 Apr 1984 (fl), J. C. Solomon 12268 (LPB, MO, NY). Entre Cotapata y Chuspipata, 16° 16' S, 67° 49' W, 3200 m, 11 Apr 1989 (fl), S. G. Beck 14927 (NY). La Paz–Coroico rd., Camino Prehispanico Sillutinkara, ca. 5 km below Unduavi, Parque Nacional Cotopata, 16° 18' S, 67° 54' W, 3100−3300 m, 26 Apr 2007 (fl, fr), J. L. Luteyn 15734 (NY). La Paz–Coroico rd., 16° 17' S, 67° 52' W, 3300 m, 27 Apr 1999 (fl), E. Hennipman 8003 (LPB). Near Unduavi, 16° 19' S, 67° 53' W, 3000 m, 15 Apr 1939 (fl), T. H. Goodspeed 25400 (K). Chuspipata 5 km via Unduavi, 16° 16' S, 67° 49' W, 3150 m, 2 Apr 1982 (fl), S. G. Beck 7603 (L, NY). Yungas, Cotapata, 8.8 km E Unduavi por el camino a Coroico, 16° 16' S, 67° 49'−50' W, 3200–3290 m, 30 Mar 1977 (fl), J. D. Boeke 1395 (NY, US); 11 Apr 1988 (fl, fr), J. C. Solomon 18223 (NY). Unduavi, 16° 19' S,
Etymology. The specific epithet makes reference to the way corolla ages after anthesis, tearing along a longitudinal slit.

*Orthaea fissiflora* is characterized by its small leaves (up to $6.6 \times 2$ cm), short inflorescence axis (up to 20 mm long), and small green corollas (14–18 mm long) that very often tear apart longitudinally after anthesis, exposing the style and stamens. Morphologically, the closest species is *O. pinnatinervia,* from which it differs by the characters mentioned in the diagnosis.

Most of the specimens were previously annotated as *Orthaea ignea* Sleumer, which type specimen (*Herrera 3656*) was destroyed during World War II. Sleumer (1934) did not cite other specimens in the protologue, but it is clear from the description that *O. ignea* cannot be conspecific with *O. fissiflora* because of its bigger leaves (8.5–11.5 $\times$ 2–2.8 vs. 2.6–6.6 $\times$ 0.5–2 cm), connate stamens (vs. distinct), and shorter staminal filaments (long cycle 2.2 mm long vs. 3.9–4.4 mm, short cycle 1.5 mm long vs. 2.5–3 mm). Without doubt all known specimens previously annotated as *O. ignea* were missidentified.

Figure 3.11: Geographic distribution of *Orthaea fissiflora*.

m, 25 May 1984 (fl), *J. L. Luteyn 10727* (holotype JAUM!; isotypes AAU!, CAS!, COL!, E!, F!, L!, MO!, MEXU, NY!, STE, U!, US!, W!).

*Orthaea oedipus* Luteyn, Nordic J. Bot. 7(1): 36, fig. 1F-G. 1987, **syn. nov.** Type. Colombia. Chocó: Bolívar–Quibdó road, 37–40 km W of El Cármen, 5° 50′ N, 76° 14′ W, 671–1360 m, 21 May 1984 (fl), *J. L. Luteyn 10652* (holotype JAUM!; isotypes AAU!, CAS!, COL!, NY!, US!).
Terrestrial or epiphytic shrubs 3–8 m tall. Young branchlets terete, 1.0–3.0 mm diam., smooth, pubescent or glabrous, the hairs glandular and multicellular; mature branchlets glabrescent, the hairs glandular and multicellular, bark not exfoliating. Axillary buds complanate or globose, stipitate, stalk 0.40–1.00 mm long; prophylls 2, valvate, ovate, 0.80–1.50 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex rounded or obtuse, abaxial side glabrous. Leaves alternate, nodes 0.60–3.80 cm long; petiole canaliculate or semiterete, 2–4 mm long, rugose or smooth in dried material, glabrous; lamina chartaceous, ovate or elliptic, 4.00–10.80 × 1.20–4.50 cm, base rounded, obtuse or cuneate, margin entire, slightly revolute in dried material, eciliate, apex acuminate, adaxial side glabrous; venation acrodromous, basal, perfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation brochidodromous, prominent lateral veins 1–2, raised on abaxial side, impressed on adaxial side. Inflorescence terminal or axillary, a 6–15-flowered raceme or solitary flower; axis 17.0–50.0 mm long, red or pink, puberulous or glabrous, hairs glandular and multicellular, peduncle 1.0–6.0 mm long, rachis 11.0–49.0 mm long; bracts of the inflorescence persistent or early caducous, membranose, oblong or ovate, 1.0–15.0 × 2.0–7.0 mm, striate, margin entire, eciliate, apex obtuse, glabrous on both sides; floral bracts early caducous, membranose, shape and size heterogeneous along the rachis, elliptic, 2.5–5.0 × 1.5–2.0 mm, smooth, margin entire, ciliate, the hairs glandular and multicellular, apex acute, glabrous on both sides; pedicel pink or red, stout or slender, 10.0–42.0 mm long, markedly swollen at apex, 0.5–1.0 mm diam. at base, 2.5–6.0 mm diam. at apex, scarcely puberulent or...
glabrous, the hairs glandular and multicellular; bracteoles early caducous, basal, subopposite, lanceolate or elliptic, 2.0–3.0 × 1.0 mm, margin entire, ciliate, the hairs glandular and multicellular, apex acute, adaxial side puberulent, the hairs glandular and multicellular, abaxial side glabrous. **Calyx** aestivation valvate, pink or red, tubular, 4.0–6.0 mm long (6.0–7.0 mm *in vivo*), sessile, terete, apophysate at base, apophysis perpendicular, entire, scarcely puberulent or glabrous, the hairs glandular and multicellular; tube cylindric, 2.0–4.0 mm long (3.50–4.80 mm *in vivo*), 2.5–4.0 mm diam. (4.50–5.30 mm *in vivo*); limb straight or flaring (straight *in vivo*), membranose, 2.20–4.00 mm long, lobes deltoid, 0.40–1.00 × 1.20–2.50 mm, margin eciliate or ciliate, the hairs glandular and multicellular, marginal gland absent, apex acute or obtuse, sinuses u-shaped or v-shaped. **Corolla** aestivation valvate, white at base, white at apex, membranose, tubular, terete, 25.0–33.0 mm long (26.0–35.0 mm *in vivo*), 5.50–9.00 mm diam. at base, 3.00–4.80 mm diam. at throat, abaxial side pubescent or glabrous, the hairs glandular and multicellular, adaxial side glabrous; lobes deltoid, 0.80–1.00 × 1.00–1.50 mm. **Stamens** distinct, adherent to corolla in the basal 2.00–4.50 mm or not adherent. Long stamens 7.50–10.30 mm long; filaments straight, 5.80–8.00 × 1.20 mm, apically puberulous or glabrous, the hairs eglandular and unicellular; anthers 2.30–3.20 mm long; thecae nonprognathous, 1.50–1.80 mm long, 0.80 mm wide, glabrous, not appendiculate; tubules parallel, 0.70–1.30 mm long, 0.60 mm diam., dehiscing by acroscopic pores, pores 0.10–0.30 mm long, margin entire. Short stamens like those of the longer cycle except for 6.50–8.20 mm long, filaments 4.10–6.00 × 1.90 mm, anthers 2.40–3.40 mm long, thecae 1.50–2.00 mm long, tubules 1.00–1.50 mm long. Nectary disk flat, glabrous; style 27.0–33.0 mm long, exerted. **Berry** spherical,
6.0–9.0 mm long, 6.0–10.0 mm diam., lobes ascending, glabrous, the hairs purple; seeds ellipsoidal, 1.00–1.50 × 0.70–0.90 mm.

**Distribution and ecology.** Northwestern Colombia, along the western slope of the western Cordillera and the northern limit of the Central Cordillera, at 800–3200 m (Fig. 3.12). Usually found in rain forests, but occasionally collected in vegetation remnants of perturbed areas. Flowering and fruiting throughout the year.


Etymology. The specific epithet refers to the glandular hairs that sometimes cover the inflorescence axis, pedicel and calyx.

Luteyn (1987) distinguished Orthaea glandulifera from O. oedipus because of the pedicel apex (slightly swollen vs. greatly in O. oedipus), the leaf base (rounded and cordate vs. obtuse to rounded), the glandular indument in the inflorescence axis (absent vs. present), and the calyx lobes (elongated and ciliate vs. reduced and eciliate). Four collections were
then cited by Luteyn (1987), two from eastern Chocó, along Quídbó–Medellín road (O. oedipus), and two from Yarumal, northern Antioquia (O. glandulifera). Certainly, those collections agree with the diagnostic characters noted by Luteyn (1987). However, many new collections are now available from other regions in north-western Colombia, such as western Antioquia (Frontino and Urrao), southern Chocó (San José del Palmar), and Risaralda. From their study it is now evident that the diagnostic characters fail to set the two species apart; therefore, they are here synonymized. Furthermore, the Ecuadorian specimens previously considered O. oedipus by Luteyn (1996a) represent an undescribed species and morphologically the closest taxon to O. oedipus (see discussion under O. eteocles).

Type. Colombia. Valle: El Cairo, Corregimiento El Boquerón, Vereda El Brillante, Cerro El Inglés (Corporación Serraníaigua), en la Serranía de Los Paraguas, 4° 44' N, 76° 18' W, 2100 m, 23 Jul 2004 (fl, fr), L. P. Pedraza-Penalosa 1125 (holotype COL!; isotypes AAU!, CUVC!, NY!).

Terrestrial shrubs 2–4 m tall. Young branchlets 3-ridged or slightly complanate, 2.0–4.0 mm diam., smooth, strigose and glabrescent, the hairs glandular and multicellular; mature branchlets glabrous, bark not exfoliating. Axillary buds compressed, stipitate, stalk 0.80–1.30 mm long; prophylls 2, imbricate or valvate, ovate, 1.20–1.90 mm long, ecarinate, margin entire or erose, eciliate, apex obtuse, abaxial side glabrous. Leaves
Figure 3.12: Geographic distribution of *Orthaea glandulifera*.

Alternate, nodes 1.20–3.10 cm long; petiole canaliculate, 4.0–6.0 mm long, rugose in dried material, glabrous; lamina coriaceous, ovate or elliptic, 5.00–9.00 × 1.90–4.40 cm, base obtuse or cuneate, margin entire, slightly revolute in dried material, eciliate, apex acuminate, adaxial side glabrous or glabrescent, the hairs eglandular and unicellular, abaxial side strigose and glabrescent, the hairs eglandular and unicellular; venation acrodromous, basal, perfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation brochidodromous, prominent lateral veins 1–3, raised on abaxial side, impressed
Inflorescence axillary, a 36–56-flowered panicle; axis 30.0–63.0 mm long, elongating up to 180.0 mm when fruiting, dark red or green, glabrous, peduncle 1.0–10.0 mm long, rachis 20.0–62.0 mm long; bracts of the inflorescence early caducous, red, membranose, ovate, 2.00 × 1.00–1.20 mm, smooth, margin entire, ciliate, the hairs glandular and multicellular, apex acute, glabrous on both sides; floral bracts early caducous, red, membranous, shape and size homogeneous along the rachis, ovate, 2.00 × 1.00–1.20 mm, smooth, margin entire, ciliate, the hairs glandular and multicellular, apex acute, glabrous on both sides; pedicel red, carnose, 8.0–15.0 mm long, markedly swollen at apex, 0.40–0.70 mm diam. at base, 1.80–2.40 mm diam. at apex, glabrous; bracteoles early caducous, basal, opposite or subopposite, red, ovate, 1.50–2.30 × 1.00–1.40 mm, margin entire, ciliate, the hairs glandular and multicellular, apex acute, glabrous on both sides. Calyx aestivation valvate, red, urceolate, 4.20–5.60 mm long, stipitate (sessile in vivo), terete, rounded at base, glabrous; tube globose, 2.60–3.00 mm long, 2.50–4.00 mm diam.; limb flaring, chartaceous, 1.60–2.50 mm long, lobes triangular, 1.00–1.70 × 1.50–2.30 mm, margin eciliate, marginal gland present, apex acute, sinuses v-shaped. Corolla aestivation valvate, red at base, red at apex, carnose, bistratose, urceolate, terete, 7.50–8.30 mm long (9.0–12.0 mm in vivo), 3.0–5.0 mm diam. (5.0-6.0 mm in vivo), 1.5–2.0 mm diam. at throat (2.5–3.5 mm in vivo), abaxial side pilose, the hairs glandular and multicellular, adaxial side glabrous; lobes triangular, 1.00–1.40 × 1.20–2.20 mm. Stamens connate, adherent to corolla. Long stamens 5.0–6.5 mm long; filaments geniculated, 3.00–4.70 × 0.60–0.70 mm, glabrous; anthers 2.60–3.00 mm long; thecae nonprognathous or slightly prognathous, 1.50–1.70 mm long, 0.50 mm wide, glabrous, appendiculate at
base; tubules parallel, 1.00–1.70 mm long, 0.40–0.60 mm diam., dehiscing by latrorse pores, pores 0.40–0.60 mm long, margin erose. Short stamens like those of the longer cycle except for 3.90–4.20 mm long, filaments 2.90–3.30 mm long, anthers thecae slightly prognathous or nonprognathous, tubules dehiscing by introrse pores. Nectary disk flat, glabrous; style 8.0–9.0 mm long, included. **Berry** white, spherical, 7.0 mm long, 7.0 mm diam., lobes ascending, glabrous; seeds fusiform or ellipsoidal, 0.60–0.70 × 0.30–0.40 mm, embryo white.

**Distribution and ecology.** *Orthaea medusula* is found in humid montane forests on the western slope of western Cordillera (Chocó and Valle del Cauca), at 2100–2500 m (Fig. 3.13). Flowering and fruiting specimens have been collected in July, August, and December.

**Specimens examined.** **COLOMBIA. Chocó:** San José del Palmar, Cerro del Torrá, 4° 46' N, 76° 29' W, 2450–2550 m, 17 Aug 1988 (fr), P. A. Silverstone-Sopkin 4516 (CHOCO, CUVC×3, MO, NY); 25 Aug 1988 (fl), 4743 (CUVC×3, NY); 25 Aug 1988 (fr), 4757 (CUVC×2, NY). **Valle:** El Cairo, corregimiento El Boquerón, vereda El Brillante, 4° 44' N, 76° 18' W, 2150–2260 m, 30 Dec 2007 (fl), N. R. Salinas 653 (COL, CUVC, NY).

**Etymology.** The specific epithet refers to the particular kind of hairs that covers the corolla (gland-tipped and multiseriate).
*Orthaea medusula* is characterized by paniculate inflorescences and relatively small (7.5–8.3 mm long), urceolate, and uniformly red corollas at anthesis, which are covered by multicellular and multiseriate hairs (Salinas and Pedraza-Peñaosa 2014). It is morphologically similar to *O. eteocles*, *O. glandulifera*, and *O. peregrina*, and they are discussed under *O. eteocles*.

**Figure 3.13:** Geographic distribution of *Orthaea medusula*.

Terrestrial or occasionally epiphytic shrubs 1.5–3 m tall. **Young branchlets** com-planate, terete or ridged, 1.5–3.0 mm diam., striate or smooth, glabrous or scarcely pubescent, the hairs glandular and multicellular; mature branchlets glabrous, bark not exfoliating. **Axillary** buds globose, sessile; prophylls 4, imbricate or alternative, ovate or oblate, 0.50–0.90 mm long, ecarinate, margin entire, ciliate or eciliate, the hairs glandular and multicellular, apex obtuse or rounded, abaxial side glabrous. **Leaves** alternate, nodes 1.50–3.70 cm long; petiole terete, 2.0–4.0 mm long, rugose in dried material, glabrous; lamina coriaceous or chartaceous, elliptic or occasionally slightly obovate, 8.20–13.10 × 2.20–5.00 cm, base obtuse, cuneate or rounded, margin entire, revolute or occasionally flat in dried material, eciliate, apex acuminate, cuspidate or rostrate, glabrous on both sides; venation acrodromous, suprabasal or basal, imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 1–2, raised on abaxial side, impressed or raised on adaxial side. **Inflorescence** terminal or axillary, a 12–18-flowered raceme; axis 34.0–79.0 mm long, elongating up to 43.0–72.0 mm when fruiting, scarcely pubescent, hairs glandular and multicellular, peduncle 0.5–5 mm long, rachis 29–78.5 mm long; bracts of the inflorescence early caducous, membranose, triangular or linear, 1.40–1.90 × 0.20–0.30 mm, smooth, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate or rounded, glabrous on both sides; floral bracts early caducous, membranous, shape and size homogeneous along the rachis, triangular or linear, 1.40–1.90 × 0.20–0.30 mm, smooth, margin entire, ciliate, the hairs
glandular and multicellular, apex rounded or acuminate, glabrous on both sides; pedicel orange, slender, 19.0–32.0 mm long (21.0–22.5 mm \textit{in vivo}), not markedly swollen at apex, 0.50–0.70 mm diam. at base (1.00–1.20 mm \textit{in vivo}), 1.10–2.20 mm diam. at apex (2.50–2.70 mm \textit{in vivo}), scabrous, scarcely puberulous or glabrous, the hairs glandular and multicellular; bracteoles early caducous or persistent, basal or medial, opposite or subopposite, triangular, linear or lanceolate, 1.40–1.90 $\times$ 0.20–0.70 mm, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate, acute or rounded, glabrous on both sides. \textbf{Calyx} aestivation tubular or campanulate (subprismatic \textit{in vivo}), 4.50–5.70 mm long (5.00–5.40 mm \textit{in vivo}), sessile, terete, slightly angulate or truncate at base, apophysate or truncate at base, apophysis perpendicular, entire, scarcely pubescent or glabrous, the hairs glandular and multicellular; tube cylindric or obconic, 1.00–2.50 mm long (3.20–3.60 mm \textit{in vivo}), 3.00–6.40 mm diam. (5.00–5.40 mm \textit{in vivo}); limb flaring (straight \textit{in vivo}), membranose or coriaceous, 1.40–4.00 mm long, lobes deltoid, 0.30–1.50 $\times$ 1.70–4.50 mm, margin eciliate or ciliate, the hairs glandular and multicellular, marginal gland absent, apex obtuse or acute, sinuses u-shaped. \textbf{Corolla} aestivation valvate or quincunx, red at base, white at apex, membranose, bistratose, tubular, terete, 19.0–31.0 mm long (28.0–30.0 mm \textit{in vivo}), 7.0–10.0 mm diam. (5.0–6.5 mm \textit{in vivo}), 3.0–3.5 mm diam. at throat (2.2–4.0 mm \textit{in vivo}), glabrous on both sides; lobes deltoid, 0.30–0.60 $\times$ 0.70–1.20 mm. \textbf{Stamens} distinct, not adherent to corolla. Long stamens 7.80–9.50 mm long; filaments geniculate, 5.20–6.50 $\times$ 0.70–1.10 mm, apically puberulous, the hairs eglandular and unicellular; anthers 3.30–3.50 mm long; thecae slightly prognathous or nonprognathous, 1.40–1.90 mm long, 0.40–0.90 mm wide, glabrous, not appendiculate; tubules parallel,
1.40–1.90 mm long, 0.60–0.80 mm diam., dehiscing by acroscopic pores, pores 0.10–0.20 mm long, margin slightly erose. Short stamens like those of the longer cycle except for 6.10–8.00 mm long, filaments straight, 3.90–5.20 × 0.80–1.10 mm, anthers 3.20–3.50 mm long, thecae nonprognathous, 1.50–1.90 mm long, 0.50–0.80 mm wide, tubules 1.30–1.60 mm long. Nectary disk flat, glabrous, style 17.0–29.0 mm long, included. **Berry** green or pale green, 5.5–8.0 mm long, 7.0–10.0 mm diam., lobes reflexed, glabrous.

**Distribution and ecology.** *Orthaea oriens* is found in the eastern slope of Ecuadorian Andes, in primary forests or perturbed areas, at 1000–2000 m (Fig. 3.14). Flowering in April, May, July, November, December, and January. Fruiting in April, September, October, and December.

m, 30 Jan 1996 (fl), B. Merino 4781 (LOJA). Loja-Zamora rd., 79.9 km E of summit and border with Loja Province, 3° 59′ S, 79° 1′ W, 1402 m, 31 May 2003 (fl), T. B. Croat 89846 (MO). Morona-Santiago/Zamora-Chinchipe: E slope of the cordillera, valley of the ríos Negro and Chupianza, Sevilla de Oro–Méndez trail, between Hacienda Chontal and Santa Elena, 2° 46′ S, 78° 27′ W, 1000–1400 m, 1 Nov 1944 (fl), W. H. Camp E-799 (NY).

**Etymology.** The epithet *oriens* refers to the eastern part of Ecuador (Amazonian low-lands and adjacent Andean slope). This region is locally known as “El Oriente”.

*Orthaea oriens* is easily identified from the other species of *Orthaea* s.s. because of its strongly apophysiate calyx and the presence of glandular hairs on the inflorescence axis.


Terrestrial shrubs 1.5 m tall. Young branchlets terete, ridged or complanate, 2–4 mm diam., smooth, glabrous; mature branchlets glabrous, bark not exfoliating. Axillary buds globose, stipitate, stalk 1.0–2.0 mm long; prophylls 2, valvate, ovate, 1.50–2.50 mm long, ecarinate, margin entire, eciliate, apex obtuse, abaxial side glabrous. Leaves alternate, nodes 1.30–3.40 cm long; petiole semiterete, 4.0–10.0 mm long, rugose in dried material,
Figure 3.14: Geographic distribution of *Orthaea oriens*.

glabrous; lamina coriaceous, elliptic or ovate, 6.60–10.90 × 2.30–5.60 cm, base rounded, cuneate or obtuse, margin entire, revolute in dried material, eciliate, apex acuminate or cuspidate, adaxial side glabrous, abaxial side strigose and glabrescent or scarcely strigose, the hairs glandular and multicellular; venation acrodromous, suprabasal, imperfect or perfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 1–2, raised on abaxial side, impressed on adaxial side. **Inflorescence** axillary, a 25–85-flowered panicle; axis 35.0–95.0 mm long, green
with red, glabrous, peduncle 0.5–10.0 mm long, rachis 25.0–94.5 mm long; pedicel red, slender, 14.0–29.0 mm long, markedly swollen at apex, 0.5–1.0 mm diam. at base, 2.7–3.7 mm diam. at apex, glabrous; bracteoles early caducous, basal, subopposite, red, ovate, 1.20 \times 1.00 \text{ mm}, margin entire, ciliate, the hairs glandular and multicellular, apex obtuse, glabrous on both sides. Calyx aestivation valvate, red, campanulate (tubular \textit{in vivo}), 4.0–7.0 \text{ mm} long (6.5–8.0 \text{ mm} \textit{in vivo}), stipitate (sessile \textit{in vivo}), terete, apophysate at base, apophysis perpendicular, entire, glabrous; tube cylindric, 3.0–4.0 \text{ mm} long (3.5–4.0 \text{ mm} \textit{in vivo}), 4.0–5.0 \text{ mm} diam. (5.5–6.5 \text{ mm} \textit{in vivo}); limb flaring or straight (straight \textit{in vivo}), coriaceous, 3.0–4.5 \text{ mm} long, lobes deltoid, 1.5–2.5 \times 2.5–3.5 \text{ mm}, margin eciliate, marginal gland present, apex acute, sinuses v-shaped. Corolla aestivation valvate, red or rose at base, white at apex, carnose, bistratose, urceolate, terete, 15.0–17.0 \text{ mm} long (16.0–19.0 \text{ mm} \textit{in vivo}), 5.0–7.0 \text{ mm} diam. (7.0 \text{ mm} \textit{in vivo}), 3.0 \text{ mm} diam. at throat (3.0–5.0 \text{ mm} \textit{in vivo}), glabrous on both sides; lobes deltoid, 1.5 \times 1.5–2.0 \text{ mm}. Stamens connate, 4.1.0–4.30 \text{ mm}, not adherent to corolla. Long stamens 9.0 \text{ mm} long; filaments straight, 6.50 \times 0.80–1.00 \text{ mm}, apically puberulous, the hairs eglandular and unicellular; anthers 3.40–3.60 \text{ mm} long; thecae nonprognathous, 2.10–2.20 \text{ mm} long, 0.50–0.60 \text{ mm} wide, glabrous, not appendiculate; tubules parallel, 1.10–1.40 \text{ mm} long, 0.40–0.50 \text{ mm} diam., dehiscing by latrorse pores, pores 0.50–0.60 \text{ mm} long, margin entire. Short stamens like those of the longer cycle except for 7.70–7.90 \text{ mm} long, filaments 4.60–4.90 \times 1.00–1.20 \text{ mm}, anthers thecae 1.90–2.20 \text{ mm} long, 0.60 \text{ mm} wide, tubules 1.40–1.60 \text{ mm} long, dehiscing by introrose pores. Nectary disk flat, glabrous; style 14.0–16.0 \text{ mm} long, included. Berry not seen.
**Distribution and ecology.** *Orthaea paniculata* is only known from the type specimen, collected in Cauca, in the western slope of the Andes of Colombia, at 2300–2600 m (Fig. 3.15). Flowering in April.

**Etymology.** The specific epithet refers to the distinctive paniculate inflorescence.

Morphologically, this is an isolated species in the genus. The paniculate inflorescences, and the glabrous and short corollas (15–17 mm long) set *Orthaea paniculata* apart from the other members of the genus.


Terrestrial shrubs 2 m tall. **Young branchlets** complanate or terete, 2.0–5.0 mm diam., smooth, glabrous; mature branchlets glabrous, bark not exfoliating. **Axillary** buds complanate or globose, stipitate, stalk 0.40–0.80 mm long, imbricate or valvate, ovate, 0.70–1.50 mm long, ecarinate, margin entire, eciliate or ciliate, the hairs glandular and multicellular, apex rounded, rounded-mucronate or obtuse, abaxial side glabrous. **Leaves** alternate, nodes 0.60–3.30 cm long; petiole canaliculate or terete, 3.0–8.0 mm long, smooth or rugose in dried material, glabrous; lamina coriaceous, ovate or elliptic, 4.40–8.50 × 1.70–4.20 cm, base obtuse, cuneate or rounded, margin entire, revolute in
dried material, eciliate, apex cuspidate or acuminate, adaxial side glabrous or strigose and glabrescent, the hairs glandular and multicellular, abaxial side strigose and glabrescent, the hairs glandular and multicellular; venation acrodromous, basal or suprabasal, perfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 1–2, raised on abaxial side, impressed or raised on adaxial side. **Inflorescence** axillary or terminal, a 5–20-flowered raceme; axis 28.0–60.0 mm long, elongating up to 54.0–108.0 mm when fruiting, pink or red, scabrous or glabrescent,
hairs glandular and multicellular, peduncle 1.0–25.0 mm long, rachis 21.0–57.0 mm long; bracts of the inflorescence early caducous, chartaceous, ovate, 3.0–10.0 × 3.0–8.0 mm, striate or smooth, margin entire, eciliate or ciliate, the hairs glandular and multicellular, apex obtuse, rounded or acute, glabrous on both sides; floral bracts early caducous; pedicel pink or red, stout or slender, 14.0–42.0 mm long, markedly swollen at apex, 0.5–1.0 mm diam. at base, 2.0–6.5 mm diam. at apex, glabrous or scarcely scabrous, the hairs glandular and multicellular; bracteoles early caducous, basal or medial, subopposite, red or pink, oblanceolate, ovate or linear, 2.0–7.0 × 1.20–2.00 mm, margin entire, ciliate, the hairs glandular and multicellular, apex obtuse or acute, glabrous on both sides. **Calyx** aestivation valvate, pink or red, tubular or cupuliform, 10.0–15.0 mm long (15.0–17.0 mm *in vivo*), stipitate or sessile (sessile *in vivo*), terete, apophysate or rounded at base, apophysis perpendicular, entire, glabrous or scarcely scabrous, the hairs glandular and multicellular; tube cylindric or cupuliform, 4.0–6.0 mm long (4.0–5.0 mm *in vivo*), 3.0–7.0 mm diam. (8.0–9.0 mm *in vivo*); limb flaring, chartaceous, 6.0–9.0 mm long, lobes ovate, 2.5–5.5 × 2.0–4.0 mm, margin eciliate, marginal gland present, apex acute, sinuses v-shaped. **Corolla** aestivation valvate, white with pink or white at base, white with pink or white at apex, carnose, bistratose, tubular, terete, 14.0–20.0 mm long, 3.0–8.0 mm diam. (7.0 mm *in vivo*), 2.0–4.0 mm diam. at throat (4.0 mm *in vivo*), abaxial side pubescent, the hairs glandular and multicellular, adaxial side glabrous; lobes ovate or deltoid, 1.0–3.0 × 1.30–3.00 mm. **Stamens** distinct, not adherent to corolla. Long stamens 7.50–9.80 mm long; filaments straight, 4.30–6.30 × 1.10 mm, glabrous or apically puberulous, the hairs eglandular and unicellular; anthers 3.30–4.40 mm long; thecae slightly
prognathous or nonprognathous, 2.10–3.00 mm long, 0.70–0.80 mm wide, glabrous, not appendiculate; tubules parallel, 1.20–2.00 mm long, 0.60 mm diam., dehiscing by latrorse pores, pores 0.50–0.80 mm long, margin entire. Short stamens like those of the longer cycle except for 5.50–8.40 mm long, filaments 3.30–5.00 × 1.40 mm, anthers 3.10–4.40 mm long, thecae nonprognathous or slightly prognathous, 2.30–2.60 mm long, tubules 0.60–0.70 mm diam., dehiscing by introrse pores. Nectary disk flat, glabrous; style 16.0–27.0 mm long, included. Berry not seen.

**Distribution and ecology.** *Orthaea peregrina* is found in the western slope of the Andes of Colombia, in Chocó and Valle del Cauca departments, at 2000–3000 m (Fig. 3.16). Flowering specimens have been collected in April, July, and August; fruiting in February, April, and August.


**Etymology.** “Peregrina” means exotic or strange. Thus the name makes reference to the multiseriate glandular hairs of the corolla, a very rare type of hair in neotropical Vaccinieae.
Orthaea peregrina belongs to a group of species from western Colombia and Ecuador characterized by the glandular hairs in the abaxial side of corolla. This group also includes O. eteocles, O. glandulifera, and O. medusula. Their differences are discussed under O. eteocles.

Figure 3.16: Geographic distribution of Orthaea peregrina.

Cruces and Tambomayo, 13° 11' S, 71° 36' W, 3300–3400 m, 25 Apr 1914 (fl), A. Weberbauer 6925 (holotype B, destroyed; lectotype MOL [designated by Luteyn et al. (2008, p. 132)]; isolectotypes F!, G!, GH!, US!).

Terrestrial shrubs 4 m tall. Young branchlets ridged, complanate or angular, 1.0–3.0 mm diam., smooth, puberulous, the hairs glandular or eglandular, unicellular or multicellular; mature branchlets glabrous or puberulous, the hairs eglandular and unicellular, bark not exfoliating. Axillary buds complanate, stipitate, stalk 0.50–1.00 mm long; prophylls 2, imbricate, ovate, 1.00–2.20 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate, abaxial side glabrous. Leaves alternate, nodes 0.40–2.00 cm long; petiole semiterete, 2.0–4.0 mm long, smooth in dried material, puberulous or glabrous, the hairs glandular or eglandular, unicellular or multicellular; lamina chartaceous, elliptic or ovate, 3.60–6.60 × 1.10–2.20 cm, base cordate or rounded, margin entire, flat or revolute in dried material, minutely ciliate, apex acuminate, adaxial side glabrous or strigose, the hairs glandular and multicellular, abaxial side strigose, the hairs glandular and multicellular; venation acrodromous or pinnate, suprabasal, perfect or imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous or brochidodromous, prominent lateral veins 1–5, raised on abaxial side, impressed on adaxial side. Inflorescence axillary, a 10–18-flowered raceme; axis 14.0–24.0 mm long, scarcely puberulous or glabrous, hairs eglandular and unicellular, peduncle 1.0–3.0 mm long, rachis 11.0–23.0 mm long; bracts of the inflorescence early caducous, chartaceous, ovate or elliptic, 3.0–6.5 × 1.0–3.0 mm, smooth, margin entire, eciliate or ciliate, the hairs glandular and multicellular, apex acute, obtuse or rounded, glabrous on
both sides; floral bracts early caducous, shape and size homogeneous along the rachis, ovate or elliptic, 3.0–6.5 × 1.0–3.0 mm, smooth, margin entire, eciliate or ciliate, the hairs glandular and multicellular, apex rounded, acute or obtuse, glabrous on both sides; pedicel slender or stout, 5.0–9.0 mm long, not markedly swollen at apex, 0.50–0.70 mm diam. at base, 0.50–1.50 mm diam. at apex, glabrous; bracteoles early caducous or persistent, basal, opposite, ovate, 0.80–3.00 × 0.70–1.10 mm, margin entire, ciliate or eciliate, the hairs eglandular and unicellular, apex acute, obtuse or obtuse-mucronate, glabrous on both sides. **Calyx** aestivation valvate, red, campanulate, 3.50–5.00 mm long, sessile, terete, apophysate at base, apophysis perpendicular or parallel, ridged or entire, glabrous; tube cylindric, 2.0–2.5 mm long, 1.80–3.00 mm diam.; limb flaring, chartaceous, 2.0–3.0 mm long, lobes deltoid, 0.50–1.00 × 1.50–2.00 mm, margin eciliate, marginal gland absent, apex acuminate, sinuses u-shaped. **Corolla** aestivation valvate, red at base, carnose, tubular, splitting longitudinally 1.0–5.5 mm in anthesis, terete, 12.0–18.0 mm long, 2.50–3.00 mm diam., 2.0–4.0 mm diam. at throat, glabrous on both sides; lobes deltoid, 0.70–1.00 × 0.90–1.50 mm. **Stamens** distinct, not adherent to corolla. Long stamens 6.50–7.00 mm long; filaments straight, 3.00–3.50 × 0.30–0.50 mm, apically puberulous, the hairs eglandular and unicellular; anthers 3.40–4.80 mm long; thecae nonprognathous, 2.00–3.00 mm long, 0.40 mm wide, glabrous, not appendiculate; tubules parallel, 1.30–1.70 mm long, 0.40–0.60 mm diam., dehiscing by latrorse pores, pores 1.20–1.40 mm long, margin entire. Short stamens like those of the longer cycle except for 4.80–5.50 mm long, filaments 0.80–2.00 × 1.0 mm, anthers 3.60–4.80 mm long, thecae 1.80–2.50 mm long, 0.30–0.50 mm wide, tubules 1.50–2.80 mm long, 0.50–0.70 mm diam., dehiscing by
introrse pores. Nectary disk flat, glabrous; style 12.0–17.0 mm long, exerted. **Berry** not seen.

**Distribution and ecology.** Endemic to Cuzco Department, Peru, at 3000–3400 m (Fig. 3.17). Flowering specimens have been collected in January and April.

**Specimens examined.** **PERU. Cuzco:** Quispicanchi, Marcapata, 13° 30' S, 70° 52' W, 3000 m, 17 Feb 1929 (fl), A. Weberbauer 7814 (F, NY).

**Etymology.** The specific epithet refers to the pinnate venation of the type collection; however acrodromous venation is also present in the species.

*Orthaea pinnatinervia* is morphologically similar to *O. fissiflora*, however the former differs from the latter by the basally red corolla (vs. green in *O. fissiflora*), distinct staminal filaments (vs. connate), and shorter stamens (long cycle 6.5–7.0 mm vs. 7.4–8.4 mm, short cycle 4.8–5.5 mm vs. 6.3–7.0 mm).


Terrestrial or epiphytic **shrubs** 2–12 m tall. **Young branchlets** terete, angular or complanate, 3–7 mm diam., smooth, glabrous; mature branchlets glabrous, bark not exfoliating. **Axillary** buds complanate or globose, stipitate, stalk 0.5–2.0 mm long; prophylls 2, valvate, ovate, triangular or orbicular, 0.80–3.80 mm long, carinate or ecarinate, margin
entire, ciliate or eciliate, the hairs glandular and multicellular, apex caudate, obtuse or obtuse-mucronate, abaxial side glabrous. Leaves alternate, nodes 0.20–5.50 cm long; petiole semiterete, terete or canaliculate, 4.0–11.0 mm long, rugose in dried material, glabrous; lamina coriaceous, elliptic or ovate, 7.70–19.00 × 2.20–7.80 cm, base cuneate, rounded or obtuse, margin entire, revolute or flat in dried material, eciliate, apex acuminate, acute or rostrate, adaxial side glabrous, abaxial side scarcely strigose or strigose and
glabrescent, the hairs glandular and multicellular; venation acrodromous, suprabasal, imperfect or perfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous or brochidodromous, prominent lateral veins 1–3, raised on abaxial side, impressed or raised on adaxial side. Inflorescence axillary or terminal, a 10–30-flowered raceme; axis 20.0–54.0 mm long, elongating up to 38.0–51.0 mm when fruiting, pink or cream with pink, glabrous, peduncle 0.5-3.0 mm long, rachis 17.0–53.5 mm long; bracts of the inflorescence persistent or early caducous, yellow, chartaceous or membranose, lanceolate, triangular or oblong, 10.0–25.0 × 2.0–8.0 mm, smooth, margin entire, ciliate or eciliate, the hairs glandular and multicellular, apex acumin ate, acute, caudate or obtuse, glabrous on both sides; floral bracts early caducous, chartaceous, shape and size heterogeneous or homogeneous along the rachis, triangular or obovate, 4.0–7.0 × 1.0–2.0 mm, smooth, margin entire, eciliate, apex acute or acuminate, glabrous on both sides; pedicel pink or cream with pink, stout, 6.0–27.0 mm long (30.0–31.0 mm in vivo), not markedly swollen at apex, 0.5–1.0 mm diam. at base (1.5–2.0 mm in vivo), 0.5–2.0 mm diam. at apex (3.0–3.5 mm in vivo), glabrous; bracteoles early caducous, basal, subopposite or opposite, pink, lanceolate, linear or triangular, 0.70–2.50 × 0.20–0.70 mm, margin entire, ciliate or eciliate, the hairs glandular and multicellular, apex acuminate, caudate or acute, glabrous on both sides. Calyx aestivation valvate, dark pink, pink or red, campanulate, tubular or cupuliform (tubular, urceolate, subglobose or subconic in vivo), 2.0–6.0 mm long (4.50–8.70 mm in vivo), sessile, terete, truncate or rounded at base, glabrous; tube cylindric or obconic, 1.50–4.50 mm long (3.20–6.50 mm in vivo), 1.5–5.0 mm diam. (4.70–8.50 mm in vivo); limb flaring or straight (flaring in
vivo), chartaceous or membranose, 0.5–3.0 mm long, lobes deltoid, 0.20–1.00 × 0.30–3.00 mm, margin eciliate, marginal gland absent, apex acute or obtuse-mucronate, sinuses u-shaped. **Corolla** aestivation valvate, pink or red at base, white at apex, membranose, bistratose, tubular, terete, 24.0–34.0 mm long (28.0 mm in vivo), 5.0–6.5 mm diam. (7.5 mm in vivo), 3.0–4.5 mm diam. at throat (2.5 mm in vivo), glabrous on both sides; lobes ovate or deltoid, 0.5 × 0.5–1.0 mm. **Stamens** distinct, not adherent to corolla. Long stamens 6.00–9.50 mm long; filaments straight, 3.60–6.00 × 0.50–1.10 mm, apically puberulous, the hairs eglandular and unicellular; anthers 2.70–4.20 mm long; thecae nonprognathous or prognathous, 1.50–2.00 mm long, 0.40–0.70 mm wide, glabrous, not appendiculate; tubules parallel, 1.00–2.20 mm long, 0.40–0.70 mm diam., dehiscing by acroscopic pores, pore margin entire, hypocrateriform or usually hypocrateriform. Short stamens like those of the longer cycle except for 3.90–7.10 mm long, filaments 2.20–4.60 × 0.50–1.40 mm, anthers 2.60–4.50 mm long, thecae prognathous, nonprognathous or slightly prognathous, 1.20–2.00 mm long, 0.40–1.10 mm wide, tubules 1.00–2.20 mm long, 0.40–0.60 mm diam., pores 0.10–0.20 mm long, margin entire, hypocrateriform, erose or usually hypocrateriform. Nectary disk flat, glabrous; style 21.0–33.0 mm long, exerted. **Berry** black, spherical, 5.0–8.0 mm long, 5.0–7.0 mm diam., lobes ascending, glabrous; seeds ellipsoidal, prismatic, luniform or isodiametric, 1.00–1.40 × 0.50–0.80 mm, without mucilaginous coat.

**Distribution and ecology.** Eastern slope of the Andes, from Tungurahua, Ecuador, south to Pasco, Peru, at 900–2650 m (Fig. 3.18). Flowering and fruiting year round.

**Specimens examined.** ECUADOR. Loja: Loja–Zamora rd. km 9–10, 3° 58′ S,

1310 m, 19 Sep 2003 (fl, fr), *J. Perea* 392 (NY×2). Oxapampa–San Alberto, 1850 m, 10 Oct 1980 (fr), *C. Díaz* 1613 (MO). **San Martín**: Rioja, San Martín side (E) of Puente Nieva over Rió Nieva (ca. Km 372-373 along Carretera Marginal), ca. 150 km NNE of Chachapoyas, 5° 40′ S, 77° 46′ W, 2040 m, 6 Jul 2002 (fl), *J. L. Luteyn* 15515 (NY).

**Unknown department**: Cuchero, Sep 1829 (fl), *E. F. Poeppig* 1305 (W); 1830 (fl), 1513 (F, W×2). Unknown locality, 27 Dec 1878 (fl), *M. Martinet* 1624 (P).

**Etymology**. The epithet *secundiflora* refers to the secund inflorescence.

As one of the most widely distributed species the genus, *Orthaea secundiflora* displays a range of morphological plasticity hardly seen in other species of *Orthaea* s.s. Most of the Ecuadorian collections tend to have small prophylls with caudate apex, thicker leaves with strongly revolute margins, and obtuse inflorescence bracts. Peruvian specimens have elongated prophylls with caudate apex, thinner leaves with almost flat margin, and acuminate or caudate inflorescence bracts. Populations with intermediate morphology are restricted to the Nangaritza river basin (eastern Zamora-Chinchipe province, Ecuador). The type collection cannot be unambiguously assigned to any of these morphotypes because it displays a combination of features from all three. Despite the geographic correlation of characters observed in this species, there are no clear boundaries among morphotypes as they overlap to some extent. Thus, all the cited specimens are considered a single entity and any further taxonomical segregation is avoid at this time.

Terrestrial or epiphytic shrubs 1.5–3 m tall. Young branchlets ridged or complanate, 1.0–3.0 mm diam., smooth, glabrous or scarcely strigose, the hairs glandular and multicellular; mature branchlets glabrous, bark not exfoliating. Axillary buds globose, stipitate,
stalk 0.40–1.50 mm long; prophylls 2, valvate or imbricate, ovate or oblate, 1.00–3.30 mm long, ecarinate or carinate, margin entire, ciliate or eciliate, the hairs glandular and multicellular, apex obtuse, obtuse-mucronate or acute, abaxial side glabrous. **Leaves** alternate or subopposite, nodes 0.10–3.40 cm long; petiole semiterete or terete, 2.5–7.0 mm long, rugose in dried material, glabrous or strigose, the hairs glandular and multicellular; lamina coriaceous or chartaceous, elliptic or ovate, 4.00–12.00 × 0.80–3.60 cm, base obtuse, cuneate or rounded, margin entire, flat or revolute in dried material, eciliate, apex acuminate or acute, adaxial side glabrous, scarcely strigose or scarcely scabrose, the hairs glandular and multicellular, abaxial side scabrose or strigose, the hairs glandular and multicellular; venation acrodromous, suprabasal or basal, imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 1–3, raised on abaxial side, impressed on adaxial side. **Inflorescence** axillary, a 13–30-flowered raceme; axis 16.0–70.0 mm long, elongating up to 57.8–69.0 mm when fruiting, red, glabrous, peduncle 2.0–7.0 mm long, rachis 9.0–68.0 mm long; bracts of the inflorescence early caducous or persistent, red or green, membranose or chartaceous, obovate, ovate, oblate or orbicular, 2.0–15.0 × 4.0–10.0 mm, smooth, margin entire, eciliate, apex rounded, glabrous on both sides; floral bracts early caducous, red or green, membranose, shape and size heterogeneous along the rachis, elliptic or lanceolate, 8.0–15.0 × 2.5–6.0 mm, smooth, margin entire, eciliate or ciliate, the hairs glandular and multicellular, apex acute or obtuse, adaxial side strigose or glabrous, the hairs glandular and multicellular, abaxial side glabrous or strigose; pedicel red, stout, 8.0–15.0 mm long, not markedly swollen at apex, 0.5–1.0 mm diam. at base, 0.5–1.0 mm diam. at apex,
glabrous; bracteoles early caducous, medial or basal, subopposite or opposite, red, ovate or elliptic, 1.10–4.50 × 0.60–1.50 mm, margin entire, ciliate or eciliate, the hairs glandular and multicellular, apex acute, adaxial side glabrous or strigose, the hairs glandular and multicellular, abaxial side glabrous. **Calyx** aestivation valvate, red, reddish green or dark green, campanulate or tubular (obclavate *in vivo*), 3.0–7.0 mm long (5.5–7.0 mm *in vivo*), sessile, terete, angulate or occasionally slightly angulate, apophysate or occasionally truncate at base, apophysis parallel or perpendicular, entire or ridged, glabrous; tube cylindric or obconic, 1.5–3.0 mm long (1.5–3.5 mm *in vivo*), 2.0–3.5 mm diam. (4.0–5.7 mm *in vivo*); limb flaring (straight *in vivo*), chartaceous or membranose, 1.5–4.0 mm long, lobes ovate or deltoid, 0.40–2.40 × 1.70–3.00 mm, margin eciliate, marginal gland present or occasionally absent, apex obtuse-mucronate, acute or obtuse, sinuses v-shaped or occasionally u-shaped. **Corolla** aestivation valvate, red or occasionally dark red at base, white, red, dark red or pink at apex, chartaceous or carnose, bistratose, tubular or urceolate, splitting longitudinally 1.0–8.0 mm in anthesis, terete or slightly angulate, 13.0–25.0 mm long (15.0–21.0 mm *in vivo*), 2.0–6.0 mm diam. (4.00–8.60 mm *in vivo*), 1.5–4.0 mm diam. at throat (3.00–4.40 mm *in vivo*), glabrous on both sides; lobes deltoid or ovate, 0.50–2.50 × 0.50–2.80 mm. **Stamens** distinct or connate, not adherent to corolla. Long stamens 6.20–9.50 mm long; filaments straight, 3.00–5.50 × 0.70–0.80 mm, apically puberulous, the hairs eglandular and unicellular; anthers 3.40–4.70 mm long; thecae nonprognathous, 1.70–3.00 mm long, 0.50–0.60 mm wide, glabrous, not appendiculate; tubules divergent or slightly divergent, 1.20–2.30 mm long, 0.50–0.60 mm diam., dehiscing by latrorse pores, pores 0.90–1.20 mm long, margin entire. Short stamens like those
of the longer cycle except for 4.50–7.40 mm long, filaments 2.00–4.00 × 0.60–1.00 mm, anthers 3.20–4.20 mm long, thecae 1.80–2.50 mm long, tubules parallel, 1.10–2.00 mm long, dehiscing by introrse pores. Nectary disk flat, glabrous or slightly raised, glabrous; style red, 16.0–27.0 mm long, exerted. Berry black or green with red, spherical, 6.0–11.0 mm long, 5.5–9.0 mm diam., lobes ascending, glabrous; seeds prismatic or ellipsoidal, 0.70–1.60 × 0.40–0.90 mm, mucilaginous coat absent.

**Distribution and ecology.** *Orthaea weberbauerii* is found in northern Bolivia (La Paz department) and southern Peru (Cuzco and Puno departments), at 2000–3700 m (Fig. 3.19). Flowering in October–July. Fruiting in March–September and December.


**Etymology.** Named after August Weberbauer, German botanist who collected the type specimen.

Peruvian populations of *Orthaea weberbauerii* have floral bracts and bracteoles with glandular hairs on the adaxial surface and margin, whereas Bolivian collections are completely glabrous. Overall, indumentum seems to be progressively lost as the plants are collected southwards; however, specimens from central Peru with well-preserved bracts and bracteoles are needed to fully understand the intraspecific variability of this species. *O. weberbauerii* is morphologically close to *O. fissiflora* and *O. pinnatinervia*, but the former has globose axillary buds (vs. complanate in the other two species), larger floral bracts (8–15...
mm vs 2.5–6.5 mm) that have different sizes along the inflorescence axis (vs. homogeneous size along the axis), and glandular calyx limb margin (vs. eglandular calyx limb margin).

Figure 3.19: Geographic distribution of *Orthaea weberbauri*. 

*Figure 3.19: Geographic distribution of Orthaea weberbauri.*
3.7 Excluded taxa


Excluded *Orthaea* s.l. taxa

Several species of *Orthaea* s.l. were not included in the taxonomic treatment of *Orthaea* s.s. Phylogenetic analyses suggest such taxa are more closely related to other lineages of Vaccinieae than to *Orthaea* s.s. Unfortunately, the exact phylogenetic affinities of most of the excluded species are still unknown, therefore precluding the proposal of new combinations for them. Their correct taxonomic placement is pending of phylogenetic analyses of related clades to *Orthaea* s.l. that include type species of putative genera. Lastly, the species previously known as *Empedoclesia* do form a robust group and valid combinations are already available for them.


**Illegitimate names**


**Incertae sedis**


Type. Peru. Cuzco: Valle de Pillahuata, Infiernillo, 3350 m, June 1933, F. L. Herrera 3656 (holotype B, destroyed). The holotype was the sole specimen cited in the protologue (Sleumer 1934). Several collections from Peru were previously annotated as O. ignea; however, after a detailed examination, none of these specimens and neither any from Peru and Bolivia matched the description (Sleumer 1934). Thus, the taxonomic status of this species remains unresolved.

### 3.8 Index of examined specimens

**Numerical list of taxa**

1. Orthaea abbreviata Drake

2. Orthaea boliviensis Fedtsch. & Basil.
3. *Orthaea carnosiflora* N. R. Salinas & Pedraza

4. *Orthaea ecuadorensis* Luteyn

5. *Orthaea eteocles* N. R. Salinas

6. *Orthaea ferreyrae* A. C. Sm.

7. *Orthaea fissiflora* N. R. Salinas & Pedraza

8. *Orthaea glandulifera* Luteyn

9. *Orthaea medusula* Pedraza

10. *Orthaea oriens* Luteyn

11. *Orthaea paniculata* Luteyn

12. *Orthaea peregrina* A. C. Sm.


14. *Orthaea secundiflora* (Poepp. & Endl.) Klotzsch

15. *Orthaea weberbaueri* Hoerold

**List of exsiccate**

C. Antezana 1548 (7).

A. C. Araújo 215 (2).
J. Aronson 1024 (1).

P. J. Barbour 2941 (1).

S. G. Beck 3188 (15), 7256 (2), 7603 (7), 9255 (2), 13572 (15), 13957 (2), 14927 (7), 18553 (2), 24435 (2), 28925 (15), 31065 (15).

H. Beltrán 811 (1), 842 (1).

J. C. Betancur 2815 (8).

J. D. Boeke 1395 (7).

A. E. Brant 1406 (8), 1606 (8).

T. C. Bridges 103 (2), s.n. (2).

O. Buchtien 2902 (7), 5515 (2), 5517 (2), 5518 (2), 7432 (2).

G. Calatayud 1196 (3), 1340 (15).

R. Callejas Posada 9864 (8).


J. Campos 4202 (1), 4606 (1), 5884 (14).

A. Cano E. 2866 (3), 3855 (15), 5332 (15).

G. Cárdenas 35 (1).
D. Cárdenas López 3289 (8).

L. Cayola 2768 (2).

C. Cerón Martínez 2915 (10).

J. L. Clark 5977 (1), 6673 (15).

A. Cogollo 3100 (8).

T. B. Croat 51531 (15), 84239 (5), 89846 (10).

J. Cuatrecasas 21771 (12).

H. Cuming 180 (2).

C. Díaz 1613 (14), 8770 (1), 10157 (1), 10297 (1).

C. H. Dodson 15361 (4).

L. J. Dorr 5912 (1), 6711 (15).

T. R. Dudley 10547 (2).

C. Dziedzioch 128 (1).

R. A. Ferreyra 1671 (6), 1671-A (14), 6709 (6).

R. Fonnegra G. 5435 (8), 5517 (8).

E. Forero 2155 (12), 2871 (12).
A. Freire Fierro 2276 (1).

A. Fuentes 8706 (15), 8842 (2), 8863 (15), 11355 (15), 11824 (2), 12188 (15).

W. Galiano Sánchez 4187 (15), 6357 (3).

A. Garmendia 1421 (14).

M. C. Gay 885 (15), s.n. (15).

A. H. Gentry 22903 (1), 35883 (6), 44690 (15), 70107 (5), 76172 (8), 79992 (14).

A. Gerique 101 (14).

T. H. Goodspeed 25400 (7).

G. W. Harling 12678 (1), 21371 (1), 24406 (10), 26839 (1).

E. Hennipman 8003 (7).

L. B. Holm-Nielsen 3564 (14), 4087-B (10).

I. Huamantupa Chuquimaco 3225 (3), 3784 (6), 3834 (3), 9628 (15).

F. Hurtado 446 (10).

P. L. Ibisch 93.0096 (2), 93.0288 (2).

J. Jones 9110 (6).

A. Juncosa 2431 (8).
C. Kajekai 777 (1).

T. Katan 479 (1).

S. D. Knapp 7741 (1).

B. A. Krukoff 10800 (2).

L. R. Landrum 4584 (6).

G. P. Lewis 3585 (14).

Lobb 734 (2).

H. Lugo S. 1157 (4).

J. L. Luteyn 5430 (6), 5431 (6), 5486 (3), 5491 (6), 5785 (14), 6415 (15), 7073 (8), 7210 (8), 7402 (11), 10540 (8), 10652 (8), 10727 (8), 11302 (14), 12072 (8), 12083 (8), 12179 (8), 12438 (8), 12700 (12), 13425 (1), 13613 (15), 13618 (7), 13710 (15), 13758 (7), 14568 (14), 14661 (10), 14997 (8), 15094 (14), 15375 (1), 15391 (1), 15439 (7), 15445 (7), 15449 (7), 15468 (7), 15479 (15), 15515 (14), 15603 (7), 15609 (7), 15610 (7), 15611 (7), 15620 (15), 15634 (7), 15639 (15), 15693-A (15), 15709 (15), 15734 (7).

M. T. Madison 2488 (10), 3277 (14), 3365 (14).

J. E. Madsen 7648 (1).

G. Mandon s.n. (2).
M. Martinet 1624 (14).

S. Matezki 330 (1), 336 (1).

B. Merino 4742 (1), 4781 (10).

Y. E. Mexia 8200 (14).

A. Monteagudo M. 4514 (6), 4799 (6), 4803 (3), 7484 (14), 12020 (3), 12309 (3), 13618 (6).

C. Morales 1896 (1), 1991 (1).

D. A. Neill 6100 (4), 14922 (1).

R. Orellana 1817 (15).

E. M. Ortiz Valencia 99 (15), 334 (3), 348 (3), 381 (6), 423 (6), 475 (3), 505 (6), 720 (3), 842 (3), 1039 (6), 1067 (14), 1085 (14).

W. A. Palacios 8449 (14), 8620 (14), 13036 (1).

R. W. Pearce 731 (2), s.n. (15).

L. P. Pedraza-Peñalosa 1084 (8), 1092 (8), 1125 (9), 1753 (8), 1932 (8), 2071 (8).

T. D. Pennington 16791 (1).

J. Perea 392 (14), 1376 (3), 2452 (1), 2813 (14), 3023 (14), 3151 (2).
J. J. Pipoly 16633 (8).

T. C. Plowman 5634 (6).

E. F. Poeppig 1305 (14), 1513 (14), 1525 (14).

Poortmann 314 (1).

W. Quizhpe 1531 (1), 2143 (1), 2298 (1), 2367 (1), 2779 (1), 2856 (1).

J. G. Ramírez 4026 (8).

D. Reyes 1181 (1).

N. R. Salinas 653 (9), 710 (1), 711 (1).

N. Salinas 2144 (7), 2542 (7).

D. Sánchez 1720 (8).

I. M. Sánchez Vega 10037 (14).

C. Sandeman 4514 (6), 4588 (6).

J. Schönenberger 494 (7).

J. M. Schunke-Vigo 5237 (6).

P. A. Silverstone-Sopkin 4516 (9), 4743 (9), 4747 (12), 4757 (9).

D. R. Simpson 852 (6).
D. N. Smith 4568 (1), 4846 (1), 5951 (6), 7674 (3), 7767 (6).

J. C. Solomon 9219 (15), 10842 (2), 12268 (7), 12311 (7), 12987 (2), 16371 (7), 16538 (7),
18223 (7), 18697 (15).

B. A. Stein 2279 (6), 3310 (8).

E. Suelli 1434 (6), 1445 (6).

L. Suin 1721 (14), 1844 (14), 1943 (14).

L. Valenzuela G. 743 (6), 3897 (2), 8082 (15).

V. Van den Eynden 588 (1), 778 (1).

H. H. van der Werff 9497 (5), 13077 (1), 13215 (1), 15613 (1), 15638 (1), 19380 (1), 21680
(1).

C. Vargas 305 (15), 9782 (15).

R. Vásquez Martinez 26328 (1), 26459 (1), 26474 (1), 30262 (6), 31077 (6), 33762 (3).

G. Villa 2021 (5).

A. Weberbauer 684 (15), 4753 (), 6925 (13), 7814 (13).

M. Weddell s.n. (2).

M. Weigend 2000/437 (15).
F. Werner 1870 (1), 1882 (1), 2168 (1), 2189 (14), 2272 (10).

J. West 7057 (15).

F. Woytkowski 34513 (14), 34521 (14), 35482 (6).

B. L. Wrigley 133 (10).

F. Zenteno 944 (15).

F. O. Zuloaga 1857 (2)
Appendix A

Molecular sequences used in the biogeographic study

Genebank accessions order: ITS, matK, ndhF. NA: sequence not available yet in Genbank (collector and collection number then are cited).

*Agapetes hosseana*, AF382651.1, U89752.1, AF419720.1; *Andromeda polifolia*, AF358872.1, AF124569.1, AF419722.1; *Anthopterus cuneatus*, AF382656.1, AF382746.1, AY331921.1; *Anthopterus revolutus*, AF382655.1, AY331893.1, AY331920.1; *Bejaria aestuans*, AF404817.1, GU176669.1, DQ002362.1; *Bejaria racemosa*, U48604.1, U61327.1, DQ002367.1; *Bejaria resinosa*, GU176622.1, DQ002352.1, DQ002368.1; *Calluna vulgaris*, HQ58884.1, U61326.1, GU176722.1; *Cavendishia angustifolia*, KJ78823.1, KJ788254.1, KJ788192.1; *Cavendishia arizonensis* (Luteyn 15286), NA, NA, NA; *Cavendishia axillaris* (Luteyn 15311), NA, NA, NA; *Cavendishia bracteata*, AY331867.1, AY331894.1, AY331922.1; *Cavendishia callista*, (Clarke 5241), NA, NA, NA; *Cavendishia calycina*, (Powell 8), NA, NA, NA; *Cavendishia capitulata*, AY331868.1, AY331895.1, AY331923.1; *Cavendishia chiriensis* (Luteyn 15540), NA, NA, NA; *Cavendishia grandifolia*, AY331869.1, AY331896.1, AY331924.1; *Cavendishia isernii var. isernii* (Salinas 704), NA, NA, NA; *Cavendishia isernii var. pseudospicata* (Salinas 707), NA, NA, NA; *Cavendishia mariae* (Luteyn 15198), NA, NA, NA; *Cavendishia martii*, AF382658.1, AF382747.1, AY331925.1; *Cavendishia aff. martii* (Pedraza 1551), NA, NA, NA; *Cavendishia micayensis*, KJ788228.1, KJ788259.1, KJ788197.1; *Cavendishia nobilis* (Lewis 3414), NA, NA, NA; *Cavendishia oligantha* (Luteyn 15179), NA, NA, NA; *Cavendishia quereme* (Luteyn 15312), NA, NA, NA; *Cavendishia tarapotana* (Salinas 703), NA, NA, NA; *Cavendishia zamorensis* (Salinas 721), NA, NA, NA; *Ceratiola ericoides*, AF519552.1, AF519564.1, GU176717.1; *Ceratostema lanigerum*, AY331870.1, AY331897.1, AY331926.1; *Ceratoste-ma rauhii*, AY331871.1, AY331898.1, AY331927.1; *Ceratoste-ma regi-naldii*, AY331872.1, AY331899.1, AY331928.1; *Ceratoste-ma silvicola*, AY331873.1,
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## Appendix B

### Biogeographic matrix


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Appendix C

Genbank accession numbers of the sequences used in the phylogenetic study study

Genebank accessions order: ITS, matK, ndhF. If the sequence has not yet been submitted to Genbank, the collector’s name and collection number is cited. NA: accession number not available.

*Agapetes hosseana*, AF382651.1, U89752.1, AF419720.1; *Anthopterus cuneatus*, AF382656.1, AF382746.1, AY331921.1; *Anthopterus revolutus*, AY331866.1, AY331893.1, AY331920.1; *Cavendishia aff. martii* (Pedraza 1551), NA, NA, NA; *Cavendishia angustifolia*, KJ788223.1, KJ788254.1, KJ788192.1; *Cavendishia arizonensis* (Luteyn 15286), NA, NA, NA; *Cavendishia axillaris* (Luteyn 15311), NA, NA, NA; *Cavendishia bracteata*, AY331867.1, AY331894.1, AY331922.1; *Cavendishia callista* (Clarke 5241), NA, NA, NA; *Cavendishia calycina* (Powell 8), NA, NA, NA; *Cavendishia capitulata*, AY331868.1, AY331895.1, AY331923.1; *Cavendishia chiriquiensis* (Luteyn 15540), NA, NA, NA; *Cavendishia grandifolia*, AY331869.1, AY331896.1, AY331924.1; *Cavendishia isernii* var. *isernii* (Salinas 704), NA, NA, NA; *Cavendishia isernii* var. *pseudospicata* (Salinas 707), NA, NA, NA; *Cavendishia mariae* (Luteyn 15198), NA, NA, NA; *Cavendishia martii*, AF382658.1, AF382747.1, AY331925.1; *Cavendishia micayensis*, KJ788228.1, KJ788259.1, KJ788197.1; *Cavendishia nobilis* (Lewis 3414), NA, NA, NA; *Cavendishia oligantha* (Luteyn 15179), NA, NA, NA; *Cavendishia quereme* (Luteyn 15312), NA, NA, NA; *Cavendishia tarapotana* (Salinas 703), NA, NA, NA; *Cavendishia zamorensis* (Salinas 721), NA, NA, NA; *Ceratostema lanigerum*, AY331870.1, AY331897.1, AY331926.1; *Ceratostema rauhii*, AY331871.1, AY331898.1, AY331927.1; *Ceratostema reginaldii*, AY331872.1, AY331899.1, AY331928.1; *Ceratostema silvicola*, AY331873.1,
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Appendix D

Description of the morphological characters

**Continuous characters**

0. Inflorescence main axis length during flower anthesis (cm).
   If the inflorescence is branched, only the main axis was measured.

1. Calyx length (mm).
   Only dried specimens at anthesis were considered.

2. Calyx lobes length (mm).
   Only dried specimens at anthesis were considered.

3. Corolla length (mm).
   Only dried specimens at anthesis were considered.

4. Corolla sinus ridge length (mm).
   In bistratose corollas, the inner stratum of the corolla is exposed in the sinuses. The length of this exposure is here reported. Only dried specimens were considered.

5. Small stamens cycle: corolla length ratio.


7. Anther length (mm).
8. Anther: corolla length ratio.  
If there are size differences among the anthers of the same flower, the average ratio was then scored. Most of the sampled OTUs do not have noticeable anther size differences.

**Discrete characters**

9. Axillary bud shape: complanate (0), globose (1), lenticular (2).  
Only vegetative buds subtending fully mature leaves were scored.

10. Axillary bud prophylls aestivation: imbricate (0), valvate (1).  
Only the outermost prophylls in vegetative buds subtending fully mature leaves were scored.

11. Axillary bud prophylls apex: $< 90^\circ$ (0), $> 90^\circ$ (1).

12. Axillary bud prophylls abaxial eglandular hairs: present (0), absent (1).

13. Axillary bud prophylls abaxial glandular hairs: absent (0), present (1).

14. Axillary bud prophylls marginal glandular hairs: absent (0), present (1).

15. Leaf eglandular hairs: present (0), absent (1).  
On both sides of young leaves.

16. Leaf glandular hairs on the adaxial side: absent (0), present (1).

17. Leaf glandular hairs shape: filiform (0), muricate (1).

18. Leaf glandular hairs duration: persistent until leaf maturity (0), caducous on early stages of leaf development (1).

19. Leaf glands on the adaxial side: absent (0), present (1).  
Some species bear glandular punctuations on the abaxial side of leaves.

20. Leaf margin glandular protrusions along the margin: absent (0), present (1).  
Glandular tissue on the lamina margin include glandular hairs or teeth.

21. Leaf basal glandular invaginations: absent (0), present (1).  
Restricted to the base of the lamina or, less commonly, to the petiole-lamina junction.

22. Leaf primary venation framework: pinnate (0), acrodromous (1).

23. Leaf prominent lateral veins origin: suprabasal (0), basal (1).

24. Organization of reproductive units: inflorescences (0), solitary flowers (1).
25. Inflorescence a fascicle: absent (0), present (1).
26. Inflorescence a raceme: present (0), absent (1).
27. Inflorescence a panicle: absent (0), present (1).
28. Inflorescence flower orientation: secund (0), spiral (1).
29. Inflorescence rachis glandular hairs: absent (0), present (1).
30. Inflorescence rachis eglandular hairs: present (0), absent (1).
31. Inflorescence bracts: persistent during floral anthesis (0), early deciduous (1).
32. Floral bracts persistence: most of the bracts persistent during floral anthesis (0), most of the bracts early deciduous (1).
33. Floral bract: pedicel relative length: floral bract longer than the pedicel (0), floral bract smaller than the pedicel (1).
34. Floral bract apex: $>90^\circ$ (0), $<90^\circ$ (1).
35. Floral bracts glandular hairs: absent on both sides (0), present on at least one of the bract sides (1).
36. Floral bract eglandular hairs: present on at least one of the bract sides (0), absent on both sides (1).
37. Floral bract marginal glandular hairs: present (0), absent (1).
38. Pedicel diameter: not swollen at the apex (0), apically swollen (1).
39. Bracteole duration: persistent through flower anthesis (0), early cadudous (1).
40. Bracteole attachment on the pedicel: basal (0), medial (1), apical (2).
41. Bracteole marginal glandular hairs: absent (0), present (1).
42. Calyx hypanthium shape in cross section: terete (0), ridged (1), alate (2).
   The shape of hypanthium usually remains unchanged after drying, but it is easily scored in fresh or liquid-preserved material.
43. Calyx apophysis: absent (0), present (1).
   The apophysis definition proposed by Luteyn (1976) is followed: “a proliferation of the tissue at the very base of the calyx tube”.
44. Calyx apophysis orientation: parallel to flower longitudinal axis (1), perpendicular to flower longitudinal axis (0).
   This character is easily observed in fresh or liquid-preserved material.
45. Calyx apophysis margin: entire (0), lobed (1).
   This character is easily observed in fresh or liquid-preserved material.

46. Calyx limb texture after drying: membranaceous (0), chartaceous (1), coriaceous (2).

47. Calyx glandular hairs: present (0), absent (1).

48. Calyx eglandular hairs: present (0), absent (1).

49. Calyx merosity: 5-merous (0), 3-merous (1).

50. Calyx marginal glandular hairs: absent (0), present (1).

51. Calyx marginal glandular hairs shape: filiform (0), clavate (1).

52. Calyx marginal gland: absent (0), present (1).
   Some species bear a thin strip of glandular tissue along the margin of calyx lobes.

53. Calyx lobes fusion: irregularly fused in pairs (0), regular non fused (1).
   Adjacent calyx lobes can be fused partially. Although this fusion can be almost complete, tips of each lobe are always visible.

54. Calyx sinus shape: V-shaped (0), U-shaped (1).
   If the sinus were a laminar structure, “V-shaped” would correspond to acute, and “U-shaped” to rounded.

55. Corolla color at base: white (0), red or pink (1), green (2), orange (3).

56. Corolla color variation: homogeneous (0), apical color is different from basal color (1).
   This character aims to code the color variation within a single corolla. This character is independent from color variation among different flowers.

57. Corolla general shape: urceolate (0), tubular (1).

58. Corolla shape in cross section: terete (0), angular (1).

59. Corolla texture after drying: membranaceous (0), coriaceous (1).

60. Corolla eglandular hairs on the abaxial surface: present (0), absent (1).

61. Corolla eglandular hairs on the adaxial surface: present (0), absent (1).

62. Corolla glandular hairs on the abaxial surface: present (0), absent (1).
63. Corolla longitudinal split at anthesis: absent (0), present (1).
   During anthesis, corolla tears longitudinally from the sinuses towards the base. Although this phenomenon does not occur in all the flowers of a specimen, it becomes dominant as all the flowers in a plant mature.

64. Corolla epidermal layers: monostratose (0), bistratose (1).
   Bistratose corollas have its tissue arranged in two layers. The outer layer covers almost the whole abaxial surface of the corolla, and it is interrupted in the area between adjacent lobes. In that region only the inner layer is developed. In other groups of plants (e.g., Solanaceae), this thin layer between perianth parts is called “interpetalar tissue”.

65. Stamen length dimorphism: isomorphic (0), dimorphic (1).
   Most of the Vaccinioideae have flowers with two stamen cycles that usually differ to some extent. Some groups develop widely dissimilar stamens, but in others this differences are almost negligible. OTU were coded as isomorphic if this difference is noteworthy and consistent.

66. Staminal filament fusion: distinct (0), connate (1).
   OTU were coded as connate if stamens were fused even only in a small portion of their length.

67. Staminal filament length dimorphism: isomorphic (0), dimorphic (1).

68. Staminal filament indument: present (0), absent (1).
   Indument on filaments is mainly distributed along the apical half of the margins. Even the presence of a small section covered by indument was coded as “present”.

69. Staminal disintegration tissue: absent (0), present (1).
   Many Andromedeae and some Vaccinioideae produce small crystals in the back of the anther, which is usually called disintegration or granular tissue in specialized literature (Hermann and Palser 2000). To the naked eye, disintegration tissue looks like a white, powder-like overlay on the anther, filament, or connective.

70. Staminal disintegration tissue location: filament apical connective (0), tubule (1).

71. Anther length dimorphism: isomorphic (0), dimorphic (1).

72. Anther dehiscence of inner (=longer) cycle of stamens: introrse (0), latrorse (1), terminal (2), extrorse (3).

73. Anther dehiscence of outer (=shorter) cycle of stamens: introrse (0), terminal (1), latrorse (2), extrorse (3).
74. Anther pore orientation of adjacent stamens in the inner (=longer) cycle: open (0), facing the adjacent stamen pore (1).

In some species, when the inner cycle of stamens are latrorsely dehiscent, pores of neighbor stamens are opposite, facing each other.

75. Anther pore orientation of outer (=shorter) cycle of stamens: open (0), blocked by a stamen of inner cycle (1).

In some Vaccinieae, dehiscence of outer cycle stamens is affected by the presence of another floral structure that blocks the pores—the anther or the pore of another stamen. If there is not another stamen closely located above the pores of inner stamens, it was coded as “open”.

76. Theca papillae distribution: homogeneously papillate (0), irregularly papillate (1).

Usually stamens have papillate evenly distributed over the thecae surface, but some taxa have thecae where papilla are just concentrated towards the base or the angles of pollen sacs.

77. Theca and tubule relative length: theca smaller than the tubule (0), theca and tubule of equal length (1), theca longer than the tubule (2).
Bibliography


