EPIPHYTIC GROWTH HABITS OF CHILEAN GESNERIACEAE AND THE EVOLUTION OF EPIPHYTES WITHIN THE TRIBE CORONANTHEREAE[1]

M. Fernanda Salinas,[2,3] *Mary T. K. Arroyo,*[3] *and Juan J. Armesto*[2,3]

ABSTRACT

Three monotypic and endemic genera of epiphytic Gesneriaceae (Gesnerioideae, Coronanthereae) occur in temperate rainforests of southern South America. In this article, intraspecific differences in rooted substrate and interspecific variation in epiphytic growth habits among these three Gesneriaceae species were assessed. The presence or absence of plants on the ground and main rooted substrate when growing epiphytically on trees were used to characterize epiphytic growth habits in two old-growth temperate rainforests of northern Chiloé Island (42°30′S) in Chile. An evolutionary interpretation based on reported phylogenies and morphologies within the Coronanthereae is proposed. Two species of Chilean Gesneriaceae, *Mitraria coccinea* Cav. and *Asteranthera ovata* (Cav.) Hanst., originate from the forest floor, then climb on trees while maintaining their main roots in the ground, and are classified as secondary hemiepiphytes. The third species, *Sarmienta repens* Ruiz & Pav., was found exclusively on tree trunks and branches of living and dead trees and thus may be classified as a holoepiphyte. Based on reported phylogenies and biogeographical, ecological, and morphological data, the mechanically independent arboreal habit appears to be the ancestral condition in the Coronanthereae, which in turn gave rise to the climbing habit and finally the holoepiphytic habit. This may be a common evolutionary pathway toward holoepiphytism within other lineages in the Gesneriaceae.

Key words: *Asteranthera*, Chile, Coronanthereae, Gesneriaceae, holoepiphyte, *Mitraria*, *Sarmienta*.

Epiphytes are plants that use other plants (phorophytes) as substrates, without drawing water or nutrients from the living tissues of the phorophyte (Oliver, 1930; Barkman, 1958; Lüttge, 1989; Benzing, 1995). Among vascular plants, the epiphytic habit is represented in 83 families and some 30,000 species (Gentry & Dodson, 1987). Vascular epiphytes have been subdivided based on differences in their life cycles into: (1) holoepiphytes, which never root in the ground (Barkman, 1958) and complete their entire life cycle on the phorophyte, such as most of the epiphytic Bromeliaceae; and (2) hemiepiphytes, which root on the ground during some stage of their life cycle (Oliver, 1930). The latter can be further distinguished into: (a) primary hemiepiphytes, which germinate on the phorophyte and later send roots down to the ground, as in *Ficus* L. (Moraceae) (Holbrook & Putz, 1996) and members of the Araceae and Clusiaceae (Sandra et al., 1999); and (b) secondary hemiepiphytes, which germinate on the ground and later climb upward onto the phorophyte (Ray, 1992; Lopez-Portillo et al., 2000). Some secondary hemiepiphytes
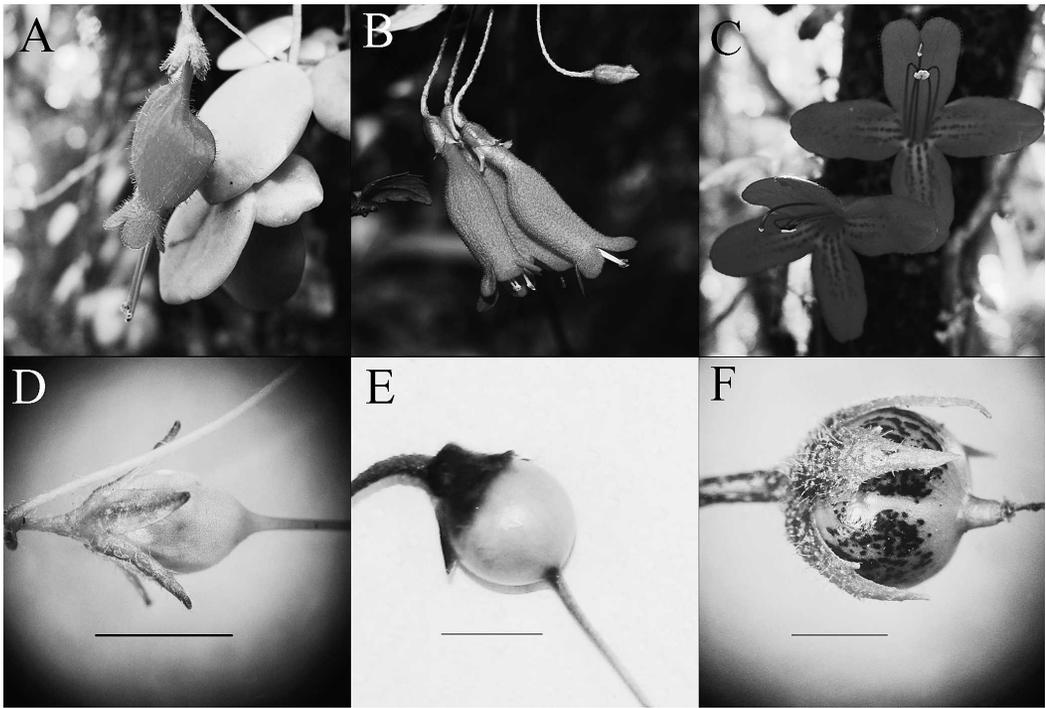
Figure 1. Flowers and fruits of the endemic monotypic genera of the Coronanthereae (Gesneriaceae) present in central-southern Chile and adjacent Argentina. —A. *Sarmienta repens* Ruiz & Pav. —B. *Mitraria coccinea* Cav. —C. *Asteranthera ovata* (Cav.) Hanst. —D. *Sarmienta repens* fruit. —E. *Mitraria coccinea* fruit. —F. *Asteranthera ovata* fruit. Scale bars in D–F = 1 cm.

are freestanding when young, if no support is available (Moffett, 2000).

It is widely accepted that the epiphytic habit evolved independently in different vascular plant lineages (Benzing, 1987; Gentry & Dodson, 1987; Kremer & van Andel, 1995). Colonization of the canopy habitat has occurred repeatedly, as in the Orchidaceae, where obligate twig epiphytism has evolved several times (Gravendeel et al., 2004). In the Bromeliaceae, Pittendrigh (1948) proposed that epiphytism evolved independently within the subfamilies Tillandsioideae and Bromelioideae, and Crayn et al. (2004) greatly clarified the origin of the epiphytic habit within Bromeliaceae by conducting a phylogenetic analysis of nucleotide sequences. The epiphytic habit within Bromeliaceae evolved a minimum of three times within the family (Crayn et al., 2004). However, the origin of epiphytes should not be considered a labile character (Wilson & Calvin, 2006) because reversals to the terrestrial habit are not common.

To our knowledge, only one hypothesis has been proposed to explain the mechanisms associated with the origin of holoepiphytes by means of hemiepiphytic intermediaries. Bews (1927) recognized the appearance of the climbing habit very early in the evolution of angiosperms, as woody lianas are abundant in many ancient orders and families and in the fossil record. Bews (1927) also suggested that the evolution of holoepiphytes is in many cases connected with the lines of development of lianas.

Temperate rainforests of southern South America are characterized by a high diversity and biomass of vascular epiphytes (Armesto et al., 1996; Arroyo et al., 1996; Muñoz et al., 2003). The prolonged history of the biogeographic isolation of the temperate rainforest biota in southern South America is reflected in high levels of local endemism, 87% of the woody flora (Arroyo et al., 1996; Villagrán & Hinojosa, 1997), which also characterizes many of the epiphytes (Arroyo et al., 1996). However, no previous study has addressed the origin of the habit in epiphytic lineages represented by species in these rainforests. Among the vascular epiphytes of Chilean temperate rainforests, three endemic monotypic genera of Gesneriaceae belong to the Coronanthereae (Smith et al., 1997; Wang et al., 2002; Mayer et al., 2003) and are frequent components of the canopy. *Asteranthera ovata* (Cav.) Hanst., *Mitraria coccinea* Cav., and *Sarmienta repens* Ruiz & Pav. (Fig. 1) have generally been considered as epiphytes or climbing shrubs in the scientific literature without further precise defini-

Volume 97, Number 1
2010

Salinas et al.
Evolution of Epiphytes in Coronanthereae

119

Table 1. References to the growth habits described in the literature for three endemic epiphytic species of Gesneriaceae from southern Chile. Most authors recognize all species as epiphytes (s.l.) or climbing shrubs, ignoring differences in their epiphytic habits.*

Habit description	Asteranthera ovata	Mitraria coccinea	Sarmienta repens
Climbing shrub rooting in the ground	1	1	
Strictly epiphytic shrub			1
Epiphytic shrub	2	2	2
Facultative epiphyte		3, 8	
Climbing shrub	4, 6	4, 6	4
Epiphytic climbing shrub			6
Epiphyte	5, 8, 10, 11, 12	5, 10, 11, 12	5, 8, 10, 11, 12
Climbing vine, epiphyte	7		7
Subshrub, epiphyte		7	

* Numbers in the table correspond to the following references: (1) Reiche, 1898; (2) Muñoz, 1959; (3) Rivero & Ramírez, 1978; (4) Muñoz, 1980; (5) Villagrán & Armesto, 1980; (6) Hoffmann, 1982; (7) Wiehler, 1983; (8) Gentry & Dodson, 1987; (9) Rivero, 1991; (10) Smith-Ramírez, 1993; (11) Smith-Ramírez & Armesto, 1994; (12) Armesto et al., 1996.

tion (Table 1). No study has quantified variation in the growth habits or substrate use within or among species. It is possible that epiphytic growth habits differ among these species, as noted more than a century ago by Reiche (1898).

MATERIALS AND METHODS

STUDY SPECIES

The Gesneriaceae family is mainly tropical and subtropical in distribution, comprising about 120 genera and 2500 species (Cronquist, 1981). Species in the Gesneriaceae include herbs or half shrubs, shrubs or small trees, and lianas or epiphytes (Cronquist, 1981). About 20% of the Gesneriaceae are epiphytic, ranking among the top 10 vascular plant families in terms of absolute number of epiphytic species (Gentry & Dodson, 1987).

Gesneriaceae are represented in the Chilean temperate rainforests by *Sarmienta repens*, *Mitraria coccinea*, and *Asteranthera ovata* (Fig. 1, Appendix 1). These three species attach to trees by adventitious roots at the nodes and have reddish tubular flowers pollinated mainly by the hummingbird *Sephanoides sephaniodes* Lesson (Rivero, 1991; Smith-Ramírez, 1993). At the end of the summer and during the fall, they produce inconspicuous, greenish berries (Fig. 1D–F) with numerous small seeds. *Sarmienta* Ruiz & Pav. (Fig. 1A) frequently grows on the branches of phorophytes. The leaves of *Sarmienta* are succulent and mainly glabrous, while the leaves of *Mitraria* Cav. and *Asteranthera* Hansl. are thinner and have higher trichome density. *Mitraria* (Fig. 1B) often grows as a twiggy shrub on trees, whereas *Asteranthera* (Fig. 1C) grows tightly attached to tree trunks, its flowers occur close to the stem, and it is often found creeping on the forest floor and logs.

STUDY SITES

The percentage of frequency of the occurrence of rooting on the ground and on phorophytes was assessed in *Sarmienta*, *Mitraria*, and *Asteranthera* in two old-growth stands of North Patagonian rainforest (sensu Veblen et al., 1995) located in the lowlands of northern Chiloé Island, Chile (Fig. 2): (1) Fundo Los Cisnes, Caulín, and (2) Senda Darwin Biological Station, El Quilar. The prevalent climate is wet-temperate, with a strong oceanic influence (Di Castri & Hajek, 1976). Meteorological records (1996–2004) at Senda Darwin Biological Station indicate a mean annual rainfall of 2124 mm and a mean annual temperature of 8.7°C. The mean maximum monthly summer temperature is 17.5°C, and the mean minimum monthly winter temperature is 2.5°C.

Evergreen broad-leaved trees and a few narrow-leaved conifers dominate the rainforest canopy in both stands. *Nothofagus nitida* (Phil.) Krasser (Nothofagaceae), *Podocarpus nubigenus* Lindl. (Podocarpaceae), *Saxegothaea conspicua* Lindl. (Podocarpaceae), *Eucryphia cordifolia* Cav. (Cunoniaceae), and *Weinmannia trichosperma* Cav. (Cunoniaceae) shape the emergent layer over 25 m tall (Table 2). *Drimys winteri* J. R. Forst. & G. Forst. (Winteraceae) and several Myrtaceae tree species are frequent in the main canopy layer. *Amomyrtus luma* (Molina) D. Legrand & Kausel, *A. meli* (Phil.) D. Legrand & Kausel, *Tepualia stipularis* (Hook. & Arn.) Griseb. (Myrtaceae), and *Caldcluvia paniculata* (Cav.) D. Don. (Cunoniaceae) are abundant also in the lower canopy and understory of the forest (Table 2).

Other vascular epiphytes in these rainforests included *Luzuriaga polyphylla* (Hook.) J. F. Macbr. (Luzuriagaceae), *Fascicularia bicolor* (Ruiz & Pav.) Mez (Bromeliaceae), and 12 species of filmy ferns (Hymenophyllaceae) (Salinas, 2008). The ground is
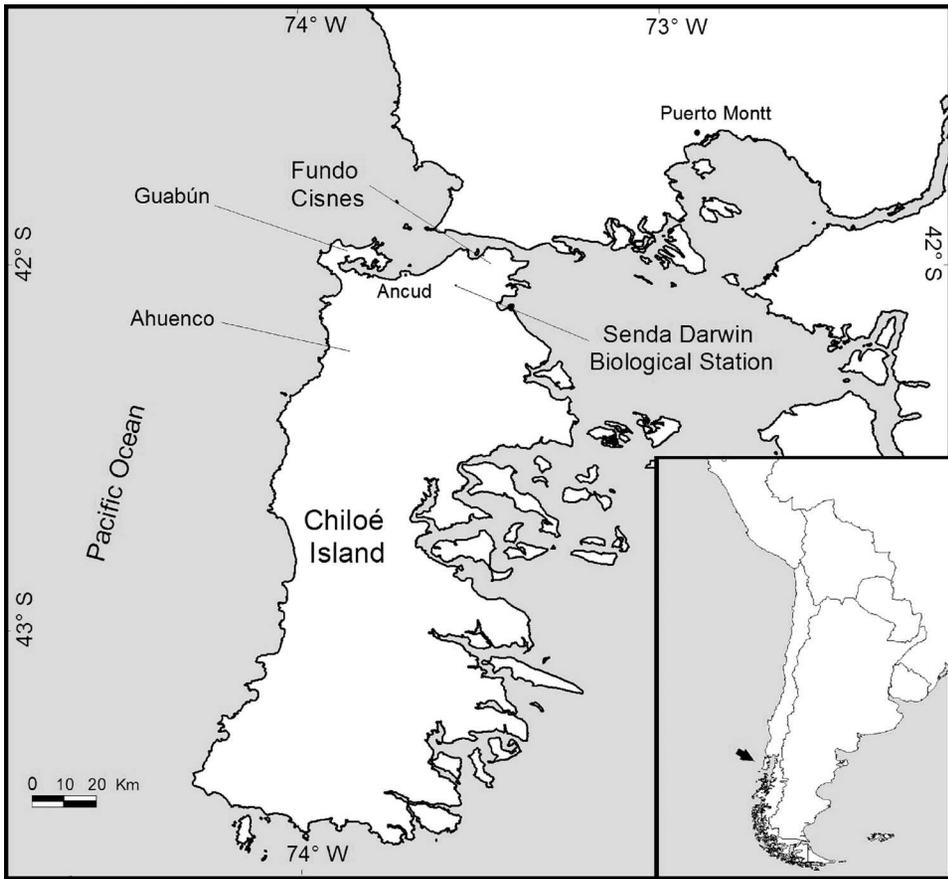
Figure 2.   Geographic location of study sites in northern Chiloé Island. Arrow in the inset box shows Chiloé Island in southern South America. Narrow lines show Senda Darwin Biological Station (SD), near El Quilar, Ancud, and Fundo Los Cisnes (FC) at the locality of Caulín.

Table 2.   Parameters of 0.1-ha. permanent plots sampled in North Patagonian rainforests of northern Chiloé Island, Chile. Tree stems measured had more than 5 cm DBH.

Stand code	SD I	SD II	FC I	FC II
Total basal area (m² 0.1 ha.⁻¹)	71.8	80.4	97	115.1
Density of trees (individuals 0.1 ha.⁻¹)	334	225	235	277
No. of tree species	9	12	11	13
Mean DBH (cm)	12.5	14.1	15.8	16.0
Maximum DBH (cm)	109.4	127	148	129
Main emergent tree species	*Nothofagus nitida, Weinmannia trichosperma*	*Podocarpus nubigena, W. trichosperma, N. nitida*	*P. nubigena, Saxegothaea conspicua, Eucryphia cordifolia*	*N. nitida, E. cordifolia, S. conspicua*
Main canopy tree species	*Tepualia stipularis, Drimys winteri, Caldcluvia paniculata*	*T. stipularis, D. winteri, C. paniculata*	*D. winteri, Amomyrtus luma, A. meli*	*S. conspicua, A. luma, D. winteri*

Abbreviations: SD I, Senda Darwin I; SD II, Senda Darwin II; FC I, Fundo Cisnes I; FC II, Fundo Cisnes II.

covered with abundant woodfalls, often covered by a carpet of bryophytes, filmy ferns, and lichens.

FIELD SAMPLING

Within each forest stand we set up two 50×20-m plots (Fundo Cisnes I, Fundo Cisnes II, Senda Darwin I, Senda Darwin II). Each plot was located at least 200 m away from any forest edge and was free of signs of recent human disturbances such as fire or clearcutting. Total basal area per plot was calculated as Σ ($\pi \times$ [DBH]^2) / 4 per tree. Sampling plots did not differ statistically in terms of total basal area and density of trees, number of tree species, and mean tree DBH ($\chi^2 = 4$, $df = 3$, $P > 0.05$ for all cases). Within each plot, we conducted two surveys.

Coronanthereae on the forest floor. To determine the frequency of each species on the forest floor, within each plot, four equidistant 50-m-long transects were traced. Along each transect, 25 quadrats of 1 m^2 were placed every 2 m, where the presence or absence of each Gesneriaceae species was recorded. A total of 400 quadrats were sampled within the four 50×20-m^2 plots in two old-growth North Patagonian forests.

Frequency and rooted substrate of Coronanthereae on trees. To characterize the frequency of each Gesneriaceae species on trees, their presence or absence on all trees greater than 5 cm DBH within each forest plot was recorded, while the presence of epiphytes on trunks, branches, and on the crowns of trees was checked with Pentax (Tokyo, Japan) 12.5 × 50 DCF SP binoculars. To characterize the rooting substrates, the epiphytic stem toward the base of the tree was carefully followed. If the plant was rooted on the ground, it was recorded as a hemiepiphyte. When the epiphytic stem did not reach the forest floor, the plant was recorded as a holoepiphyte. A total of 1071 trees greater than 5 cm DBH within the four plots of old-growth North Patagonian forests were surveyed (Table 2).

DATA ANALYSIS

Randomizations of data using RT 2.1 (Otago, New Zealand; Manly, 1997) software were performed because frequencies had non-normal distribution. The proportion of each Coronanthereae species occurring on the ground and on trees was compared independently, while one-way ANOVAs with 10,000 randomizations of the data were performed. The proportion of each species on the forest floor was compared using the 16 transects as replicates. The proportion of trees showing each

Gesneriaceae species was compared using the four plots as replicates. Mann-Whitney U tests were performed for post-hoc analysis.

BIOGEOGRAPHIC AND PHYLOGENETIC DATA
FOR CORONANTHEREAE

Available phylogenetic (Smith et al., 1997; Wang et al., 2002; Mayer et al., 2003), systematic, ecological, biogeographical, and morphological information for the species in the Coronanthereae (Bentham, 1869; Reiche, 1898; Petrie, 1903; Guillaumin, 1948; Allan, 1961; Morley, 1978; Morley & Toelken, 1983; Wiehler, 1983; Nicholson & Nicholson, 1991; Walsh & Entwisle, 1999; Friedman et al., 2004) and field observations of *Fieldia australis* A. Cunn. (Victoria, Australia), *Rhabdothamnus solandri* A. Cunn. (Auckland, New Zealand), *Coronanthera sericea* C. B. Clarke (Mont Koghi, New Caledonia), and *C. clarkeana* Schltr. (Plateau de Dogny, New Caledonia) were used for generating hypotheses about the evolution of the epiphytic habit within the tribe.

RESULTS

FREQUENCY DISTRIBUTION AND ROOT SUBSTRATES

Coronanthereae on the forest floor. Differences in the frequencies of the three species of Gesneriaceae on the forest floor were found (one-way ANOVA with randomized data, $P < 0.001$). *Mitraria* and *Asteranthera* were found to root on the ground in both forest stands (Fig. 3A). In contrast, *Sarmienta* was not found on ground quadrats in either of the two forest stands (Fig. 3A). *Mitraria* had a mean frequency on the ground quadrats of 0.31 per transect and was more frequent than *Asteranthera* (Mann-Whitney U test, Z = 2.92, $P < 0.005$), which had a mean occurrence of 0.15 per transect (Fig. 3A). Both *M. coccinea* and *A. ovata* were significantly more frequent than *S. repens* on the forest floor (Mann-Whitney U test, $P < 0.05$ in both cases). Growth patterns on the ground differed: *Mitraria* was able to grow without support for up to 10–20 cm in height on the forest floor, and erect stems were separated 10–50 cm from others and were connected by buried lateral shoots. Instead, *Asteranthera* had a creeping habit on the ground and was never found growing erect more than 10 cm in height on the ground.

Frequency and rooted substrate of Coronanthereae on trees. No statistical difference in the proportions of trees bearing each Gesneriaceae species was found (one-way ANOVA with randomized data, $P = 0.0829$). *Mitraria* (n = 297) occurred on a proportion of 0.29 of
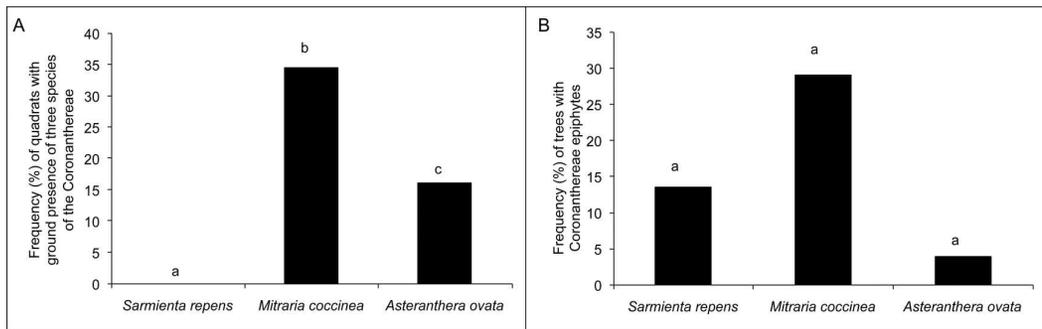
Figure 3. —A. Mean percentage of Coronanthereae species in quadrats within transects traced on the ground of two North Patagonian rainforests, N = 8 transects within each site, N = 25 sampling quadrats per transect for a total of 400 quadrats. Different letters above the bars indicate significant differences between species (ANOVA with randomized data, $P < 0.05$). *Sarmienta repens* Ruiz & Pav. was completely absent from the ground (a), while *Mitraria coccinea* Cav. was the most frequent Coronanthereae species on the forest ground (b), and *Asteranthera ovata* (Cav.) Hanst. was less frequent than *M. coccinea* on the forest floor (c). —B. Mean percentage of trees with Coronanthereae epiphytes within two North Patagonian rainforests, including both hemiepiphytes and holoepiphytes. N = 2 plots, 0.1 ha. at each forest stand. Sample size, N = 1071 trees. Same letter (a) above bars indicates no statistical differences in frequency on trees among Coronanthereae species (ANOVA with randomized data, $P > 0.05$). Significantly different frequencies between species were found only on the forest ground. Epiphytic *M. coccinea* and *A. ovata* were found always rooted on the ground and were classified as secondary hemiepiphytes, while epiphytic *S. repens* was never found rooted on the ground and was classified as holoepiphyte.

trees greater than 5 cm DBH sampled, and *Sarmienta* (n = 139) occurred on a proportion of 0.14 of trees sampled (Fig. 3B). *Asteranthera* (n = 40) had the lowest proportion of 0.04 on trees sampled (Fig. 3B).

Differences in the rooted substrates of the epiphytes growing on trees were revealed. Only *Mitraria* and *Asteranthera* rooted on the ground. Consequently, these species may be classified as secondary hemiepiphytes, germinating and growing on the floor and climbing on trees afterward. In contrast, *Sarmienta* did not root on the ground, and thus *Sarmienta* may be classified as holoepiphyte, germinating on trees and not rooting on the ground.

BIOGEOGRAPHY AND PHYLOGENY OF CORONANTHEREAE

The Coronanthereae consists of nine genera and 20 species (Table 3), with a vicariant South Pacific distribution. Recently, Coronanthereae has received considerable attention in discussions related to the origin of the Gesneriaceae (Weber, 2004). The tribe is present in the southern South American temperate rainforests of Chile and adjacent Argentina, mainly in the North Island of New Zealand, Lord Howe Island, and in the provinces of Queensland, Victoria, and New South Wales in Australia. Seven genera are monotypic (Table 3). *Depanthus* S. Moore, with two species, and *Coronanthera* Vieill. ex C. B. Clarke, with 11 species, are largely endemic to New Caledonia (Table 3). Only one species of *Coronanthera* is present in the Solomon Islands (Wiehler, 1983; Table 3). Present-day distribution patterns and available fossil evidence of Gesneriaceae from south-

ern South America (Villagrán & Hinojosa, 1997) suggest an ancient clade that precedes the breakup of Gondwana (Dalziel, 1992). The elevated proportion of monotypic genera (78% of the genera) and the endemism of species to isolated and restricted areas (Table 3) support the contention that current Coronanthereae represent relictual taxa of a more diversified group in the past (Burtt, 1963, 1998; Wiehler, 1983; Weber, 2004), which was affected by subsequent extinctions (Wiehler, 1983; Weber, 2004).

Phylogenetic studies and isocotylous seedlings support the position of the Coronanthereae within the Gesnerioideae (Burtt, 1963; Smith et al., 1997; Wang et al., 2002; Mayer et al., 2003) in a fairly basal position (Wang et al., 2002). Our literature review indicated a diversity of growth habits among living species of Coronanthereae, varying from trees to holoepiphytes. Among genera, the functional stamen number in the flowers varied from two to five, and the fruit type varied from a dehiscent capsule to a fleshy fruit. All species within the Coronanthereae occur in rainforests, ranging from tropical to temperate regions (Table 3).

DISCUSSION

EPIPHYTIC HABITS OF SOUTHERN SOUTH AMERICAN GESNERIACEAE

Mitraria and *Asteranthera* are considered secondary hemiepiphytes as they were regularly found as terrestrial plants as well as epiphytic climbers with

Table 3. Number of species, geographic distribution, habitat, habit, stamen numbers, and fruit characteristics of nine genera in the gesneriad tribe Coronanthereae.*

Genus	Species number	Geographic distribution	Habitat	Habit	Stamen number	Fruit type
Depanthus	2	New Caledonia	montane forest	tree	5	capsule
Negria	1	Lord Howe Island	montane forest	tree	4	capsule
Coronanthera	11	New Caledonia, Solomon Islands	montane forest	tree	4	capsule
Rhabdothamnus	1	New Zealand, North Island	montane forest	shrub	4	capsule
Lenbrassia	1	Australia, Queensland	rainforest	tree	4	berry
Fieldia	1	Australia, Victoria and New South Wales	montane rainforest	secondary hemiepiphytes	4	berry
Asteranthera	1	Chile and adjacent Argentina	temperate rainforest	secondary hemiepiphytes	4	berry
Mitraria	1	Chile and adjacent Argentina	temperate rainforest	secondary hemiepiphyte	4	berry
Sarmienta	1	Chile	temperate rainforest	holoepiphyte	2	berry

* Modified from Whieler (1983).

the main stem rooting on the forest floor. As noted in many other species of Gesneriaceae, both species showed that the development of lateral shoots on the prostrate stem may lead to multiplication and to the patchy habit (Weber, 2004). In contrast, *Sarmienta* was never found rooted on the ground and hence is not a terrestrial plant, but rather a holoepiphyte. These results support early observations reported by Reiche (1898).

EVOLUTION OF THE EPIPHYTIC HABIT WITHIN CORONANTHEREAE

Considering stamen number in genera of Coronanthereae (Table 3), there appears to have been at least two reductions in number within the tribe. From a putative ancestral number of five functional stamens, as present in *Depanthus*, a first reduction of one stamen to staminoid is present in seven genera within Coronanthereae (Table 3). A second reduction has taken place in the lineage, now present in the flowers of *Sarmienta*, which have three staminodes, two longer than the third (Reiche, 1898), and only two functional stamens (Table 3), which support two reductions to staminodes in the lineage of *Sarmienta*. The presence of rudimentary, reduced, or functionless structures has traditionally been used to establish the direction of evolutionary change since de Candolle (1813). The 5-stamen condition present in *Depanthus* flowers has traditionally been regarded as a secondary acquisition within the lineage (Wiehler, 1983; Weber, 2004), a hypothesis that has never been challenged or demonstrated. However, considering the relative ancestral position of Coronanthereae in Gesneriaceae (Burtt, 1963; Wiehler, 1983; Smith et al., 1997; Wang et al.,

2004; Weber, 2004), five functional stamens could likely represent the ancestral condition for the family.

Within the Gesneriaceae, fleshy fruits are considered a derived fruit type with respect to dehiscent capsules (Wiehler, 1983). Within the Beslerieae and Napeantheae, dehiscent capsules have been described as ancestral contrasting with the derived state of fleshy fruits (Smith, 2000a). The sister family considered ancestral to Gesneriaceae, the Calceolariaceae (Soltis et al., 2005), also presents dehiscent capsules, which would support the ancestral character of dehiscent capsules across the entire Gesneriaceae. Within Coronanthereae, genera bearing dehiscent capsules seem to have maintained the ancestral character state (as in *Depanthus*, *Coronanthera*, *Negria* F. Muell., and *Rhabdothamnus* A. Cunn.). Fleshy fruits, present in the Australian *Fieldia* A. Cunn. and *Lenbrassia* G. W. Gillett, and in the South American *Asteranthera*, *Mitraria*, and *Sarmienta* (Table 3), may have originated at least once within the tribe, potentially representing a derived character.

Growth habits within the living genera of Coronanthereae include trees (*Depanthus*, *Negria*, *Coronanthera*, and *Lenbrassia*), shrubs (*Rhabdothamnus*), climbers (*Fieldia*, *Mitraria*, and *Asteranthera*), and holoepiphytes (*Sarmienta*, Table 3). At least three reductions in vegetative size associated with shifts in growth habits seem to have occurred within the Coronanthereae. One trend would have been from the arboreal condition to the shrub habit. Another trend is the reduction in stem thickness from the arboreal to the secondary hemiepiphytic habit. A further reduction in plant size within this lineage would have

accompanied the shift from the secondary hemiepiphytic to the holoepiphytic habit (Table 3).

Coronanthera sericea, which occurs in the tropical rainforest of Mont Koghi, New Caledonia (Appendix 1), and is described as a tree (Wiehler, 1983; Table 3), was also found growing as a secondary hemiepiphyte on the trunk of a tree fern, much as the climber *Fieldia australis*, which grows on tree-fern trunks in Australian rainforests (Walsh & Entwisle, 1999). Considering the reduction in size from tree to secondary hemiepiphyte, the morphological phenotypic plasticity in the growth habit of *C. sericea* supports this evolutionary shift: this unusual secondary hemiepiphytic habit in the lineage of *Coronanthera* could have been genetically assimilated in related lineages such as those from *Fieldia* and *Mitraria* in evolutionary time, thus altering the shape of the reaction norm in the derived lineage (see Pigliucci et al., 2006).

Leaves of *Coronanthera sericea* and *C. clarkeana* (Appendix 1) in the rainforests of New Caledonia showed variation from early development to adulthood. Such leaves show ontogenetic modification in terms of (1) leaf margin, from toothed or crenated to smooth, and (2) trichome density, from pubescent to glabrous or nearly so. Early developmental stages of an organism can recapitulate early stages found in its ancestors (Stebbins, 1974; Thorne, 1976), making heterochrony a potential mechanism for morphological change (Olson & Rosell, 2006). If the derived organism is neotenic, a common phenomenon in plant evolution (Takhtajan, 1959, 1969, 1976; Doyle, 1977, 1978) that has been previously reported in Gesneriaceae (Jong & Burtt, 1975; Nieder & Barthlott, 2001; Mayer et al., 2003), early developmental traits of the ancestor will be shown in mature plants (Gould, 1970; McKinney & McNamara, 1991). Hemiepiphytic species in Coronanthereae exhibit toothed or crenated leaf margins and rather pubescent leaves as seen in early stages of previously mentioned arboreal rainforest *Coronanthera* leaves. These observations suggest that the mechanism involved in the evolution from tree to secondary hemiepiphytes in Coronanthereae is heterochronic, and leaf margin and trichome density of secondary hemiepiphytes are neotenic (see Gould, 2002).

Epiphytes are more specialized than terrestrial plants with regard to physiological, morphological, and ecological traits (Oliver, 1930; Pittendrigh, 1948; Strong & Ray, 1975; Winter et al., 1983; Nobel & Hartsock, 1990; Lambers et al., 1998; Helbsing et al., 2000), and the increase in specialization has been considered a common evolutionary trend (Takhtajan, 1991). It is suggested that plants present in microhabitats in the forest canopy receive more and a different quality of sunlight than plants present on the forest ground (Parker, 1995), are subjected to wider variation in moisture supply (Bohlman et al., 1995), and may present specialized seed dispersal vectors (Kleinfeldt, 1978). Consequently, the hypothesis proposed by Bews (1927), indicating that in many cases the evolutionary line of development of lianas results in the production of epiphytes, seems reasonable. Essential differences between climbing taxa and holoepiphytes lie in seed dispersal sites (ground or phorophyte) and physiologically in the early stages of the life cycle. The specific characteristics of the holoepiphytic habit in the Coronanthereae tribe are most likely to have been developed from the climbing habit, such as seen in *Fieldia*, *Mitraria*, and *Asteranthera*. Furthermore, Wiehler (1983) argues that most common Gesneriaceae taxa are found in the warm, humid, and shaded tropical forests, where a significant number of Gesneriaceae have abandoned the terrestrial habit in search of more light, with a few becoming lianas and the rest evolving into holoepiphytes.

OTHER ORIGINS OF THE EPIPHYTIC HABIT WITHIN THE GESNERIACEAE

Within the Gesneriaceae there are 598 epiphytic species within 28 genera (Gentry & Dodson, 1987). Epiphytic Gesneriaceae are present in circumglobal tropical regions (Neotropics, Paleotropics, and Australasia) and belong to two different subfamilies (Wiehler, 1983). The distribution of the epiphytic habit in different phylogenies based on DNA sequences in the Gesnerioideae subfamily has been considered by Smith and Sytsma (1994), Smith and Carroll (1997), Smith (2000b), and Perret et al. (2003). The conservative estimate derived from these studies is that the epiphytic habit has evolved independently at least four times within the subfamily Gesnerioideae in (1) the Episcieae (Smith & Carroll, 1997; Smith, 2000b); (2) the genus *Columnea* L., with 160 species that include lianas and epiphytes (Smith & Sytsma, 1994); (3) the Sinningieae (Perret et al., 2003); and (4) the Coronanthereae (present results).

Whenever holoepiphytes are present within these analyses in Gesnerioideae, their closest relatives are either terrestrial and/or secondary hemiepiphytic habit. Therefore, we suggest that holoepiphytes evolved through the increased use of other plants for structural and mechanical support from terrestrial or secondary hemiepiphytes to holoepiphytes in these lineages. The evolution of the secondary hemiepiphytic habit in Gesnerioideae would involve a potentially terrestrial ancestral condition, considering the terrestrial habit in the closest ancestral relatives to Gesneriaceae, within the Calceolariaceae (Soltis et al., 2005). The derived form would be a climbing herb or shrub, associated with the canopy habitat. For the

climbing habit, specialized physiological, morphological, and ecological traits associated with the holoepiphytic habit derive. Similar steps leading to the holoepiphytic habit postulated for *Sarmienta* within the Coronanthereae may have evolved in parallel within the tribes previously mentioned in Gesnerioideae. Future well-supported phylogenies within Gesneriaceae and Coronanthereae and its relative position within the Gesnerioideae will provide a test of these hypotheses.

Follow-up articles will explore ecological differences in vertical distribution patterns among Chilean Coronanthereae species, their dynamics and requirements for germination and seedling survival, and comparative anatomy of their leaves and stems in relation to specialization to the epiphytic habit.

Literature Cited

Allan, H. H. 1961. Flora of New Zealand. R. E. Owen, Government Printer, Wellington, New Zealand.

Armesto, J. J., P. León & M. Arroyo. 1996. Los bosques templados del sur de Chile y Argentina: Una isla biogeográfica. Pp. 23–28 in J. J. Armesto, C. Villagrán & M. Arroyo (editors), Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Santiago.

Arroyo, M. T. K., L. Caviares, A. Peñaloza, M. Riveros & A. M. Faggi. 1996. Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. Pp. 71–92 in J. J. Armesto, C. Villagrán & M. Arroyo (editors), Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Santiago.

Barkman, J. J. 1958. Phytosociology and Ecology of Cryptogamic Epiphytes. Van Gorcum, Assen, The Netherlands.

Bentham, G. 1869. Flora Australiensis, Vol. 4. Stylidieae–Pedalineae. L. Reeve & Co., London.

Benzing, D. H. 1987. Vascular epiphytism: Taxonomic participation and adaptive diversity. Ann. Missouri Bot. Gard. 74: 183–204.

———. 1995. Vascular epiphytes. Pp. 175–211 in M. Lowman & N. Nadkarni (editors), Forest Canopies. Academic Press, San Diego.

Bews, J. W. 1927. Studies in the ecological evolution of angiosperms. New Phytol. 26: 65–84.

Bohlman, S., T. Matelson & N. Nadkarni. 1995. Moisture and temperature patterns of dead organic matter in the canopy and soils of the forest floor of a montane cloud forest, Costa Rica. Biotropica 27: 13–19.

Burtt, B. L. 1963. Studies in the Gesneriaceae of the Old World, XXIV: Tentative keys to the tribes and genera. Notes Roy. Bot. Gard. Edinburgh 24: 20–220.

———. 1998. Climatic accommodation and phytogeography of the Gesneriaceae of the Old World. Pp. 1–27 in P. Mathew & M. Sivadasan (editors), Diversity and Taxonomy of Tropical Flowering Plants. Mentor Books, Calicut, India.

Candolle, A. P. de. 1813. Théorie élémentaire de la botanique, ou exposition du principe de la classification naturelle et de l'art de décrire et d'etudier les végétaux. Déterville, Paris.

Crayn, D. M., K. Winter & J. A. C. Smith. 2004. Multiple origins of crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. Proc. Natl. Acad. Sci. U.S.A. 101: 3703–3708.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press, New York.

Dalziel, I. W. 1992. Antarctica: A tale of two supercontinents? Annual Rev. Earth Planet. Sci. 20: 501–526.

Di Castri, F. & E. R. Hajek. 1976. Bioclimatología de Chile. Vicerrectoría de Comunicaciones, Pontificia Universidad Católica de Chile, Santiago.

Doyle, J. A. 1977. Early Cretaceous fossil evidence for angiosperm evolution. Bot. Rev. 43: 3–104.

———. 1978. Origin of angiosperms. Annual Rev. Ecol. Syst. 9: 365–392.

Friedman, W. E., R. C. Moore & M. D. Purugganan. 2004. The evolution of plant development. Amer. J. Bot. 91: 1726–1741.

Gentry, A. H. & C. H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. Ann. Missouri Bot. Gard. 74: 205–233.

Gould, S. J. 1970. Dollo on Dollo's law: Irreversibility and the status of evolutionary laws. J. Hist. Biol. 3: 189–212.

———. 2002. The Structure of Evolutionary Theory. Harvard University Press, Cambridge.

Gravendeel, B., A. Smithson, F. J. W. Slik & A. Schuiteman. 2004. Epiphytism and pollinator specialization: Drivers of orchid diversity. Philos. Trans., Ser. B 359: 1523–1535.

Guillaumin, A. 1948. Flore analytique et synoptique de la Nouvelle-Caledonie. Office de la Recherche Scientifique Coloniale, Paris.

Helbsing, S., M. Riederer & G. Zotz. 2000. Cuticles of vascular epiphytes: Efficient barriers for water loss after stomatal closure? Ann. Bot. 86: 765–769.

Hoffmann, A. 1982. Flora Silvestre de Chile. Zona Araucana. Fundación Claudio Gay, Santiago.

Holbrook, N. M. & F. E. Putz. 1996. From epiphyte to tree: Differences in leaf structure and leaf water relations associated with the transition in growth form in eight species of hemiepiphytes. Pl. Cell Environm. 19: 631–642.

Jong, K. & B. L. Burtt. 1975. The evolution of morphological novelty exemplified in the growth patterns of some Gesneriaceae. New Phytol. 75: 297–311.

Kleinfeldt, S. E. 1978. Ant-gardens: Interaction of *Codonanthe crassifolia* (Gesneriaceae) and *Crematogaster longispina* (Formicidae). Ecology 59: 449–456.

Kremer, P. & J. van Andel. 1995. Evolutionary aspects of life forms in angiosperm families. Acta Bot. Neerl. 44: 469–479.

Lambers, H., F. S. Chapin & T. L. Pons. 1998. Plant Physiological Ecology. Springer-Verlag, New York.

Lopez-Portillo, J., F. W. Ewers, G. Angeles & J. B. Fisher. 2000. Hydraulic architecture of *Monstera acuminata*: Evolutionary consequences of the hemiepiphytic growth form. New Phytol. 145: 289–299.

Lüttge, U. 1989. Vascular epiphytes: Setting the scene. Pp. 1–14 in U. Luttge (editor), Vascular Plants as Epiphytes. Evolution and Ecophysiology, Ecological Studies: Analysis and Synthesis, Vol. 76. Springer-Verlag, Berlin.

Manly, B. F. J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. Chapman and Hall, London.

Mayer, V., M. Moller, M. Perret & A. Weber. 2003. Phylogenetic position and generic differentiation of Epithemateae (Gesneriaceae) inferred from plastid DNA sequence data. Amer. J. Bot. 90: 321–329.

McKinney, M. L. & K. McNamara. 1991. Heterochrony: The Evolution of Ontogeny. Plenum Press, New York.

Moffett, M. W. 2000. What's "up"? A critical look at the basic terms of canopy biology. Biotropica 32: 569–596.

Morley, B. D. 1978. Variation in Lenbrassia G.W. Gillet (Gesneriaceae). J. Adelaide Bot. Gard. 1: 187–192.

——— & H. R. Toelken. 1983. Flowering Plants in Australia. Rigby Publishers, Adelaide.

Muñoz, A. A., P. Chacon, F. Pérez, E. S. Barnert & J. J. Armesto. 2003. Diversity and host tree preferences of vascular epiphytes and vines in temperate rainforest in southern Chile. Austral. J. Bot. 51: 381–391.

Muñoz, C. 1959. Sinopsis de la Flora Chilena. Editorial Universitaria, Santiago.

Muñoz, M. 1980. Flora del Parque Nacional Puyehue. Editorial Universitaria, Santiago.

Nicholson, N. & H. Nicholson. 1991. Australian Rainforest Plants II. Hugh & Nan Nicholson, New South Wales.

Nieder, J. & W. Barthlott. 2001. Epiphytes and their role in the tropical forest canopy. Pp. 23–86 in J. Nieder & W. Barthlott (editors), Results of the Bonn-Quito Epiphyte Project, funded by the Volkswagen Foundation, Vol. 2. Books on Demand, Bonn.

Nobel, P. S. & T. L. Hartsock. 1990. Dial patterns of CO_2 exchange for epiphytic cacti differing in succulence. Physiol. Pl. (Copenhagen) 78: 628–634.

Oliver, W. R. B. 1930. New Zealand epiphytes. J. Ecol. 18: 1–50.

Olson, M. E. & J. Rosell. 2006. Using heterochrony to infer modularity in the evolution of stem diversity in Moringa (Moringaceae). Evolution 60: 724–734.

Parker, G. 1995. Structure and microclimate of forest canopies. Pp. 73–106 in M. Lowman & N. Nadkarni (editors), Forest Canopies. Academic Press, San Diego.

Perret, M., A. Chautems, R. Spichiger, G. Kite & V. Savolainen. 2003. Systematics and evolution of tribe Sinningieae (Gesneriaceae): Evidence from phylogenetic analyses of six plastid DNA regions and nuclear ncpGS. Amer. J. Bot. 90: 445–460.

Petrie, M. A. 1903. On the pollination of Rhabdothamnus solandri, A. Cunn. Trans. & Proc. New Zealand Inst. 35: 321–323.

Pigliucci, M., C. J. Murren & C. D. Schichting. 2006. Phenotypic plasticity and evolution by genetic assimilation. J. Exp. Biol. 209: 2362–2367.

Pittendrigh, C. S. 1948. The Bromeliad–Anopheles–Malaria complex in Trinidad. 1. The Bromeliad flora. Evolution 2: 58–89.

Ray, T. S. 1992. Foraging behaviour in tropical herbaceous climbers (Araceae). J. Ecol. 80: 189–203.

Reiche, K. 1898. Flora de Chile. Estudios críticos sobre la flora de Chile, Vol. 5. Imprenta Cervantes, Santiago.

Rivero, M. 1991. Aspectos sobre la Biología Reproductiva en Dos Comunidades del Sur de Chile, 40° S. Doctoral Thesis, Universidad de Chile, Santiago.

——— & C. Ramírez. 1978. Fitocenosis epífitas de la asociación Lapagerio-Aetoxiconetum en el Fundo San Martín (Valdivia-Chile). Acta Ci. Venez. 29: 163–169.

Salinas, M. F. 2008. Ecological Niche Differentiation of Three Epiphytic Gesneriad Species of the Temperate Forest of Southern Chile. Ph.D. Dissertation, Facultad de Ciencias, Universidad de Chile, Santiago.

Sandra, P., G. S. Gilbert, G. Zotz & M. T. Tyree. 1999. Growth and survival of aerial roots of hemiepiphytes in a lower montane tropical moist forest in Panama. J. Trop. Ecol. 15: 651–665.

Smith, J. F. 2000a. A phylogenetic analysis of tribes Beslerieae and Napeantheae (Gesneriaceae) and evolution of fruit types: Parsimony and maximum likelihood analyses of ndhF sequences. Syst. Bot. 25: 72–81.

———. 2000b. Phylogenetic resolution within the tribe Episcieae (Gesneriaceae): Congruence of ITS and ndhF sequences from parsimony and maximum-likelihood analyses. Amer. J. Bot. 87: 883–897.

——— & K. J. Sytsma. 1994. Evolution in the Andean epiphytic genus Columnea (Gesneriaceae). II. Chloroplast DNA restriction site variation. Syst. Bot. 19: 317–336.

——— & C. L. Carroll. 1997. A cladistic analysis of the tribe Episcieae (Gesneriaceae) based on ndhF sequences: Origin of morphological characters. Syst. Bot. 22: 713–725.

———, J. C. Wolfram, K. D. Brown, C. L. Carroll & D. S. Denton. 1997. Tribal relationships in the Gesneriaceae: Evidence from DNA sequences of the chloroplast gene ndhF. Ann. Missouri Bot. Gard. 84: 50–66.

Smith-Ramírez, C. 1993. Los picaflores y su recurso floral en el bosque templado de la isla de Chiloé, Chile. Revista Chilena Hist. Nat. 66: 65–73.

——— & J. J. Armesto. 1994. Plant phenology in a South American temperate rain forest, Chiloé, Chile. J. Ecol. 82: 353–365.

Soltis, D. E., P. K. Endress & M. W. Chase. 2005. Phylogeny and Evolution of Angiosperms. Sinauer Associates, Sunderland, Massachusetts.

Stebbins, G. L. 1974. Flowering Plants: Evolution above the Species Level. Harvard University Press, Cambridge.

Strong, D. R. & T. S. Ray. 1975. Host tree location behavior of a tropical vine (Monstera gigantea) by skototropism. Science 190: 804–806.

Takhtajan, A. L. 1959. Die Evolution der Angiospermen. G. Fischer, Jena.

———. 1969. Flowering Plants: Origin and Dispersal. Oliver & Boyd, Edinburgh.

———. 1976. Neoteny and the origin of flowering plants. Pp. 207–219 in C. B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia University Press, New York.

———. 1991. Evolutionary Trends in Flowering Plants. Columbia University Press, New York.

Thorne, R. F. 1976. A phylogenetic classification of the Angiospermae. Evol. Biol. 9: 35–106.

Veblen, T. T., B. R. Burns, T. Kitzberger, A. Lara & R. Villalba. 1995. The ecology of the conifers of southern South America. Pp. 120–155 in N. J. Enright & R. S. Hill (editors), Ecology of the Southern Conifers. Melbourne University Press, Melbourne.

Villagrán, C. & J. J. Armesto. 1980. Relaciones florísticas entre las comunidades relictuales del Norte Chico y la Zona Central con el bosque del sur de Chile. Bol. Mus. Nac. Hist. Nat. Santiago de Chile 37: 87–101.

——— & L. Hinojosa. 1997. Historia de los bosques del sur de Sudamérica II: Análisis fitogeográfico. Revista Chilena Hist. Nat. 70: 241–267.

Walsh, N. G. & T. J. Entwisle. 1999. Flora of Victoria. Inkata Press, Melbourne.

Wang, C., M. Moller & Q. C. B. Cronk. 2004. Phylogenetic position of Titanotrichum oldhamii (Gesneriaceae) inferred from four different gene regions. Syst. Bot. 29: 407–418.

Wang, Y. Z., Z. Y. Li, K. Y. Pan & X. H. Zou. 2002. Pattern and significance of seedling development in Titanotrichum oldhamii (Gesneriaceae). Acta Bot. Sin. 44: 903–907.

Weber, A. 2004. Gesneriaceae. Pp. 63–158 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. VII. Flowering Plants—Dicotyledons. Lamiales (Except Acanthaceae Including Avicenniaceae). Springer, Berlin.

Wiehler, H. 1983. A synopsis of the neotropical Gesneriaceae. Selbyana 6: 1–219.

Wilson, C. A. & C. L. Calvin. 2006. An origin of aerial branch parasitism in the mistletoe family, Loranthaceae. Amer. J. Bot. 93: 787–796.

Winter, K., B. J. Wallace, G. C. Stocker & Z. Roksandic. 1983. Crassulacean acid metabolism in Australian vascular epiphytes and some related species. Oecologia 68: 224–230.

APPENDIX 1. Voucher specimens for the two study sites from old-growth stands of North Patagonian rainforest located in the lowlands of northern Chiloé Island, Chile: (1) Fundo Cisnes (FC, 41°50′S, 73°36′W), Caulín, and (2) Senda Darwin Biological Station (SD, 41°52′S, 73°40′W), El Quilar. Voucher specimens are given for other Coronanthereae from the coastal temperate rainforest of Wenderholm (WE, 36°32′S, 174°42′E), Waiwera, Auckland, New Zealand; the temperate rainforest located at the head of Bunyip Valley Road (BU, 37°54′S, 145°41′E), Gembrook, Eastern Highlands, Victoria, Australia; and two tropical rainforests in the South Province, New Caledonia: (1) Mont Koghi (KO, 22°11′S, 166°30′E), main trail to Pic Malaoui, 20 km northeast from Noumea, and (2) main trail to Plateau de Dogny (DO, 21°37′S, 165°52′E), Dogny. Taxa with epiphytic habit are boldfaced.

Species	Site	Collector number (herbarium)
Asteranthera ovata (Cav.) Hanst.	FC	*Salinas 823* (CONC)
A. ovata	SD	*Salinas 816* (CONC)
Mitraria coccinea Cav.	FC	*Salinas 824* (CONC)
M. coccinea	SD	*Salinas 815* (CONC)
Sarmienta repens Ruiz & Pav.	FC	*Salinas 822* (CONC)
S. repens	SD	*Salinas 814* (CONC)
Coronanthera sericea C. B. Clarke	KO	*Salinas 776* (AK, CONC, NOU)
C. clarkeana Schltr.	DO	*Salinas 782* (AK, CONC, NOU)
Rhabdothamnus solandri A. Cunn.	WE	*Salinas 759* (AK, CONC)
Fieldia australis A. Cunn.	BU	*Salinas 756* (CONC, MEL)