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Evolutionary diversification and historical biogeography of orchidaceae in Central America with emphasis on Costa Rica and Panama

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General Introduction

Chapter 1

Introduction

1.1 Evolutionary diversification and historical biogeography of Orchidaceae in Costa Rica and Panama

The floristic richness of the Neotropics has a complex origin. The most diverse plant family in the American continent is made up of the Orchidaceae with more than 13,000 species (Ulloa et al., 2017) and the most diverse genera of angiosperms are *Piper* L. (1,804) and *Peperomia* Ruiz & Pav. (1,133) (Piperaceae), *Miconia* Ruiz & Pav. (1,110) (Melastomataceae) and the orchid genera *Epidendrum* L. (1,459 species), *Lepanthes* Sw. (1,125) and *Stelis* Sw. (1,128). In contrast, most genera of American angiosperms (5,975) contain less than 100 species (Ulloa et al., 2017). Orchidaceae is also the most diverse plant family in Central America, concentrating 13% of the species and the number of species is triple that of other well-represented angiosperm families. Although we are still far from knowing the exact number of orchid species extant in both countries nowadays, at present Costa Rica (1,620 spp.) and Panama (1,372 spp.) together contain more than 2,000 species of orchids; representing about 8.0% of all orchid species on just about 1% of the Earth's land surface. In this region, Cymbidiae, Pleurothallidinae and Laeliinae are the most diverse groups and contain the largest genera: *Maxillaria* Ruiz & Pav. *s.l.*, *Lepanthes*, *Oncidium* Sw., *Pleurothallis* R.Br., *Stelis* and *Epidendrum* showing the same global pattern observed in the Neotropics.

Historically, the isthmus of Costa Rica and Panama has been a source of fascination for its strategic position linking North America to South America. The geological events that led to the closure of the isthmus that started with the formation of a volcanic arc, dating from the Cretaceous to Eocene, 67 to 39 million years ago (Ma) (Montes et al., 2015), have been studied extensively but are still controversial. There is no consensus about when the isthmus closed the Central American Seaway (CAS) separating the Pacific from the Atlantic Ocean and favoring the Great American Biotic Interchange (GABI). Traditionally, it was assumed that this closure was established between 3.5-5.0 Ma, but other studies that include new information suggest a closure much earlier, between 13-15 Ma in the middle Miocene (Bacon et al., 2015; Montes et al., 2015). Despite this controversy, it is clear that with the initial emergence of a volcanic arc in the Cretaceous, orchids had millions of years to colonize some of these oceanic islands by wind dispersal of seeds and evolve there. According to a phylogenomic analysis and net diversification regimes across lineages using BAMM analysis, Givnish *et al.*, (2015) proposed that Orchidaceae arose around 112 Ma in the Cretaceous, long before the formation of the arc and subsequent closure of the Isthmus of Panama. However, the most diverse Neotropical subtribes Laeliinae, Oncidi-

inae, Maxillariinae and Pleurothallidinae probably diversified between 10-25 Ma after the last acceleration of net diversification rate that occurred about 25 Ma, overlapping with the possible closure of the Isthmus proposed recently (Bacon et al., 2015; Givnish et al., 2015; Montes et al., 2015). Indeed the flora of the Isthmus is dominated mainly by species of Cymbidiae, Laeliinae and Pleurothallidinae that diversified in the past 20 Ma. Consequently, we can assess some of the factors that shaped this extraordinary diversity in the isthmus by analyzing the current floristic composition of selected orchid groups with phylogenetics, floral trait evolution, pollination evidence and biogeographical analyses (Fig. 1.1).

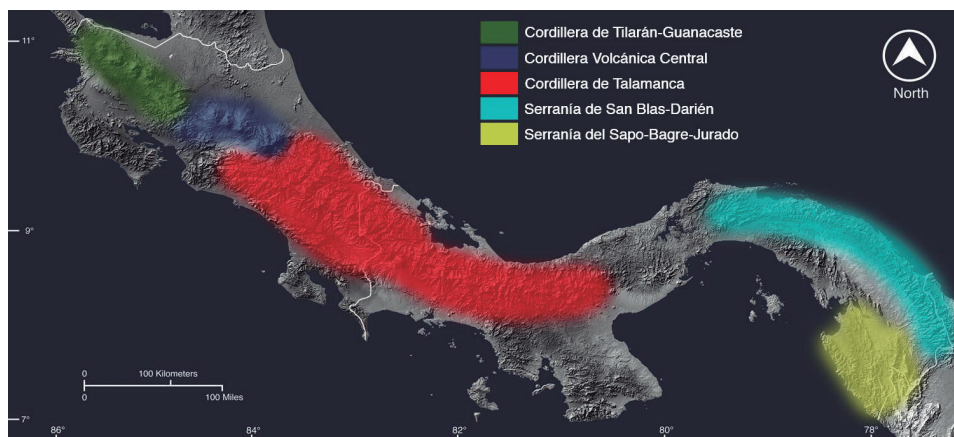


Figure 1.1. Geography of southern Central America (Costa Rica and Panama) showing the main ranges: Talamanca crossing both countries and San Blas-Darién on the southeast of Panama towards Colombia.

1.2 Orchid diversity in the hotspot of Costa Rica and Panama

Updated floristic inventories of Costa Rica and Panama (both countries treated as a biogeographic unit) resulted in the detection of 2012 species of orchids of which 934 are shared (Bogarín et al., 2014b). From these figures, 784 (39%) species are endemic to the Isthmus (Table 1.1). A strategy to analyze the current evolutionary and floristic relationships of the Orchidaceae of the Isthmus is to study the most diverse groups in the region. An analysis of the various genera in both Costa Rica and Panama shows that *Epidendrum* L., *Lepanthes* Sw. and *Stelis* s.s. Sw. contain the highest number of species and the highest percentages of endemism (Tables 1.2–1.3). These genera are also monophyletic (Pridgeon et al., 2001) and therefore there is no bias due to the use of different nomenclatural circumscriptions that might cause variations in the number of species assigned to a genus. One factor that can affect the interpretation of evolutionary and biogeographic data is the intensity of the alpha-taxonomic work. The most diverse genus in the Isthmus is *Epidendrum*, the taxonomy of which has been developed in detail and consistently by Hágsater and colleagues. *Lepanthes* is a diverse genus, and despite extensive work by (Luer, 2003a) it is expected that there are still many undiscovered species new to science, especially in the relatively unexplored areas of the Cordillera de Talamanca and Panama. If this expectation is correct, *Lepanthes* may exceed *Epidendrum* in number of species recorded in the Isthmus (Pupulin and Bogarín, 2014).

Table 1. 1. Number of species, endemics and genera in Costa Rica and Panama

	Costa Rica	Panama	Total
Species	1574	1372	2012
Endemics	485	299	784
Genera	199	187	211

Moreover, the taxonomy of *Stelis* s.s. is the least developed, and conclusions based on these data are likely biased (Luer, 2003b). Botanical exploration and alpha-taxonomy are therefore tasks that must be promoted with impetus in the region. Some other diverse groups in the Isthmus are *Camaridium* Lindl., *Dichaea* Lindl., *Oncidium*, *Pleurothallis*, *Scaphyglottis* Poepp. & Endl., *Sobralia* Ruiz & Pav., *Specklinia* Lindl. and *Telipogon* Kunth. (Fig. 1.2) These groups also maintain a tendency to hold many endemic species. The taxonomic work in these genera has also revealed new species and expanded knowledge on their geographic distributions, encouraging more potential case studies to understand the evolution and diversification of Orchidaceae in the Isthmus (Bogarín et al., 2014a; Dressler and Pupulin, 2015; Pupulin et al., 2012).

Table 1.2. The most diverse genera in Costa Rica and Panama

Costa Rica		Panama	
Genus	Number of species	Genus	Number of species
<i>Epidendrum</i>	207	<i>Epidendrum</i>	221
<i>Stelis</i>	88	<i>Lepanthes</i>	151
<i>Lepanthes</i>	66	<i>Stelis</i>	103
<i>Pleurothallis</i>	54	<i>Camaridium</i>	48
<i>Camaridium</i>	48	<i>Pleurothallis</i>	48
<i>Scaphyglottis</i>	39	<i>Specklinia</i>	44
<i>Sobralia</i>	39	<i>Scaphyglottis</i>	38
<i>Specklinia</i>	34	<i>Sobralia</i>	38
<i>Oncidium</i>	32	<i>Telipogon</i>	37
<i>Dichaea</i>	26	<i>Masdevallia</i>	34

1.3 Biogeography and endemism of orchids in Costa Rica and Panama

About 40% of the orchid species are endemic to the Isthmus. The highest percentages of endemism recorded could be related to geological events of its volcanic arc, vicariance and *in situ* speciation produced by the lifting of the Cordillera de Talamanca. For example, allopatric speciation in *Lycaste bruncana* Bogarín and *L. tricolor* Rchb.f. (Fig. 1.3), among other examples found in *Brassia* R.Br., *Epidendrum*, *Kefersteinia* Rchb.f., *Oncidium*, *Pleurothallis* and *Stelis*, indicate an important role of the altitudinal division in vicariance speciation induced by the Talamanca and its climate barrier effect blocking the Caribbean trade winds (Bogarín, 2007; Pupulin, 2001; Pupulin and Bogarín, 2009). The highest percentages of endemism are found in the most diverse genera. For instance, 90% of the species of *Lepanthes* are endemic and about 50% of the species of *Stelis* and *Epidendrum* (Table 1.4) occur nowhere else. The study of the factors favoring this high

Table 1.3. Genera with most endemic species in Costa Rica and Panama.

Costa Rica		Panama	
Genus	Endemic species	Genus	Endemic species
<i>Lepanthes</i>	102	<i>Epidendrum</i>	53
<i>Epidendrum</i>	80	<i>Pleurothallis</i>	23
<i>Stelis</i>	37	<i>Stelis</i>	23
<i>Telipogon</i>	31	<i>Lepanthes</i>	21
<i>Pleurothallis</i>	15	<i>Telipogon</i>	17
<i>Sobralia</i>	15	<i>Sobralia</i>	16
<i>Camaridium</i>	14	<i>Masdevallia</i>	9
<i>Specklinia</i>	14	<i>Camaridium</i>	8
<i>Masdevallia</i>	13	<i>Specklinia</i>	7

Table 1.4. The most diverse genera and the % of endemis in the Isthmus of Panama

Genus	Species in the Isthmus	% endemic species
<i>Lepanthes</i>	155	90.12
<i>Epidendrum</i>	133	46.18
<i>Stelis</i>	60	43.80

endemism in *Lepanthes* is key to understanding its diversification and will be further discussed in the upcoming chapters of this PhD thesis. Other genera also deserve more attention because, although not as diverse, they show high rates of endemism; one of these is *Telipogon*, in which more than 70% of the species are endemic. Current floristic relationships with other groups of orchids of the Andes is evident. For example, *Telipogon* is a diverse genus in the highlands of the Isthmus, and its northern distribution is limited. Other genera of South American affinities are *Brachionidium* Lindl., *Fernandezia* Lindl. and *Pterichis* Lindl. that almost reach their northernmost distribution in the Cordillera de Talamanca. About 10 genera are present in Panama but not in Costa Rica. These genera have a strong South American affinity: *Discyphus* Schltr., *Eloyella* P.Ortiz, *Koellensteinia* Rchb.f., *Neomoorea* Rolfe, *Rudolfiella* Hoehne and *Selenipedium* Rchb.f. They range from Central Panama to the southeast of Darien and towards Colombia, indicating a common geological history of this area but different from western Panama and southeast Costa Rica. The geological formation of foothills of Maje, Darien and San Blas in Panama and western Colombia is reflected in the species composition data. Geographical distributions of *Dinema* Lindl., *Euryblema* Dressler, *Helleriella* A.D. Hawkes and *Horichia* Jenny suggests that these genera might be present in Costa Rica (Bogarín et al., 2014b). On the other hand, 18 genera present in Costa Rica are still not recorded from Panama. Some of them show a northern distribution such as *Arpophyllum* La Llave & Lex. and *Restrepiella* Garay & Dunst. However, *Epistephium* Kunth, *Funkiella* Schltr., *Lankesterella* Ames, *Trevoria* F.Lehm., *Tropidia* Lindl. and *Warmingia* Rchb.f., all with representatives in South America, might be distributed in Panama after all. The bias resulting from less floristic and alpha-taxonomic work in Panama should be reduced in the upcoming years (Bogarín et al., 2013).

1.4 Evolutionary diversification and orchid floristic composition

There are many factors that can enhance orchid species diversifications such as orogeny, past climatic fluctuations, interactions with other organisms such as mycorrhiza, pollinators, seed dispersers or key innovations such as colonization (extrinsic) or trait evolution (intrinsic). The main aim of my PhD thesis consisted of studying the factors that led to the formation of the current species composition of Orchidaceae in the Isthmus. Based on our taxonomic experience we have selected *Lepanthes* and closely related genera as a model group to study the extraordinary species richness and evolution in Costa Rica and Panama and its relationship with the Andean flora. We intend in the future to extend this model to other diverse groups such as *Stelis*. *Epidendrum* is



Figure 1.2. Some representatives of the major groups of Orchidaceae present in Lower Central America. From left to right: *Camaridium campanulatum*, *Epidendrum nocturnum*, *Epidendrum* (*Oerstedella*) *walisii*, *Lepanthes matamorosii*, *L. bradei*, *Pleurothallis anthurioides*, *Scaphyglottis pulchella*, *Stelis transversalis*, *Telipogon panamensis*. Photographs by Diego Bogarín.

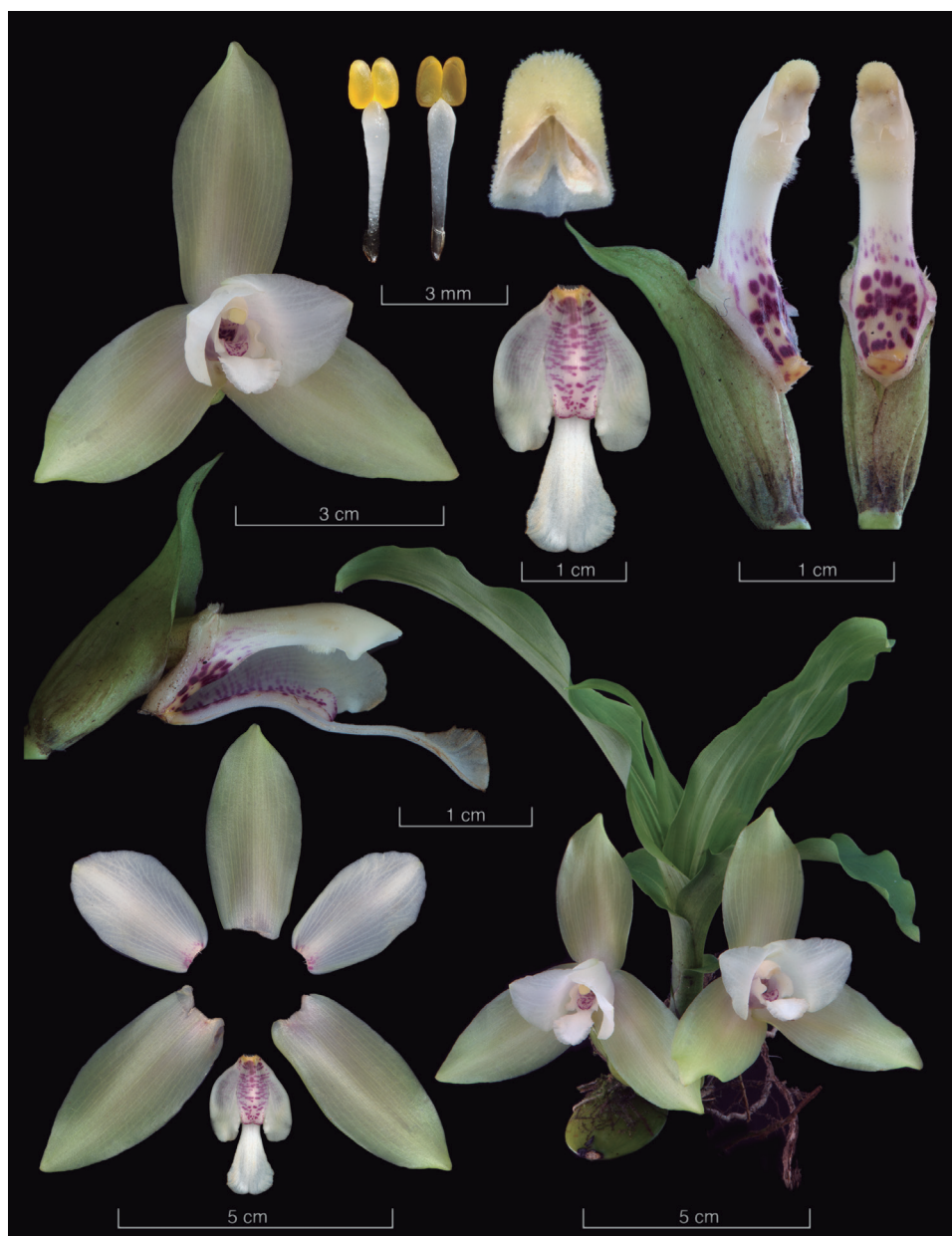


Figure 1.3. Lankester Composite Digital Plate of *Lycaste bruncana*, a species from Costa Rica and Panama restricted to the Pacific watershed of Cordillera de Talamanca.
Photograph by Diego Bogarín.

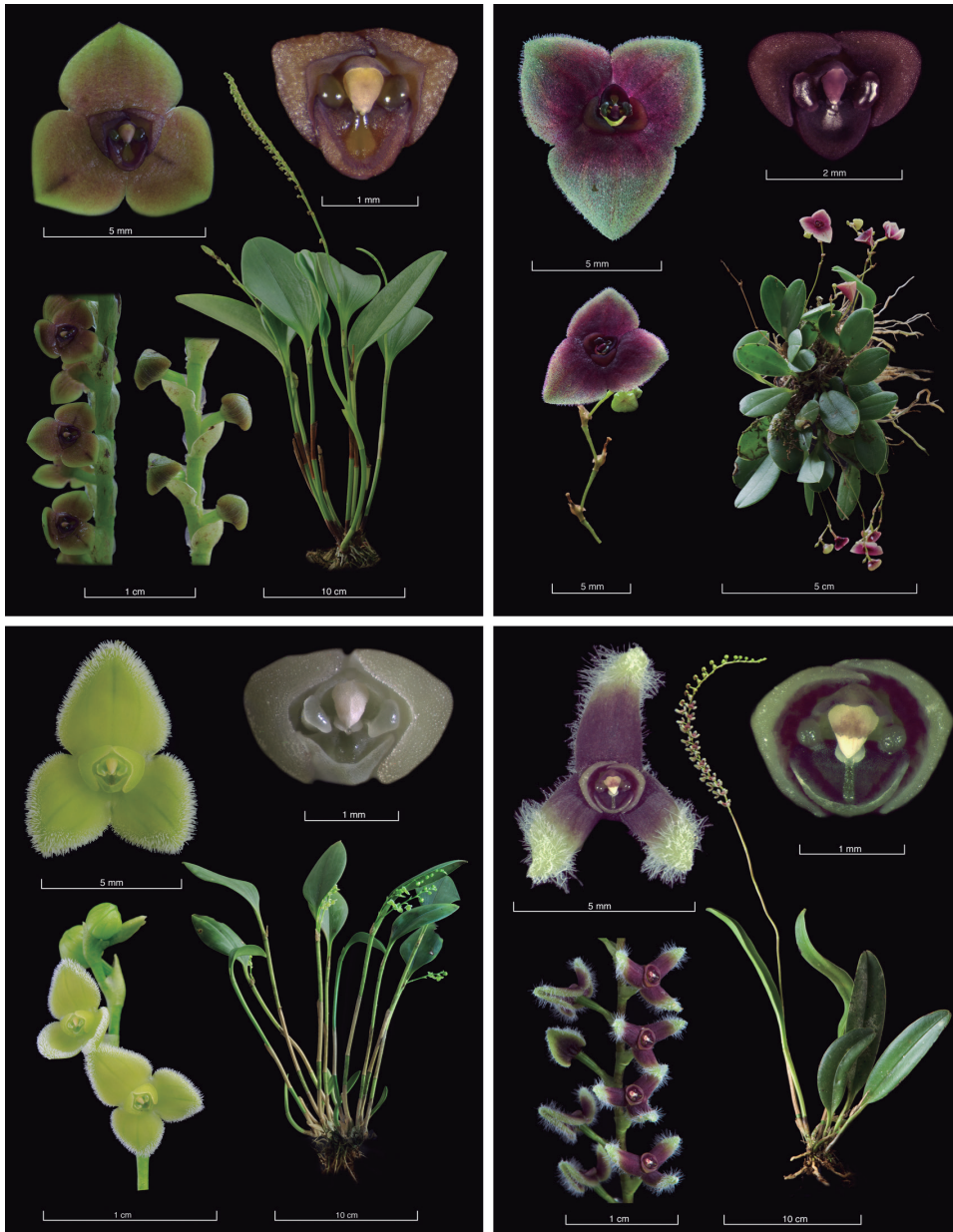


Figure 1.4. Lankester Composite Dissection Plates (LCDP) of some representative species of the highly diverse genus *Stelis* from Costa Rica and Panama. Species are currently under taxonomic review. Photographs by Diego Bogarín.

another interesting group, and it is being evaluated by Hågsater and co-workers so there will be information available in the future. Although *Stelis* s.s. remains an excellent group as a candidate to study their high evolutionary diversification, the limited taxonomic expertise and little ecological information available so far prevented us to address this group (Fig. 1.4). However, some clues about its pollination mechanism (hitherto little-known) indicate that it may be pollinated by gall midges of Cecidomyiidae under conditions that we are still exploring.

1.5 The orchid genus *Lepanthes*

Lepanthes is one of the major genera in the Pleurothallidinae. With over 1,000 spp., the genus ranges from southern Mexico and the Antilles to Peru and Bolivia, with few species in the Guianas and Brazil. Plants grow mostly from 1,500 to 3,000 m elevation in humid, often shady places. Highest diversity is found in the Andean region of Colombia and Ecuador with more than 300 species in each country (Luer, 1996b; Luer and Thoele, 2012) (Fig. 1.6-1.7). *Lepanthes* is represented in Costa Rica and Panama with about 150 spp. Only two species are shared with Colombia and Ecuador. This may reflect the floristic influence of the Andean region in Costa Rica and Panama at the genus level but not the species level. Species are usually restricted to specific ranges or mountains, and endemism is high. Plants are recognized by the monophyllous ramicauls, enclosed by a series of lepanthiform sheaths and congested, distichous inflorescences. Floral morphology distinguishes *Lepanthes* from other genera with lepanthiform sheaths (*Draconanthes* (Luer) Luer, *Trichosalpinx* Luer and *Lepanthopsis* (Cogn.) Hoehne among others). Flowers are characterized by the ovate to elliptic sepals and the transversely bilobed petals. Lip morphology is complex (Fig. 1.6); the lip is usually bilaminar with the two blades supported by connectives that often lift the blades above the column. The central part of the lip is made up by the body, which is attached to the column. The appendix is developed from the sinuous between the connectives and varies morphologically among the species in different combinations of lobes,

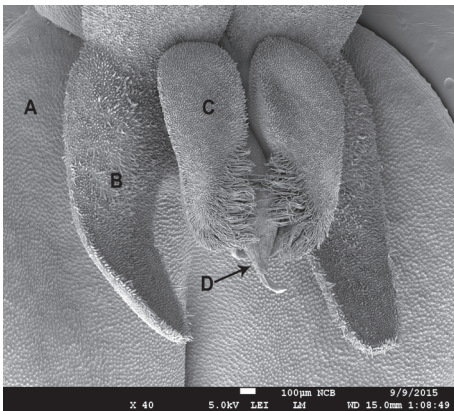


Figure 1.6. Scanning electron microscopy (SEM) of a flower of *Lepanthes horichii* showing the complex morphology in detail. **A.** Sepal. **B.** Petal (lower lobe). **C.** Lip (lobe). **D.** Column showing the apical anther. Photographs by Diego Bogarín

hairs, projections, trichomes and membranes. *Lepanthes* taxonomy has been studied by Luer and Thoele (2012) and particularly in Costa Rica and Panama by Luer and Dressler (1986), Luer (2003a), Pupulin *et al.* (2009), Pupulin and Bogarín (2014). Givnish *et al.*, (2015) pointed out that the role of limited dispersal of seeds and ineffective pollinators, limited gene flow, population bottlenecks and genetic drift deserve to be further studied, and that *Lepanthes* would be one of the best study cases for that so we focused on its systematics in Chapters 2 and 3. Although *Lepanthes* is considered a monophyletic group, it has been poorly sampled phylogenetically (Pridgeon *et al.*, 2001). Phylogenetic analyses of the Pleurothallidinae showed that *Andinia* (Luer) Luer (including *Neooreophilus* Archila) is not closely related to *Lepanthes*, and



Figure 1.7. Some species of *Lepanthes* from Costa Rica and Panama. Species are mostly endemic and show a wide range of morphological variation around the same scheme. Note the coloration of the flowers, which might be involved in attraction of pollinators. Photographs by Diego Bogarín.

flower similarities are homoplastic (Wilson et al., 2017) (Fig. 1.8). *Neooreophilus* species have a similar flower morphology as *Lepanthes*, and there is some evidence of its pollination by pseudocopulation (S. Vieira-Urbe, pers. comm. 2015). *Neooreophilus* is absent in Mesoamerica, and it might be a younger group when compared to *Lepanthes*, which is widespread in the Neotropics. Phylogenetics of these two groups could help to shed light on this hypothesis. Furthermore, the floral morphology of *Lepanthes* varies astonishingly around the same scheme in all the >1,000 species known. The flowers are developed above or beneath the leaves or sometimes in inflorescences surpassing the leaves and the petals and lip tend to be reduced or almost absent in some species. The most common colors of flowers are yellow, red, orange, purple (rarely green) or a combination of these. The appendix of the lip plays an important role in pollination of *Lepanthes* flowers. Blanco and Barboza (2005) described the first case of pseudocopulation in the



Figure 1.8. Floral convergence among the species of *Neoreophila*. A-B, and *Lepanthes* C. Photos: A-B, by Sebastián Vieira-Urbe. C, by Diego Bogarín.

genus in which male fungus gnats of *Bradysia floribunda* (Diptera: Sciaridae) visit flowers of *L. glicensteinii* Luer, apparently attracted by sexual pheromones. The male adheres to the flower appendix during copulation. In this attempt the insect removes the pollinarium with the abdomen. Calderón-Sáenz (2012) observed the same phenomenon in *L. yubarta* E. Calderon, which is visited by another species of *Bradysia* in Valle del Cauca, Colombia. Sciaridae flies, commonly known as dark-winged fungus gnats, are a diverse group of flies with more than 8,000 species worldwide. Eggs are deposited between the lamina of sporocarps of fungi, and the larvae feed on sporocarps and other decaying organic matter such as rotten trunks or plant roots or leaves. Some species are pests of important economic crops such as mushrooms. Blanco and Barboza (2005) and Calderón-Sáenz (2012) clearly described the pollination of *Lepanthes* but left many evolutionary questions unanswered. We are studying more cases of pollination in other *Lepanthes* species where morphological evidence indicates that other parts of the body of fungal gnats are being used such that the pollinia are not always attached to the abdomen. Probably, flowers produce pheromone-like compounds to attract pollinators and we have some preliminary evidence that flowers indeed use this strategy to attract males.

The anatomy of the flower was studied in order to find possible secretory structures involved in pollinator attraction (Fig. 1.7). Sciarids are attracted by yellow colors. Special traps were designed to catch flies in greenhouses made up by yellow cardboard and petroleum jelly. Although this method proved to be less effective in studying *Lepanthes* pollination (Godden, 2002), the approach works well in large populations of plants to increase the probabilities of catching gnats carrying pollinia. Sciarid flies have short life cycles (Wilkinson and Daugherty, 1970). Adults usually live less than 7 days, and they are considered poor flyers. Thus the chance to deceive inexperienced males may be high. Sciaridae is a highly diverse group but poorly known. The behavior and natural history of Sciaridae are key to understanding the evolution of *Lepanthes*. Why is *Lepanthes* more diverse than closely related genera such as *Anathallis* Barb. Rodr., *Draconanthes*, *Lankesteriana* Karremans, *Lepanthopsis*, *Trichosalpinx* and *Zootrophion* Luer? A hypothesis is that pseudocopulation triggered the high speciation levels in *Lepanthes*. To study the evolutionary diversification of *Lepanthes* and the possible triggers of speciation, it was necessary to extend the molecular phylogenetic sampling of the “*Lepanthes* clade” as described by Pridgeon *et al.*, (2001) in order to find answers to the evolutionary success of *Lepanthes* as compared to its sister genera (see **Chapters 2-5**). However, the pollination mechanisms

that operate in the sister genera are also important for comparisons with *Lepanthes*. Observations on the pollination of *Trichosalpinx* revealed a frequent visitation by biting midges of the Ceratopogonidae family (see **Chapters 6-7**). Finally, we also used biogeographical areas within the Neotropics in order to draw accurate conclusions about endemism and species distribution in biogeographical analyses (**Chapters 8-9**).

Aims of the thesis

In this thesis, I targeted the orchid genus *Lepanthes*, one of the six genera of angiosperms that surpasses 1,000 species in the Neotropics, as a study model to investigate the evolutionary processes that promoted species diversifications. To investigate some of the possible factors that shaped the diversification in *Lepanthes* and related genera we improved the taxonomy of the group by providing a solid phylogenetic framework combined with ancestral state reconstructions, assessing inter-specific relationships in species complexes with hundreds of molecular markers, and describing new species, (**Chapters 2-5**), disclosed a new pollination system, identified morphological characters associated with similar pollination mechanisms (**Chapters 6-7**) and discussed the impact of biogeographical events and orogeny (formation of the Andes and Central America) on the extant species richness and biodiversity of *Lepanthes* (**Chapter 8-9**). This thesis provides new insights in the complex evolution of one of the most species-rich angiosperm lineages in the Neotropics.

Outline of the thesis

Lepanthes contains more than 1,130 species and new species are constantly being discovered in the Neotropics. An approximate number of the actual species diversity is not yet known and this number tends to increase partially due to the extreme diversity of the genus but also because several regions of the Neotropics continue to be explored and the boost of alpha-taxonomic studies (Luer and Thoele, 2012; Pupulin et al., 2018; Pupulin and Bogarín, 2019). In addition, the phylogenetic relationships of the *Lepanthes* and allied genera were problematic at the start of my PhD project, not because of the lack of sufficient DNA markers but because of insufficient taxonomic sampling and the widespread convergences in reproductive characters. Therefore, in **Chapter 2** (Bogarín et al. in review) we presented the integral discussion on the phylogenetics of the *Lepanthes* clade integrating phylogenetics and morphological evolution of character states. Consequently, in **Chapter 3** we proposed a new classification of the *Lepanthes* clade based on a more extensive taxonomic sampling and the information obtained in Chapter 2 (Bogarín et al., 2018). Similar to the poor understanding of inter-generic relationships, some inter-specific relationships are difficult to understand because of the high morphological similarity, especially in floral traits. In addition, these species complexes are challenging to resolve using standard DNA barcoding markers such as nrITS or *matK*. Therefore, in **Chapter 4** we assessed the performance of hundreds of innovative molecular markers derived from an anchored hybrid enrichment approach (AHE) to resolve phylogenetic relationships and improve species recognition in the *Lepanthes horrida* species group (Bogarín et al., 2018). Further, some areas of the Neotropics are rich in *Lepanthes* species but much floristic work still needs to be done. This

is for instance the case for Panama, where an underestimation of species is well known but an increase of taxonomic studies is revealing new species or new records from neighboring regions (Bogarín et al., 2013). In this way, in **Chapter 5** we revealed two new species of *Lepanthes* detected during fieldwork (Bogarín et al., 2017). In addition to the systematics and the evolution of morphological traits, pollination studies are key in understanding homoplastic characters in closely related genera and the role of pollinators as drivers of species diversity. However, this is largely unknown because knowledge of pollination systems in the group is still scarce and only the pollination system of *Lepanthes* is known. Therefore, in **Chapter 6** we addressed the pollination of *Lepanthes*' closely related genus *Trichosalpinx* through study of floral anatomy, pollinator behaviour and floral traits shared with other angiosperms to elucidate its pollination mechanism (Bogarín et al., 2018). The similar floral morphology and homoplastic characters described in **Chapter 5** among *Trichosalpinx* and the closely related genera *Anathallis* and *Lankesteriana* suggest that they are pollinated by a similar system as shown in **Chapter 6**. Hence, in **Chapter 7** we assessed the micromorphological and histochemical features of floral organs to test a hypothesis on floral convergence in this clade (Bogarín et al., 2018). And finally, to understand the role of abiotic factors such as the impact of the Andean mountains in the diversification of *Lepanthes* in **Chapter 8-9** we inferred the biogeographical history and diversification dynamics of the two largest Neotropical orchid groups (Cymbidieae and Pleurothallidinae), using two unparalleled, densely sampled phylogenies coupled with geological and biological datasets (Pérez-Escobar et al., 2017a). In **Chapter 10**, I discuss further steps needed to complement the findings presented in my PhD thesis to fully understand and better protect orchid species radiations in the Neotropics.