

# DAVIS EXPEDITION FUND

## REPORT ON EXPEDITION / PROJECT

**Expedition/Project Title:** The Evolution of *Begonia* Section *Gireoudia* in Central America

**Travel Dates:** 28<sup>th</sup> February – 26<sup>th</sup> April 2010

**Location:** Southern Mexico

**Group Members:** Alex Twyford

**Aims:** Population level sampling of two *Begonia* species and their putative hybrid for DNA analysis

---

**Outcome (not less than 300 words):-**

**The Evolution of *Begonia* Section  
*Gireoudia* in Central America**  
Davis Expedition Fund Grant Report



**Alex Twyford**

**University of Edinburgh    Royal Botanic Gardens Edinburgh**

## Summary

Collections of *Begonia* were made during a 7 week field trip to Mexico. Collecting was focused in the south of the country in the states of Chiapas, Oaxaca and Veracruz. These collections were completed with Mark Hughes (Royal Botanic Gardens Edinburgh, RBGE) as well as Mexican collaborators Hector Domínguez (Herbario Eizi Matuda, Tuxtlas Gutierrez, Chiapas) and Arturo Sanchez (Sociedad para el Estudio de los Recursos Bióticos de Oaxaca, SERBO). The primary aims were: a) to collect population level samples of *Begonia nelumbiifolia* and *B. heracleifolia*, as well as their putative hybrid, for population genetic analysis, and b) to collect DNA, living material and herbarium specimens of the *Begonia* species from Southern Mexico, for phylogenetic analysis and to enrich the living collection at RBGE. Secondary aims were to document the *Begonia* herbarium collections from Mexico for future fieldtrip planning and to develop collaborative links with botanical researchers in Mexico.

In total 1027 *Begonia* collections were made, of which 715 were for population genetic analysis. Putative hybrids between *B. nelumbiifolia* and *B. heracleifolia* were found at 4 localities. A total of 29 species were collected, of which 16 are new to the research collections of the RBGE. Herbarium specimens were collected in duplicate and distributed to the herbaria of Southern Mexico. These collections will greatly improve the living collection and herbarium at RBGE, and these samples provide valuable material for current and future research into speciation, hybridisation and adaptation of Central American *Begonia*.

## Introduction

Mesoamerica is recognised as one of the outstanding areas of biodiversity on the planet, and this is reflected in its incredible species richness of vascular plants (Myers et al., 2000). The evolutionary process and patterns that have resulted in this species diversity are poorly understood, however advances in molecular approaches are shedding light on this fascinating topic (see Cody, 2008 and references therein). We are using these methods to understand the evolutionary history of the angiosperm genus *Begonia* in Central America. *Begonia* is represented by some 450 species in the Americas (Neale et al., 2006), and different species are adapted to a huge range of habitats, making it the ideal system to test evolutionary hypotheses about speciation and adaptation.

The primary focus of the project is to collect two widespread *Begonia* species, *B. nelumbiifolia* and *B. heracleifolia*. These species are frequently encountered along roadside verges, however ecological preferences generally keep these species apart (Hoover, 1979). There are a number of cases where the two species occur in sympatry, and hybrids have been reported (Burt-Utley, 1985; Morris, 2008). I am interested in whether introgression, the exchange of genes between species, occurs within hybrid swarms. This is of particular interest due to the dynamic changes in distribution ranges caused by the expansive programme of road building in Mexico, and predicted future changes in climate. Therefore I will use population genetic approaches to investigate gene flow within and between species, which is important in understanding patterns of speciation.

The secondary aim of the project is to supplement the living collection and herbarium at the Royal Botanic Gardens Edinburgh (RBGE) with *Begonia* species collections from the South of Mexico. The genus *Begonia* is one of the four flagship research groups at the RBGE. In recent years the *Begonia* flora of Africa and South East Asia has been documented, and the biogeography and taxonomy of these groups investigated (Forrest, 2000; Forrest and Hollingsworth, 2003; Plana et al., 2003). However the collections from the highly speciose Central American flora at RBGE is limited, being represented by horticultural plants and species collections of unknown provenance. In order to study the evolution of this group the number of species in the living collection needs to be expanded, to allow for experimental work on the group. It is also important to supplement the herbarium with specimens of *Begonia*. Herbaria act as important long term stores of specimens for future classification and taxonomic work. With this data being increasingly digitalised and available via the internet these resources are increasingly important, and in many groups this material can even be used for DNA extractions.

## Fieldwork plan and justification

Begonias are reported to have limited dispersal capabilities, as indicated by their high between population genetic differentiation ( $F_{st}$  values) and species frequently having limited ranges (high endemism)(Hughes and Hollingsworth, 2008). Most population genetic studies focus on rare species in order to assess conservation priorities(Hughes and Hollingsworth, 2003), however the patterns of population structure are likely to be different for widespread weedy species that disperse along roads. Therefore in order to understand within and between species population structure I have chosen to work on two of the most widespread and common *Begonia* species from the species rich section

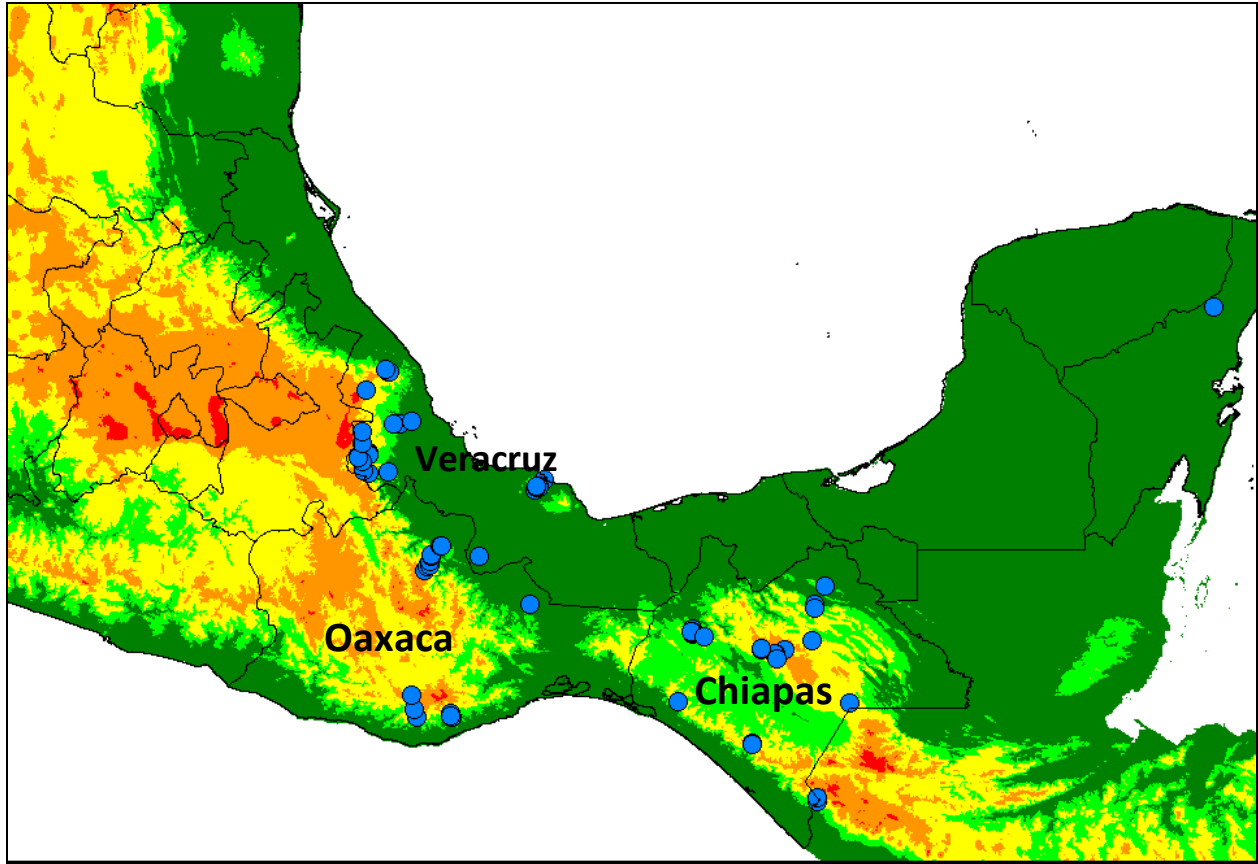
*Gireoudia*, *Begonia nelumbiifolia* and *B. heracleifolia*. To capture the variation in population structure it is necessary to make collections from throughout the distribution range of the species of interest.

In order to meet the second goal, of collecting different species, it is important to target the areas with highest species richness of *Begonias*. Prior to fieldwork myself and Dr Keith Gardner (University of Edinburgh/Royal Botanic Gardens Edinburgh) compiled a database of species locations based on a variety of sources, including monographic descriptions (Burt-Utley, 1985; Burt-Utley and Utley, 1999), internet databases (GBIF, tropicos), *Begonian* articles (e.g. Ziesenhenné, 1950, 1952, 1981, 1988). Many of these descriptions are old and vegetation clearance since the articles were published is likely to make them redundant. Also, due to the lack of a complete monograph of the section synonymy is likely to be a problem. However, this database allows for the most species rich localities to be targeted.

Based on this literature survey the most diverse states in Mexico for *Begonias* were identified as the southern states of Chiapas, Oaxaca and Veracruz. Oaxaca is arguably the most biodiverse state in Mexico, largely due to its variation in ecological zones. These can be divided into humid tropical (45%), sub-humid tropical (35%) and temperate (about 20%) ([www.sipaz.org](http://www.sipaz.org)). The state contains some 9000 plant species, half of the national total, with Chimalapas representing the most outstanding area of biodiversity. However, the state is complex to navigate with large areas of inaccessible forest, permission from local people is required for collections, and the literature on *Begonia* species found here is diffuse. Veracruz contains a different complement of *Begonia* species as it contains large dry canyons, where xerophytic *Begonia* species grow. There are small patches of protected biosphere reserve where *Begonia* species are reported to flourish, however extensive expansion of coffee plantations across the region has resulted in a complete absence of lowland and mid elevation habitats. Chiapas, bordering Guatemala, contains a number of regionally endemic species in the southern mountains. The presence of biosphere reserves next to world famous tourist sites such as Palenque and the Sumidero Canyon has preserved some of the areas of greatest biodiversity.

## Itinerary

The summary below details the itinerary of the 7 weeks of *Begonia* field collections that took place in Mexico in the spring 2010. Figure 1 indicates the sites where *Begonia* collections were made.



**Figure 1 – Map of *Begonia* collections in Southern Mexico.** Topographic map (high altitudes in red, low altitudes in dark green) highlights the widespread effect of deforestation in lowland areas, indicating that many lowland areas are now devoid of *Begonia*s. *Begonia* collections indicated by blue dots.

28<sup>th</sup> February - 2<sup>nd</sup> March. Mexico City. Acclimatization and planning

3<sup>rd</sup> March. Travel to Xalapa, Veracruz

4<sup>th</sup> -7<sup>th</sup> March. UNAM Biological Station at Los Tuxtlas, Veracruz

8<sup>th</sup> March. Palenque, Chiapas

9<sup>th</sup> March. South of Palenque and Agua Azul, Chiapas

10<sup>th</sup> -11<sup>th</sup> March. San Cristobal, Lagunas de Montebello, Chiapas

12<sup>th</sup> March. Comitan, Chiapas

13<sup>th</sup> March. Huixtla, Chiapas

14<sup>th</sup> March. Tapachula and Siltepec, Chiapas

15<sup>th</sup> March. Volcan Tacana, Chiapas

16<sup>th</sup> March. Drive to Tuxtla Gutierrez, Chiapas

17<sup>th</sup> – 20<sup>th</sup> March. Around Tuxtla Gutierrez: Ocozucuatla, Berriozabel, Villaflores, El Truinfbiosphere reserve, Chiapas

21<sup>st</sup>-23<sup>rd</sup> March. Return to Mexico City

24<sup>th</sup>-28<sup>th</sup> March. Herbarium work and specimen processing

29<sup>th</sup> March. Travel to Cordoba, Veracruz, and planning

30<sup>th</sup> March. Zongolica, Veracruz

31<sup>st</sup> March. Huatusco, Veracruz

1<sup>st</sup> April. Misantla, Veracruz  
2<sup>nd</sup> April. Around Misantla, Veracruz  
4<sup>th</sup> -7<sup>th</sup> April. Around Oaxaca  
8<sup>th</sup> April. Highway 175 north of Oaxaca  
9<sup>th</sup> April. Valle Nacional, Oaxaca  
10<sup>th</sup> April. Tehuantepec, Oaxaca  
11<sup>th</sup> April. Santa Maria Xanabi, Oaxaca  
12<sup>th</sup> April. return to Oaxaca City  
13<sup>th</sup>-17<sup>th</sup> April. Specimen processing  
18<sup>th</sup>-21<sup>st</sup> April. Herbarium work at UNAM  
26<sup>th</sup> April. Return flight to Scotland

Further collections are planned to complement these from Costa Rica in July 2010. These were originally scheduled as part of this fieldtrip but were cancelled due to the collaborators in Costa Rica being unavailable.

## Collection methods

Different collection methods were employed for species level and population level samples. For the population genetic survey of *B. heracleifolia* and *B. nelumbiifolia*, collections were made in populations of the species occurring away from the other species (allopatric), where the two species grow in close proximity (sympatric), and where hybrids were present. In each case 30 individuals of each species per population were sampled. For the species level survey three plants per population were sampled.

In each case photographs of the plants were taken to allow for identification and further analysis. Where possible these included a habitat shot, overall photo of the plants' growth habit and macro photo of key details such as the inflorescence structure. In addition to this, in one hybrid swarm photos were taken of a single leaf per plant with a scale in the image for 30 plants each of *B. heracleifolia*, *B. nelumbiifolia*, and as many of the putative hybrid that were present at the site. The delayed flowering season caused by the cold wet winter prevented the collection of seed pods, and rhizomes were collected instead. A single side branch (or whole rhizome for abundant species) was collected, packaged in dry newspaper, and couriered back to the UK. Herbarium specimens were collected in duplicate for the Royal Botanic Gardens Edinburgh (E), Universidad Nacional Autónoma de México (UNAM), Royal Botanic Gardens Kew (K), Sociedad para el Estudio de los Recursos Bióticos de Oaxaca (SERBO, Oaxaca collections only),

Herbario Eizi Matuda (Tuxtlas Gutierrez, Chiapas, selected Chiapan collections only), Los Tuxtlas UNAM field station (collections in the vicinity of Los Tuxtlas only).

## Results

### Population genetic collections

A total of 715 collections of *B. heracleifolia* (378 plants), *B. nelumbiifolia* (323 plants), and the putative hybrid (14 plants) were made. The largest population of putative hybrids were found near the biological station at Los Tuxtlas, Veracruz, where 10 hybrids were recorded. Three other small populations of hybrids between *B. heracleifolia* and *B. nelumbiifolia* were found. Putative hybrids could easily be distinguished based on intermediate leaf morphology between the two putative parents, as well as intermediate flower time. Near Motzorongo, Oaxaca, a large population of hybrids (30 plants) between *B. heracleifolia* and *B. sericoneura* were collected. A selection of these hybrids, as well as species collections, are illustrated in Appendix 2.

### Species collections – Chiapas

Collections were made of 16 different *Begonia* species in Chiapas, of which 8 were from section Gireoudia, 6 from section Weilbachia and 2 from other *Begonia* sections. This represents 40% of the 40 species described in the literature for Chiapas. In Chiapas recollections of species in the literature was successful for recently described collections, but also for a number of very old collections. *Begonia mazaе*, restricted to Pico Carrizal was successfully recollected, the first time since 1941. *Begonia purpusii* was collected near Union Juarez, another old Ziesenhenné collection that was surprising to find. The complete list of species collected on the fieldwork are listed in Appendix 1.

We were unsuccessful in recollected xerophytic species such as *B. peltata* in Chiapas. A number of dry habitats were investigated, however none of these yielded any *Begonia* collections. Particularly of note was the difficulty in collecting the widespread *B. plebeja*. This species is deciduous through much of its range, and due to the late start of the season this plant was not in leaf. However, inspection of the herbarium material (once received from Mexico) may be able to establish whether some of the unidentified *Begonia* collections with distinctive spots on the leaf are *B. plebeja* collected from sites where it remains evergreen.



## Species collections – Veracruz

Out of the 30 species described in Veracruz collections were made of 17 species, representing 55% of the *Begonia* flora of the state. These collections were complementary to those from Chiapas, with 7 of the species collected not being found in Chiapas. These included the dry-adapted species *B. hydrocotylifolia*, *B. peltata* and *B. carolineifolia*. Collections in Veracruz were more difficult due to the widespread deforestation of lowland and mid-elevation terrain, making collections only possible from mountainside, canyons, biosphere reserve and some roadsides. Therefore older accounts of the flora of Veracruz, even the 13 year old account by Jimenz and Schubert (1997) are now largely out-of-date as a guide to the *Begonia* species present in lowland areas. Other notable collections were the narrowly distributed *B. multistaminea* and *B. sousae*, which were found to be highly localised but locally abundant.

## Species collections - Oaxaca

A large number of *Begonia* collections were made in the state of Oaxaca, including many of *B. heracleifolia* and *B. nelumbiifolia* for population genetic analysis (total 270 plants). In total 9 species were identified in the field, and at least 4 other unknown species were collected. We will identify these when the herbarium material is received. Two recently described species from near Santa Maria Xanabi were collected, *B. pseudodaedelea* and *B. morrisiorium*, both described in section Gireoudia despite them being very different morphologically from other collections (Morris and McMillan, 2010). We will now molecularly characterise these accessions to establish whether they group with other species from section Gireoudia.

## Herbarium documentation

A photo was taken of each *Begonia* specimen from Central America from the following herbaria: UNAM, SERBO, Herbario Eizi Matuda and Los Tuxtlas UNAM field station. A total of 918 images were taken. The most informative of these are the collections at UNAM, which are the most complete record of the *Begonia* flora of Central America. These collections also seem well curated with limited synonymy and incorrect idents, as well as relatively few unidentified specimens. This compares with Herbario Eizi Matuda which is a useful repository of local Chiapan collection, though many specimens are incorrectly identified. This compilation of images is freely available from the author via email, and it is currently organised by herbarium and then species. In the future a database of herbarium specimens would be a valuable resource for future fieldwork planning.

## Discussion and further work

*Begonia* species generally occur in isolated populations and frequently have limited distributions (Hughes and Hollingsworth, 2008). This distribution pattern may be due to poor dispersal capacities or very specific ecological envelopes and habitat requirements. On this fieldtrip collections were made from a large number of different species representative of the range of habitats that *Begonias* can grow in. This will allow a phylogeny of the group to be constructed using both nuclear and chloroplast markers. Interpretation of these results will give us an insight into the biogeographic patterns in central American *Begonia*, and shed light on the evolution of the group.

Putative hybrids were found between *B. nelumbiifolia* and *B. heracleifolia* in four localities. Notes on the two species ecology highlight their different ecological preferences, with *B. nelumbiifolia* being present in moist shaded roadside banks and *B. heracleifolia* being encountered on dry sun baked roadside verges. The two species occur in sympatry only on some disturbed roadside verges, and hybrids tend to be uncommon. As both these species are widely distributed and are found along dispersal corridors (such as roadsides), population genetic analysis will show how related these populations are and indicate whether the dispersal capacities are different to previously study rare endemics.

Whilst most central American *Begonia* species are found in Mexico, due to their limited distributions are frequent endemism other countries do have different species. An expedition to Costa Rica in July (previous scheduled as part of this trip, however this was cancelled due to the collaborator being unavailable) is now planned.

## Conclusion

The overall aims of the field collection, to a) collect population-level samples of two widespread *Begonia* species and their putative hybrid and b) to collect species-level collections from Southern Mexico, were both fulfilled in the fieldtrip. With regards to the first aim, a large number of collections were made across the central region of the two species range (covering many hundreds of kilometres), and populations of putative hybrids were also collected. With regards to the second aim, 29 identifiable species were collected, many of which are new to the living collections at RBGE. In addition to the above, all *Begonia* specimens from the national herbarium in Mexico and 3 smaller herbariums were photographed for future *Begonia* fieldwork in Central America, and collaborative links forged between

the RBGE and researchers in Chipas, Oaxaca and Veracruz. It is hoped that these links will be valuable for future collections and publications.

The living material of the species collections is successfully coming into leaf at RBGE. As this is the first *Begonia* fieldtrip to Central America, a level of uncertainty was present with the methods of collecting. However collecting rhizomatous *Begonias*, which many species in Central America are, in dry newspaper and storing them in open polythene bags, to prevent the rhizomes sweating, proved to be effective – and the plants survived a month in such conditions. During the trip a large number of skills were learnt, including practical plant collecting techniques, improvements with macro photography and a better understanding of herbarium arrangements.

Descriptions of new *Begonia* species in Central America have been constant over the last 30 years (see Burt-Utley, 1985; Burt-Utley and Utley, 1999; Morris and McMillan, 2010; Ziesenhenné, 1988), highlighting the fact that even relatively well developed countries with good transport infrastructure can be under-collected. Collection trips such as this one provide important material for both scientific research into plant evolution, ecology and taxonomy, as well as for ex-situ conservation and education. It is hoped that future fieldwork in Central America will document more of this horticulturally important genus.

## Financial statement

### Grants awarded:

Davis Expedition Fund (University of Edinburgh) £3000 (total spent £1054, rest returned)

Genetics Society Heredity Fieldwork Grant	£1500
Merlin Trust	£800
MacIntyre <i>Begonia</i> Fund	£2000
Stanley Smith Horticultural Trust	£1000
Total	£8300*

\*Dr Mark Hughes (RBGE) was awarded £2350 to fund his flights, food and accommodation, as well as a large contribution to the cost of car hire.

## Acknowledgements

I would like to thank Mark Hughes, Héctor Domínguez and Arturo Sanchez for help in the field. Thanks are due to thank Keith Gardner for assistance in fundraising and planning the fieldwork, and additional help for fieldwork planning was given by Marie-Stéphanie Samain and Carolina Granados Mendoza. I am thankful to Hilda Flores, Miguel Farrera, Silvia Salas and Rosammond Coates for their assistance in Mexican herbariums and guidance on suitable collection localities. Guidance for project design was given by Catherine Kidner and Richard Ennos. I would also like to thank Stephan Helfer, James Tosh, Martin Gardner, James Richardson, Toby Pennington, Susana Magallón, RBGE *Begonia* group and RBGE tropical group for their contributions and advice. I would like to thank the funding bodies on page 11 for providing financial support for the trip.

## Appendix 1: *Begonia* species collected

*Begonia* species collected in Mexico, ordered alphabetically. Note that final identification of species is reliant on detailed analysis of herbarium specimens once received from Mexico. The section the species is assigned to is indicated in brackets. Those in bold are new to the research collections at the RBGE.

***B. almedana*** (Weilbachia)

***B. barkeri*** (Gireoudia)

*B. carolineifolia* (Gireoudia)

***B. faustinoi*** (Weilbachia)

***B. fusca*** (Gireoudia)

***B. glabra*** (Wageneria)

***B. gracilis*** (Quadriperigonina)

*B. heracleifolia* (Gireoudia)

*B. hydrocotylifolia* (Gireoudia)

*B. imperialis* (Weilbachia)

***B. incarnata*** (Knesebeckia)

***B. lynceorum***(Weilbachia)

***B. manicata*** (Gireoudia)

*B. mazaе* (Gireoudia)

***B. morrisiorum*** (Gireoudia)

***B. multistaminea*** (Gireoudia)

*B. nelumbiifolia* (Gireoudia)

*B. peltata* (Gireoudia)

***B. pinetorum*** (Gireoudia)

*B. plebeja* (Gireoudia)

***B. pseudodaedelea*** (Gireoudia)

***B. pudica*** (Gireoudia)

***B. purpusii***(Weilbachia)

*B. pustulata*(Weilbachia)

*B. sartorii* (Gireoudia)

*B. sericoneura* (Gireoudia)

***B. sousae*** (Gireoudia)

*B. aff. squarrosa* (Gireoudia)

*B. thiemei* (Gireoudia)

## Putative hybrids collected

***B. heracleifolia* x *B. nelumbiifolia*** (Gireoudia)

***B. heracleifolia* x *B. sericoneura*** (Gireoudia)

## Appendix 2: Colour plates of selected *Begonia* collections and habitats

Pictures labeled a – h from top left to bottom right

### Plate 1: Variation in *Begonia* habitats in Southern Mexico

a) canyon near Coyol Veracruz, habitat of *Begonia peltata*, b) waterfall at Gucamaya Veracruz, with *B. multistaminea* growing in abundance, c) Sumidero Canyon Chiapas, surrounded by seasonally dry forest – reported locality for *B. plebeja*, d) degraded tropical rainforest near El Triunfo Chiapas, roadside clearing with *B. sartorii* e) canyon near Calchualco Veracruz, locality with abundant drought adapted *B. hydrocotylifolia*, f) roadsides frequently have a number of weedy *Begonia* species such as *B. heracleifolia*, *B. nelumbiifolia* or *B. pinetorum*, g) primary rainforest at union Juarez where *B. lyniceorum* can be found h) transitional zone between dry forest and cloud forest sees a clear demarcation in species, *B. fusca* grows near by

### Plate 2: Widespread *Begonia* species

a) *B. peltata* is frequently reported to grow in dry canyons in the literature, b) *B. sartorii*, common in mixed woodland, c) deciduous *B. plebeja*, note the symmetrical inflorescence, d) *B. fusca*, the largest leaved *Begonia* in Mexico, inset shows male flower details, e) Dense stand of *B. pinetorum*, inset shows male flower details, f) compound leaved *B. theimeii* with dense understory forest cover, g) *B. manicata*, h) *B. barkeri*

### Plate 3: Narrow endemic *Begonia* species

a) Recently described *B. morrisiorium*, b) *B. mazae*, only known from Picco Carizal where a few hundred plants grow, c) *B. multistaminea*, abundant in moist microhabitats, inset shows leaf details, d) *B. pseudodaedelia*, e) *B. hydrocotylifolia*, inset shows rhizome and leaf details, f) *B. sousae* has distinctive hairs on the adaxial leaf margin, inset shows flower structure, g) drought adapted *B. carolineifolia*, inset shows inflorescence structure, h) *B. aff. stigmosa* from santa Maria Xanabi

### Plate 4: *Begonia*s of section *Weilbachia*, *Knesbeckia*, *Quadriperigonia* and *Wagneria*

a) *B. tacana* b) *B. alemdana*, one of a dozen plants remaining near the roadside to Ocosingo, c) *B. faustinoi* endemic to Berrizobal, d) *B. lyniceorum*, note the similar leaf morphology to *B. conchifolia* (*Gireoudia*), e) *B. pustulata*, f) *B. gracilis*, g) *B. incarnata*, h) *B. glabra*, frequently encountered epiphyte on trees

### Plate 5: *Begonia* hybrids observed in the field

a) *B. heracleifolia* frequently grows on dry roadside verges, b) *B. nelumbiifolia* forms large stands on shady roadside banks with moist soils, c) white flowered form of *B. heracleifolia*, d) *B. sericoneura*, e) *B. heracleifolia* x *B. sericoneura* putative hybrid, growing in abundance at motzorongo, f) *B. heracleifolia* and *B. nelumbiifolia* growing in sympatry on disturbed roadside in Veracruz, g + h) *B. heracleifolia* x *B. nelumbiifolia* putative hybrid shows intermediate leaf morphology between the two parents.



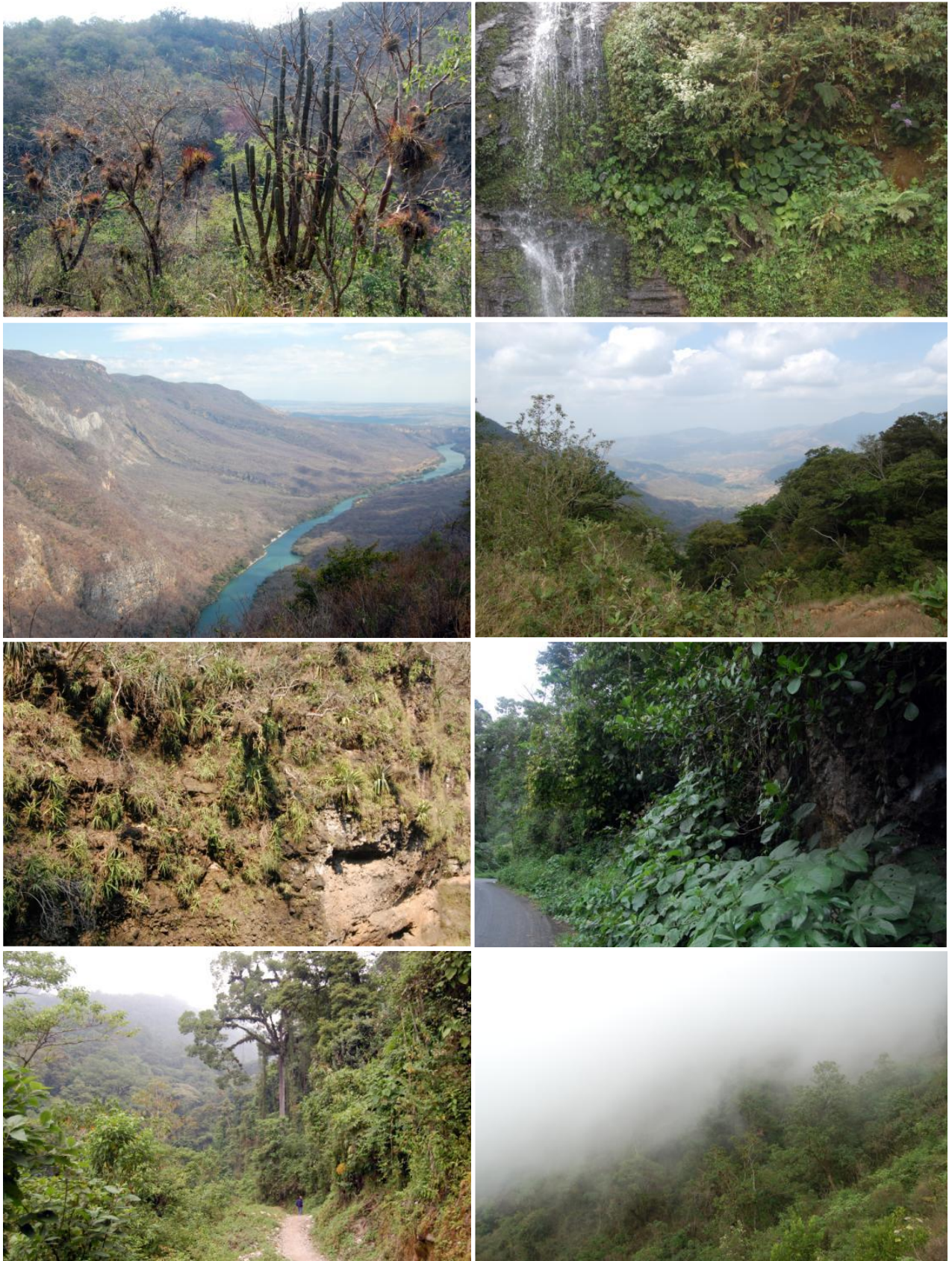


Plate 1: Variation in *Begonia* habitats in Southern Mexico





Plate 2: Widespread *Begonia* species





Plate 3: Narrow endemic *Begonia* species





Plate 4: Begonias of section *Weilbachia*, *Knesbeckia*, *Quadriperigonia* and *Wagneria*





Plate 5: *Begonia* hybrids observed in the field



## References

- Burt-Utley, K., 1985. A revision of Central American species of *Begonia* section *Gireoudia* (Begoniaceae). *Tulane studies in zoology and botany* 25.
- Burt-Utley, K., Utley, J.F., 1999. Contributions towards a revision of *Begonia* Section *Weilbachia* (Begoniaceae). *Novon* 9, 483-489.
- Cody, S., 2008. The use of plant and animal dated phylogenies to explore the effects of the closure of the Panama Isthmus. *Royal Botanic Gardens Edinburgh & University of Edinburgh*.
- Forrest, L.L., 2000. A phylogeny of the Begoniaceae Bercht. & J. Presl. *University of Glasgow*.
- Forrest, L.L., Hollingsworth, P.M., 2003. A recircumscription of *Begonia* based on nuclear ribosomal sequences. *Plant systematics and evolution* 241, 193-211.
- Hoover, S., 1979. Notes on the spatial distribution patterns for three Mexican species of *Begonia*. *Phytologia* 34, 107-132.
- Hughes, M., Hollingsworth, P.M., 2003. Population structure in the endemic *Begonia* of the Socotra archipelago. *Biological Conservation* 113, 277-284.
- Hughes, M., Hollingsworth, P.M., 2008. Population genetic divergence corresponds with species-level biodiversity patterns in the large genus *Begonia*. *Molecular Ecology* 17, 2643-2651.
- Jimenez, R., Schubert, B., 1997. *Begoniaceae*. *Flora de Veracruz*.
- Morris, R., 2008. Personal communication via email.
- Morris, R., McMillan, P., 2010. Two new *Begonia* (Begoniaceae, section *Gireoudia*) species from Oaxaca, Mexico Part 1: *B. U535* now *B. morrisiorum*. *The Begonian* 77, 51-53.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., de Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858.
- Neale, S., Goodall-Copestake, W., Kidner, C.A., 2006. *Floriculture, Ornamental and Plant Biotechnology Volume IV*. Global Science Books.
- Plana, V., Gascoigne, A., Forrest, L.L., Harris, D.J., Pennington, R.T., 2003. Pleistocene and pre-Pleistocene *Begonia* speciation in Africa. *Molecular Phylogenetics and Evolution* 31, 449-461.
- Ziesenhenné, R., 1950. *Begonia hispidavillosa* Ziesenhenné. *The Begonian* 17, 12-14.
- Ziesenhenné, R., 1952. *Begonia aridicaulis* Zies. *The Begonian* 19, 105-106.
- Ziesenhenné, R., 1981. *B. boweae* and 583 of its many hybrids. *The Begonian* 48, 248-252.
- Ziesenhenné, R., 1988. *Begonia manicata* Brongniart and its varieties. *The Begonian* 55, 84-89.