FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE ORIGIN, PHYLOGENETICS AND NATURAL HISTORY OF *DARWINIOTHAMNUS* (ASTERACEAE: ASTEREAE), AN ENDEMIC SHRUB OF THE GALAPAGOS ISLANDS

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To: Dean Arthur W. Herriott
College of Arts and Sciences

This thesis, written by Nicole Genet Andrus, and entitled The Origin, Phylogenetics and Natural History of Darwiniothamnus (Asteraceae: Astereae), an Endemic Shrub of the Galapagos Islands, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

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The thesis of Nicole Genet Andrus is approved.

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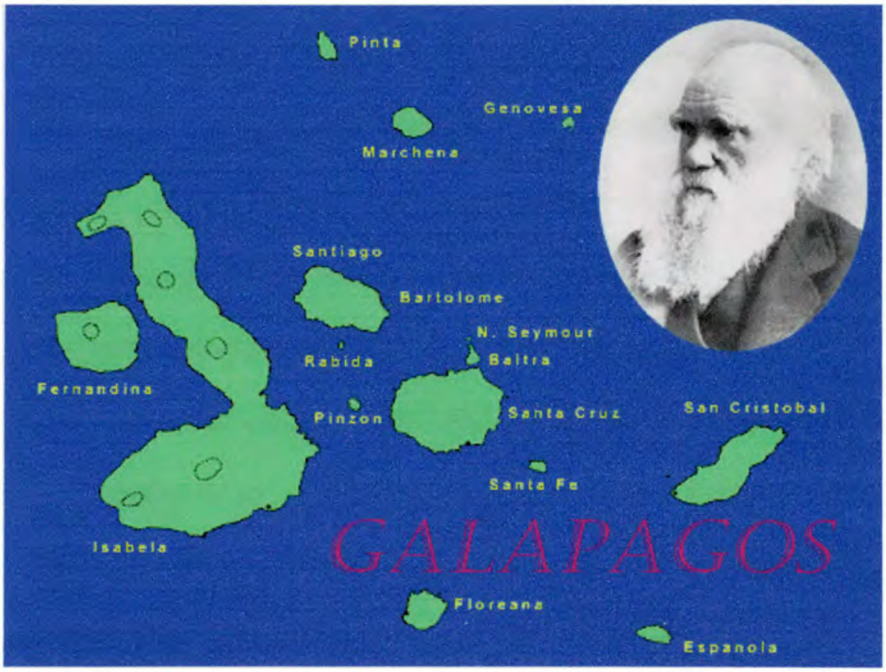
DEDICATION

I dedicate this thesis to my parents, without their patience, understanding and support, the completion of this work would not have been possible; and to my grandmothers Irene Furman and Gail Andrus, who's love and strength has given me more inspiration than they know.



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ABSTRACT OF THE THESIS

THE ORIGIN, PHYLOGENETICS AND NATURAL HISTORY OF *DARWINIOTHAMNUS* (ASTERACEAE: ASTEREAE), AN ENDEMIC SHRUB OF THE GALAPAGOS ISLANDS

by

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Miami, Florida

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Darwiniothamnus (Asteraceae:Astereae), one of seven plant genera endemic to the Galápagos Islands, has until recently had an unknown origin, number of species, and conservation status. The purpose of this master's thesis was to determine the origin and phylogenetics of *Darwiniothamnus* and to outline the major ecological factors influencing the survival of this genus.

Material for this thesis was sequenced from the ITS (Internal Transcribed Spacer) region of 18-26S nuclear ribosomal DNA of putative sister taxa from South, Central and North America, Mexico and the Caribbean. A molecular phylogeny was then constructed using fifty-four representatives from the tribe Astereae. Sequence data suggested that *Darwiniothamnus* is polyphyletic, nested within the paraphyletic *Erigeron-Conyza* complex, and stems from two separate introductions into the Galápagos. Additional information regarding the current biological threats on extant populations of

Darwiniothamnus, nomenclatural suggestions for potential new taxa, and hypotheses on the disjunct distribution of *Darwiniothamnus* throughout the archipelago are also provided within the thesis.

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CHAPTER I: INTRODUCTION INTO THE THESIS AND THE GENUS *DARWINIOTHAMNUS*

1. General Introduction:

The origin of species endemic to oceanic islands has fascinated evolutionary biologists ever since the pioneering work of Charles Darwin's publication on the origin of species (Darwin, 1859). However, tracing the origin of insular endemics based on morphological data can be trying because of the major morphological shifts that typically occur after long distance dispersal and insular diversification (Givnish and Systma, 1997, Carlquist, 1965, 1974, 1995, Aradhya *et al*, 1991, Rees, *et al.* 2001, Fuertes-Aguilar *et al.* 2002). *Darwiniothamnus (*Asteraceae: Astereae), one of the seven plant genera endemic to the Galápagos Islands, is a model example of this situation.

Darwiniothamnus, as currently defined, comprises three species of suffrutescent (*D. alternifolius*) to woody (*D. tenuifolius* and *D. lancifolius*) perennials, which can be found on seven major islands throughout the archipelago. The genus ranges from coastal beach strands to mesic or humid scrub and forestlands, through lava and scoria fields and up to high elevation fern and sedge zones. Morphologically, these taxa are considered to be highly divergent from their continental relatives and have been suggested to be most closely related to woody Chilean members of the genus *Erigeron* (Asteraceae: Astereae) (Harling, 1962). Until recently, however, there have been no molecular studies completed on *Darwiniothamnus* in regards to finding its origin and clarifying its relationship to other taxa. Thus, there exists a serious need for a rigorous phylogenetic study on this genus in order to confirm or disprove the monophyly of *Darwiniothamnus* and to clarify the existing relationships between this genus and its putative South American relatives.

This thesis is composed of three interrelated, yet independent papers, each addressing several topics critical to the conservation and taxonomy of all species of *Darwiniothamnus*. The introduction is followed by a discussion of the history of research on *Darwiniothamnus*, which includes a review of historical taxonomical and morphological treatments. This section is followed by the purpose and design of my study, which incorporates the specific investigative questions that I aimed to answer during the course of master's research.

Chapter 2 contains information on the natural history of the Galápagos Islands; included is a brief summary of the geological history of the archipelago and a synopsis of its climatic patterns and vegetation zones. This section is followed by an outline of the most relevant botanical collections within the Galápagos Islands over the past 150 years. An epigrammatic review of plant endemism within the archipelago is discussed in the next section with notes on rarity, radiation and sources of origin. Finally, the scope of this topic is narrowed further by a discussion of the endemic members of the Asteraceae within the Galápagos Islands, including information on taxonomy, morphology and phylogenetics. Notes on the ecology, habitat and conservation status are also reviewed for each of these endemic taxa, with projections on the future status of these genera within the archipelago.

Chapter 3 is composed of a discussion of my field observations, which were conducted from April 1st-July 1st, 2002. The first section deals with the distribution and habitat types of all populations that I encountered while in the field, throughout several different islands. The second section covers the various factors currently threatening the survival of the extant populations of *Darwiniothamnus*. In specific, this section discusses the effects of foraging animals and human population growth and includes information on the deleterious effects caused by the current infestation by the cottony cushion scale insect, *Icerya purchasi* Maskell (Homoptera: Margarodidae), which is perhaps the single most detrimental organism in contact with *Darwiniothamnus*. This chapter is closed with a discussion of my soil observations and analyses where I hypothesize on how the different soil types throughout the archipelago may have an effect on the successful introduction of *Darwiniothamnus* in previously unpopulated areas.

Chapter 4 is dedicated to the origin and phylogenetics of *Darwiniothamnus*. The first section of this chapter provides a brief history of research on the tribe Astereae; including notes on its distribution, morphological characteristics, and recent phylogenetic analyses performed on various members of the tribe. This section is followed by a review of the *Erigeron-Conyza* complex, which is a group comprising 24 closely related genera (including *Darwiniothamnus*) that are rather small in comparison to the size of *Erigeron* and *Conyza*, for which this complex is named. The final section of this chapter, before the introduction into the phylogenetics of *Darwiniothamnus* is covered, contains a brief discussion of the value of using the Internal Transcribed Spacer region (ITS) of nuclear ribosomal DNA (nrDNA) in various phylogenetic studies.

It should be noted that the second, third and fourth chapters of this thesis are intended to be published independently and thus contain their own reference sections at the end of each chapter. The same format applies to figures and tables, which are numbered consecutively for each chapter, where the first number refers to the chapter and the number following the period refers to the individual figure or table (e.g. Table 2.3, refers to Chapter 2, Table 3). Only the appendices for all the chapters are grouped together at the end of the thesis.

2. History of Research on *Darwiniothamnus:*

i. History of taxonomy and morphology

Members of the genus *Darwiniothamnus* were first described by J. D. Hooker (1847), who considered them to be part of *Erigeron* based primarily on floral characters taken from Darwin's collections, made some twelve years earlier. Hooker (1847) named the two species collected by Darwin *E. tenuifolius* and *E. lancifolius*. Although *Erigeron* has always been given a rather wide circumscription (Bentham and Hooker, 1873; Hoffman, 1894), the two Galápagos endemics were sufficiently morphologically divergent that both Bentham and Hooker (1873) and Andersson (1857) wrote about the unusual woody habit of these two species in comparison to other members of the genus. However, despite several differences in leaf form and plant size between these two new species and other members of *Erigeron*, the general structure of the inflorescences and flowers was sufficiently similar for Hooker to warrant grouping them together. This treatment, and Hooker's description of *E. tenuifolius* and *E. lancifolius,* were generally followed by several botanists familiar with the flora of the Galápagos for many years until Harling (1962) published his review "On some Compositae endemic to the Galápagos Islands."

Harling (1962) was the first to describe the woody composites of the Galápagos in detail and was the first to transfer *E. tenuifolius* and *E. lancifolius* into their own genus, *Darwiniothamnus*. Harling's initial reason for the transfer of these species into

Darwiniothamnus was based on his own morphological research, where he found detailed differences in characters belonging to the inflorescences, flowers, fruits, and the formation and development of the embryo-sac. Indeed, he felt these differences were great enough to remove the two Galápagos species from *Erigeron*, even though both Stewart (1911) and Christophersen (1932) had previously stated that material of *E. tenuifolius* tended to be rather variable in basic morphology.

Harling (1962) and his colleague Fagerlind (in Harling, 1962) continued to delve further into the embryological conditions of *E. tenuifolius* and *E. lancifolius*, and found that the two species of *Darwiniothamnus* also differed from other members of *Erigeron* in that they had monosporic embryo sac development and a persistent unicellular archespore. Interestingly, these two unique embryological conditions were actually very similar certain species of *Conyza*, however the two new species of *Darwiniothamnus* differed from this genus too, in that they lacked secondary cell divisions in the antipodes (Harling, 1962).

In addition to his embryological work, Harling (1962) found other differences between the species of *Darwiniothamnus* and those of *Erigeron*. For example, the former's involucres were described as "narrowly companulate or obconical" while the latter were "hemispherical to broadly campanulate." The number of phyllaries also differed, where the former had strongly imbricate and unequal phyllaries in series of 4-6, and the later had subequal or imbricate phyllaries in series of 2-3. Finally, Harling (1962) found three additional discrepancies for which to base his removal of *E. tenuifolius* and *E. lancifolius* from the rest of the genus: 1) The receptacle of all other South American species of *Erigeron* was "alveolate and sometimes 'fimbriate'" (Solbrig, 1960), whereas the species from the Galápagos were "minutely papillose but not or only indistinctly alveolate;" 2) The ray flowers were typically twice as many as the disk flowers in the Galápagos species whereas the opposite was found in the rest of the genus; 3) The two Galápagos species had "slightly but distinctly" dimorphic achenes, while the rest of the genus did not.

These differences were enough to convince Harling (1962) that *Darwiniothamnus* should exist as a separate genus from *Erigeron*; and he described it as containing two species, namely *D. tenuifolius* and *D. lancifolius*. He continued to further split these two species into four subspecies: *D. tenuifolius* ssp. *tenuifolius* from Floreana, Santíago, Pinta, Pinzón, and Isabela; *D. tenuifolius* ssp. *santacruzianus* from Santa Cruz; *D. lancifolius* ssp. *lancifolius* from south Isabela, and *D. lancifolius* ssp. *glandulosus* from north Isabela and Fernandina. Harling (1962) also mentioned that although he did not get the opportunity to study Stewart's (1911) type of *D. lancifolius* var. *glabriusculus*, he felt it may be worth retaining as a variety.

Unfortunately, the treatment of the genus *Darwiniothamnus* did not stop there, as several other taxonomists continued to comment of the placement of its two species (see Table 1.1). For example, around the same time Harling (1962) published his review of the Galápagos endemics, Solbrig (1962) was revising the South American species of *Erigeron*. Solbrig (1962) mentioned that the Galápagos species might deserve being described as their own genus, but refrained from doing so because of a lack of material. He did, however, suggest that *E. lancifolius* ought to be considered a subspecies of *E. tenuifolius*, and by doing so confounded the taxonomical treatments of *Darwiniothamnus* for years to come.

Over the next ten years new material provided by additional collection trips to the Galápagos led Cronquist (1970, 1971) to rebut Harling's previous hypotheses and to suggest lumping all of the morphological variants into a single variable species, *D. tenuifolius*, with three varieties: *D. tenuifolius* var. *tenuifolius* from Floreana, Pinta, Pinzón, Santíago and Santa Cruz; *D. tenuifolius* var. *glabriusculus* (Stewart) Cronquist from Isabela, and *D. tenuifolius* var. *glandulosus* (Harling) Cronquist from north Isabela and Fernandina. Although Cronquist (1970) did not provide any specific explanation for his decision to lump all of these taxa into one variable species, Wiggins and Porter (1971) chose to follow his treatment when publishing their flora of the Galápagos Islands, listing the genus as monotypic with the three varieties described above.

Sixteen years later Lawesson and Adsersen (1987) described yet another new species of *Darwiniothamnus*, *D. alternifolius*, which they discovered on the volcanoes of Sierra Negra and Cero Azul on the southern tip of Isabela. They felt this new species warranted inclusion within *Darwiniothamnus* because "the type flowers while still herbaceous, look very similar to *Erigeron* or *Conyza*...[the habit] gradually becomes shrubby [and] as it has many ray florets, imbricate phyllaria of unequal length, slightly dimorphic achenes and is aromatic, it is clearly within the generic limits of *Darwiniothamnus*." Lawesson and Adsersen (1987) continued to point out, however, that several differences did exist between their type specimen and the other species of the genus, as can be seen in Table 1.2.

Lawesson and Adsersen (1987) went on to state that most botanists with field experience in the Galápagos agree that Cronquist's reduction was probably exaggerated, and thus chose to rename most of the species previously delineated by Harling (1962), Hooker (1847), Cronquist (1970, 1971) and Solbrig (1962), to: *D. tenuifolius* (Hooker fil.) Harling from Floreana, Isabela, Pinta, Pinzon and Santiago; *D. lancifolius* ssp. *lancifolius* (Hooker fil) Harling from Tagus Cove, Isabela; *D. lancifolius* ssp. *glandulosus* Harling from the higher elevations of Volcan Darwin, Isabela and throughout Fernandina; and *D. lancifolius* ssp. *glabriusculus (*Stewart) Lawesson & Adsersen, from the area on and near Volcan Sierra Negra, Isabela.

The taxonomy of *Darwiniothamnus* has remained contentious, as different authors have listed it as having 2, 3, or 4 species, each with their own subspecies and/or varieties (see Table 1.1). In addition, although Harling's (1962) description of *Darwiniothamnus* may appear to have been adequate, he may have made a couple of critical mistakes when first describing the subspecies of *D. lancifolius*. For example, Harling was incorrect in stating that *D. lancifolius* ssp. *lancifolius* hailed from southern Isabela, as the taxon *lancifolius* was originally described from material from northern Isabela (Hooker, 1847). Thus, Harling may have started the nomenclatural confusion for this genus when he included Darwin's type (which was almost certainly from Tagus Cove on the northwestern edge of Isabela) and material from Sierra Negra (located on the southernmost tip of Isabela) in the same taxon *D. lancifolius* ssp. *lancifolius*. This carries the implication that each subspecies pair (*lancifolius/glabriusculus* and *lancifolius/glandulosus*) has broadly overlapping ranges, which obviously makes little biogeographical sense. However, if the ranges of the subspecies that Harling (1962) described are indeed more restricted, then the name *lancifolius* ought to belong to the type locality population at Tagus Cove; although it appears that after having personally searched this area extensively, the population that Darwin once collected is now extinct and the only taxon that remains anywhere on or near Volcan Darwin is *D. lancifolius* ssp. *glandulosus*. In lieu of all of this, it could still be worth retaining the subspecies epithet "*lancifolius*," as Darwin's type specimen for this taxon (located at CGE) is definitely morphologically different from *D. lancifolius* ssp. *glandulosus* and *D. lancifolius* ssp. *glabriusculus*. However, a rigorous morphological study must be completed before the taxonomical confusion of this genus can be sorted out once and for all.

Regardless of its circumscription, however, the genus *Darwiniothamnus* continues to thrive in a variety of habitats within the Galápagos Islands, ranging from lava fields to the moist highlands of several different islands. In general, each of the species in this genus are differentiated from one another by their leaf shape (as all members of the genus have leaves that are thick, glabrous to tomentose, and aromatic), and degree of woodiness. In specific, *D. lancifolius* has leaves that are lanceolate to broadly lanceolate and the plant can range from a small shrub to large bush spanning 1-2 meters, with a rather thick and woody trunk. *D. tenuifolius* has almost needle-like leaves and the same woody, shrub-like appearance of *D. lancifolius*, except it tends be more erect, sometimes reaching a height of 1-2 meters. Finally *D. alternifolius* has leaves that alternate and not clustered near the branch tips like the other two species, and it is almost always a small herbaceous plant with only a slightly woody stem. The flowers of all the species of *Darwiniothamnus* are also very similar, with white to purplish-white ray flowers and yellow disk flowers. Both the flowers and fruits in all species persist for several weeks and are often seen being eaten by birds. It should also be noted that the numerous, pappus-bearing fruits are very light, making them apt for both wind or bird dispersal (Lawesson and Adsersen, 1987.)

It has been suggested by Harling (1962) that the closest relatives of *Darwiniothamnus* are probably the Chilean *Erigeron berterianus* DC. and *E. litoralis* (Phil.) Skottsb. However, the molecular phylogeny presented in this thesis suggests that two members of the genus may actually be closer to *E. bellidiastroides* of the Caribbean (see Chapter 4). Chromosome counts have not been performed on this genus, and the results of my molecular phylogenetic data suggest that *Darwiniothamnus* should be regrouped within *Erigeron,* just as Solbrig mentioned in 1962 (see Chapter 4 for a detailed explanation).

ii. Purpose of study

Island ecosystems have often been considered to be biodiversity hotspots as they are generally species poor for their size, rich in forms found no place else and collectively contribute disproportionately for their area to global species totals. Because all of these peculiarities are typical of island biotas, it makes them fascinating environments on which to perform a study in molecular plant systematics. Schilling *et al.* (1994) has stated that the "study of island endemics is of particular interest for evolutionary biologists, and possession of information on their phylogenetic relationships is critical to resolving questions regarding their place and time of origin that would allow new insights into evolutionary processes." In addition, Hamann (1990) outlined a list of characteristics typical of oceanic islands which describes why they should be of particular interest in terms of importance to conservation:

1. The high degree of endemism that occurs on islands gives them a disproportionately large contribution to the diversity of species and ecosystems of the world.

2. The peculiar adaptations which occur on islands, including a loss of dispersal ability for plants and flightlessness for birds, poorly prepare the organisms for survival in the face of habitat changes, human interference and exotic herbivores or predators, thereby increasing their vulnerability to extinction.
3. Islands are seldom well endowed with natural resources, which typically are scarce in variety and quantity, and thus are particularly liable to overexploitation and mismanagement. Stated simply, islands are environmentally fragile.
4. Because of their scarcity, fragility and vulnerability of natural resources, islands require different approaches to ensure a continuous flow of raw materials, goods, and services needed by their inhabitants.
5. Although islands face important and unique difficulties they also may serve as a resource for improving approaches to conservation management. Indeed, pilot studies carried out in islands under relatively simple conditions, where the limits to the ecosystems are clear, may point to solutions to problems also faced on larger, continental scales. Therefore, islands such as the Galápagos share not only problems but also opportunities with other oceanic islands.

With all of this said, the importance of island studies in general becomes apparent, but what of molecular phylogenetic studies on the flora of the Galápagos in specific? Unfortunately, only a few studies have used molecular data in the past to assess the origin and evolution of plants from the Galápagos. Rick and Forbes (1975), Wendel and Percival (1990), and Elisens (1992) used allozyme data to compare members of *Lycopersicon* (Solanaceae), *Gossypium* (Malvaceae), and *Galvezia* (Scrophulariaceae), respectively, to potential Andean congeners. Wendel and Percival (1990) have also provided allozyme and cpDNA restriction site data suggesting a species of *Gossypium* endemic to the Galápagos is of north Mexican descent; and as noted earlier, Schilling (1994) was the first to compare the genus *Scalesia* with several potential South American sister groups from within the tribe Helianthinae. More recently, Miller (2002) studied gender dimorphism in the genus *Lycium* (Solancaceae) by looking at the phylogenetic relationships within the genus, and used *Nolana galapagensis* (Solanaceae) of the Galápagos as one of the six outgroups. Besides these few studies, however, no other molecular work has been performed on the native or endemic taxa of the Galápagos Islands.

Until recently, the same could be said for *Darwiniothamnus,* as both its origin and relationship to potential sister taxa were uncertain. Thus, there existed a significant need for a rigorous phylogenetic study on this genus in order to confirm or disprove the existing morphological hypotheses regarding its relationship with putative South American relatives, and therefore the research described in Chapters 3 and 4 was performed.

iii. Research Questions

The following is a list of questions that were assembled for my Master's thesis both while in the lab and in the field. Detailed morphological analyses and chromosome counts on all members of the genus had to be postponed as it became apparent that this was outside the scope and time range of a typical master's project. Both of these analyses will be performed in the near future, however, and may serve to complement or disprove some of the author's hypotheses discussed in the following chapters.

1. What is the conservation status of all currently recognized taxa within the genus *Darwiniothamnus* and do any new conservation measures need to be implemented?
2. Based upon field observations, do any areas contain new morphological variants that warrant in-depth morphological analyses?
3. What are the existing biological threats to *Darwiniothamnus* and what can be done to protect these populations in the future?
4. Does the lack or over-abundance of certain essential elements and/or micronutrients prevent *Darwiniothamnus* from colonizing certain areas of the archipelago?
5. Where is the origin of *Darwiniothamnus* and is the genus monophyletic?

Detailed answers to each of these questions can be found within the next the next three chapters and a precise discussion on each of the topics can also be found in the "Concluding Remarks" section at the end of Chapter 4.

Table 1.1: Synopsis of recent taxonomic classification by various authors

Species Recognized	**Ho**	**St**	**Ch**	**Ha**	**So**	**Cr**	**W & P**	**L & A**
Erigeron lancifolius	X	X	X					
Erigeron tenuifolius	X	X	X		X			
E. tenuifolius ssp. *lancifolius*					X			
E. lancifolius var. *glabriusculus*		X						
E. tenuifolius var. *tomentosus*		X						X
Darwiniothamnus tenuifolius				X				X
Darwiniothamnus lancifolius				X				X
Darwiniothamnus alternifolius						X	X	
D. tenuifolius var. *tenuifolius*						X	X	
D. tenuifolius var. *glabriusculus*						X	X	
D. tenuifolius var. *glandulosus*								
D. tenuifolius ssp. *santacruzianus*				X				X
D. lancifolius ssp. *glandulosus*				X				
D. lancifolius ssp. *glabriusculus*				X				

Where: Ho = Hooker (1847)
St = Stewart (1911)
Cr = Christophersen (1932)
Ha = Harling (1962)
So = Solbrig (1962)
Cr = Cronquist (1970, 1971)
W & P = Wiggens and Porter

Table 1.2: Description of the species of *Darwiniothamnus*:

Taxon	Leaf position	Leaf shape	Fruit type	Inflorescence type
D. alternifolius	not condensed in terminal whorls; Internodes half the length of the leaves or longer	broadly lanceolate to spatulate	all achenes two nerved	synflorescence cymiformly branched, clearly exceeding terminal terminal leaves. involucrum abruptly limited downwards
D. tenuifolius	leaves terminally in condensed whorls; Internodes much shorter than half the leaf length	filiform, linear or narrowly lanceolate	achenes of disk florets with 3 to 6 nerves	heads solitary or on somewhat branched peduncles in terminal axils, forming corymbiform synflorescences hardly exceeding terminal leaf whorl involucrum gradually terminating with bracts downwards on the pedicel.
D. lancifolius	leaves terminally in condensed whorls; Internodes much shorter than half the leaf length	lanceolate to broadly lanceolate	achenes of disk florets with 3 to 6 nerves	heads solitary or on somewhat branched peduncles in terminal axils, forming corymbiform synflorescences hardly exceeding terminal leaf whorl involucrum gradually terminating with bracts downwards on the pedicel.

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CHAPTER II: NATURAL HISTORY OF THE GALÁPAGOS ISLANDS:

1. Geology/age of the Galápagos Islands:

The Galápagos Islands, situated on the equator between 1°25'S - 1°40'N latitude and 89°14' - 92°01W longitude, lie about 960 km off the coast of Ecuador in the eastern Pacific Ocean. The age of the Galápagos archipelago has never been determined exactly and what exists of fossil material is almost all from the Pleistocene age, ca. 1.8 mya (Jackson, 1976). It is generally accepted that the westernmost islands (west of the Darwin-Española fault line) are slightly less than a million years old and the easternmost islands are somewhat older. In general, estimates such as these are based on preliminary investigations of shifts in the magnetic polarity of lava that has cooled in place, and the values vary greatly depending upon the author (Christie *et al.* 1992; Davis *et al.* 1995). A more detailed study by Cox (1983) based on geomagnetic reversal stratigraphy to age most of the major islands, suggested that Santa Cruz and San Cristóbal are amongst the oldest islands at about 4.2 ± 1.8 and 4.5 million years old respectively. The youngest islands were determined to be Isabela and Fernandina at approximately 0.09-0.5 million years old.

All of the Galápagos Islands are volcanic in origin, comprising the top of the Carnegie Ridge, which is a submarine mountain range that extends eastward from the Galápagos almost to the mainland. In addition, the entire archipelago is situated beyond the continental shelf just south of the divergent plate boundary separating the Nazca and Cocos Plates. This divergent plate boundary is the origin of an underwater line of ridges and chasms known as the Galápagos Rift, which is an area of intense geological activity that most likely played an important role in the formation of the Galápagos (Jackson, 1993).

In total, the archipelago comprises 13 major islands and several smaller islets and rocks, which altogether encompass an area of 7900 km^2. All of the islands within the archipelago contain topographic characteristics in accordance with Whittaker's (1998) definition of a true volcanic island, which he states are steep, relatively high for their area, and become highly dissected over time. Jackson (1993) has mentioned that although the most dramatic features of Galápagos geology relate to constructive volcanic processes, erosion via wind, the ocean, and rain have altered much of the Galápagos landscape as well. In the Galápagos, the shapes of ash rings and scoria cones can be used as a rough guide to direction since the prevailing winds come from the southeast and generally lead to more erosion on that side. It is thus also likely that the prevailing winds could cause more material to be deposited on the northwest side during an eruption, which may have had a bearing on the general shape of many of the islands and their volcanoes. In addition to erosion, some parts of the general topography of the archipelago are not solely due to volcanic eruptions, but instead to uplifting and subsidence. The presence of the islands of Seymour, Baltra, Plazas and parts of the northeast coast of Santa Cruz are most likely due to uplifting which is the result of subsurface movements of magma (Jackson, 1993). Subsidence, on the other hand, results in the formation of calderas and pit-craters, such as can be seen in los Gemellos, on the island of Santa Cruz.

It should also be noted that the entire archipelago is steadily moving in a southeastern direction at more than 7 cm/year and the present islands are expected to disappear into the Chile-Peru Trench about 20 million years from now, due to spreading of the sea floor along the Galápagos Rift and through the Carnegie Ridge (Cox, 1983 and Jackson, 1976). There is no evidence that suggests the archipelago was ever connected with the continent by an above-water land bridge, even though Banfield *et al.* (1956) have noted that the bottom topography of the ocean between the islands and the mainland is not fully known. The existence of such a bridge could have served for the transfer of any number of species from the mainland to the Galápagos Islands.

It is generally accepted that at least some of the islands within the archipelago were connected to each other when the Pleistocene ice sheets were at their maximum volume of about 77 million km^3 and the sea level was about 120 meters below the current level (Jackson, 1993). Such glacial advances, and their subsequent retreats, no doubt played an important role in the evolution and distribution of several Galápagos species within the archipelago.

2. Climate and vegetation types:

The Galápagos Islands are situated at the point of convergence of the principal ocean currents of the eastern Pacific and are annually influenced by the warm Panama current from the north, formerly known as "El Niño." They are also periodically affected by what have now come to be known as El Niño Southern Oscillation (ENSO) events, which are currents that influence the islands for an unusually protracted period of time, bringing exceptionally heavy rains to the archipelago. Due to their unique placement, the lowlands of the archipelago are quite arid while the highlands are generally moist. The archipelago has a mean annual precipitation range of 0-300 mm at the coast, and about 2000 or more in the mountains (Jackson, 1993; Alan Tye, personal communication). In general, the air temperature on the islands reflects that of the sea water temperature, and there are only two distinct seasons. Due largely to the Humboldt current from the Antartic, there is a cold season that lasts from July to December, and a warm season that exists during the rest of the year.

Historical climate change is known to dictate the course of botanical diversity over time in the Galápagos and throughout the world. As previously mentioned, the lower regions of the archipelago are typically desert-like and the highlands are moist where expansive forests occur. However, paleo-environmental data from lake sediments demonstrate that in the last glacial period the highlands were also dry (Whittaker, 1998). The familiar moist conditions returned to the highlands around 10,000 BP, and pollen data for El Junco Lake on Isla San Cristóbal indicate a lag of some 500-1000 years before the vegetation similar to that of the present day occupied the moist high ground (Colinvaux, 1972). Whittaker (1998) has stated that this delay may reflect the slow progress of primary succession after the expansion from relict populations in small refugia in more moist valleys, or the necessity of many plants having to disperse over wide sea gaps to reach the site. Today the vegetation of the archipelago can be divided into seven, easily characterized vegetation zones: the littoral, arid, transition, *Scalesia*, *Miconia*, brown, and fern-sedge zones. Each of these zones is primarily divided by a difference in plant species, increasing levels of rainfall over an altitudinal gradient, and depth of soil (see Figure 2.1).

3. Summary of Botanical Collections from Darwin to present:

The Galápagos Islands were first visited by Bishop Fray Tomás de Berlanga, the fourth Bishop of Panamá, in 1535. Tomás de Berlanga discovered the islands by accident when attempting to sail to Puerto Viejo, Ecuador, when he instead drifted to the Galápagos due to a lack of wind power (Wiggins and Porter, 1971). He wrote little about the plant life on the islands and mentioned only that his crew chewed cactus pads for liquid nourishment, although no known collections of such plants were made. The first real scientific exploration of the Galápagos Islands began in the early nineteenth century by British botanists such as Douglas and Scouler in 1825 (Robinson, 1902), Macrae in 1825, and Cuming in 1829 (Howell, 1941). Each of these collections yielded only a few specimens as many of the collectors had trouble transporting the specimens back to Europe or accidentally lost them along the way (see Table 2.1).

The first major collection of Galápagos flora was made by Charles Darwin in 1835, who collected over 200 specimens, two of which (*Sicyos villosa* and *Delilia inelegans*) are now considered to be extinct endemic species of which only Darwin's type collection exists (Hooker, 1847). During the month that Darwin spent in the Galápagos he collected vascular plants on the islands of Isabela, San Cristóbal, Santíago, and Floreana. Of the 209 plants which Darwin collected, 74% of them were new records for the archipelago. All of these specimens, including a few added by Scouler, Douglas, Macrae and Cuming were the basis of J.D. Hooker's (1847) seminal work on Darwin's specimens and the vegetation of the Galápagos Islands.

During the middle of the nineteenth century a few additional collections were made by Petit-Thouars and Neboux, from France, in 1838; and by Edmonstone and Goodridge, from England, in 1846 (Wiggins and Porter, 1971). These two collections represent a total of 46 taxa (Petit-Thourars and Neboux = 5 and Edmonstone & Goodridge = 41) of which 24 (Petit-Thourars and Neboux = 3 and Edmonstone &

Goodridge = 21) were new records for the archipelago (see Table 2.1). In 1852 N. J. Andersson, a Sweedish scientist, spent ten days in the Galápagos and collected 329 specimens that further contributed to the growing knowledge of the Galápagos flora. Thirty-one percent of Andersson's collecting effort represented new records for the islands and he successfully published 50 as new species (Andersson, 1857).

The end of the nineteenth and beginning of the twentieth centuries were marked by the following major and minor contributing collectors: Habel in 1869 (Robinson, 1902), Hill and Steindachner in 1872 (Wiggins and Porter, 1971), Wolf in 1875 (Wolf, 1875), Chierchia and Marcacci in 1884 (Wiggins and Porter, 1971), Lee in 1888 (Wiggins and Porter, 1971), Agassiz in 1891 (Wiggins and Porter, 1971), Baur in 1891 (Baur, 1891; and in Robinson & Greenman, 1895), Snodgrass and Heller in 1899, Stewart from 1905-1906 (Stewart, 1911), Rorud from 1926-1927 (Christophersen, 1932), Svenson in 1930 (Svenson, 1935), and Howell in 1932 (Howell, 1933, 1941, 1968). These explorers hailed from England, Italy, Germany, the USA and Sweden; and although the collection numbers for several of these explorers was quite high, the number of newly reported species was often low (see Table 2.1). This is most likely due to the fact that most of the native flora of the Galápagos Islands was already described by the early 1900's. Of these early collectors, Rorud was the first Galápagos resident to collect and catalog Galápagos plants and Baur was the first to visit 13 of the islands and collect many of the plants that had not been seen since Darwin's day (Porter, 1971).

The first two significant explorations to cover almost all reaches of the archipelago were the Hopkins and California Academy of Sciences expeditions, (McMullen, 1999). Each expedition had their own team of well-trained botanists, with

Snodgrass and Heller (Robinson, 1902) as the acting botanists in the former and Stewart (Stewart, 1911) being responsible for plant collecting in the latter. Both of these expeditions cataloged several new members of the Galápagos flora and fauna, the largest plant collections of which can be found at the Gray and California Academy of Sciences Herbaria, respectively.

Due to the economic tensions produced by World War I, the next collecting expedition to the Galápagos was not until 1923. The Harrison Williams Galápagos Expedition was described in detail by Beebe (1924), and both his and his colleagues' collections are held in the New York Botanical Garden (NY). Over the next eight years four additional collecting expeditions began in the Galápagos, the Norwegian Zoological Expedition, a British group aboard the yacht *St. George,* the British Vincent Astor and the Templeton Crocker Expeditions. All of the botanists in each of these expeditions amassed large collections from a variety of islands and what exists of the details from these collection trips is described in the papers by Christophersen (1932), Riley (1925), Svenson (1935), and Howell (1933abc, 1934ab, 1937, 1941ab), respectively.

Harling (1962) began the postwar period of publication on Galápagos botany and performed the first major work to detail solely the endemic members of the Asteraceae in the archipelago. In addition, Harling and his field collaborators also collected a total of about 1,600 specimens across several plant families that are now housed in Sweden's Naturhhistoriska Riksmuseet's herbarium (S). After Harling's 1962 publication and before the publication of the flora by Wiggins and Porter in 1971 (the first modern flora describing a total of 107 families, 348 genera, 642 species and 60 species and varieties), close to 70 different scientists visited and collected both plant and animal specimens on the islands. Many of these visits were the result of the opening of the Charles Darwin Research Station (CDRS) in 1964. The CDRS now encompasses active labs with resident and visiting research scientists who continue to study the flora and fauna of the Galápagos Islands.

Over the past forty years, new records of vascular plants in the Galápagos continue to have been published by Eliasson (1972), Weber (1973), Hamann (1974), Wiggins (1975), Adsersen (1976 a,b), Van der Werff (1977), and Lawesson and Adserson (1987) among others. A botanical bibliography has also been published by Schofield (1973) and a treatment of the endemic genera within the archipelago is discussed in this paper below.

4. Review of plant endemism within the archipelago - rarity, radiation and sources of origin:

Of the 500-560 native plant species and 550-610 native plant taxa in the Galápagos (60 are uncertainly native), close to 180 species and 230 taxa are considered endemic (A. Tye, personal communication; Adsersen, 1989; Hamann, 1991; Porter, 1983). Although several endemic plant species exist within the Galápagos, only seven plant genera (*Darwiniothamnus, Lecocarpus, Macraea* and *Scalesia* in the Asteraceae, *Brachycereus* and *Jasminocereus* in the Cactaceae and *Sicyocaulis* in the Curcurbitaceae) are endemic to the entire archipelago. When reviewing the percentage of endemic plant taxa across island groups in the Pacific Ocean, endemism in the Galápagos Islands appears to be quite low in comparison with that of other Pacific island chains. For example, Hawaii's percentage of endemics at the species level is estimated at around

94.4%, whereas that of the Galápagos is only thought to be around 37-43% (Porter, 1979).

At this point, one may wonder just how vulnerable are the endemic plant taxa of the Galápagos? In order to assess the conservation status for any plant taxon it is important to estimate its population size, geographical range, and evidence of population decline (IUCN, 2000). An example of such an estimation was discussed by Adsersen (1989), who noted that endemic plants throughout the world appear to be more vulnerable to the impacts of man than other native plants, a notion that is readily supported by his estimation of rarity in the Galápagos Islands. Adsersen (1989) found that 31% of the endemic plant species in the Galápagos were considered to be "rare" in accordance with the IUCN guidelines, and only 38% of those live in stable populations. This is in direct comparison with the native flora of the archipelago where only 20% are considered to be rare and upwards of 55% were growing in stable stands (Adsersen, 1989). Because small and/or isolated populations of any plant species are typically prone to genetic drift, rarity itself may lead to speciation (and in some instances extinction), which is one of the prime factors leading to the evolution of new plant taxa within the archipelago.

It has been stated that if the Galápagos Islands are indeed 3-5 million years old, then one introduction every 7,300-12,100 years would account for the presence of the endemics and natives in the Galápagos Islands (Porter, 1983). It is well known that the flora of the Galápagos is very closely related to that of tropical and subtropical America (e.g. Svenson 1946), where 87% of the endemics and 97% of the non-endemic indigenous species are considered to be descendants of either widespread tropical species or are otherwise restricted to the South American mainland nearest the archipelago (Porter, 1983).

Indeed, Porter (1983) has stated that many of the plants of lowland Galápagos have been suggested to be closely related to those of the semi-desert area bordering the Gulf of Guayaquil in southern Ecuador and northern Peru. Most scientists familiar with the flora of the Galápagos Islands attribute different vectors of long-distance dispersal to bringing the current diversity of species to the archipelago, including wind and air currents, oceanic drift and dispersal brought upon by birds (Adsersen, 1991; Porter, 1983; Hamann, 1991, Perry *et al.* 1984, van der Werff, 1977). All of these vectors, along with various founder events and the steady adaptation and radiation discussed above, act upon the continental species upon arrival and may be responsible for the current diversity of disharmonic endemic species within the archipelago.

5. Review of the Asteraceae within the Galápagos Islands - origin, history and modes of dispersal:

i. Introduction into the Asteraceae

The Asteraceae comprise the largest family of flowering plants in the world consisting of 1535 genera and approximately 23,000 species (Bremer, 1994). The family is distributed worldwide but is most abundant in the southwestern United States and Mexico, southern Brazil, along the Andes mountains of South America, in the Mediterranean area, in southwestern and central Asia, South Africa, and Australia (Bremer, 1994). The family's geographic origin is thought to be in northern South America (Raven and Axelrod, 1974, Turner, 1977) as several of the earliest lineages of Asteraceae (i.e. Barnadesioideae) are found in South America. Another theory (Nur and

Ben-Avraham, 1981, Humphries and Parenti, 1986) states that the possible origin of the Asteraceae is linked to the geological history of the Pacific basin. However, plate tectonics of the Pacific are complicated and involve a number of possible means for traversing the Pacific, including ancient slowly moving island areas such as the Hawaiian and Galápagos Islands (Wilson and Hey, 1995). Turner (1977) stated that it is possible the family originated in the mid-Cretaceous, which would be early enough for it to be distributed around the world as a result of plate tectonics. That theory, however, contradicts the one by Raven and Axelrod (1974), who thought that the family originated in the mid-Oligocene and felt that the migrations of the Asteraceae must be seen "in the light of present geography."

It is possible that the Asteraceae are older than the known fossil record indicates, but no direct evidence exists that proves its members were present in the Cretaceous. Another hypothesis by Bremer (1994) suggests that the family split from their present sister group in the mid-Tertiary. Although Pacific history may have influenced the distribution of the Asteraceae, the separation of the major continents of Gondwanaland was probably too early of an event to affect the distribution of the family (Bremer, 1993 a,b).

ii. Asteraceae in the Galápagos Islands

Although several global floristic studies have been done for this family, no one has published the distribution of Asteraceae solely in terms of their presence on oceanic islands, and what is known about the family in the Galápagos Islands in particular, is fragmentary. The Asteraceae are the second largest family within the Galápagos Islands, consisting of 31 genera, four of which are considered to be endemic to the archipelago

(Wiggens and Porter, 1971). In addition, although fifteen of these thirty-one genera are native and widespread with relative abundance throughout the Galápagos Islands, Lawesson (1990) has stated that in terms of their conservation status, the Asteraceae appear to be the family with the most taxa in a critical state within the Galápagos Islands. Evidence of this can be found in Tables 2.3, 2.4 and 2.5, which list all of the Galápagos taxa that are in a vulnerable state (VU), in danger of extinction (EN) or in critical danger of extinction (CR), respectively, according to the 2000 criteria of IUCN (Tye, 2000).

Of the four genera from the Asteraceae considered to be endemic to the Galápagos, three (*Scalesia*, *Lecocarpus* and *Darwiniothamnus*) paint a remarkably good picture of adaptive radiation within the archipelago; something that is rather uncommon within the islands. Tye and Callebaut (2002), stated that phyletic evolution is far more frequent in the archipelago than radiative evolution, as only 11 families and 19 genera have radiated into groups of 3 or more (up to 19) endemic taxa (see Table 2.2). The best example of adaptive radiation in the flora of the Galápagos, often considered to be on par with that of the Galápagos finches, is found in the woody endemic genus *Scalesia* (Eliasson, 1984; Hamann and Wium-Andersen, 1986; Adsersen, 1990; Porter, 1979).

***Scalesia*:**

Scalesia, is a member of the tribe Heliantheae (subtribe Helianthinae) that comprises 15 species and as many as 21 taxa (Eliasson, 1974; Hamann & Wium-Andersen, 1986), although additional specific and sub-specific taxa may still need to be described (Lawesson & Adsersen, 1987). Most members of this genus are found in the relatively dry lowlands of the archipelago, however this genus also contains three species of trees that occur in the highlands of the larger islands (Lawesson, 1990). Several scientists have focused on the woody Composites of the Galápagos (Harling, 1969; Cronquist, 1970 and 1971; Eliasson, 1972 and 1974; Carlquist, 1974; Hamann and Wium-Andersen, 1986), and a vast majority of the literature points to the overt woodiness in both *Scalesia* and *Darwiniothamnus.* However, it is not specifically known if the formation of woodiness on islands is derived secondarily, as was suggested by Carlquist (1974), or if it represents a primitive feature of continental floras that was carried over to oceanic islands via dispersal events. The lowland or coastal habitats of *Scalesia* are areas where several of the species are considered to have evolved, although most of the species remain in relatively small and geographically restricted populations (see Appendix 1 a&b for individual species distributions).

The taxonomy of the genus *Scalesia* is currently fairly stable, and there have not been many discrepancies over the taxonomic changes throughout the years (Harling, 1962; Wiggens and Porter, 1971; Schilling, 1994). At first glance the genus appears to be monophyletic based on the presence of trifid pales, gummy resin, and a tetraploid chromosome number of 2n=68 in all species (Eliasson, 1974; Schilling *et al.*, 1994), however this has never been tested by rigorous phylogenetic methods. The only extensive molecular work that has been performed on the genus is by Shilling *et al.* (1994) who used cpDNA restriction site data to compare *Scalesia* to potential sister groups within the subtribe Helianthinae. In specific, they found that *Pappobolus* was *Scalesia's* most likely sister group, even though it was formerly considered to be most closely related to Andean species of *Helianthus* and *Viguiera*, with which it shares the basic chromosome number of x = 17 (Porter, 1979). Although there is significant morphological variation within *Pappobolus*, both *Scalesia* and *Pappobolus* are similar in that both genera include shrubs or small trees and both contain considerable variation in the features of the pappus (Schilling, 1994.)

The original introduction of *Scalesia* to the Galápagos was most likely by birds. It has been suggested that the ancestor of *Scalesia* first colonized the arid lowlands of a single island, which was then followed by adaptation to moister sites and to other islands (Carlquist, 1966). Currently, *S. penduncula**ta* occurs on the islands of Santa Cruz, Santíago, Floreana and San Cristóbal; *S. cordata* is restricted to Isabela south of Isthmus Perry, and *S. microcephala* can be found on Fernandina and the volcanoes north of Isthmus Perry on Isabela (Eliasson, 1984). A fourth and fifth species, *S. atractyloides* and *S. darwinii*, are considered in critical condition as only 80 and 500 trees are left in the archipelago, respectively (Williams, 1998). During the process of this adaptation to different island habitats, not only did the leaves of these plants become markedly different from each other in shape and size, but the plant heights also began to range from small shrubs to tall trees reaching upwards of 15 meters. Because this genus is one of the few Galápagos plant genera to include trees, its forest stands have acquired their own ecological zone, known throughout the Galápagos as the "*Scalesia* Zone."

***Lecocarpus*:**

Until recently, *Darwiniothamnus* and *Lecocarpus* have also been noted for their successful adaptive radiation within the Galápagos Islands (Adsersen, 1980), however the taxonomic status of the former should be reconsidered, as is discussed in detail in Chapter 4. *Lecocarpus*, on the other hand, is a well-defined, distinct genus within the tribe Heliantheae with three currently recognized species, *L. darwinii* Adsersen, *L. lecocarpoides* (Robins. & Greenm.) Cronq. & Stuessy, and *L. pinnatifidus* Decne.; all of which are woody shrubs and considered to be threatened. *Lecocarpus darwinii* is only found on the island of San Cristóbal, *L. lecocarpoides* is only on Espanola and surrounding islets, and *L. pinnatifidus* only inhabits the island of Floreana (Adsersen, 1980). Although each species occupies a different island, they all prefer the arid lowlands of each island, which seems to promote the morphological uniformity among its species. In specific, all of species are shrub-like, 1-1.5 meters in height, with opposite, deeply pinnately dissected leaves and yellow flowers.

Although two species of *Lecocarpus* have been referred to the related genus *Acanthospermum* (Adsersen, 1980), each of the three species are closely allied and the general unity of the group has been supported by several different authors within Wiggins and Porter's (1971) flora of the archipelago. It is generally believed that the genus is most likely related to *Acanthospermum* and *Melampodium,* both of which contain a number of tropical American species. Although the exact sister relationship is unclear, chromosome counts and phylogenetic studies have not been performed on this genus to suggest otherwise (Stuessy, 1970; Eliasson, 1971).

***Macraea*:**

The third endemic Composite genus in the Galápagos, *Macraea*, is also a member of the tribe Heliantheae and was named after James Macrae, who first collected this plant on the island of Isabela during a visit to the archipelago in 1825. *Macraea* is a shrub about 2.5 meters tall, with numerous slender branches and a chromosome number of 2n=28 (Eliasson, 1984). The opposite leaves are simple, linear, and very narrow, and give rise to the species' name, *M. laricifolia*, which alludes to the clusters of narrow leaves similar to those of the conifer genus *Larix* (McMullen, 1999). The flowers of

Macraea are tiny and yellow with the disc flowers more prevalent than the ray flowers. This genus is currently considered to be monotypic with its only species, *M. laricifolia*, found on the islands of Fernandina, Floreana, Isabela, Pinta, Rabida, San Cristóbal, Santa Cruz and Santíago.

Harling (1962) stated that the greatest affinities to *Macraea* are most likely found in *Wedelia*, particularly among the American species of this genus, yet its origin is currently unknown. It is generally thought that adaptive radiation has not occurred in *Macraea*, nor in two other endemic genera of the Galápagos, *Brachycereus* and *Sicyocaulis* (Wiggens and Porter, 1971); however I and other botanists of the Charles Darwin Research Station have seen *Macraea* with several different morphological types at varying locations. The slight, yet obvious, morphological variation that exists within this genus thus warrants an in-depth morphological analysis across the entire archipelago.

The fouth and final endemic member of the Asteraceae in the Galápagos, *Darwiniothamnus,* will be covered in the next two chapters of this thesis. In addition, a comprehensive list of the introduced, native and endemic members of the Asteraceae in the Galápagos Islands is also included in Appendix 1 a&b. This list is primarily adapted from Duncan Porter's chapter on Endemism and Evolution in Galápagos Islands Vascular Plants (1979) and his checklist of the vascular plant of the Galápagos Islands (1983). A few additions and revisions have been made to the list where new data has been made available since the publication of Porter's papers, however the list is not entirely complete for introduced species, as many more introduced Asteraceae have been discovered in the Galápagos in recent years.

From the list in Appedix 1a one can readily note that the most widespread endemic species from the Asteraceae appear to be: *Pectis subsquarrosa,* which according to Porter (1983) is spread throughout at least 16 different islands, islets and rocks; *Macraea laricifolia,* which is spread throughout nine different islands and islets; *Chrysanthellum pusillum*, which is spread throughout seven islands and islets; *Jaegeria gracilis*, which is spread throughout six; *Pectis tenuifolia,* which is spread through out five; and *Baccharis steetzii*, *Darwiniothamnus tenuifolius, Delilia repens, Encelia hispida*, and *Scalesia pedunculata* which are all spread across four islands and/or islets.

Again, by looking at Appendix 1a it is apparent that the Galápagos (at least at the time of Porter's 1979 and 1983 publications) contained 43 endemic taxa from the Asteraceae, comprising various genera, species, subspecies and varieties. The genus with the largest number of endemic taxa is by far *Scalesia*, followed by *Darwiniothamnus*, *Delilia*, *Lecocarpus* and *Pectis*. In addition to the endemic taxa, there are also 24 introduced weeds and 6 native species that represent the Asteraceae in the Galápagos.

Table 2.1: History of collections in the Galápagos Islands from 1825-1930:

Collector	Year	Total # of plant taxa collected	New record for the Galápagos	New spp to science
Douglas & Scouler	**1825**	**18**	**18**	**18**
Macrae	**1825**	**41**	**34**	**20**
Cuming	**1829**	**9**	**4**	**4**
Darwin	**1835**	**209**	**155**	**78**
Petit-Thouars & Neboux	**1838**	**5**	**3**	**?**
Edmonstone & Goodridge	**1846**	**41**	**21**	**5**
Wood	**1846**	**27**	**15**	**0**
Andersson	**1852**	**69**	**8**	**2**
Habel	**1869**	**69**	**8**	**2**
Hill & Steindacher	**1872**	**96**	**2**	**1**
Wolf	**1875**	**7**	**?**	**?**
Chierchia & Marcacci	**1884**	**44**	**22**	**2**
Lee	**1888**	**42**	**4**	**0**
Agiz	**1891**	**41**	**1**	**0**
Baur	**1891**	**385**	**37**	**37**
Snodgrass & Heller (Hopkins Expedition)	**1898-1899**	**949**	**?**	**?**
Stewart (California Academy of Sciences Expedition)	**1905-1906**	**3000**	**615**	**10**
Beebe, Rose & Wheeler	**1923**	**n/a**	**n/a**	**n/a**
Wollebaek	**1924**	**n/a**	**0**	**0**
Riley	**1925**	**?**	**3**	**1**
Rorud	**1927**	**262**	**4**	**4**
Svenson	**1930**	**300**	**several**	**5**

Table 2.2: Radiative groups in the Galápagos of at least 3 endemic taxa:

(Tye and Callebaut, 2002)

Family	Genus	No. of taxa in group
Amaranthaceae	***Alternanthera* Forssk.**	**8**
	***Froelichia* Monech**	**5**
Asteraceae	***Darwiniothamnus* Harling**	**4**
	***Lecocarpus* Decne.**	**3**
	***Scalesia* Arn. Ex Lindl.**	**19**
Boraginaceae	***Cordia***	**3**
	***Tiquilia* Pers.**	**3**
Cactaceae	***Jasminocereus* Britton & Ros**	**3**
	***Opuntia* Mill.**	**14**
Euphorbiaceae	***Acalypha* L.**	**6**
	***Chamaesyce* Raf.**	**9**
	***Croton* L.**	**4**
	***Lamiaceae* Salvia LO.**	**3**
Molluginaceae	***Mollugo* L.**	**9**
Piperaceae	***Peperomia* Ruiz & Pav.**	**4**
Poaceae	***Aristida* L.**	**4**
	***Paspalum* L.**	**3**
Polygalaceae	***Polygala* L.**	**5**
Rubiaceae	***Borreria* G. Mey.**	**6**

Table 2.3: Taxa in vulnerable status (VU) according to the 2000 criteria of IUCN (adapted from Tye, 2000)

Family	Species
Monocotyledons	
Orchidaceae	*Epidendrum spicatum* Hook. f.
Poaceae	*Paspalum redundans* Chase
Poaceae	*Trisetum howellii* Hitchc.
Dicotyledons	
Amaranthaceae	*Alternanthera flavicoma* (Anderss.) Howell
Amaranthaceae	*Alternanthera galapagensis* (Stewart) Howell
Amaranthaceae	*Alternanthera helleri* (Robins.) Howell
Amaranthaceae	*Alternanthera snodgrassii* (Robins.) Howell
Amaranthaceae	*Amaranthus furcatus* Howell
Amaranthaceae	*Froelichia juncea* Robins. & Greenm.
Amaranthaceae	*Lithophila radicata* (Hook.f.) Standl.
Apiaceae	*Hydrocotyle galapagensis* Robins
Asteraceae	*Acmella darwinii* (D.M. Porter) R.K. Jansen
Asteraceae	*Lecocarpus lecocarpoides* Cronq. & Stuessy
Asteraceae	*Scalesia aspera* Anderss.
Asteraceae	*Scalesia baurii* Robins. & Greenm.
Asteraceae	*Scalesia gordilloi* Hamann & Andersen
Asteraceae	*Scalesia helleri* Robins.
Asteraceae	*Scalesia incisa* Hook. f.
Asteraceae	*Scalesia villosa* Stewart
Boraginaceae	*Cordia revoluta* Hook.f.
Boraginaceae	*Cordia scouleri* Hook.f.
Boraginaceae	*Heliotropium anderssonii* Robins.
Boraginaceae	*Tiquilia nesiotica* (Howell) Richard.
Boraginaceae	*Tournefortia rufo-sericea* Hook.f.
Burseraceae	*Bursera malacophylla* Robins.
Cactaceae	*Opuntia echios* Howell
Cactaceae	*Opuntia helleri* K. Schum.
Cactaceae	*Opuntia megasperma* Howell
Caryophyllaceae	*Drymaria monticola* Howell
Convolvulaceae	*Ipomoea tubiflora* Hook. f.
Euphorbiaceae	*Acalypha abingdonii* O. Seberg
Euphorbiaceae	*Acalypha baurii* Robins. & Greenm.
Euphorbiaceae	*Acalypha wigginsii* Webster
Euphorbiaceae	*Chamaesyce abdita* Burch
Euphorbiaceae	*Chamaesyce nummularia* (Hook.f.) Burch
Lamiaceae	*Salvia prostrata* Hook. f.
Lamiaceae	*Salvia pseudoserotina* Epling
Linaceae	*Linum harlingii* Eliass.
Malvaceae	*Fuertesimalva insularis* (Kearney) Fryxell
Malvaceae	*Gossypium klotzschianum* Anderss.
Mimosaceae	*Acacia rorudiana* Christoph.
Molluginaceae	*Mollugo crockeri* Howell
Myrtaceae	*Psidium galapageium* Hook.f.
Passifloraceae	*Passiflora colinvauxii* Wiggins
Plantaginaceae	*Plantago galapagensis* Rahn
Polygalaceae	*Polygala anderssonii* Robins.

Cont.

Polygalaceae	***Polygala sancti-georgii***
Polygonaceae	***Polygonum galapagense* Caruel**
Rubiaceae	***Borreria dispersa* Hook.f.**
Rubiaceae	***Borreria ericaefolia* Hook.f.**
Rubiaceae	***Borreria linearifolia* Hook.f.**
Rubiaceae	***Borreria perpusilla* Hook.f.**
Rubiaceae	***Psychotria rufipes* Hook.f.**
Sapindaceae	***Cardiospermum galapageium* Robins. & Greenm.**
Solanaceae	***Iochroma ellipticum* (Hook.f.) Hunz.**
Solanaceae	***Jaltomata werffi* D'Arcy**
Verbenaceae	***Lippia rosmarinifolia* Anderss.**
Verbenaceae	***Verbena grisea* Robins. & Greenm.**

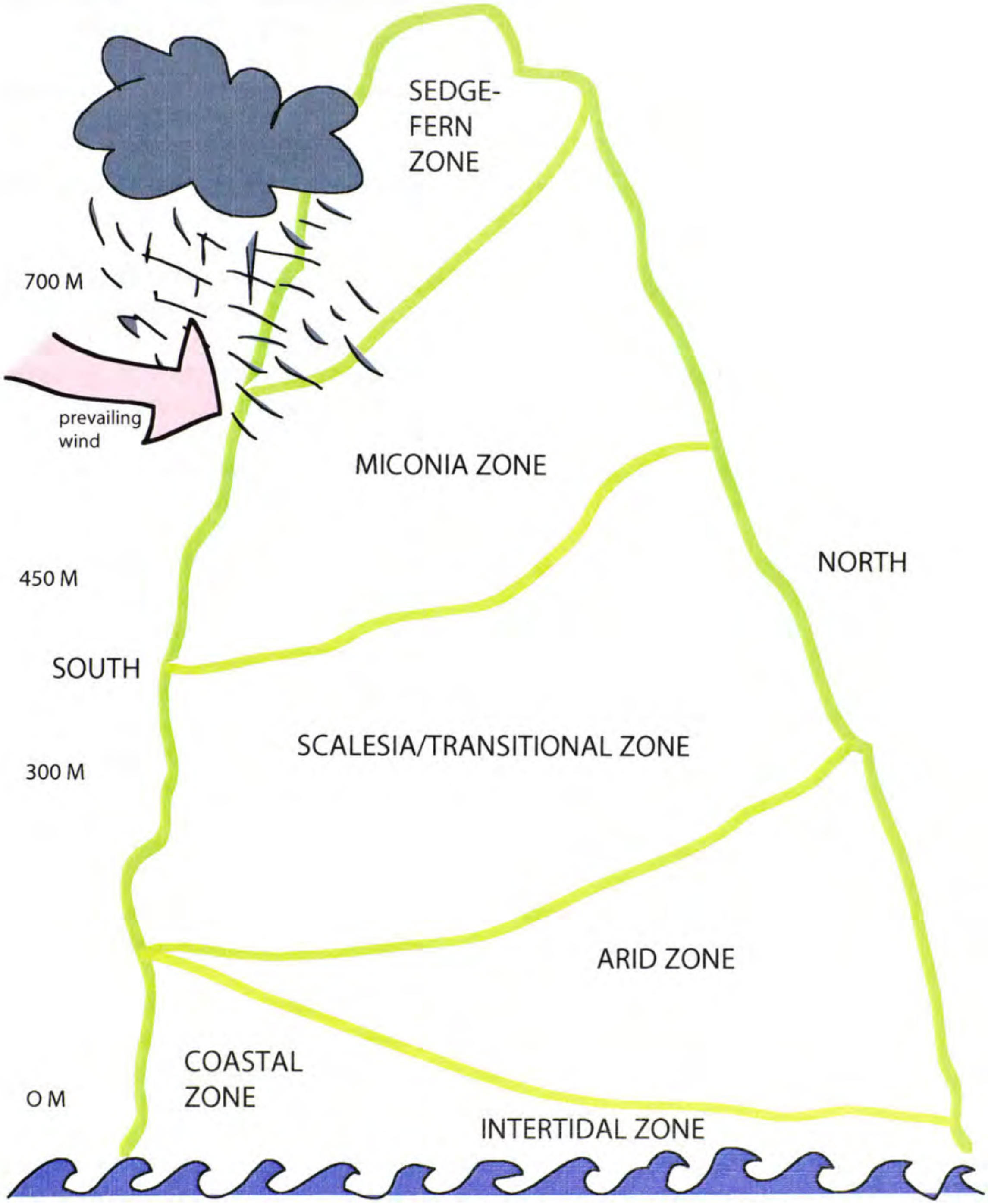
Table 2.4: Taxa in danger of extinction (EN) according to the 2000 criteria of IUCN (adapted from Tye, 2000)

Family	Species
Pteridophyta	
Cyatheaceae	*Cyathea weatherbyana* (Morton) Morton
Monocotyledons	
Cyperaceae	*Cyperus grandifolius* Anderss.
Dicotyledons	
Amaranthaceae	*Alternanthera nesiotes* Johnston
Amaranthaceae	*Pleuropetalum darwinii* Hook.f.
Asteraceae	*Baccharis steetzii* Anderss.
Asteraceae	*Darwiniothamnus alternifolius* Lawesson & Ads.
Asteraceae	*Encelia hispida* Anderss.
Asteraceae	*Lecocarpus darwinii* Adsersen
Asteraceae	*Lecocarpus pinnatifidus* Decne.
Asteraceae	*Scalesia cordata* Stewart
Asteraceae	*Scalesia stewartii* Riley EN
Asteraceae	*Scalesia microcephala* Robins.
Asteraceae	*Scalesia pedunculata* Hook. f.
Cactaceae	*Opuntia galapageia* Hensl.
Cactaceae	*Opuntia insularis* Stewart
Ericaceae	*Pernettya howellii* Sleumer
Lamiaceae	*Salvia insularum* Epling
Melastomataceae	*Miconia robinsoniana* Cogn.
Rubiaceae	*Galium galapagoense* Wiggins
Scrophulariaceae	*Galvezia leucantha* Wiggins
Solanaceae	*Capsicum galapagoense* Heiser & Smith

Table 2.5: Taxa in critical danger of extinction (CR) according to the 2000 criteria of IUCN (adapted from Tye, 2000)

Family	Species
Monocotyledons	
Orchidaceae	Cyclopogon werffii Dodson
Dicotyledons	
Amaranthaceae	Lithophila subscaposa (Hook.f.) Standl.
Asteraceae	Scalesia atractyloides Arn.
Asteraceae	Scalesia divisa Anderss.
Asteraceae	Scalesia retroflexa Hemsley
Cactaceae	Opuntia saxicola Howell
Cucurbitaceae	Sicyocaulis pentagonus Wiggins
Euphorbiaceae	Euphorbia equisetiformis Stewart
Lamiaceae	Hyptis gymnocaulos Epling
Linaceae	Linum cratericola Eliass.
Portulacaceae	Calandrinia galapagosa St. John
Rubiaceae	Psychotria angustata Andersson
Verbenaceae	Lippia salicifolia Anderss.

Figure 2.1: Vegetation Zones of a typical Galápagos Island:
(Adapted from a Teacher's Resource Guide to the Galápagos)



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CHAPTER 3: FIELD OBSERVATIONS AND ECOLOGICAL NOTES

1. Distribution and habitat of *Darwiniothamnus*:

Most species of *Darwiniothamnus,* as the genus is currently recognized, range from woodlands to open lava beds, and from rocky shorelines to the rims and sometimes inside of many volcano craters. Historically the genus has been known to inhabit the four largest islands of the Galápagos (Fernandina, Isabela, Santíago, and Santa Cruz), and to occur on three of the smaller islands, namely Pinta, Pinzón, and Floreana. The geographical range of the three species overlap in only one small region on the southern slopes of Volcán Sierra Negra, located on the southeast tip of the island of Isabela. It is currently unknown to what extent the three species form hybrid swarms at this location, as has been reported for several congeneric species of most oceanic islands (Baldwin *et al.*, 1998). Preliminary field observations suggest, however, that some degree of hybridization does exist.

Natural hybridization is known to occur throughout the world in areas of sympatry and is a major factor influencing the evolution of plants on islands (Borgen 1976, Brochmann 1984). In addition, hybridization has long been considered to be an important factor in the evolution of certain clades of Asteraceae (e.g. in those of *Argyranthemum* and the Silverswords) both in Macaronesia and the Hawaiian islands, respectively (Francisco-Ortega, *et al.*, 1997, Baldwin, 1992). Because introgression is hypothesized to generate genetic diversity in otherwise uniform plants, it could have been a way in which the ancestors of *Darwiniothamnus* that were once located on relatively small islands and/or areas were able to increase their heterogeneity.

Visible, but well separated from Isabela, are three additional islands, Fernandina, Santíago and Santa Cruz; each with an area exceeding 500 sq km. Two species of *Darwiniothamnus* with several apparent varieties inhabit these islands and a recognized subspecies of *D. tenuifolius*, ssp. *santacruzianus*, grows exclusively in very small populations at the upper elevations of the island of Santa Cruz near Cerro Crocker. Beyond Santa Cruz in the far east lies a fifth major island, San Cristóbal, which historically has never been known to contain any members of *Darwiniothamnus*. The rest of the smaller islands, in descending order of size, are: Floreana, Marchena, Española, Pinta, Baltra, Santa Fe, Pinzón and Genovesa. Previously, *Darwiniothamnus* was known only to inhabit three of these smaller islands, Pinta, Pinzón, and Floreana (Wiggens and Porter, 1971). However, after having searched quite extensively on the island of Pinzón and not having found any members of the genus, it appears that the genus has been extirpated from the island, perhaps as the result of foraging by a now extinct feral goat population.

An island-by-island account of the species I found at each collection site throughout the archipelago is listed in Appendix 2. My first trip covered all areas on the island of Santa Cruz where *Darwiniothamnus tenuifolius* ssp. *santacruzianus* was known to exist. My second trip covered the island of Pinzon, all the major coves and northern volcanoes of Isabela, and included two stops on the island of Fernandina. My third trip was a return to Isabela, to the volcanoes of Sierra Negra, Cerro Azul, and surrounding areas. And finally, my fourth collecting trip was to Santiago, Marchena and Pinta (a map of all these areas and the species distributions can be found in Figure 3.1).

Appendix 2 also contains remarks on the hypothesized stability of each population of *Darwiniothamnus* I encountered on the different islands, and if I noticed any unusual forms which might be examined for new specific or subspecific recognition in the future (a general consensus of my findings can be found in the concluding remarks section of this paper and is discussed further in the Chapter 4 as well). Special attention is also paid to leaf form and degree of hairiness, as these are some of the major characteristics by which the genus is divided. Additional information on the factors directly threatening the stability of individual populations is also discussed in more detail below.

2. Biological threats on extant populations of *Darwiniothamnus*:

The three most significant biological threats to the native and endemic flora of the Galápagos Islands are introduced animals, aggressive alien plants, and agricultural encroachment (e.g. Hamann, 1984, 1991; Hoeck, 1984; Brockie *et al.*, 1988; Adsersen, 1989; Loope, Hamann and Stone, 1988; Scofield, 1989). No less important, however, are several additional biological threats including: habitat fragmentation, over-exploitation of native woody species, increasing pressure from resident human populations due to the sharp increase in immigration to the islands, increasing tourist pressure, and man-made fires (Davis *et al.*, 1995).

Currently there are approximately 600 exotic plant species in the archipelago, of which 250 are considered to be naturalized introduced weeds and 37 are considered to be disruptive invasives (see Tables 3.1 and 3.2) (Tye, 2001; Tye, Soria and Gardener, 2002). These numbers, however, continue to grow each year as a result of the increase in traffic to and among the islands over the past 30 years. Hamann (1984, 1991) has stated that the most dangerous invasives directly affecting the native vegetation are most likely *Psidium guajava* (Myrtaceae), *Cinchona succirubra* (Rubiaceae), *Lantana camara* (Verbenaceae), *Rubus* spp. (Rosaceae), *Pennisetum purpureum* (Poaceae), and perhaps *Passiflora edulis* (Passifloraceae) and *P. ligularis*. These plant species not only compete directly with endemics and natives for space and resources, but also may be responsible for the introduction of other pest organisms, such as *Icerya purchasi*, the cottony cushion scale insect.

Icerya purchasi is a known predator of many native and endemic plant species of the Galápagos including *Cordia lutea* (Boraginaceae), *Hibiscus tiliaceus* (Malvaceae), *Laguncularia racemosa* (Combretaceae), *Merremia aegyptica* (Convolvulaceae), *Parkinsonia aculeata* (Fabaceae), *Piscidia carthagenesis* (Fabaceae), *Darwiniothamnus tenuifolius* (including all ssp.), and *D. lancifolius* (including all ssp) (McMullen, 1999). Once infested by *I. purchasi*, all of these plant species and many others die rapidly as a direct result of the insect feeding on the plants' xylem and phloem.

The origin of this pest is thought to be California, where it was introduced, probably from Australia, in the mid 1800s (McMullen, 1999). Upon arrival in South America, *I. purchasi* was introduced into the Galápagos almost certainly from mainland Ecuador on imported citrus (Tye, personal communication). This insect has no known natural enemies in the Galápagos, but California's valuable citrus population was spared by using a species of lady bug (*Rodolia cardinalis*) and cryptochetum fly (*Cryptochetum iceryae*) in order to control the spread of the scale insect. Although the introduction of exotic insects to the Galápagos for biological control is controversial due to possible unforeseen detrimental effects (McMullen, 1999), controlled studies at the CDRS using

Rodolia cardinalis suggested that the ladybug would not adversely affect native scale insects, their predators, nor bird species that might eat it. It was therefore released as the first biological control attempt in the Galápagos, in January of 2002.

In addition to invasive plant and insect species, several introduced animal species have also caused severe and possibly irreversible effects on the native flora and fauna of the Galápagos Islands. Lawesson (1990), has given a number of examples of endemic plant genera that suffer from the introduction of both alien plants and animals, and one specific example is that of *Lecocarpus pinnatifidus* (Asteraceae). This species inhabits the arid zone and humid highlands of Floreana, and has a range that has been steadily decreasing in recent years, possibly due to the invasion of introduced plants such as *Lantana camara* L. (Cruz *et al.*, 1986; Lawesson & Ortiz, 1990). Although *L. pinnatifidus* was still known from some localities at the time Lawesson wrote his paper, he feared it could quickly become extinct due to the increasing goat population on Floreana, which was at about 10,000 in 1987 (Lawesson, 1990). However, since the late 1980's better goat control has been used on this island and the species now appears to be somewhat stable (Tye, personal communication).

Another related example is that of two arid zone taxa of *Scalesia (S. atractyloides*, var. *atractyloides* and var. *darwinii;* Asteraceae), which are also in extreme danger of extinction due to the depletion by feral goats (McMullen, 1999). Feral goats, pigs and cattle were once introduced to many islands of the archipelago several years ago as a sustainable food source for both local fishermen and residents of the archipelago. However, the impact these large feral animals have had on the local flora of the archipelago is considerable; not only do these animals feed on several different plant species (including most species of *Darwiniothamnus*), but they also trample and wear paths through the vegetation. Because these once small ruminant populations have now reproduced to such large proportions, several eradication measures are currently underway to remove them completely from as many islands as possible.

3. Soil observations and analyses:

i. Introduction:

During my field research throughout the islands, it became evident that there was no individual soil type that was preferred by all members of *Darwiniothamnus*. The type of volcanism found in the Galápagos is such that the upper slopes of the islands have a different soil type than the lower ones, due to differences in parent rock (van der Werff, 1977). Because members of this genus can be found at multiple elevations and in various climatic zones, I decided to investigate what some of the limiting nutrients might be for the successful introduction of this genus into new ecological niches. I therefore collected soil samples across all the islands that I visited, both at locations where different taxa of *Darwiniothamnus* were found growing and in places where they were not. My initial hypothesis is that there is not an individual nutrient that currently acts as the limiting factor for the successful growth of *Darwiniothamnus*, however a combination of missing nutrients could be enough to prevent this genus from colonizing new, or previously uninhabited, areas of the archipelago.

ii. Soil collection methodology

Twenty-nine soil samples were collected in 150 ml plastic "Whirl-pak" bags. One combined sample was taken for each collection site in most cases, each weighing approximately 100 grams. In some instances we were able to sample different root zones and have them analyzed separately. Typically, after removal of the top organic layer, soil samples were obtained from a depth ranging between 5 and 35 centimeters. A few of the samples were located near juvenile plants growing in areas with almost no top soil, and where the species of *Darwinothamus* appeared to be a pioneering plant growing in volcanic sump holes protected from the wind.

Once the samples were collected, GPS locations and photos of the surrounding vegetation were taken at their resident soils and correlated. With the permission of the CDRS, the samples were then exported and sent to the Growers Testing Service (Visalia, California) where the analyses were run. All soil samples were autoclaved prior to analysis, as required by the USDA, and a list of all the analyses run, including their methodology can be found in Table 3.3.

Upon receiving the results of the soil analyses, a Mann-Whitney U test (with 2-tailed p values of ≤ 0.05) was run on each taxon across all of the analyses performed to see if any of the soil characters were significantly correlated with the presence or absence of species of *Darwiniothamnus* (see Table 3.6 for all of the significant results).

iii. Results

As previously mentioned, the soils collected for analysis were chemically analyzed for elements of agriculture suitability. The results of each test performed on each individual sample are located in Appendix 3 and a description of the collection sites and qualitative soil descriptions are located in Table 3.4. The means and average for each analysis run in the saturation extract, nutrients by dry soil estimate and the trace metals, are also cross referenced in Table 3.5 with the geographical locations listed and the species of *Darwiniothamnus* present at each site. In addition to these tables,

Appendix 3 contains general information on each of the analyses run, in terms of their ecological importance, and briefly describes some qualitative correlations between each sample site. These findings are briefly summarized below, followed by the significant results of the study.

Soil pH levels are known to have a direct influence over the availability of both macro and micronutrients and their uptake by plants (Brady, 1990). From all of the sites where soil was collected, the highest pH values of 8.6 and 8.5 were found at both locations collected near the base of Volcan Ecuador (soil sample numbers 7 and 16, respectively). The first location, which was quite near the shore, contained a sparse population of *D. lancifolius* ssp. *glandulosus*. The second location, however, was bare of any species of the genus. Thus, highly basic soils could be a reason for the absence of *Darwiniothamnus* at this location, however further analyses should be run before any strict hypothesis is developed.

Electrical conductivity (Ece) is an estimate of the relative amount of salt in a given area. Generally speaking, Ece values of less than 2.0 indicate no salt excess, where as values of 2.0-4.0 may restrict the growth of certain agricultural crops. Ece values of 4.0-8.0 are known to restrict the growth of many crops, and locations that contain Ece values of 8.0-16 and above are known to house only very salt tolerant plants (Rivers, 2002). In general, all of the Ece values for the sites collected in the Galápagos were below 2.0 (see table 4.1), except at Cartago Bay (soil sample numbers 1-4). This location varied from 2.0-5.9 with an average Ece of 4.15. This is expected, however, as the location is located very close to the ocean and receives both spray and wind from the seaside. This location was also home to a robust population of *D. tenuifolius*, which suggests that soils with either a high or low salt content are not a limiting factor for the survival of *Darwiniothamnus*.

Brady (1990) listed six nutrient elements, N, P, K, Ca, Mg, and S, that are essential for the growth of plants. All of these elements are provided to plants in the form of soil solids and are used in relatively large amounts by most plant species. Due to the relatively small sample size of soil collected at each location, only Ca, Mg, Ca+Mg, and P were tested from the saturation extract, and K and NO_3-N were both tested from the saturation extract and as a dry soil estimate.

The highest levels of Ca and Mg were found on the islands of Fernandina, near Roca Tarzan (15.27 meq), and at Cartago Bay (17.93 meq), respectively; and the lowest levels for both (0.4 and 0.28 meq) were found at Volcan Ecuador. Sumner (2000) has stated that environments containing considerable amounts of Ca and Mg are often the result of other components in the soil such as limestone, fertilizers and animal manures. This could explain the high level of Mg at Cartago Bay where feral goats were known to exist for several years, however the same explanation cannot be used for the high level of Ca on the island of Fernandina, which is void of all animals except for birds. In any case, it could be that low levels of each of these two nutrients may inhibit the successful germination and subsequent growth of all species of *Darwiniothamnus*, as the site that produced the two lowest values of Ca and Mg, Volcan Ecuador, was completely void of any members of this genus. However, additional evidence for another area besides this one site is needed before any concrete hypotheses can be made.

Rivers (2002) has stated that NO_3-N values below 5 ppm, P values below 7 ppm and K values below 80 ppm are extremely low for most soil environments and could prevent the successful growth of many plant species. Nutrient dry soil estimates of all of each of these elements shows that the lowest level of NO_3-N (1 ppm) was found at two locations: Volcan Ecuador (where no species of *Darwiniothamnus* were present) and on the southern coast of Santiago, near Cabo Nepean (where only a very few plants of *Darwiniothamnus* were found over a 3 km square radius). The lowest level of P (2 ppm), however, was found on the coast of Fernandina, where oddly the healthiest stand of *D. lancifolius* ssp. *glandulosus* throughout all of the islands was found. Finally, the lowest level of K (48 ppm) was also found on the southern coast of Santiago, near Cabo Nepean, where again, only a very few plants of *Darwiniothamnus* were found.

Brady (1990) also listed eight elements, or micronutrients, obtained from soil solids (Fe, B, Mo, Mn, Cu, Zn, Cl, Co) that are used in relatively small amounts by most plants, but which are nonetheless essential for their proper growth. With the amount of soil collected, I was able to test for Cl, B, Zn, Mn, Fe and Cu from each location I visited within the Galápagos. Rivers (2002) has stated that while standard levels for Mn, Fe and Cu have not been well established, if any of the values fall below 2 ppm, 5 ppm and .1 ppm respectively, a possible deficiency could exist. Two of these three elements were below or close to below these limits (Mn = 1.5 ppm and Cu = 0.4), and both were collected from Volcan Ecuador, where no species of *Darwiniothamnus* were found. Coincidently, this is also the site where the lowest level of Zn was found among all of the soil samples collected.

Although some interesting trends were readily detected from the raw soil data, as described above, additional significant results were also obtained using a Mann-Whitney U test. This test was performed in order to investigate whether any of the soil characters were significantly correlated with the presence or absence of species of *Darwiniothamnus*. The results for this test are located in Table 3.6 and it should be noted that while a brief summary of the potentially limiting factors is discussed below for each species, subspecies and variety of *Darwiniothamnus*; the results are based on limited data and thus ought to be treated only as preliminary data.

By looking at the results in Table 3.6, it appears that water could be the major limiting resource for successful growth of *D. tenuifolius*, a notion that is tenuously supported by the species' range across the archipelago. Zn (Z=-1.5, p=.037), Fe (Z=-2.08, p=.038), Na (Z=-1.86, p=.063) and organic matter (Z=-1.86, p=.063) could also be the limiting factors for *D. tenuifolius* var. *tomentosus,* as the data appears to be supported by the fact that across all the sample sites, Pinta contained the highest amount of Zn. In addition, this site also contained relatively high amounts of Fe, Na and organic matter.

Exchangeable Na (Z=-2.08, p=.038), pH (Z=-2.04, p=.037) and NO_4-N (Z=-1.94, p=.053) may all represent the limiting factors for this successful growth of *D. alternifolius*, since this species is limited to two relatively small areas on the southern tip of Isabela. The same can be said for *D. lancifolius* ssp. *glabriusculus*, which could have the limiting factors of Fe (Z=-2.77, p=.006), pH (Z=-3.12, p=.002) and Carbonate (Z=-2.86, p=.004), as it also is only found on Volcan Sierra Negra which also had the lowest values for pH and carbonates, and the highest values of Fe (see table 3.5). It must be noted, however, that *D. alternifolius* and *D. lancifolius* ssp. *glabriusculus* may have always been restricted to Volcan Sierra Negra for another reason altogether.

Finally, by looking at the results from Table 3.6, Saturation % (Z=-3.16, p=.002), Zn (Z=-1.84, p=.066) and organic matter (Z=-2.00, p=.045) could also be the limiting factors for *D. lancifolius* ssp. *glandulosus,* which is somewhat interesting as this species grows predominantly in non-lava areas where there's plenty of soil and several other species growing

In addition to these results, soil samples taken where there were no species of *Darwiniothamnus* present appear to be lacking in Ca (Z=-1.93, p=.053), Ca+Mg (Z=-2.01, p=.045), NO_4-N (Z=-1.94, p=.053) and organic matter (Z=-2.00, p=.045). These results are supported by the fact that when looking at the raw data across all 29 soil samples, the locations which had the lowest values for Ca, Ca +Mg and NO4-N are indeed where no species of *Darwiniothamnus* were found growing (see Table 3.5). It is therefore possible that these elements are the ultimate limiting factors for the successful introduction of *Darwiniothamnus* into previously uncolonized areas of the Galápagos Islands.

iv. Discussion

When considering the results of the soil analyses it appears evident that Volcan Ecuador is the one location that is void of several of the element and micronutrients necessary for the successful growth of most plants. In specific, the lowest levels for Calcium (0.4 meq), Magnesium (0.28 meq), Nitrate-nitrogen (1 ppm), Manganese (1.4 ppm) and Copper (.4 ppm) were all found at the sample site from this location where no species of *Darwiniothamnus* were found growing. Brady (1990) has listed the following importance of each of these elements: Copper (Cu) is involved in photosynthesis and respiration and in the use of iron, stimulates lignifcation of all plant cell walls; a deficiency in Boron (Bo) can decrease the rate of water absorption, root growth and translocation of sugars in plants; Manganese (Mn) is essential for certain nitrogen transformations in microorganisms as well as in plants; both Zinc (Zn) and Manganese function in enzyme systems necessary for important reactions in plant metabolism; and both Copper and Iron (Fe) act as electron carriers in enzyme systems that help bring about oxidation-reduction reactions in plants' biochemical processes.

The lack of the several elements and micronutrients described above may explain the lack of healthy populations of *Darwiniothamnus* at the upper elevations of Volcan Ecuador. Similar results were also found on the southern coast of Santiago, near Cabo Nepean, where very low levels of Nitrate-nitrogen (1 ppm) and Potassium (48 ppm) were found. Although this location is home to a few plants of *D. tenuifolius* the small population size could be a result of the limited amount of these essential elements present in their environment. However, because typically only one soil sample was collected per site across the archipelago, the data is not sufficient enough to draw any strong conclusions, and all deductions made here are only based on preliminary data.

It is also worth pointing out that the only other location where soil was collected and where no species of *Darwiniothamnus* were found growing was on the island of Marchena. This island has been known for decades to be completely void of all members of the genus, however all of the values for each of the soil analyses run were within the accepted limits for healthy plant growth. It is therefore my preliminary hypothesis that some factor other than soil (such as chance or location of the island), is responsible for the complete lack of *Darwiniothamnus* on this island. All of the numerical data for the results described above can again be found in Tables 4.3, 5.3 and 6.3.

Table 3.1: Invasive species in Galapagos, known or suspected to be causing significant ecological change (adapted from Tye, 2001)

Family	**Species**
Agavaceae	*Furcraea cubensis* (Jacq.) Vent.
Bombacaceae	*Ochroma pyramidale* (Lam.) Urban
Boraginaceae	*Cordia alliodora* (R. & P.) Chum.
Capparidaceae	*Cleome viscosa* L.
Crassulaceae	*Kalanchoe pinnata* (Lam.) Pers.
Cucurbitaceae	*Cucumis dipsaceus* Ehr.
Euphorbiaceae	*Ricinus communis* L.
Lauraceae	*Persea americana* Mill.
Leguminosae	*Caesalpinia bonduc* (L.) Roxb.
Leguminosae	*Cassia tora* L.
Leguminosae	*Leucaena leucocephala* (Lam.) de Wit
Meliaceae	*Cedrela odorata* L.
Myrtaceae	*Eugenia jambos* L.
Myrtaceae	*Psidium guajava* L.
Passifloraceae	*Passiflora edulis* Sims.
Poaceae	*Brachiaria mutica* (Forssk.) Stapf
Poaceae	*Digitaria decumbens* Stent.
Poaceae	*Melinis minutiflora* Beauv.
Poaceae	*Panicum maximum* Jacq.
Poaceae	*Panicum purpurascens* Raddi
Poaceae	*Pennisetum clandestinum* Hochst.
Poaceae	*Pennisetum purpureum* Schum.
Rosaceae	*Rubus niveus* Thunb.
Rubiaceae	*Cinchona pubescens* Vahl
Rutaceae	*Citrus aurantiifolia* (Christm.) Swingle
Rutaceae	*Citrus limetta* Risso
Rutaceae	*Citrus limon* (L.) Burn.
Solanaceae	*Cestrum auriculatum* L'Her.
Solanaceae	*Datura stramonium* L.
Solanaceae	*Lycopersicon esculentum* Mill.
Ulmaceae	*Trema micrantha* (L.) Blume
Verbenaceae	*Lantana camara* L.

Table 3.2: Naturalized species, which are still relatively uncommon but are known to be damaging aggressives in other parts of the world or suspected of capacity to be so in Galapagos (adapted from Tye, 2001).

(note: Most of those listed will probably move into Table 1 unless action is taken to control them)

Family	Species
Amaranthaceae	***Amaranthus gracilis* Desf.**
Anacardiaceae	***Spondias purpurea* L.**
Annonaceae	***Annona cherimolia* Mill.**
Annonaceae	***Annona muricata* L.**
Araceae	***Colocasia esculenta* (L.) Schott**
Asclepiadiaceae	***Asclepias curassavica* L.**
Asteraceae	***Bidens cynapiifolia* HBK.**
Asteraceae	***Flaveria bidentis* (L.) Kuntze**
Asteraceae	***Gnaphalium purpureum* L.**
Asteraceae	***Porophyllum ruderale* (Jacq.) Cass.**
Bixaceae	***Bixa orellana* L.**
Brassicaceae	***Raphanus sativus* L.**
Cannaceae	***Canna lutea* Mill.**
Caricaceae	***Carica papaya* L.**
Chenopodiaceae	***Chenopodium ambrosioides* L.**
Chenopodiaceae	***Chenopodium murale* L.**
Convolvulaceae	***Ipomoea pulchella* Roth**
Cyperaceae	***Cyperus rotundus* L.**
Euphorbiaceae	***Chamaesyce hirta* (L.) Millsp.**
Euphorbiaceae	***Jatropha curcas* L.**
Leguminosae	***Acacia nilotica* (L.) DeLisle**
Leguminosae	***Cassia bicapsularis* L.**
Leguminosae	***Geoffroea spinosa* Jacq.**
Leguminosae	***Inga edulis* Mart.**
Leguminosae	***Lablab purpureus* (L.) Sweet**
Leguminosae	***Mimosa pigra* L.**
Lythraceae	***Cuphea carthagenesis* (Jacq.) Macbr.**
Malvaceae	***Hibiscus diversifolius* Jacq.**
Malvaceae	***Hibiscus rosa-sinensis* L.**
Malvaceae	***Malachra alceifolia* Jacq.**
Malvaceae	***Malvastrum coromandelianum* (L.) Garcke**
Meliaceae	***Melia azederach* L.**
Nyctaginaceae	***Mirabilis jalapa* L.**
Papaveraceae	***Argemone mexicana* L.**
Passifloraceae	***Passiflora ligularis* Juss.**
Passifloraceae	***Passiflora quadrangularis* L.**
Phytolaccaceae	***Rivina humilis* L.**
Piperaceae	***Pothomorphe peltata* (L.) Mig.**
Poaceae	***Axonopus compressus* (Sw.) Beaur.**
Poaceae	***Bambusia guadua* HBK.**
Poaceae	***Cynodon dactylon* (L.) Pers.**
Poaceae	***Dactylotenium aegypticum* (L.) Beauv.**

Cont.

Poaceae	***Echinochloa colonum* (L.) Link**
Poaceae	***Eragrostis pilosa* (L.) Beauv.**
Polemoniaceae	***Phlox* sp.**
Rubiaceae	***Coffea arabica* L.**
Solanaceae	***Brugmansia candida* L.**
Solanaceae	***Datura innoxia* Mill.**
Solanaceae	***Nicotiana tabacum* L.**
Solanaceae	***Physalis peruviana* L.**
Tiliaceae	***Triumfetta semitriloba* Jacq.**
Urticaceae	***Urera caracasana* (Jacq.) Griseb.**
Verbenaceae	***Verbena brasiliensis* Vell.**
Zingiberaceae	***Hedychium* sp.**

Table 3.3: List of Soil Analyses run and methods used at the Growers Testing Service, Visalia, California:

Test:	Type of Analysis:
pH	Measured in the saturated paste after 1 hour.
EC_e (mmhos/cm or dS/m)	Electrical conductivity of the saturation extract.
Soluble CALCIUM/MAGNESIUM (meq/l)	Measured in the saturation extract by Atomic Absorption, response enhanced with Lanthanum.
Soluble SODIUM/POTASSIUM (meq/l)	Measured in the saturation extract by Flame Emission.
CARBONATE+BICARBONATE (meq/l)	Measured in the saturation extract by titration with 0.01N Sulfuric Acid to Methyl Orange endpoint.
CHLORIDE (meq/l)	Measured in the saturation extract by titration with 0.01N Silver Sulfate with Potassium Chromate indicator (Silver Chromate precipitate).
FREE LIME (Calcium Carbonate)	Fizz Test (none, low, medium or high)
SATURATION PERCENTAGE	Usually start with 200 grams of dried and ground soil and add deionized water until the paste meets the usual criteria. The saturated paste sits for at least 1 hour before further tests are begun.
NITRATE-NITROGEN (ppm in saturation extract; ppm in dry soil)	Measured in the saturation extract using Phenoldisulfonic Acid detection colorimetric method.
PHOSPHORUS (ppm in dry soil)	0.5N Sodium Bicarbonate extraction, Ammonium Molybdate detection colorimetric method.
Exchangeable K, Ca, Mg, Na (ppm, meq/100 grams)	1N Ammonium Acetate extraction, Atomic Absorption/Flame Emission detection.
Zn, Mn, Fe, Cu (ppm in dry soil)	DPTA extraction, Atomic Absorption detection.
BORON (ppm in saturation extract)	Azomethine H detection colorimetric method (AOAC)

Cont.

ORGANIC MATTER (%)	Weight loss by combustion.
SAR	Calculated from measured soluble Ca, Mg & K.
NH_4-N (ppm in dry soil)	Extracted from soil with 1N Sulfuric Acid. Distilled from acid solution after making the extract alkaline (like a kjeldahl analysis without the digestion).

Table 3.4: Description of Soil collection sites:

Sample no.	Species present	General Location
1	*Darwiniothamnus tenuifolius*	Cartago Bay, Isabela
2	*D. tenuifolius*	Cartago Bay, Isabela
3	*D. tenuifolius*	Cartago Bay, Isabela
4	*D. tenuifolius*	Cartago Bay, Isabela
5	*D. tenuifolius*	trail up to V. Alcedo, Isabela
6	*D. tenuifolius*	Cerro Cartago
7	*D.lancifolius*	Volcan Ecuador
8		Volcan Ecuador
9	*D. tenuifolius*	2/3 of the way up to V. Alcedo
10	*D. lancifolius* ssp. *glandulosus*	Volcan Wolff, Isabela
11	*D. lancifolius* ssp. *glandulosus*	Cabo Douglas, Fernandina
12	*D. lancifolius* ssp. *glandulosus*	Lava near Roca Tarzan, Fernandina
13	*D. lancifolius* ssp. *glandulosus*	Base of V. Fernandina, Fernandina (lea. oddly very long and thin)
14	*D. lancifolius* ssp. *glandulosus*	Volcan Darwin, Isabela
15	same data as #5	
16	none	Volcan Ecuador
17	*D. tenuifolius*	rim of Volcan Sierra Negra, Isab.
18	*D. lancifolius* ssp. *glabriusculus*	ca. down trail from rim to parking area, Volcan Sierra Negra, Isabela
19	*D. alternifolius*	Pampa "El Alemania," base of VSN, Isa.
20	*D. tenuifolius*	Sanitago highlands, in area around GNPS house
21	*D. tenuifolius* ssp. *santacruzianus*	Santa Cruz, south of Cerro Crocker
22	none	Marchena, inland from landing place by Playa Negra
23	none	Marchena, inland close to Pta. Mejia, facing Pinta
24	*D. tenuifolius*, var. *tomentosus*?	Pinta, up the new trail across from top of Red Hill
25	*D. tenuifolius*, var. *tomentosus*?	Pinta, approx. 1/2 km from last collection site
26	*D. tenuifolius*, var. *tomentosus*?	Pinta, down old trail from Peak, heading east
27	*D. tenuifolius*	Santiago, southern coast, south of Cabo Nepean
28	none	Cerro Azul, Isabela
29	*D. alternifolius* and *D. lancifolius*	Cerro Azul, Isabela

Table 3.4 cont.: Description of Soil collection sites:

Sample no.	Location site information from field notes:
1	Dry rocky lava, good drainage
2	Dry rocky lava, good drainage
3	Dry rocky lava, some dk. woody soil present
4	Dry rocky lava, some dk. woody soil present
5	Scrub lands, muy cerado, not quite savannah, not far from new trail - browish soil, no lava present
6	Rocky lava, undulating and some yellowish soil present as well; soil collected near Cerro Cartago, where no *Darwiniothamnus* was found growing (soil much more yellow)
7	Plants growing in dirt between very dark (black) lava
8	Soil in transition zone between black lava and light brown lava, sample taken on hillside
9	Fern/sedge zone, plants surrounded by various grass spp.
10	Light brown lava/dirt, plants both in soil and directly on rocks
11	Medium dark grey and fine, taken inbetween lava stands
12	Sample taken in dirt past initial coastal strand of lava at first sight of a huge population of *Darwiniothamnus*
13	Sample taken in a rocky river bed at interface with black lava where another large population was found
14	Lava-gravel interface right before start of reddish lava, past tourist trail where first *Darwiniothamnus* pop was found
15	Repeat of sample # 5
16	Hillside, ascending base of volcano - sandy soil, no spp. of *Darwiniothamnus* present from here on out, why?
17	Sample collected ca 6 km around crater from end of trail past sulfur plumes; rocky soil and +/- volcanic, with orange bits of pumice, soil very wet and constitutes top most veg zone, fog abundant.
18	Sample taken off trail in +/- pasture-land, still very moist, soil dark, no lava present
19	+/- pasture land, still very moist, soil dark, no lava present
20	Sample taken near a fenced off quadrant, lush veg, wet, rocky, dark brown soil
21	On way to Los Picachos, area densely covered with *Pteridium aquilinum*, moist ground, brown clay-like soil
22	Soil very dry, light brown, somewhat rocky, lava present, but sample taken away from lava
23	Again, sample taken from soil/lava stand, very dry, light brown
24	Reddish, dry soil, no lava present at this particular location
25	Soil very dark, almost black, also dry and no lava present, dense vegetation
26	Scrub zone, soil also black, nice clean, almost woody soil but not rocky
27	Very dry and hot area, huge lava stand, sample taken from within cracks of lava, very shallow
28	Along the cassadores trail, up from Calleta Iguana and before reaching Media Luna
29	Just south of Media Luna

Table 3.4 cont.: Description of Soil collection sites:

Sample no.	GPS data	Qualitative assessment of the presence of *Icerya purchasi* (Cottony-cushion scale insect)
1	90 56 88 W, 00 37 35 S	no data
2	90 56 88 W, 00 37 33 S	all plants ca. 50% infected
3	90 57 13 W. 00 37 16 S	none
4	90 57 06 W, 00 37 16 S	none
5	91 02 16 W, 00 23 90 S	most plants only 20-30% alive due to insect
6	90 57 15 W, 00 37 20 S	
7	91 35 27 W, 00 00 91 S	no data, but black dot insect (feces?) abundant and plants w/ ca 50% dieback
8	91 35 22 W, 00 00 98 S	
9	91 03 37 W, 00 24 33 S	present, but not too abundant, healthiest plants yet seen
10	91 13 04 W, 00 01 25 S	none found
11	no GPS data,	none present
12	91 39 04 W, 00 23 34 S	none present, but black dot "insects" mentioned above are present
13	91 37 08 W, 00 23 01 S	none present
14	91 21 93 W, 00 14 95 S	no notes
15		
16	about1 km north of 91 35 15 W 00 00 86 S	none found
17	91 10 25 W, 00 48 25 S	no notes
18	91 66 26 W, 00 50 34 S	no notes
19	91 10 57 W, 00 50 26 S	none present
20	90 46 03 W, 00 13.18 S	none present
21	90 19 00 W, 00 38 66 S	none present
22	no data	yes, on Rinchosa minima
23	91 32 07.1W, 00 21 21.71S	yes, on Rincosa minima
24	90 44 94 W, 00 33 84 N	yes, everywhere!!! Several plants of *Darwiniothamnus tenuifolius* are dead and/or dieing
25	90 45 16 W, 00 34.12 N	yes, everywhere!!! Several plants of *D. tenuifolius* dead and/or dieing
26	90 44 84 W, 00 34 95 N	none present
27	90 49 15 W, 00 19 15 S	none appears to be present at this location
28	91 25.92 W, 00 59 16 S	none
29	91 25 52 W, 00 58 12 S	another kind of scale insect, but doesn't appear to be *I. purchasi*

Table 3.5: Results of soil analyses for each collection site within the Galápagos Islands:
(Note: if more than one value is given, the first two numbers are the range and the second, followed by a comma, is the mean)

Island and collection location:	**soil sample #s:**	**species present:**
Isabela		
Cartago Bay	1,2,3,4	*D. tenuifolius*
Cerro Cartago	6	*D. tenuifolius*
Volcan Alcedo	5, 9	*D. tenuifolius*
Volcan Wolff	10	*D. lancifolius* ssp. *glandulosus*
Volcan Ecuador, lava strand near shore	7, 8	*D. lancifolius* ssp. *glandulosus*
Volcan Ecuador, base of Volcano	16	none
Volcan Darwin	14	*D. lancifolius* ssp. *glandulosus* & *D. tenuifolius*
Sierra Negra (base of volcano)	18	*D. lancifolius*, ssp. *glabriusculus* only
Sierra Negra (El velasco)	19	*D. lancifolius* ssp. *glabriusculus*, *D. tenuifolius*, *D. alternifolius*
Sierra Negra rim only	17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius* only
Cerro Azul		
Just north of Media Luna, up from Calletta Iguana	28, 29	*D. lancifolius* ssp. *glabriusculus* & *D. alternifolius* only
Fernandina		
Lava near Roca Tarzan & base of V. Fernandina	12, 13	*D. lancifolius* ssp. *glandulosus*
Cabo Douglas	11	*D. lancifolius* ssp. *glandulosus*
Santa Cruz		
South of Cerro Crocker, near los Picachos	21	*D. tenuifolius* ssp. *santacruzianus*
Santiago		
highlands, near GNPS house	20	*D. tenuifolius*
southern coast, south of Cabo Nepean	27	*D. tenuifolius*
Marchena		
Playa Negra & inland near Pta. Mejia	22, 23	none
Pinta		
up new trail	24, 25	*D. tenuifolius*
down old trail	26	*D. tenuifolius*

Table 3.5 cont: Results of soil analyses for each collection site within the Galápagos Islands:
(Note: if more than one value is given, the first two numbers are the range and the second, followed by a comma, is the mean)

Soil sample #	**Spp. present**	**pH**	**Ece**	**Ca (meq)**
1,2,3,4	*D. tenuifolius*	5.6-7.6, 6.93	2.0-5.9, 4.15	7.69-15.82, 11.42
6	*D. tenuifolius*	7.3	0.3	1.6
5, 9	*D. tenuifolius*	7.3-7.4, 7.35	1.1-3.1-2.1	6.39-13.22, 9.81
10	*D. lancifolius* ssp. *glandulosus*	8.2	1.3	5.34
7, 8	*D. lancifolius*	8.2-8.6, 8.4	1.1-3.1-2.1	4.83-14.52, 9.68
	none	8.5	0.3	0.4
14	*D. lancifolius* ssp. *glandulosus* & *D. tenuifolius*	8.1	0.9	3.18
18	*D. lancifolius* ssp. *glabriusculus*	5.4	0.3	0.77
19	*D. lancifolius* ssp. *glabriusculus*, *D. tenuifolius*, *D. alternifolius*	5.4	1.1	8.33
17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius* only	4.8	0.5	1.78
28, 29	*D. lancifolius* ssp. *glabriusculus* & *D. alternifolius* only	5.8-5.9, 5.85	.7-1.2, .95	2.83-6.64, 4.84
12, 13	*D. lancifolius* ssp. *glandulosus*	6.9-7.0, 6.96	.8-3.4, 2.1	2.85-27.69, 15.27
11	*D. lancifolius* ssp. *glandulosus*	6.6	2.5	11.83
21	*D. tenuifolius* ssp. *santacruzianus*	5	0.4	1.09
20	*D. tenuifolius*	6.1	1.4	3.22
27	*D. tenuifolius*	7.5	0.2	0.89
22, 23	none	6.7-7.9, 7.3	.2-1.2, .7	.78-3.61, 2.20
24, 25	*D. tenuifolius*	7.3-7.8, 7.55	.8-.8, .8	3.43-4.10, 3.77
26	*D. tenuifolius*	7.3	1.5	8.48

Table 3.5 cont: Results of soil analyses for each collection site within the Galápagos Islands:

Soil sample #s	**Spp. present**	**Mg (meq)**	**Ca + Mg (meq)**	**Na (meq)**
1,2,3,4	*D. tenuifolius*	2.88-17.93, 10.94	10.57-29.01, 22.18	4.35-32.19, 18.05
6	*D. tenuifolius*	0.68	2.28	0.61
5, 9	*D. tenuifolius*	2.63-3.78, 3.2	9.02-17.00, 13.0	4.78-6.53, 5.66
10	*D. lancifolius* ssp. *glandulosus*	2.06	7.4	4.31
7, 8	*D. lancifolius* ssp. *glandulosus*	2.55-7.16, 4.86	7.38-21.68, 14.53	3.39-10.0, 6.70
16	none	0.28	0.68	2.61
14	*D. lancifolius* ssp.p . *glandulosus* & *D. tenuifolius*	0.82	4	3.92
18	*D. lancifolius*, ssp. *glabriusculus*	0.81	1.58	1.17
19	*D. lancifolius* ssp. *glabriusculus*, *D. tenuifolius*, *D. alternifolius*	1.1	9.43	0.91
17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius*	0.94	2.72	1.7
28, 29	*D. lancifolius*, ssp. *glabriusculus* & *D. alternifolius*	2.55-3.54, 3.05	5.38-10.18, 7.78	1.35-1.61
12, 13	*D. lancifolius* ssp. *glandulosus*	2.63-6.33, 4.48 5	.48-34.02, 19.75	1.74-2.18, 1.96
11	*D. lancifolius* ssp. *glandulosus*	7.57	19.4	7.4
21	*D. tenuifolius santacruzianus*	1.32	2.41	1.52
20	*D. tenuifolius*	5.92	9.14	2.09
27	*D. tenuifolius*	0.48	1.37	0.5
22, 23	none .	54-3.29, 1.92	1.32-6.9, 1.01	.96-2.26, 1.61
24, 25	*D. tenuifolius*	2.39-2.72, 2.55	5.82-6.82, 6.32	.96-1.13, 1.05
26	*D. tenuifolius*	3.87	12.35	1.74

Table 3.5 cont: Results of soil analyses for each collection site within the Galápagos Islands:
(Note: if more than one value is given, the first two numbers are the range and the second, followed by a comma, is the mean)

Soil sample #:	Spp. present	K (meq)	K (ppm)	P (ppm)
1,2,3,4	*D. tenuifolius*	2.15-7.39, 4.62	700-2020, 1400	6-42, 28.5
6	*D. tenuifolius*	0.2	1990	29
5, 9	*D. tenuifolius*	4.19-4.54, 4.33	2190-2340, 2265	18-29, 23.5
10	*D. lancifolius* ssp. *glandulosus*	1.13	1010	16
7, 8	*D. lancifolius* ssp. *glandulosus*	.15-1.92, 1.04	148-1000, 574	27-100, 75.25
16	none	0.15	204	2
14	*D. lancifolius* ssp. *glandulosus* & *D. tenuifolius*	1.15	128	7
18	*D. lancifolius,* ssp. *glabriusculus*	0.68	306	6
19	*D. lancifolius* ssp. *glabriusculus,* *D. tenuifolius,* *D. alternifolius*	0.39	222	35
17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius* only	0.63	214	32
28, 29	*D. lancifolius,* ssp. *glabriusculus* & *D. alternifolius* only	0.41-0.5, 0.455	180-236, 208	3-6, 4.5
12, 13	*D. lancifolius* ssp. *glandulosus*	0.56-2.33, 1.45	108-510, 309	15-32, 23.5
11	*D. lancifolius* ssp. *glandulosus*	0.56	118	68
21	*D. tenuifolius* ssp. *santacruzianus*	0.2	144	4
20	*D. tenuifolius*	2.81	1090	6
27	*D. tenuifolius*	0.1	48	7
22, 23	none	0.15-2.51, 1.33	344-720, 532	5-31, 18
24, 25	*D. tenuifolius*	0.39-0.74, 0.57	860-970, 915	20-27, 23.5
26	*D. tenuifolius*	1.23	830	11

Table 3.5 cont: Results of soil analyses for each collection site within the Galápagos Islands:
(Note: if more than one value is given, the first two numbers are the range and the second, followed by a comma, is the mean)

Soil sample #:	**Spp. present**	**Carb (meq)**	**Cl (meq)**	**Na adsorption ratio**
1,2,3,4	*D. tenuifolius*	3.4-27.8, 16.05	8.4-61.1, 30.93	1.31-8.45, 5.19
6	*D. tenuifolius*	0.9	0.8	0.57
5, 9	*D. tenuifolius*	2.4-4.9, 3.65	3.5-9.8, 6.65	1.64-3.08, 2.36
10	*D. lancifolius* ssp. *glandulosus*	4.3	4.4	2.24
7, 8	*D. lancifolius* ssp. *glandulosus*	3.2-8.7, 6.0	5.9-17.9, 11.9 1	0.77-3.04, 2.4
16	none	0.7	2.2	4.48
14	*D. lancifolius* ssp. *glandulosus* & *D. tenuifolius*	4.1	2.5	2.77
18	*D. lancifolius*, ssp. *glabriusculus*	0.2	1.7	1.32
19	*D. lancifolius* ssp. *glabriusculus*, *D. tenuifolius*, *D. alternifolius*	0.2	0.9	0.42
17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius* only	0.2	0.2	1.46
28, 29	*D. lancifolius*, ssp. *glabriusculus* & *D. alternifolius* only	0.4-0.6, 0.5	1.3-1.6, 1.45	0.71-.83, 0.77
12, 13	*D. lancifolius* ssp. *glandulosus*	0.3-1.9, 1.1	0.3-0.6, 0.45	0.42-1.32, 0.87
11	*D. lancifolius* ssp. *glandulosus*	1.2	19.8	2.38
21	*D. tenuifolius* ssp. *santacruzianus*	0.2	0.5	1.39
20	*D. tenuifolius*	0.3	0.7	0.98
27	*D. tenuifolius*	0.5	1	0.6
22, 23	none	0.7-3.1, 1.9	0.6-1.3, 0.95	1.18-1.22, 1.2
24, 25	*D. tenuifolius*	2.7-4.2, 3.45	0.6-3.2 3.63	0.56-0.61, 0.59
26	*D. tenuifolius*	2.6	2.5	7.1

Table 3.5 cont: Results of soil analyses for each collection site within the Galápagos Islands:
(Note: if more than one value is given, the first two numbers are the range and the second, followed by a comma, is the mean)

Soil sample #:	**Spp. Present**	**Na exchangeable %**	**NO_4-N, saturation extract (ppm)**	**NO_4-N dry soil estimate (ppm)**
1,2,3,4	*D. tenuifolius*	.7-10.1, 5.88	30.0-62.0, 43.25	47-117, 70
6	*D. tenuifolius*	0.1	18	9
5, 9	*D. tenuifolius*	1.2-3.2, 2.2	39.0-156.0, 97.5	28-147, 87.5
10	*D. lancifolius* ssp. *glandulosus*	2	9	3
7, 8	*D. lancifolius* ssp. *glandulosus*	1.4-3.1, 2.25	4.0-7.1, 5.55	2-36, 19
16	none	5.1	2	1
14	*D. lancifolius* ssp. *glandulosus* & *D. tenuifolius*	2.8	47	14
18	*D. lancifolius* ssp. *glabriusculus*	0.7	39	43
19	*D. lancifolius* ssp. *glabriusculus*, *D. tenuifolius*, *D. alternifolius*	0.1	102	111
17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius* only	9	3	3
28, 29	*D. lancifolius*, ssp. *glabriusculus* & *D. alternifolius* only	0.1-0.1, 0.1	76-153, 114.5	50-104, 77
12, 13	*D. lancifolius* ssp. *glandulosus*	0.1-0.7, 0.4	81-497, 289	27-249, 138
11	*D. lancifolius* ssp. *glandulosus*	2.2	26	8
21	*D. tenuifolius* ssp. *santacruzianus*	0.8	44	40
20	*D. tenuifolius*	0.2	195	201
27	*D. tenuifolius*	0.1	2	1
22, 23	none	0.5-0.5, 0.5	3-46, 24.5	1-30, 15.5
24, 25	*D. tenuifolius*	0.1-0.1, 0.1	16-20, 18	15-22, 18.5
26	*D. tenuifolius*	0.1	144	219

Table 3.5 cont: Results of soil analyses for each collection site within the Galápagos Islands:
(Note: if more than one value is given, the first two numbers are the range and the second, followed by a comma, is the mean)

Soil sample #:	Spp. present	Boron (ppm)	Zinc (ppm)
1,2,3,4	*D. tenuifolius*	0.89-1.0, 0.95	9.6-67.0, 45.4
6	*D. tenuifolius*	0.3	1.6
5, 9	*D. tenuifolius*	0.45-0.82, 0.64	6.4-10.8, 8.6
10	*D. lancifolius* ssp. *glandulosus*	1.41	2.4
7, 8	*D. lancifolius* ssp. *glandulosus*	0.27-0.48, 0.38	0.9-1.4, 1.15
16	none	0.24	0.4
14	*D. lancifolius* ssp. *glandulosus* & *D. tenuifolius*	0.48	2.4
18	*D. lancifolius* ssp. *glabriusculus* only	0.24	2.4
19	*D. lancifolius* ssp. *glabriusculus, D. tenuifolius, D. alternifolius*	0.22	10.8
17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius*	0.27	2.2
28, 29	*D. lancifolius*, ssp. *glabriusculus* & *D. alternifolius*	0.2-0.2, 0.2	1.0-1.4, 1.2
12, 13	*D. lancifolius* ssp. *glandulosus*	0.27-0.3, 0.29	1.2-2.6, 1.9
11	*D. lancifolius* ssp. *glandulosus*	0.3	1.8
21	*D. tenuifolius* ssp. *santacruzianus*	0.13	2.4
20	*D. tenuifolius*	0.22	2.2
27	*D. tenuifolius*	1	0.6
22, 23	none	0.22-0.22, 0.22	1.0-2.7, 1.35
24, 25	*D. tenuifolius*	0.2-0.22, 0.21	9-50, 29.5
26	*D. tenuifolius*	0.3	53

Table 3.5 cont: Results of soil analyses for each collection site within the Galápagos Islands:

Soil #:	Spp. present	Mn (ppm)	Fe (ppm)	Cu (ppm)
1,2,3,4	*D. tenuifolius*	42.0-72.0, 53.0	12.0-70.0, 17.5	2.0-3.8, 2.95
6	*D. tenuifolius*	2.8	56	1.2
5, 9	*D. tenuifolius*	4.0-5.4, 4.7	36.0-37.0, 36.5	.8-2.0, 1.4
10	*D. lancifolius glandulosus*	3.1	27.8	2
7, 8	*D. lancifolius* ssp. *glandulosus*	.8-3.8, 2.3	35.6-43.0, 39.3	1.2-1.2, 1.2
16	none	1.5	16.2	0.4
14	*D. lancifolius* ssp. *glandulosus* & *D. tenuifolius*	2.5	20	0.9
18	*D. lancifolius* ssp. *glabriusculus*	12.8	184	7.8
19	*D. lancifolius* ssp. *glabriusculus*, *D. tenuifolius*, *D. alternifolius*	2.8	85	6
17	*D. lancifolius* ssp. *glabriusculus* & *D. tenuifolius*	5	342	1.9
28, 29	*D. lancifolius*, ssp. *glabriusculus* & *D. alternifolius*	2.2-2.7, 2.45	57-60, 58.5	1.1-1.2, 1.15
12, 13	*D. lancifolius* ssp. *glandulosus*	3.4-3.6, 3.5	23-37.6, 30.3	1.2-1.5, 1.35
11	*D. lancifolius* ssp. *glandulosus*	4.8	86	1.8
21	*D. tenuifolius* ssp. *santacruzianus*	12	20	0.8
20 Cont:	*D. tenuifolius*	6.4	15.8	1
27	*D. tenuifolius*	0.2	43	0.5
22, 23	none	1.2-4.1, 2.65	24.8-6.1, 42.9	1.0-2.6, 1.8
24, 25	*D. tenuifolius*	7.2-8.4, 7.8	78-78, 78	1.8-2.2, 2.0
26	*D. tenuifolius*	10.7	103	2.4

Table 3.6: Significant results of soil analyses (Mann-Whitney U test, p< .05):
(note: the number after each taxon represents the number of locations where each species was found growing out of all of the locations sampled)

Taxa	**Fe**	**Na (ad)**	**Na (ex)**
D. ten. (12/29)			
D. ten. ssp. s.c.(1/29)			
D. ten. var. tomen. (3/29)	Z= -2.08, p=.038	Z= -1.86, p=.063	
D. lanc. ssp. glab. (5/29)	Z= -2.77, p=.006		
D. lanc. ssp. gland. (7/29)			
D. altern. (3/29)			Z= -2.08, p=.037
None (3/29)			

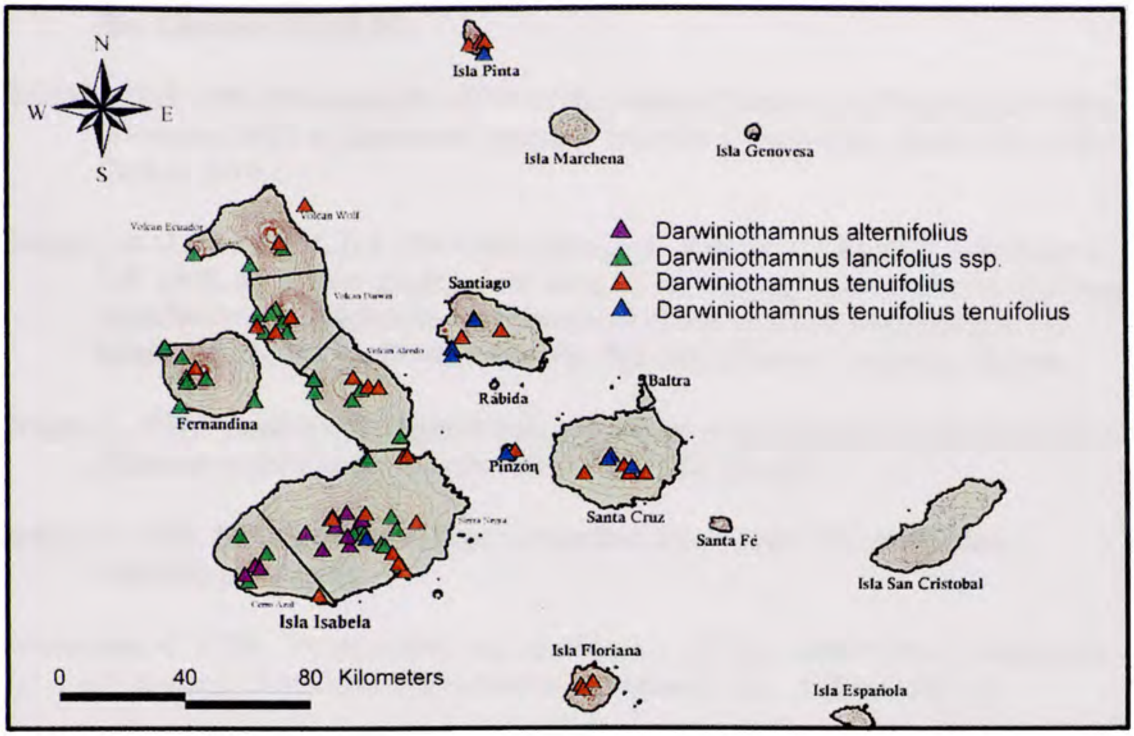
Taxa	**NO4-N**	**Carb**	**Ca**
D. ten. (12/29)			
D. ten. ssp. s.c (1/29)			
D. ten var. tomen. (3/29)			
D. lanc. ssp. glab. (5/29)		Z= -2.86, p=.004	
D. lanc. ssp. gland. (7/29)			
D. altern. (3/29)	Z= -1.93, p=.037		
None (3/29)	Z= -1.94, p=.053		Z=-1.93, p=.053

Taxa	**Organic matter**	**Saturation %**	**Ca+Mg**
D. ten. (12/29)		Z= -1.99, p=.046	
D. ten. ssp. s.c (1/29)			
D. ten var. tomen. (3/29)	Z= -1.86, p=.063		
D. lanc. ssp. glab. (5/29)			
D. lanc. ssp. gland. (7/29)	Z= -2.905, p=.004	Z=-3.16, p=.002	
D. altern. (3/29)			
None (3/29)	Z= -2.00, p=.045		Z=-2.01 p=.045

Taxa	**pH**	**Zn**
D. ten. (12/29)		
D. ten. ssp. s.c (1/29)		
D. ten var. tomen. (3/29)		Z= -1.50, p=.037
D. lanc. ssp. glab. (5/29)	Z= -3.12, p=.002	
D. lanc. ssp. gland. (7/29)		Z= -1.84, p=,066
D. altern. (3/29)	Z= -2.04, p=.037	
None (3/29)		

Where: D. ten. = *Darwiniothamnus tenuifolius*
D. ten. ssp. s.c. = *D. tenuifolius* ssp. *santacruzianus*
D. ten. var. tomen. = *D. tenuifolius* var. *tomentosus*
D. lanc. ssp. glab = *D. lancifolius* ssp. *glabriusculus*
D. lanc. ssp. gland. = *D. lancifolius* ssp. *glandulosus*
D. altern. = *D. alternifolius*
None = no species of *Darwiniothamnus* present at soil sample site

Figure 3.1: Distribution of *Darwiniothamnus* throughout the Galápagos Islands:
(courtesy of the CDRS plant science department GIS archives)



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Chapter IV: ORIGIN AND PHYLOGENETICS OF *DARWINIOTHAMNUS*

1. Introduction:

Darwiniothamnus (Asteraceae: Astereae), as it is currently recognized, is one of seven endemic plant genera in the Galápagos Islands that has an unknown origin, although previous hypotheses have been made based upon various morphological analyses (Harling, 1962; Nesom, unpublished). Harling (1962) suggested that *Darwiniothamnus'* closest putative relatives may occur off the central coast of Chile, citing *Erigeron berterianus* DC. and *E. litoralis* (Phil.) Skottsberg as examples. He also mentioned, however, that the closest relative of *Darwiniothamnus* might instead be found in the Juan Fernández Islands, citing *Erigeron fernandezianus* (Colla), one of six species of *Erigeron* endemic to the Juan Fernandez Islands, as the primary example (Harling, 1962; Valdebenito *et al.*, 1992). These two hypotheses were based primarily upon Harling's (1962) morphological research on the collections of Skottsberg and Sparre deposited in S; where he stated that the species mentioned above might be related to *Darwiniothamnus* as they are all endemic and possess "a more or less suffrutescent habit" (Harling, 1962 and Skottsberg, 1922).

At the time of Harling's publication the best known of the species mentioned above was *E. fernandezianus* and Harling noticed that this species resembled *Darwiniothamnus* more than any other species of *Erigeron*. In specific, Harling stated that the two taxa were strikingly similar in that they both possessed inflorescences with pistillate flowers that were much more numerous than the hermaphroditic ones. However, he also reported several morphological differences between the two species that kept him from making any firm conclusions as to the definite origin of *Darwiniothamnus*. For example, the involucre of *E. fernandezianus* is hemispheric or broadly campanulate; its phyllaries are unequal in length, in imbricate series of 2-3; and the achenes of *E. fernandezianus* are homomorphic, rather than flat with an incrassate margin (Harling, 1962; Solbrig *et al.*, 1969; cf. Skottsberg, 1922).

Harling went on to mention one additional potential biogeographical connection between *Darwiniothamnus* and two rather shrubby species of *Erigeron* (*E. socorrensis* and *E. crenatus*) from the Revillagigedo Islands, off the Pacific coast of Mexico (Harling, 1962; Johnston, 1931). However, he was uncertain of this connection as well, as although he recognized that Johnston (1931) had grouped these Revillagigedo species within the section *Coenotus*, he believed that this was not the same section to which the species of *Darwiniothamnus* and *E. fernandezianus* belonged.

A more recent study by Nesom (1989) has suggested that *Darwiniothamnus* may be more closely related to members of the primarily Mexican and Caribbean group *Erigeron* sect. *Cincinnactis,* due to their similarity in habit and form. Indeed, members of this group and the species of *Darwiniothamnus* are similar in that they all have leaves with toothed margins, rays that are filiform and numerous, achenes that are short-oblong and very small, and all are perennials with short, somewhat woody rhizomes (Nesom, 1989).

Nesom's (1989) hypothesis seems reasonable as the tendency for the evolutionary development of a woody habit in insular plants is well documented and can been observed in all of the examples listed above and in the previous chapter. In addition, Cronquist (1947) has stated that although the genus *Erigeron* is primarily herbaceous in its earliest lineages, it almost always becomes non-herbaceous in its more recently derived species. Carlquist (1974) has also provided examples of the Asteraceae and many other plant families in which genera with herbaceous mainland species have developed woody, insular species. Among those in the Asteraceae are insular species of *Argyanthemum*, *Bidens*, *Centaurea*, *Daubautia*, *Dendroseris*, *Pertyle*, *Pulicaria*, *Remya*, *Robinsonia*, *Senecio*, *Sonchus* and *Stephanodoria* (e.g. see Nesom, 1989; Carr, 1998; Sang, *et al.*, 1994; Francisco-Ortega *et al.*, 2001a,b; Crawford, *et al.*, 1992; Crawford and Stuessy, 1987; Lowe and Abbott, 1996; Sanders *et al.*, 1987). As in *Darwiniothamnus*, most of these species are rosette trees or rosette shrubs with long, mostly unbranched stems and leaves clustered near the stem tips.

Besides those of the Galápagos Islands, suffrutescent species of *Erigeron* with similar habits also have developed on the Revillagigedo Islands (*E. socorrensis* and *E. crenatus*), Caribbean (e.g. *E. bellidiastroides*, *E. paucilobus*, *E. quercifolius*, and *E. karvinskianus*), Canary (e.g. *E. cabrerae* Ditr.) and Juan Fernandez Islands (e.g. *E. fernandezianus*, *E. ingae*, and *E. luteoviridis*); suggesting that a connection based on the morphological similarity of *Darwiniothamnus* to another woody species from any one of these three areas could be possible (Johnston, 1931; Solbrig, 1962; Correl and Correll, 1982; Adams, 1972; and Alain, 1962).

2. A brief description of the Astereae:

The tribe Astereae is one of the largest tribes within the Asteraceae, both with respect to number of genera and number of species, and comes only second in number of species to the Senecioneae (Bremer, 1994). Most members of the Astereae are annual or perennial herbs or shrubs, however four genera including small to rarely tall trees are known to exist in South America (*Baccharis*), Australia-New Zealand (*Olearia*), and the island of St. Helena (*Commidendron* and *Melanodendron*). The Astereae are worldwide in distribution, but primarily concentrated in southwestern North America, South America along the Andes, South Africa, Australia and New Zealand (Bremer, 1994). Grau (1977) has further stated that most of the genera within the Astereae are distributed in and around land close to the Pacific and Indian oceans.

Grau (1977) performed one of the most detailed studies on members of the Astereae and found four characters by which members of the tribe could be recognized: the style (with special branch appendages), the anthers (which are typically obtuse at the base and without tails and spurs), the pollen (which is typically helianthoid) and the anatomy of the fruit (which have a testa epidermis with thick inner and radial cell walls, and thin outer walls). Both Bremer (1987) and Jones (1976) have also stated that the acute shape of the style branch appendages, which cross over during late anthesis, is also a good synapomorphy for the tribe. A limited amount of other anatomical characters have been listed by Baagoe (1978), Herz (1977) and Seaman (1982) that have been used to characterize members of the Astereae, however Bremer (1994) has stated that, in general, there are apparently few reliable synapomorphies for the tribe. In lieu of this fact, however, there are as of yet no indications that the tribe should be nonmonophyletic. Almost all of the genera hold together morphologically, and their tribal position is not questioned except in a few cases (Bremer, 1994).

More recently, various cpDNA (chloroplast) and nrDNA (nuclear ribosomal) studies of primarily North American members of the tribe Astereae have helped to clarify the phylogenetics of the Astereae (e.g. by Nesom (1989), Suh and Simpson (1990), Morgan and Simpson (1992), and Noyes (2000)). Morgan and Simpson (1992), in particular, studied 55 taxa of the Astereae and their work was extremely influential in helping to clarify relationships within the subtribe Solidagininae. Zhang and Bremer (1993) also performed a detailed cladistic analysis using 26 different morphological characters on 24 different genera from within the Grangeinae, Solidagininae and Asterinae subtribes. Their work helped to elucidate the phylogenetic relationships among these 24 genera and established the sister relationship between *Erigeron* and *Vittadinia* within the Asterinae.

3. Relevant historical research on the genus *Erigeron*:

The group of 24 genera that comprise the *Conyza-Erigeron* complex is one that is primarily united together based upon complex geographical distribution patterns and agamospermy (Noyes, 2000). This group comprises a major part of the tribe Astereae, and as stated by Bremer (1994) the group shows a "gradual trend from *Aster* with uniseriate, long ray florets through *Erigeron* with multiseriate rays to *Conyza* with multiseriate, more or less eradiate to filiform-tubular outer female florets, having been postulated by several authors (e.g. Cronquist, 1974)." The *Erigeron/Conyza* complex *sensu lato* includes the highly specialized genera *Archibaccharis*, *Baccharis*, and *Heterothalamus*, which collectively constitute the subtribe Baccharidinae; and *Brachyactis, Chamaegeron, Conyza, Conysanthus, Darwiniothamnus, Erigeron, Heteroplexis, Hysterionica, Lachnophyllum, Laqennecia, Microglossa, Nidorella, Oreostemma, Oritrophium, Psiadia, Psiadiella, Psychrogeton, Rochonia, Sarcanthemum, Sommerfeltia* and *Trimorpha* (Bremer, 1994). Zhang and Bremer (1993) have stated that multiseriate female florets, whether radiate (e.g. *Erigeron*) or minutely radiate to tubular (as in *Conyza*, *Baccharis*, and others), should be considered a potential synapomorphy for the entire group.

The genus *Erigeron sensu stricto* contains approximately 400 species, and a molecular phylogenetic study conducted by Noyes (2000) suggested a North American origin for Erigeron. This study also showed that *Aphanostephus, Conyza*, and three small genera to South America (*Apropyros, Hysteronica* and *Neja*) are all nested within *Erigeron*. Currently 20 sections have been recognized within *Erigeron* (Nesom 1989, 1990, 1994) which are all predominantly North American except for one which is from Brazil (sect. *Leptostelma* (D. Don) Benth and Hook). The most extensive taxonomic monographs of *Erigeron* have been completed for the species from North America by Cronquist (1947) and Nesom (1989); South American by Solbrig (1962); Europe by Halliday (1976); and Eurasia by Botschantzev (1959).

A "typical" species of *Erigeron* is one which Noyes (2000) states grows in a montane habitat and is a "monocephalous 'caudex'-branched herbaceous perennial with narrow white to pinkish rays, yellow disk, and oblanceolate leaves." This is not standard for all species of the genus, however, as considerable variation is known to occur in certain species. In specific, variation within *Erigeron* can often be seen in the following forms: members of the genus can be primarily herbaceous annuals or somewhat woody perennials; the ray color and ray to disk floret ratio may vary (e.g. from white to purple, pink or yellow); the amount of leaf dissection can vary (e.g. from highly dissected as in *E. jamaicensis*, to not dissected at all as in the currently recognized *D. lancifolius*); the breeding system of certain species can be outcrossing to selfing or agamospermus; and finally minute and/or technical floral variation also exists (Nesom, 1989). It should also be noted that while this variation may make it easier to identify a certain number of species, most members of this genus are often delimited using rather plastic microcharacters of achene type, and leaf, stem and/or involucre shape. These subtle differences often make it difficult to identify many species of *Erigeron* while in the field or in the herbarium. Indeed, as Noyes (2000) has stated: "there are surprisingly few hypotheses on either relationships within *Erigeron* or between *Erigeron* and related genera."

The systematics and evolution of *Erigeron* are considered to be closely linked with the morphologically similar genus *Conyza* (Noyes, 2000). *Conyza* comprises approximately 40 species, which span across both North and South America. The closest relatives to *Conyza* appear to be a number of widespread paleotropical (e.g. *Nidorella* and *Microglossa*; Wild, 1969) and Madagascan-Mascarene genera (e.g. *Psiadia*, *Psiadiella*, *Rochonia*, and *Sarcanthemum*; Bremer, 1994), and recent work by Nesom (1990b) and Noyes and Riesberg (1999) has shown that approximately 40 African species that were once traditionally included within *Conyza* are in fact more closely related to other African genera such as *Nidorella*.

4. The value of using ITS sequences in phylogentic studies:

The use of the ITS region for systematic botany was first described in Baldwin's 1992 paper on the phylogenetic utility of the ITS region in Hawaiian plants, specifically those within the Asteraceae family. Baldwin (1992) was one of the first to point out the shortcomings of studies based solely on cpDNA data and stated that "mounting evidence demonstrates that species-lineage reconstructions using the cytoplasmically inherited cpDNA may be prone to significant error from hybridization and introgression events or lineage sorting." Nuclear DNA is not without its shortcomings, however, and when seeking potentially useful nrDNA regions for phylogenetic use one should make sure the region is evolutionarily conservative, phylogenetically interpretable, easily examined in the laboratory, and sufficiently large to provide enough informative characters for analysis (Soltis *et al.* 1998; Baldwin, 1992).

The ITS region fits most of these characteristics, as its gene family (the 18-26S nrDNA region) often appears to undergo rapid concerted evolution making the many copies homogeneous and useful for phylogenetic reconstruction (Sanderson and Doyle, 1992). Noyes (2000) has also pointed out that because nrDNA is present in numerous copies, it is relatively easy to amplify from dried herbarium specimens of *Erigeron* and related genera. In addition, the results of Baldwin's study showed no ITS length variants or major sequence variants in any of the DNA he examined, which made the comparison and alignment of his sequences much easier. He did mention, however, that stabilizing selection on the ITS region has not been altogether sufficient to prevent broad-scale evolutionary diversity in ITS secondary structures, as can be seen when one tries to align two ITS sequences from different plant families. This therefore suggests a lack of long-term evolutionary constraint on much of the ITS region.

Since the time of Baldwin's initial study these spacers have been widely used to study members of the Asteraceae family and are especially useful at the infrageneric level (e.g. Baldwin *et al.*, 1995, Kornkven *et al.*, 1998, Noyes and Rieseberg, 1999 Torrell, *et al.*, 1999, and Clevinger and Panero, 2000). Indeed, although the ITS region has been especially useful for sorting out the phylogenetics of organisms at the species and genus level, it is rarely used to detect within-species variation (Wem-Hsiung Li, 1997). In addition to the utility of the ITS region with members of the Asteraceae, several authors have used this spacer region to find the origin of genera such as *Saintpaulia* (Gesneraiaceae: Moller, M. and Cronk, Q, 1997) and *Sanicula* (Apiaceae: Vargas, *et al.*, 1998) and to sort out the phylogenetics of the Apiaceae subfamily, the Apioideae (Downie, S. and Katz-Downie, D., 1996).

In relevance to this study, this region has also been successfully used to study the phylogenetics of various island endemic taxa. Downie *et al.* (2000) examined the evolutionary relationships among representatives of Old World Apiaceae, including several narrowly distributed endemic species. Francisco-Ortega *et al.* (2001) also used the ITS region to study the origin and evolution of the ten endemic Macaronesian members of the tribe Inuleae (Asteraceae), including three endemic genera *Allagopappus*, *Schizogyne*, and *Vierea*. This region has also been used successfully to establish phylogenetic relationships within *Erigeron* (Noyes, 2000) and between 55 genera of the tribe Astereae (Noyes and Rieseberg, 1999).

5. Introduction into the phylogenetics of *Darwiniothamnus*:

i. Objectives of this study

As previously mentioned, *Darwiniothamnus,* as currently defined, comprises three species of suffrutescent (*D. alternifolius*) to woody (*D. tenuifolius* and *D. lancifolius*) perennials. Ranging from coastal beach strands to mesic or humid scrub and forestlands, through lava and scoria fields and up to high elevation fern and sedge zones, it exists on seven different islands within the archipelago. Morphologically, these taxa are considered to be highly divergent from their continental relatives and have been suggested to be most closely related to woody Chilean members of the genus *Erigeron*

(Asteraceae: Astereae) (Harling, 1962). However, a rigorous phylogenetic study of *Darwiniothamnus* is needed in order to confirm or disprove its monophyly and to clarify the existing relationships between this genus and its putative South American relatives.

ii. Materials and Methods

a. Sampling scheme:

Any rigorous, non-circular study to trace the origin of island endemics must be based on a phylogeny derived from all available data. In order to test the origin of the genus currently recognized as *Darwiniothamnus,* I developed a molecular phylogeny based on the ITS region of the nrDNA gene. This region was chosen for this particular study because it has already been successfully used to establish phylogenetic relationships within *Erigeron* (Noyes, 2000) and between 55 genera of the tribe Astereae (Noyes and Rieseberg, 1999). Several of the 77 taxa included in Noyes' (2000) study (representing 20 different sections of *Erigeron* and four additional genera from the *Erigeron-Conyza* group) have been submitted to the GenBank database; and 28 of these sequences, representing an even sample of the six total clades produced in Noyes' (2000) phylogeny, were exported for use in this project.

In addition, in order to help trace the origin of *Darwiniothamnus* I also sequenced all the putative relatives listed in Harling's (1962) paper and 16 additional taxa from previously unsampled areas, including: Ecuador, the island of Socorro, Mexico, the Caribbean and Central America (see Table 4.1 for voucher information on all taxa included in this study). It should also be mentioned that leaf samples of all taxa sequenced in this study, save the ones collected by the author, were either sent from or collected by our colleagues in Chile, Argentina, Uruguay, Cuba, the Dominican Republic, Ecuador, Mexico, the United States, the Revillagigedo Islands and Puerto Rico. Additional material was made available for study from herbarium specimens on loan from the following herbaria: FTG, HPPR, JBSD, S, GCD, HUMO, SGO, NY, AAU, ARIZ, C, CDS, CONC, GH, HUH, MO, Q, QCA, UC, and US.

Material of *Darwiniothamnus* included in this study was collected from six different islands within the Galápagos archipelago by the author and sequenced upon return to FTG/FIU. A few additional taxa were amplified or sequenced but not included in the phylogenetic analyses as their sequences were not clean enough to warrant their inclusion into my existing data matrix. These taxa, in no particular order are: *Sommerfeltia spinulosa, Neja filiformis, Erigeron procumbens, E. fuertesii, E. vegaensis, E. subalpinus* and *E. othonaefolius.*

b. Outgroup selection:

Species chosen for the outgroup in this study are *Oritrophium hieracioides, Pteronia incana, Chiliotrichum rosmarinifolium, Nardophyllum bryoides* and *N. obtusifolium.* The first two species of this group were chosen based upon Noyes and Rieseberg's (1999) paper on the origin of the tribe Astereae. Both *O. hieracioides* and *P. incana* are of the subtribe Hinterhuberinae and were part of the basal group in Noyes and Reiseberg's (1999) paper, separated from all other Astereae included in their phylogeny by bootstrap values of 76-96%.

The other two genera included in my outgroup, *Chiliotrichum* and *Nardophyllum,* are restricted to South America, contain very few species and are nested within the tribe Astereae. The three species from these two genera included in my study (*Chiliotrichum rosmarinifolium, Nardophyllum bryoides* and *N. obtusifolium)* were initially added as members of my ingroup; however, in all of the prelimiary phylogenetic analyses performed, each came out included within the outgroup so I chose to leave them there as additional taxa were added to my phylogeny.

c. Molecular methodology:

All leaf material used in this study came from one of two sources: 1.) picked fresh and stored in silica gel, or 2.) taken from dried leaf material from herbarium samples. A list of the voucher specimens and locality information can be found in Table 4.1, along with the accession numbers for the sequences imported from GenBank for use in my phylogeny.

DNA was extracted using the following protocols, depending on whether freshly dried or dried herbarium leaf material was used: freshly dried leaf material stored in silica gel was first frozen in liquid nitrogen and then ground to a fine powder, whereas leaf fragments taken from herbarium specimens were ground dry using fine white sand. CTAB (hexadecyltrimethylammonium bromide) was occasionally added to this grinding process if it proved difficult to extract DNA from a pure, frozen or sand-induced grind. For the most part, DNeasy Plant Mini Kit (Qiagen, Inc., Valencia, CA) columns were used for DNA extractions; however, if the herbarium specimens used to extract DNA in this project were over 25 years old, better extractions resulted when using the 2X CTAB protocols of Doyle and Doyle (1987).

Prior to amplification by the polymerase chain reaction (PCR) the DNA samples were further purified by the Geneclean procedure (Bio. 101, Vista, CA), a process that entails binding DNA to tiny silica beads, washing with an ethanol/salt solution, and eluting the purified DNA in TE. The entire ITS1-5.8S-ITS2 region of the nuclear ribosomal DNA was then amplified using the P1A and P4 ITS primers and following the PCR protocols of Francisco-Ortegta et al (1999) on a PTC-200 thermal cycler (MJ Research, Watertown, MA). It should be noted that in a few cases the initial amplification of certain taxa was problematic, and ITS 1 and ITS 2 had to be amplified separately using the primers described in the next paragraph. Upon successful amplification, the PCR product was then purified using a QIAquick PCR purification kit (Qiagen Inc., Valencia, CA) according to the instructions of the manufacturer, or following the Geneclean procedures described above. Total nr DNA (18S-26S) was then quantified by fluorometry.

After purification, the PCR product was sequenced using the ABI Prism BigDye™, Terminator Cycle Sequencing Ready Reaction Kit (Perkin Elmer, Applied Biosystems, Foster City, CA) with AmpliTaq DNA polymerase. Sequencing was performed in both the forward and reverse directions using the P1A (GGA AGG AGA AGT CGT AAC AAG G) and P2 (CTC GAT GGA ACA CGG GAT TCT GC) primers for ITS 1, and the P3 (GCA TCG ATG AAG AAC GCA GC) and P4 (TCC TCC GCT TAT TGA TAT GC) primers for ITS 2 (Integrated DNA Tech: White et al., 1990; Downie and Katz-Downie, 1996). Reactions were carried out in 10 μl volumes, with the Terminator Mix diluted 50:50 with Aplitaq FS buffer.

Cycle sequencing conditions consisted of an initial denaturation at 96° for 2 minutes, followed by 35 cycles of 96° denaturation for 10 seconds, 55° primer annealing for 5 seconds, and 60° extension for 4 minutes. The product of this sequencing reaction was then precipitated with EtOH/$NaNH_4Oac$ (6:1), the pellet dried under vacuum, resuspended in formamaide/blue dextran loading dye (5:1) and loaded on an ABI 377 automated sequencer.

d. Phylogenetic Analyses:

DNA fragments were assembled using Sequencher version 3.0 (Gene Codes Corporation, Ann Arbor, MI) or Seqapp (Gilbert, 1993), and aligned using Clustal X (Thompson *et al.*, 1997) with minor manual adjustments. Default Clustal X parameters were used for gap opening costs (10.00) and gap extension costs (0.05). All nucleotide characters were unordered, with equal weight. Fifty-three gaps were coded in MacClade version 4.03 (Maddison & Maddison) as binary characters, A or C, according to their presence or absence (Simmons and Ochoterena's, 2000). Phylogenetic reconstruction was conducted using maximum parsimony methods as implemented in PAUP* version 4.0 (Swofford, 1990), following the perameters described below.

A heuristic search was performed on the 53 sequences using the following criteria: maxtrees 20,000; 1,000 random taxon addition replicates; tree bisection and reconstruction (TBR) branch swapping; no more than 10 trees saved for each repetition. TBR branch swapping was performed on all of the trees retained in memory from the first search. The Consistency Index (CI) (Kluge and Farris, 1969) and Retention Index (RI) (Farris, 1989) were also computed for each analysis.

Bootstrap support values were calculated by conducting 100 bootstrap replicates with the following criteria: maxtrees 20,000; 1,000 random taxon addition replicates; tree bisection and reconstruction (TBR) branch swapping; no more than 10 trees saved for each repetition. TBR branch swapping was performed on all of the trees retained in memory from the first search.

Constraint trees with all the species of *Darwiniothamnus* forming a monophyletic group were also executed in order to test the hypothesis that all the species of this genus form a monophyletic assemblage. Tree scores of the constraint trees were compared to those of unconstrained trees and the results are confered in the discussion section below.

Finally, nine areas of endemism were also defined for the purpose of a biogeographical study. These areas include the following geographical locations and the numbers in parentheses indicate the number of taxa included in my phylogeny that occur in each area: SE USA (5); SW USA (9); Central/Northern USA (12); The Caribbean basin, including Mexico (19); Central America (2); West (Pacific) South America (7); East (Atlantic) South America (2); The Galápagos Islands (6); South Africa and Asia (2). It should be noted that some species' ranges (e.g. *Erigeron scaberrimus, E. quercifolius, E. tenuis, Aphanosstephus skirrhobasis, A. ramosissimus, Hetertheca villosa, Chrysopsis gossypina, Rigiopappus leptocladus, Aster amellus* and *Chiliotrichum rosmarinifolium*) extend into more than one geographical range, and were thus coded as multistate characters.

This biogeographic analysis was performed in order to identify the ancestral areas of *Darwiniothamnus.* In specific, after the 10 separate areas of endemism (listed above) were defined, they were coded as unordered characters in MacClade version 4.03 (Maddison & Maddison) and the character state changes were traced on one of the most parsimonious trees imported from Paup*, using the parsimony methods implemented in MacClade.

iii. Results

Unweighted parsimony analyses yielded 96 most parsimonious trees, each 778 steps long (c.i. = 0.486, r.i. = 0.712, and r.c = 0.338), from the 4,181,138 rearrangements performed in the final heuristic search. One of these 96 trees can be found in Figure 4.1 and dashed lines show where the branches collapse in a strict consensus tree. Seven groups can be identified in the strict consensus tree, which are easily depicted in the phylogeny of Figure 4.1. Group I is a monophyletic clade and it is composed of 6 species of *Erigeron* from Mexico, the Caribbean Islands and North America. Group II is a clade that contains three independent, monophyletic subclades. The first of these clades includes four shrubby taxa of *Darwiniothamnus* and is sister to *E. bellidiastroides* of the Caribbean. The second clade within Group II is composed of three species also from the Caribbean Islands and one that is from Mexico. The third subclade comprises two species of the genus *Aphanosstephus*, which is from the Southwestern U.S. and Mexico.

Group III contains species from the following three genera: *Erigeron, Darwiniothamnus* and *Conyza*. The two semi-herbaceous members of *Darwiniothamnus* are sister to two species of *Erigeron* from the coast of Chile and are nested within a larger clade comprising of species primarily found in South America. Group IV, comprises two genera (*Erigeron* and one species of *Conyza*) that are distributed only throughout North America and Mexico, and the same is true for Group V. Group VI constitutes a grade of six assemblages and contains species of *Erigeron, Hetertheca, Chrysopsis, Rigiopappus, Aster* and *Kalimeris* from Mexico, North America and South America. Finally, Group VII consists of all the outgroup species which were discussed in the previous section of this paper.

One of the most significant results produced from this phylogeny is the dissolution of the previously held notion that all members of the genus *Darwiniothamnus* constitute a monophyletic group. This is clearly not the case, as the woody shrub-like members of the genus, *D. tenuifolius* and *D. lancifolius*, come out in a completely separate clade from the single semi-herbaceous species, *D. alternifolius*, recently described by Lawesson and Adsersen (1987). Two representatives of both *D. tenuifolius* and *D. lancifolius* were included in this phylogeny and while all four taxa comprise a monophyletic group they are nested within a clade containing some of the Caribbean species of the genus *Erigeron.*

In addition, two representatives of *D. alternifolius* were also included in this phylogeny from the two separate locations where the species is known to exist on the southern tip of Isabela in the Galápagos Islands. Both sequences of this species were resolved within a clade of primarily South American species of *Erigeron,* and the results suggest that *Darwiniothamnus* stems from two separate introductions into the Galápagos Islands.

The formation of the constraint tree in both MacClade and Paup*, which forced all taxa of *Darwiniothamnus* included in this study to be monophyletic, was 799 steps long, or 21 steps longer than the 96 most parsimonious trees found after an unconstrained heuristic search was performed.

Finally, the biogeographic analysis performed in order to identify the ancestral areas also yielded some results relevant to the origin of *Darwiniothamnus* (see Figure 4.2). For example, based on our sampling, it appears that *D. lancifolius* and *D. tenuifolius* have their ancestral area, or location of origin, in the Caribbean basin as evidenced by the pattern-coded areas of endemism on the phylogeny in Figure 4.2. It also appears clear that the second introduction of *Darwiniothamnus* was from South America as *D. alternifolius* clearly stems from this region, again evidenced by the tracing of ancestral areas in Figure 4.2. Both of these findings support the notion that *Darwiniothamnus*, as it is currently recognized, arose from two separate introductions into the Galápagos Islands.

iv. Discussion

Data from the ITS region of nrDNA provided strong support for the inclusion of *Darwiniothamnus* within *Erigeron.* Both groups of the polyphyletic *Darwiniothamnus* were nested well within clades consisting solely of members from the *Erigeron-Conyza* complex. Based on our sampling, *Erigeron bellidiastroides* of Cuba is the sister group (Fig. 4.1) of *Darwiniothamnus tenuifolius* and *D. lancifolius*; whereas *Erigeron luxurians* and *E. fasciculatus* from the central coast of Chile are the sister group of *Darwiniothamnus alternifolius* (Fig. 4.1). Therefore, it appears that *Darwiniothamnus*, as the genus is currently recognized, not only stems from two separate introductions into the Galápagos Islands, but also represents two separate evolutionary lineages whose current taxonomy ought to be reconsidered.

Although the habit of *Darwiniothamnus tenuifolius* and *D. lancifolius* (both ssp. *glandulosus* and *glabriusculus*) appears to be greatly divergent from *Erigeron bellidiastroides* (the former are rather large woody shrubs while the latter is a small herbaceous-suffrutescent perennial), the evolution of a woody habit from an herbaceous one is a common island syndrome that has been discussed by many authors (e.g.

Cronquist, 1970, 1971; Carlquist, 1974; Harling, 1962; Nesom, 1989; Shilling *et al.*, 1994; Whittaker, 1998).

Sanders *et al.* (1987) have mentioned the importance of the environment in dictating ways in which different members within a certain clade can be found to be both very morphologically divergent and genetically similar at the same time. Two prime examples of this idea can be found in the Silversword alliance and the genus *Dendroseris*, from the Hawaiian and Juan Fernandez Islands, respectively. The mainland counterparts of these two groups are both much smaller and less woody, yet genetically rather similar to their island relatives. Carlquist (1974) has also provided several examples from the Asteraceae, and many other plant families, where genera with herbaceous mainland species have developed woody, insular species. Among those in the Asteraceae are insular species of *Bidens, Centaurea, Daubautia, Pertyle, Remya, Robinsonia, Senecio, Sonchus* and *Stephanodoria* (e.g. see Nesom, 1989; Carr, 1998; Sang, *et al.*, 1994; Francisco-Ortega *et al.*, 2001a,b; Crawford, *et al.*, 1992; Crawford and Stuessy, 1987; Lowe and Abbott, 1996; Sanders *et al.*, 1987).

In addition, although the plant sizes of the Galápagos (*D. tenuifolius* and *D. lancifolius*) and Cuban *(E. bellidiastroides*) endemic sister taxa are not the same, several similarities do exist between them. For example, the leaves of both plants are ovate-obovate, puberulent and condensed in either basal (as in *E. bellidiastroides*) or terminal (e.g. *D. tenuifolius* & *D. lancifolius*) whorls. In addition both groups are monocephalous, with filiform pedicels and linear-lancolate bracts making up the capitula.

Several similar connections can also be drawn between the Galápagos and Chilean endemic sister taxa, *D. alternifolius* and *E. luxurians/E. fasciculatus*, respectively. Several authors have noted that *D. alternifolius* (Lawesson and Adsersen, 1987; Nesom, unpublished), does not share all of the characters by which the other members of the genus are defined. For example, the leaves of this species are alternate and not in condensed in terminal whorls, the plant is typically a suffrutescent perennial which does not exceed 1 foot in height, and it often has branching peduncles forming cymiform synflorescences. Many of these characters are also found in *E. luxurians* and *E. fasciculatus* as both of these species are subshrubs, or suffrutescent perennials; both have leaf scars readily present; and both have leaves that are pubescent to very pubescent and crowded in the basal part of the plant but rather scattered at the ends of the branches (as does *D. alternifolius*). *E. luxurians* and *E. fasciculatus* are also polycephalous and generally look more like *D. alternifolius* that the other species of the same genus. Because the two sequences of *D. alternifolius,* (from Cerro Azul and Volcan Sierra Negra, respectively), clustered together in group III far from the rest of the species of *Darwiniothamnus*, I suggest renaming this taxon as *Erigeron alternifolius* comb. nov. (see the section on Nomenclatual Conclusions).

a. A Caribbean origin

When considering the biogeographic connections between *Darwiniothamnus* and its two apparent origins, the notion of a connection between the Caribbean and the Galápagos Islands is not as novel as it might first appear. The first paper to discuss the geographic relationships of the Galápagos flora (Hooker, 1847) mentioned that the flora of the Galápagos could be divided into two distinct elements: "the peculiar or new species being for the most part allied to plants of the cooler parts of America, or the uplands of the tropical latitudes, whilst the non-peculiar are the same as abound chiefly in the hot and damper regions, as the West Indian islands and the shores of the Gulf of Mexico." Porter (1983) has stated that Hooker's "peculiar" element probably corresponded primarily to taxa of Andean origin, while the "non-peculiar" element corresponded to Tropical and Pantropical America.

In addition to Hooker's hypotheses, N. J. Andersson (1857), who generally supported the views of Hooker, stated that a number of species in the Galápagos flora also have pantropical distributions, an element which was not previously emphasized by Hooker. Takhtajan (1988) has also stated in his seminal work on plant biogeography, that the Caribbean Region has floristic ties not only with the coasts of Mexico, Florida, most of Central America and northern South America; but also may be closely allied with Cocos and the Galápagos Islands. Although Takhtajan (1988) did not specifically say how such floristic connections were developed throughout these various areas, it is clear that he understood a connection between the Caribbean and Galápagos was possible.

In addition to the papers mentioned above, Porter (1979) also placed an important emphasis on West Indian relationships and his ideas have transcended into several of the papers discussed below. For example, *Sesuvium edmonstonei*, formerly regarded as a Galápagos endemic, has been found by Eliasson (1996) to occur on the Caribbean coast of both Colombia, Venezuela and their offshore islets. Valdebenito *et al.* (1990) documented an inter-population separation (disjunction) for the plant genus *Peperomia* (Piperaceae), of more than 5,000 km, one of the longest known in flowering plants. They attributed long-distance dispersal by birds as the most likely cause of the wide disjunction. Valdebenito *et al.*'s (1990) paper is of special interest in light of the recent findings of Sato *et al.* (2001). Sato *et al.* (2001) recently discovered that the initial adaptive radiation of the *Tiaris* group, the nearest living relative of Darwin's finches, occurred on the Caribbean islands and then spread to Central and South America. Because all species of *Darwiniothamnus* have a bristle-like pappus and are considered to be transported by wind (as in grasses) and/or by birds (as in the finches), both Valdebenito's (1990) and Sato *et al.*'s (2001) hypotheses seem to provide reasonable vectors for the transportation of the ancestral lineage of *Darwinothamnus* to the Galápagos Islands.

Finally, Grehan (2001) distinguished three principal tracks that connect the Galápagos with the East Pacific, the Caribbean and the Pacific basin. In specific, he stated that the Galápagos Islands lie in a nodal position of three potential tracts (the East-Pacific, the Pacific and the Galápagos-Caribbean tracks), with respect to the biogeographic history of the region. Grehan's (2001) ideas thus support Wiggins (1966) findings which state that there are two major sources of grasses reaching the Galápagos Islands before man began to carry them about: the Mexico-West Indies area and South America. This of course, is the same biogeographical hypothesis that I propose for *Darwiniothamnus*, as it most likely also stemmed from two separate introductions.

b. A South American origin:

In spite of the research discussed above, it should be noted that in general, the flora of the Galápagos Islands has long been thought to originate and have several common elements in mainland of South America; with only a few species (1%) having been formally recognized to be of Mexican and Central American origin (Porter, 1976). Good (1964) delimited what he considered to be the major floristic regions of the world and grouped the Galápagos with the western coast of South America, and said that the floristic affinities of the Galápagos could probably only come from this region. Perry (1984) has stated that virtually all of the endemic species of the Galápagos have their closest relatives in South America except for the bryophytes, where mosses tend to show an aberrant and close correlation with Central America, most likely attributed to dispersal by the trade winds.

In addition, Porter (1983) has mentioned several other authors who support an Andean origin for most Galápagos plants including: Robinson and Greenman (1895); Stewart (1911), Wiggins (1966), and Porter (1976). The first author to document the close relationship of Galápagos plants to Ecuador and Peru, in specific, was Svenson (1935, 1946); he was followed by Harling (1962), who discussed the possibility of a relationship between several Galápagos endemics, including *Darwiniothamnus*, to certain plant species of Chile and the Juan Fernandez Islands. From the results of this thesis, it seems that Harling's hypothesis was at least partially correct as based upon my sampling, the two specimens of *D. alternifolius* included this thesis came out sister to *E. fasciculatus* and *E. luxurians* of Chile, just as Harling had hypothesized.

In closing, Carlquist (1965) interpreted both the paucity of endemic Galápagos plant genera and their close relationships with American mainland groups as evidence for recent origin (Grehan, 2001). This appears to hold true for the origin of *D. alternifolius* as its morphology has remained relatively similar to its sister taxa *E. fasciculatus* and *E. luxurians*. Carlquist (1965) also regarded the Galápagos flora as purely that of an oceanic island; where plant families with good long-distance dispersal ability were the most abundant and groups with poor dispersal ability were absent. This appears to be true, at least in the case of *D. tenuifolius* and *D. lancifolius*, which are sister to Caribbean species of *Erigeron*, appear to have reached to the Galápagos via long-distance dispersal, and then radiated into several new species and subspecies that are now spread throughout seven different islands within the archipelago.

Concluding Remarks to all the chapters:

Below is a concise response to the five research questions that I mentioned at the beginning of this thesis, namely:

1. What is the conservation status of all currently recognized taxa within the genus *Darwiniothamnus*, and do any new conservation measures need to be implemented?
2. Based upon field observations, do any areas contain new morphological variants that warrant in-depth morphological studies?
3. What are the existing biological threats to *Darwiniothamnus* and what can be done to protect these populations in the future?
4. Does the lack or over-abundance of certain essential elements and/or micronutrients prevent *Darwiniothamnus* from colonizing certain areas of the archipelago?
5. Where is the origin of *Darwiniothamnus* and is the genus monophyletic?

In regards to question #1: the current conservation status of *Darwiniothamnus* is not determined easily and appears to depend upon on the island environment in which it the plant is growing. Most taxa of *D. lancifolius* appear to be in good health, especially on the rather untouched island of Fernandina and most populations of *D. lancifolius* appear to be unaffected by the introduction of *I. purchasi*, except for the population on Bahia Urvina. It is my suggestion that biological control methods for the eradication of this insect be implemented immediately at Bahia Urvina in order to prevent the future spread of *I. purchasi* to the virgin coast of Fernandina.

The state of most populations of *D. tenuifolius* appears to be healthy, although a few populations have died back significantly over the past few years due to scale insect infestation on three separate islands (Pinta, Santa Cruz, and Isabela). Again, if put into effect in the near future, biological controls may be able to reverse these effects and ensure a healthy future for this species. The third species of the genus, *D. alternifolius*, is at the greatest risk of extinction and I recommend rapid *ex situ* reproduction and germination studies in order to facilitate the prompt reintroduction of this species to its two native habitats. A thorough collection of seeds should also be made at each site as soon as possible, to protect the genetic variation of this species for future generations. Finally, I also recommend that similar studies be performed on the species of *Darwiniothamnus* that once inhabited Pinzon, so that a reintroduction plan can be implemented for this island as soon as possible.

In regards to question #2: my two-month field research and preliminary herbarium studies suggest that a new subspecies of *D. tenuifolius* may be recognized from Pinta and Santiago; however, a detailed morphological analysis of all specimens collected from these areas will have to be completed before any new subspecies or varieties are documented. There also may be a few of hybrid populations on the island of Isabela that warrant recognition as varieties; however, further population-based studies are needed before these recommendations can be finalized.

In regards to question #3: the greatest biological threats on the existing populations of *Darwiniothamnus* are introduced animal species (such as feral pigs, goats, and cattle) and the lethal scale insect, *I. purchasi*. I therefore recommend that biological control methods for each of these pests be introduced to all of the vulnerable populations of *Darwiniothamnus* as soon as possible. The areas that warrant the most concern are Los Gemellos, on the island of Santa Cruz, the areas surrounding Cartago Bay, Volcan

Alcedo and Bahia Urvina on the island of Isabela, and the area surrounding both trails up to peak of Pinta. I also recommend that fences be put around the existing populations of *D. alternifolius* both on Volcan Sierra Negra and Cerro Azul, in order to protect them from extirpation by feral animals. In addition, because the 1985 fire on Volcán Sierra Negra nearly wiped out the entire population *D. alternifolius* at this location, I would make certain that residents from the town of Puerto Villamil, at the base of Volcán Sierra Negra, are aware of the danger that accidental fires may have on the native flora of the Galápagos.

In response to question #4: the inquiry of why members of *Darwiniothamnus* only grow in certain areas or islands is perhaps the hardest to answer. Because I have seen members of this genus range from humid coastlines, to sun-scorched lava fields, to high elevation savannahs of very low temperatures and ultimately to the inside of craters with sulpher plumes and both hot and freezing winds, I do not believe that climate is a limiting factor. The soil data I collected, although it contains some interesting correlations, does not seem to point to any one conclusive answer either. A trend was evident at one location near Volcan Ecuador, which lacked several of the elements and micronutrients necessary for the successful growth of most plants, and which interestingly was also void of any species of *Darwiniothamnus*.

Finally, my fifth question, which assessed the monophyly of *Darwiniothamnus* and what geographical area appears to be its source of origin, produced perhaps the most surprising results of the thesis. As discussed in Chapter 4, the genus is not monophyletic, but polyphyletic, and stems from two separate introductions into the Galápagos Islands.

The sister taxon to *D. tenuifolius* and *D. lancifolius*, *E. bellidiastroides,* is an endemic from the island of Cuba, further corroborating recent biogeographical hypotheses linking the biota of the Caribbean basin with the Galápagos Islands (e.g. Porter, 1979; Sato *et al.*, 2001; Wiggins, 1966; Eliasson, 1996; Grehan, 2001). The sister taxa to the third species of *Darwiniothamnus*, *D. alternifolius*, were just as Harling (1962) suggested, namely, *E. fasciculatus* and *E. luxurians* of the central coast of Chile. Furthermore, due to the results of this paper, it is the suggestion of the author that *Darwiniothamnus* be regrouped within the paraphyletic *Erigeron-Conyza* complex, until further taxonomical work is done on the group to clarify its subgeneric relationships.

Nomenclatural conclusions:

Erigeron alternifolius (Lawesson & Adsersen) Andrus **comb. nov.**
Basionym: *Darwiniothamnus alternifolius* Lawesson & Adsersen
Notes on the endemic genus *Darwiniothamnus* Harling (Asteraceae, Astereae) from the Galápagos Islands. *Op. Bot.* 92:7-15 (1987).
Type: Lawesson, Adsersen, Nowak, Velasco, Abodrabbo & Tupiza 2452. (holotype QCA, isotypes C, CDS (= *Erigeron alternifolius* (Law.Ads) Andrus))

Darwiniothamnus tenuifolius (Hooker fil.) Harling (1962)!
Erigeron tenuifolius Hooker (1847)
Type: Darwin s. num. (CGE) (probably collected on Floreana)!

D. tenuifolius* ssp. *santacruzianus Harling (1962)!
Type: Harling 5076 (S)!

Darwiniothamnus lancifolius (Hooker fil.) Harling (1962)!
Erigeron lancifolius Hooker (1847)
Type: Darwin s.num. (CGE) (probably collected at Tagus Cove, Volcan Darwin)!
Erigeron tenuifolius ssp. *lancifolius* (Hook. f.) Solbrig (1962)

D. lancifolius* ssp. *glabriusculus (Stewart) Lawesson & Adsersen (1987)!
Erigeron lancifolius var. *glabriusculus* Stewart (1911)
Type: Stewart 724 (GH) from Sierra Negra!
Darwiniothamnus tenuifolius var. *glabriusculus* (Stewart) Cronquist (1970).

D. lancifolius* ssp. *glandulosus Harling (1962)!
Darwiniothamnus tenuifolius var. *glandulosus* (Harling) Cronquist (1970)
Type: Harling 5376 (S) from Volcan Darwin!

Table 4.1: Voucher list for all species used in this study, includes GPS and geographical data. (Note: all species with accession numbers listed as "recently submitted" were sequenced by the author).

Taxon	**Voucher Origin / Collector & coll. #**
1. Aphanosstephus ramosissimus DC	E. Ventura 7924 (MO)
2. Aphanosstephus skirrhobasis DC. Trek.	A. Brant 1974 (MO)
3. Aster amellus L.	A.K. Skvortsov s.n. (MO)
4. Chiliotrichum rosmarinifolium	M. Bonifacino (#191) D. Gutierrez & P. Simon (LPS)
5. Chrysopsis gossypina (Michx.) Ell.	M. Merello 416 (MO)
6. Conyza borariensis (L.) Cronq.	R. D. Noyes 1182 (IND)
7. Conyza canadensis (L.) Cronq.	C. Ochs 248 (MO)
8. *Darwiniothamnus alternifolius* Lawesson & Adsersen	N. Andrus, 16.7/ND (FTG)
9. *Darwiniothamnus alternifolius* Lawesson & Adsersen	N. Andrus, 16.9/ND (FTG)
10. *Darwiniothamnus* tenuifolius (Hook. f.) Harling	A Tye 4/25/00 (CDS)
11. Darwiniothmanus lancefolius ssp. *glandulosus* Harling	N. Andrus, 7.1/3.1 (FTG/CDS)
12. Darwiniothmanus tenuifolius (Hook. f.) Harling	N. Andrus, 5.1/81.1 (FTG/CDS)
13. *Darwiniothamnus* lancefolius *glabriusculus* (Stewart) L & A	N. Andrus, 10.2/67.2 (FTG/CDS)
14. Erigeron arenarioides (D.C. Eaton) Rydb.	J.S. Tuhy 3619 (MO)
15. Erigeron argentatus A. Gray	M. A. Franklin 7062 (MO)
16. Erigeron bellidiastroides Griesb.	A. Urquiola, 820 (HPPR)
17. Erigeron bellioides DC.	C. Taylor 11705 (MO)
18. Erigeron coronarius E. Greene	R. M. King 9896 (MO)
19. Erigeron cunefolius DC.	P. Herrera (HAC)
20. Erigeron dissectus Urban	Jimenez, Peguero & Francisco-Ortega 3/01 (FTG/JBSD)
21. Erigeron dryophyllus A. Gray	G. B. Hinton 17777 (MO)
22. Erigeron ecuadoriensis	loan from Ximenna Aguire (QCNE)
23. Erigeron fasciculatus Colla *	ITS1: B. Sparre 2913 (S)
24. Erigeron fasciculatus Colla *	ITS2: C. Marticorena *et al* 9788 (CONC)
25. Erigeron fernandezianus (Colla) Solbrig	T. Stuessy 11441 (OS)
26. Erigeron gradiflorus Hook.	R. Hartman 55581 (RM)
27. Erigeron jamaicensis L.	Zanoni *et al.* , # 477598 (JBSD)
28. Erigeron sp.	Escobedo #305 (LL)
29. Erigeron luxurians (Skottsb) Solbrig **	P. Jorge 1759 (S)
30. Erigeron maximus (D. Don) DC.	R. Wasum 8044 (MO)
31. Erigeron podphylllus Nesom	G. Nesom 5438 (MO)
32. Erigeron philadelphicus L.	R.D. Noyes 1165 (IND)
33. Erigeron pinnatisectus (A. Gray) A. Nels	R.D. Noyes1146 (IND)
34. Erigeron pinnatus Turcz.	B. Lojtnant 13865 (MO)
35. Erigeron pygmaeus (A. Gray) E. Greene	K. Ake 215 (MO)
36. Erigeron quercifolius Lam.	S. Hill 17962 (MO)
37. Erigeron rosulatus Wedd.	T. Steussy 8508 (OS)
38. Erigeron longipes DC	G. Carmona 800 (GCD)
39. Erigeron socorrensis I.M. Johnston	R. Moran, #25455 (LL)
40. Erigeron stanfordii I.M. Johnston ex Nesom	M. Martinez, #1725 (LL)
41. Erigeron subalpinus	material sent by D. Castillo; #23179 & 08110 (JBSD)
42. Erigeron tenuis Torr. And A. Gray	G. Nesom 7224 (MO)
43. Erigeron thrincioides Griesb.	R. Oviedo and E. Gamboa 8/18/00 (HAC)
44. Erigeron tweedyi Canby	J. Grimes 2243 (MO)
45. Erigeron uniflorus L.	R. D. Noyes 1190 (IND)
46. Erigeron ursinus D. C. Eaton	L.M. Schultz 3711 (MO)
47. Erigeron veracruzensis Nesom	G. Nesom 5945 (MO)
48. Hetertheca villosa (Pursh) Shinners	B. Stein 1823 (MO)
49. Kalimeris integrifolia Turcz. Ex DC	W. Wei 6003 (MO)
50. Nardophyllum bryoides	M. Bonifacino 304 & V. Romano (LPS)
51. Nardophylum obtusifolium	M. Bonifacino 298 & V. Romano (LPS)
52. Oritrophium hieracioides (Wedd.) Cuatr.	J. C. Solomon 16570 (MO)
53. Pteronia incana (Burm.) DC.	H. Joffe 850 (MO)
54. . Regiopappus leptocladus A. Gray	A. Tiehm 11753 (MO)

Table 4.1 cont.

No. GenBank Accession number / Exact collection site, if available

1 AF046990; Mexico: Guanajuato
2 AF118521; USA: Texas
3 AF046961; Russia: N. Caucasus
4 Argentina: Paso Pino Hachado near Chilean border; 38 39.738 S: 70 53.00, 1/16/00 (recently submitted genbank acc. #: AF511590)
5 AF046993; USA: South Carolina
6 AF118513; USA: Alabama
7 AF046987; USA: Missouri
8 Galapagos Islands, Isla de Isabela, Volcan Sierra Negra, 00 50.26 S, 091 10.57 W (recently submitted genbank acc. #: AF511573)
9 Galapagos Is., Isla de Isabela, Volcan Sierra Negra, 00 50.26 S, 091 10.57 W (recently submitted genbank acc. #: AF511575)
10 Galapagos Is., Isla de Santiago 00 19.52 S and 98 46.23 W (recently submitted genbank accession number: AF511576)
11 Galapagos Is., Isla de Isabela, Volcan Darwin, 00 14.96 S, 91 21.92 W (recently submitted genbank accession #: AF511574)
12 Galapagos Is., Isla de Pinta, on trail up volcano, 00 34.63 N, 090 45.12 W (recently submitted genbank acc. #: AF511578)
13 Galapagos Is., Isla de Isabela, Volcan Sierra Negra, 00 50.37 S, 091 06.24 W (recently submitted genbank accession #: AF511577)
14 AF118528; USA: Utah
15 AF118506; USA: Utah
16 Cuba, Laguna Vieja, Santa Teresa, Pinar del Rio (recently sub. genbank acc.: #AF511580)
17 Puerto Rico: Rio Grande (recently submitted genbank accession #: AF511588)
18 AF118520; Mexico: Chihuahua
19 Cuba; Brook near Hotel Colonial on Juventud Island, 12/10/00 (recently submitted genbank accession #: AF511583)
20 Dominican Republic, collected in Prov. San Cristobal 18° 28' N, 70° 14' W (recently submitted genbank acc.: # AF511581)
21 AF118524; Mexico: Nuevo Leon
22 Ecuador; Herbario Nacional de Quito (QCNE) (recently submitted genbank accession #: AF511584)
23 Chile, near Los Vilos (31 58.0 S and 71 29.0 W) (recently submitted to genbank, pending number)
24 Chile, near Los Vilos (31 58.0 S and 71 29.0 W) (recently submitted to genbank, pending number)
25 AF118515; Chile: Juan Fernandez Island
26 AF118494; USA: Wyoming
27 Dominican Republic, Cordillera central. Jardin Botanico in Santo Domingo
28 Mexico: Michoacan; 10/3/85 (recently submitted genbank accession number: AF511589)
29 Chile, coast north of Santiago (recently submitted genbank accession number: AF511582)
30 AF118509; Brazil: Rio Grande do Sul
31 AF118542; Mexico: Chihuahua
32 AF046989; USA: Indiana
33 AF118501; USA: Wyoming
34 AF118517; Ecuador: Cotopaxi
35 AF118526; USA: California
36 AF118525; USA: South Carolina
37 AF118516; Chile; Juan Fernandez Island
38 Mexico; Xalapa, (recently submitted genbank accession number: AF511579)
39 Socorro Island; 4/18/78, plant abundant from sea cliffs to shrubby slopes (recently submitted genbank accession #: AF511587)
40 Mexico: Tamaulipas; 4/27/88, (recently submitted genbank accession number: AF511585)
41 Dominican Republic, no exact location was given
42 AF118488; USA: Texas
43 Cuba, Pinar del Rio, on river bank before reaching the waterfall (recently submitted genbank acc #: AF511586)
44 AF118529; USA: Montana
45 AF046988; Conservatoire et Jardins Botaniques de Nancy "1401", Villers les Nancy, France, ex Sweeden
46 AF118491; USA: Wyoming
47 AF118523; Mexico: Tamaulipas
48 AF046994; USA: Colorado
49 AF046960; China: Jiangsu
50 Argentina: Santa Cruz province, near El Chalten, 2/10/00 (recently submitted genbank accession number: AF511591)
51 Argentina: Chubut province, on Route 40; lat: 42 43.56 S, long: 71 04.03 W., 2/2/00 (recently submitted genbank acc. # AF511592)
52 AF046946; Bolivia: La Paz
53 AF046947; South Africa: Cape
54 AF046971; USA: California

Table 4.1 cont.

No.	Geographic Distribution
1	SW US and Mexico
2	SW US and Mexico, mostly in Texas
3	Northern Hemisphere
4	South America
5	South Eastern USA
6	South America, introduced throughout North America
7	North America
8	Galapagos Islands, southern tip of Isabela, on Cerro Azul and Volcan Sierra Negra
9	Galapagos Islands, southern tip of Isabela, on Cerro Azul and Volcan Sierra Negra
10	Galapagos Islands, Isabela, Fernandina, Santa Cruz, Santiago, Floreana and Pinta
11	Galapagos Islands, Fernandina and Isabela
12	Galapagos Islands, Isabela, Fernandina, Santa Cruz, Santiago, Floreana and Pinta
13	Galapagos Islands, Isabela only
14	Western US, especially in Utah and Nevada
15	Western US, especially in Utah, Nevada and California
16	Cuba
17	Abundant in the Dominican Republic, Puerto Rico & Cuba; but rare in Haiti, Vieques and the Bahamas
18	Mexico
19	Puerto Rico, West Indies, Central America from Guatemala to Panama, rare in Mexico
20	Hispañiola
21	Mexico
22	Higher elevations of Ecuador
23	Chile, typically north of Santiago
24	Chile, typically north of Santiago
25	Juan Fernandez Islands
26	Western USA from CA to AK and out to WY
27	Puerto Rico, Greater Antilles, Hispañiola, Central America
28	Mexico and Central America
29	Chile
30	Brazil and Paraguay
31	Centeral and Western Mexico
32	Central USA, especially in Indiana and Colorado
33	Western USA, especially in Colorado, Wyoming, and New Mexico
34	Highlands of Ecuador
35	Western USA, especially California and Nevada
36	SE USA and the West Indies
37	Bolivia, Peru, Juan Fernandez Islands and Chile
38	Mexico and Central America
39	Isla Socorro, Revillagigedo Islands
40	Mexico, extending to Central America
41	Dominican Republic
42	SW USA
43	Cuba
44	midwest USA, especially MT, WY, ID
45	N. America = lectotype for Erigeron
46	Western U.S.A.
47	Mid-northern Mexico only
48	Western USA and Mexico

49 Central, East and SE Asia
50 South America, especially Bolivia, Argentina and Chile
51 South America, especially Bolivia, Argentina and Chile
52 Along the Andes from Venezuela and Colomia to Peru and Bolivia; 1 species in Mexico
53 Southern Africa
54 Mexico, southwestern USA

Figure 4.1: Results of the phylogentic study of *Darwiniothamnus*:

(bootstrap values are indicated in red, branch lengths are in blue, all taxa of *Darwiniothamnus* included in this study are highlighted in green, and the seven groups discussed in Chapter 4 are depicted in purple.)

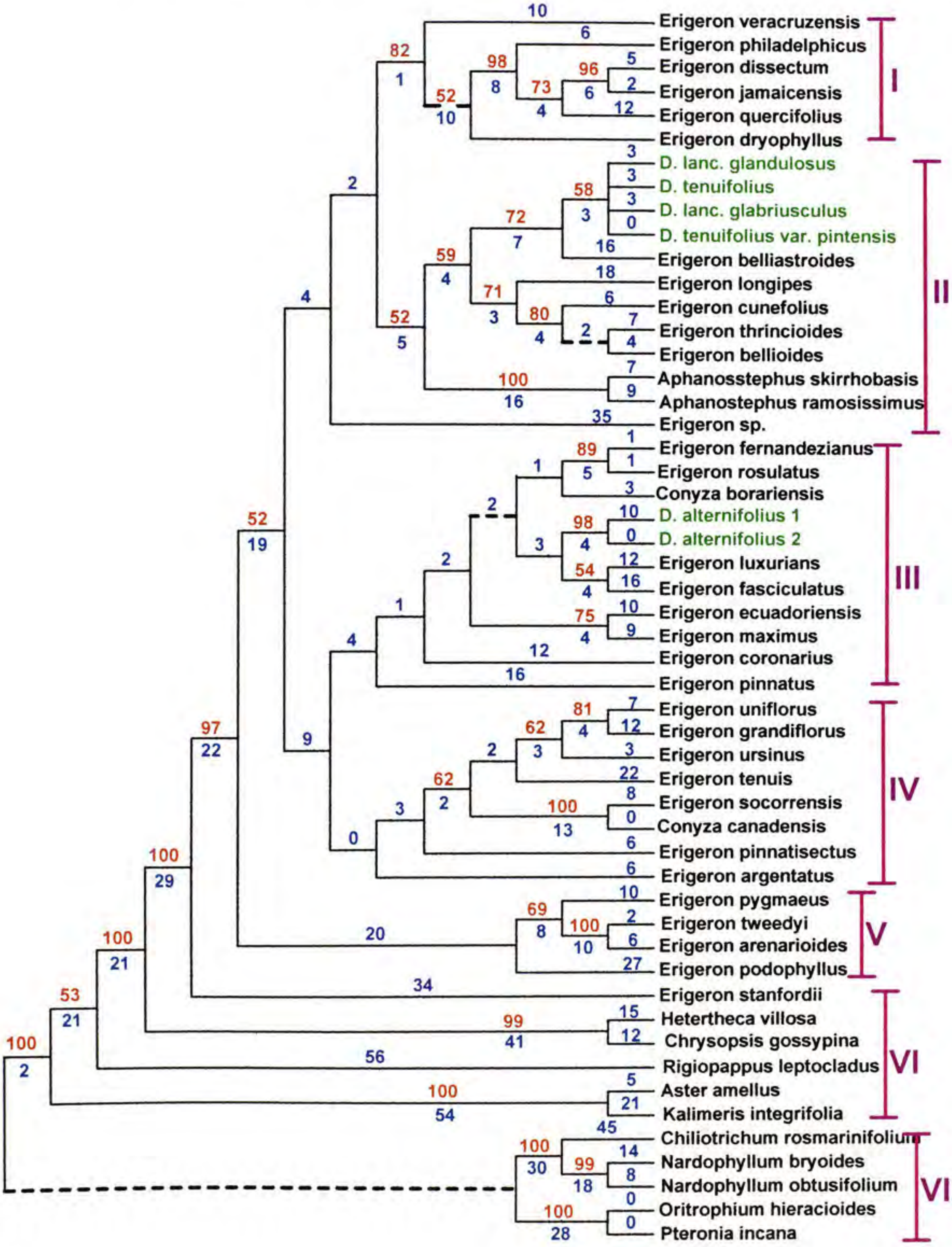
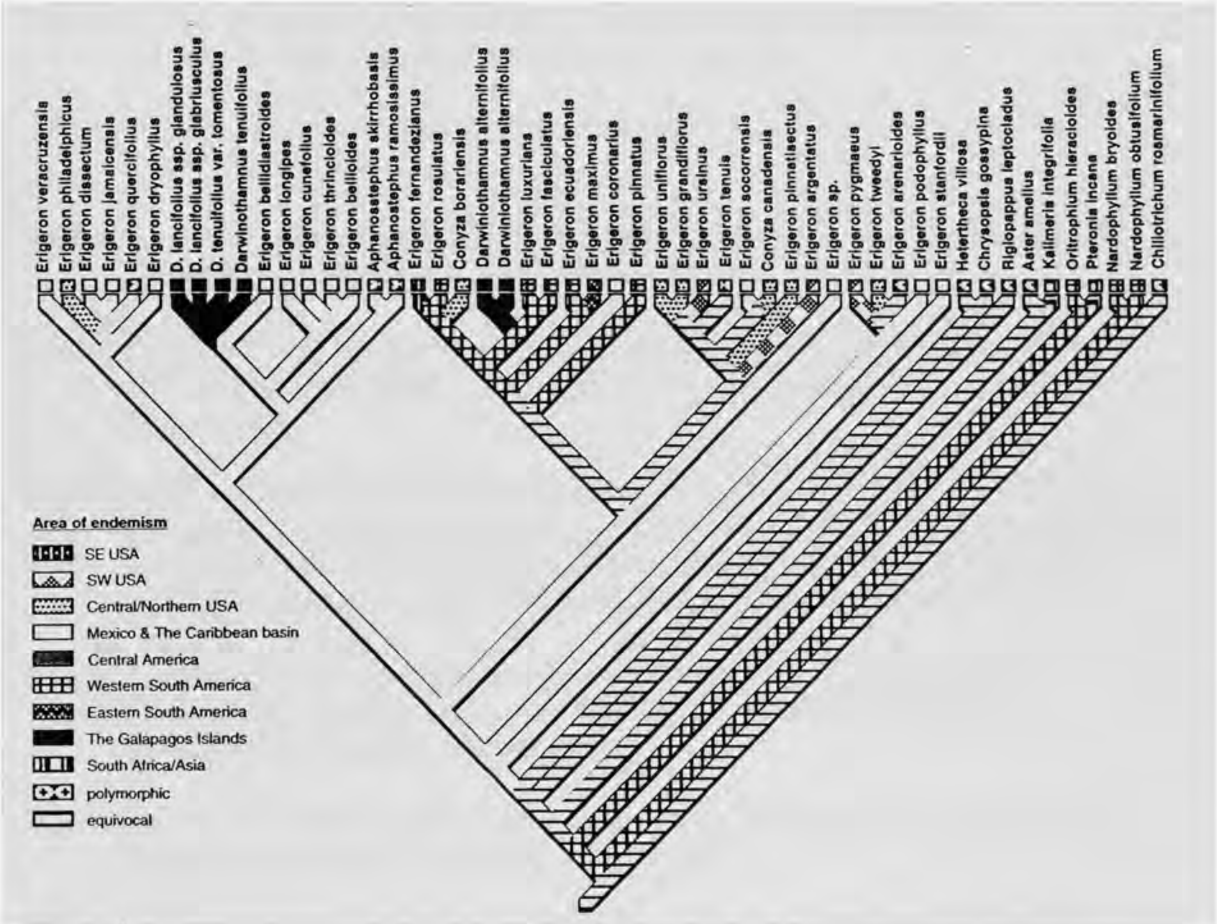


Figure 4.2: Phylogeny showing the ancestral areas for all taxa included in this study.



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APPENDIX 1a: A list adapted from Porter (1979 & 1983) of all the species from within the Asteraceae family on the Galápagos Islands. Included in this list, in order, are the names of the taxa, authors and dates of publication, their distributions by island, habitat types, chromosome numbers, discussions of their relationships, modes of dispersal and probable origin where possible. Introduced species are marked with a dash (-), native species are marked with a (^-) and endemic species are marked with an asterix (*-)

Note the following abbreviations are used for each island: **SaC** = Santa Cruz, **SaM** = Santa Maria, **SC** = San Cristobal, **I** = Isabela, **F** = Floreana, **Bal** = Baltra, **Bar** = Bartolome, **Esp** (Gar) = Espanola **Pta** = Pinta, **Pzn** = Pinzon, **R** = Rabida, and **S** = Santiago.

-*Acanthospermum microcarpum* Robins. introduced weed; Andean.
-*Adenostemma platyphyllum* Cass. (as *A. lavenia* (L.) Kuntze; King & Robinson 1975) introduced weed; Andean.
-*Ageratum conyzoides* L. ssp. *conyzoides*, introduced weed, pantropical, originally from tropical America.
-*A. conyzoide*s ssp. *latifolium* (Cav.) M.F. Johnson (Johnson, 1971) introduced weed (1835) tropical America.
-*Ambrosia artemisiifolia* L. introduced weed, pantropical, originally from the New World.
*-*Baccharis steetzii* Anderss. - I, SaC, SaM, SC; *Scalesia* Zone. Probably related most closely to the Andean (Ecuador) *B. gnidiifolia* HBK., which also occurs in the Galápagos.
^-*B. gnidiifolia* HBK. Andean (Ecuador), dispersed by wind (has a pappus with achenes 2-3 mm long).
-*Bidens cynapiifolia* HBK. Introduced weed, tropical America origin and distribution.
-*B. pilosa* L. introduced weed; pantropical distribution, originally from the Caribbean.
^-*B. riparia* HBK. Tropical America (Mexico to Peru and Brazil). Dispersed by birds externally (achenes are 10-15 mm long with a pappus of 3-5 retrorsely-barbed awns).
^-*Blainvillea dichotoma* (Murr.) Stewart, pantropical distribution, dispersed by birds externally (achenes 2-3.5 mm long, pappus awns 0.5-1.5 mm long, hirtellous).
-*Brickellia diffusa* (M. Vahl) A. Gray, introduced weed, tropical America origin and distribution.
*-*Chrysanthellum pusillum* Hook.f. - F, I, SaC, SaF, SaM, SC, SS; Arid and Transition Zones. Most closely related to *C. mexicanum* Green. from south-central Mexico (see Duncan, 1979), although Eliasson (1972) has argued for the recognition of *C. fagerlindii* Eliass. as a separate taxon, it is best included under *C. pusillum* (see Duncan, 1979), as was done by Conquist (in Wiggins and Porter, 1971), dispersed by birds externally (achenes 1-2 mm long, irregularly tuberculate).

-*Conyza bonariensis* (L.) Cronq., introduced weed, pantropical distribution, originally from tropical America.
*-*Darwiniothamnus*. Currently considered to be an endemic genus, for which Cronquist (in Wiggins and Porter, 1971) recognized one species with three varieties. Harling's (1962) treatment is followed below which up until now most accurately represented the populations in the field. Included is a third species described by Lawesson and Adsersen (1987) which after the results of this paper may no longer be considered as part of the same group. The genus is most closely related to *Erigeron.* And as previously stated by Harling: "The nearest relatives of *Darwiniothamnus* within *Erigeron*, as this genus is at present circumscribed, should probably be sought among the somewhat shrubby species from the coast of Central Chile, e.g. *E. berterianus* DC. and *E. litoralis* (Phil.) Skottsberg. (cf. Skottsberg, 1950, pp. 158-164), and the Juan Fernandez Islands."
*-*D. lancifolius* (Hook.f.) Harling ssp. *lancifolius* - F, I; common in the Transition Zone and above. Included in Wiggins and Porter (1971) under *D. tenuifolius* var. *glabriusculus* (Stewart) Cronq., dispersed by wind via the pappus.
*-*D. lancifolius* ssp. *glandulosus* Harling - F, I; common in shrubby vegetation on cinders. Included in Wiggins and Porter (1971) under *D. tenuifolius* var. *glandulosus* (Harling) Cronq., probably dispersed by wind via the pappus, although birds have been seen occasionally on and/or appearing to feed on the flowers (personal observation).
*-*D. lancifolius* ssp. *glabriusculus* Stewart (1911) I; common at higher elevations on Volcan Sierra Negra and Cerro Azul only, probably dispersed by wind via the pappus, although birds have been seen occasionally on and/or appearing to feed on the flowers (personal observation).
*-*D. tenuifolius* (Hook.f.) Harling ssp. *tenuifolius* - I, Pta, SaM, SS; common in the Transition and *Scalesia* Zones. Included in Wiggins and Porter (1971) as var. *tenuifolius*, dispersed by wind via the pappus.
*-*D. tenuifolius* (Hook.f) Harling spp. *santacruzianus* Harling - SaC; *Scalesia* Zone. Included in Wiggins and Porter (1971) under var. *tenuifolius*, dispersed by wind via the pappus.
*-*Delilia*. A genus of three species, the third being the tropical American *D. biflora* (L.) Kuntze, recently reported from the Galápagos as an introduced weed (van der Werff, 1977). Included in Wiggins and Porter (1971) as *Elvira*, but Stuessy (1975) has pointed out that the former is the older name; the Galápagos endemics are closely related to D. biflora which is the only other member of the genus.
*-*D. inelegans* (Hook.f.) Kuntze - SaM; known only from the type collection, made by Darwin in 1835. Included in Wiggins and Porter (1971) as *Elvira inelegans* (Hook.f.) Robins; dispersed by wind (achenes are housed within persistent involucral bracts which are dispersed as a unit).
*-*D. repens* (Hook.f.) Kuntze - F, I, SaC, SS; occurring in woody vegetation from sea level to 1400m. Included in Wiggins and Porter (1971) as *Elvira repens* (Hook.f.) Robins. Dispersed by wind (achenes are housed within persistent involucral bracts which are dispersed as a unit).
-*D. biflora* (L.) Kuntze (van der Werff 1977), introduced weed, tropical America distribution and origin.

^-*Eclipta alba* (L.) Hassk. Pantropical distribution, originally from tropical America. Dispersal by birds (external in mud or internal; achenes 2-2.5 mm long).

*-*Encelia hispida* Anderss. - SaF, SaM, SC, SS; Arid Zone. According to Cronquist (in Wiggins and Porter, 1971), "closely related to *E. canescens* Lam., of the Peruvian coast, and the two may eventually prove to be conspecific." Dispersed by wind (achenes are 4-5 mm long, densely pubescent, with the upper trichomes surpassing the achene body by more than 1 mm).

^-*Enydra maritime* (HBK.) DC. Andean (Pacific coast of tropical South America) distribution, dispersal by birds (external in mud or internal; achenes ca 2 mm long).

-*Erechitites hieracifolia* var. *cacaloides* (Spreng.) Griesb. (van der Werff 1977), introduced weed, pantropical distribution, originally from tropical America.

-*Flaveria bidentis* (L.) Kuntze, introduced weed, tropical America distribution.

-*Fleischmannia pratensis* (Klatt) King & Robins. (as *Eupatorium pycnocephalum* Less.; King & Robinson 1975), introduced weed, tropical America distribution..

-*Galinsoga urticaefolia* (HBK.) Benth. (van der Werff 1977), introduced weed, pantropical distribution, originally from tropical America.

-*Gnaphalium purpureum* L. introduced weed, tropical American distribution.

-*G. vira-vira* Molina, introduced weed, Andean origin.

*-*Jaegeria gracilis* Hook.f. - F, I, Sac, SaM, SC, SS; common in the *Miconia* and Fern-Sedge Zones; 2n=36, tetraploid (Torres, 1968). Most closely related to the tropical American *J. crassa* Torres (van der Werff, 1977), recognized as separate in Wiggins and Porter (1971); also closely related *J. hira* (Lag.) Less. Dispersed by birds (external in mud; achenes ca 1 mm long).

-*Jungia hirsuta* Cuatr. introduced weed, Andean origin.

^-*Koanophyllon solidaginoides* (HBK.) King and Robins. (as *Eupatorium solidaginoides* HBK.; King and Robinson (1971), topical American origin (Mexico to Ecuador), dispersed by wind (achenes 1.5-2.5 mm long, pappus abundant and longer than achenes).

*-*Lecocarpus*. An endemic genus most closely related to *Acanthospermum* and *Melampodium* (Steussy, 1970; Eliasson, 1971).

*-*L. lecocarpoides* (Robins. & Greenm.) Cronq. And Stuessy - Esp, Gar (Esp), SC; Arid Zone. Dispersed by birds (external, mechanical attachment; achenes; see Carlquist 1966; 41-42).

*-*L. darwinii* (Blake) Conq. & Stuessy - Sc; Arid Zone; known only from the type collections, made by Stewart in 1906. Perhaps not distinct from *L. lecocarpoides*. Dispersed in same manner as *L. lecocarpoides*.

*-*L. pinnatifidus* Decne. - SaM; on cinders in the Arid Zone; 2n=22 (Eliasson, 1970; as *L. foliosus* Decne.). Dispersed in same manner as *L. lecocarpoides*.

*-*Macraea*. A monotypic endemic genus, greatest affinities to *Macraea* are considered to be *Wedelia*, "particularly among the American species of this genus." (Harling, 1962, p. 98), which is a tropical and warm temperate genus of about 70 species. For centuries *Macraea* was cited as *Lipochaeta*, which belongs to the same tribe as *Macraea*, Heliantheae, but is restricted to the Hawaiian Islands. Harling (1962) was the first to do a critical study of Macraea and gave it its present name. Macraea has a diploid chromosome number of 2n=28 (Eliasson, 1984).

*-*M. laricifolia* Hook. f. - F, I, Pta, R, SaC, SaF, SaM, SC, SS; in open shrubby vegetation on cinders from near sea level to 1200 m or higher. Dispersed by birds (external, mechanical attachment; achenes; see Carlquist, 1966).

*-*Pectis*. "Both Galápagos Islands species are members of an unnamed South American section of *Pectis*" (Keil, 1977).

-*P. linifolia* L. Introduced weed, Caribbean origin.

*-*P. subsquarrosa* (Hook. f.) Schultz Bip. - Bal, Bar, Eden, Esp, F, Gar (Esp), I, Pta, Pzn, R, S, Sac, SaF, SaM, SC, SS; Arid Zone; n=36, hexaploid (Kyhos in Wiggins and porter 1971; Keil, 1977). Dispersed by birds (external, mechanical attachment; achenes 2.5-3.5 mm long, minutely hispidulous, minutely barbed pappus 2-3 mm long).

*-*P. tenuifolia* (DC.) Schultz Bip. - f, I, G, SaC, SC; Arid Zone. Dispersed by birds (external, mechanical attachment; achenes 3-4 mm long, minutely hispidulous, minutely barbed pappus 3-5 mm long).

-*Porophyllum ruderale* var. *macrocephalum* (DC.) Cronq. Introduced weed, tropical American origin.

-*Pseudelephantopus spicatus* (Aubl.) C. F. Baker; introduced weed, pantropical distribution, originally from tropical America.

*-*Scalesia*. The fourth and largest endemic composite genus. It is a member of the tribe *Heliantheae*, subtribe *Verbesininae*, being closely related to *Tithonia* and *Viguiera* (Ono, 1967a,b) or to *Helianthus* and *Viguiera* (Elisson, 1974), with which it shares the basic chromosome numbers of x=17 (all taxa of *Scalesia* so far counted are tetraploids 2n=68). *Helianthus* has about 100 species in North and South America, *Tithonia* about 10 species in Mexico, Central America, and the West Indies, and *Viguiera* about 150 species in the warmer parts of the Americas. *Scalesia* appears to be most closely related to the South American representatives of *Helianthus* (subgenus *Viguieropsis*) and *Viguiera* (Eliasson, 1974), many of which have Andean distributions. A singe original introduction has given rise to this genus, the prime example of adaptive radiation in Galápagos Plants. The treatment of *Scalesia* follows that of Eliasson's (1974) monograph. Original introduction was most likely by birds (Carlquist 1966).

*-*S. affinis* Hook.f. ssp *affinis* - SaM (W. side); Arid Zone, dispersed by birds (external, mechanical attachment; achenes 2.5-4 mm long, pappus absent or rudimentary).

*-*S. affinis* ssp. *brachyloba* Harling - SaC (S. side); Arid and Transition Zones; 2n=68 (Ono, 1967a; Eliasson, 1970; both as *S. affinis*); dispersed by birds as in ssp. *affinis*.

*-*S. affinis* ssp. *gummifera* (hook.f.)Harling - f, I; Arid Zone; 2n=68 9Eliasson, 1974); dispersed by birds (external, mechanical attachment; achenes 2.5-4 mm long, pappus rarely forming an awn to almost as long as the achene).

*-*S. aspera* Anderss. - Eden, SaC (n. side); Arid and Transition Zones; 2n=68 (Eliasson, 1974); dispersed by birds (external, mechanical attachment; achenes 4-5 mm long, pappus rarely prolonged into 2 awns to ca 4 mm long).

*-*S. atractyloides* Arn. var. *atractyloides* - SS; Arid Zone; dispersed by birds (external, mechanical attachment; achenes 3-4 mm long, pappus sometimes forming 1-2 short awns).

*-*S. atractyloides* var. *darwinii* (Hook.f.) Eliass. - SS; Arid and Transition Zone; 2n=68 (as *S. atractyloides* Eliasson, 1974;60); endemic, dispersed by birds as in var. *atractyloides*.

*-*S. baurii* Robins & Greenm. ssp. *baurii* - Pzn; *Scalesia* Zone; 2n=68 (Ono, 1971); dispersed by birds (external, mechanical attachment; achenes 3.5-4 mm long, pappus absent or rudimentary and forming 1-2 small callosities).

*-*S. baurii* ssp. *hopkinsii* (Robins.) Eliass. - Pta, W; Arid and Transition Zones; 2n=68 (Eliasson, 1970; as *S. hopskinsii*); dispersed by birds as in ssp. *baurii*.

*-*S. cordata* Stewart - I (S. half); cinder soils at both low (100-350 m) and high (1280-1600 m) elevations; dispersed by birds (external, mechanical attachment; achenes 3.5 mm long, pappus generally of 2 laciniate-margined awns to 2 mm long).

*-*S. crockeri* Howell - Bal, S, SaC (N. side); Arid Zone; 2n=68 (Eliasson, 1970); dispersed by birds (external, mechanical attachment; achenes 4-5 mm long, pappus apparently absent).

*-*S. divisa* Anderss. - SC; Arid Zone; 2n = 68 (Eliasson, 1974); dispersed by birds (external, mechanical attachment; achenes 4-5 mm long, pappus rarely present as 1-2 pointed callosities to ca 0.5 mm long).

*-*S. helleri* Robins. ssp. *helleri* - SaC (S. side), SaF; Arid Zone; 2n= 68 (Eliasson, 1974); dispersed by birds (external, mechanical attachment; achenes 2-4 mm long, pappus absent or present as low callosities).

*-*S. helleri* ssp. *santacruziana* Harling - SaC (S. side), SaF; Arid Zone; described as S. helleri; Eliasson 1974:89), dispersed by birds (external, mechanical attachment; achenes 2-4 mm long, pappus absent or present as low callosities).

*-*S. incisa* Hook. f. - SC (N. side); Arid Zone; 2n=68 (Ono, 1971; Eliasson, 1974); dispersed by birds (external, mechanical attachment; achenes 4-4.5 mm long, pappus apparently absent).

*-*S. microcephala* Robins var. *microcephala* - F, I; more common at higher elevations; 2n=68 (Eliasson, 1970; Ono, 1971); dispersed by birds (external, mechanical attachment; achenes 3-4 mm long, pappus rarely present, of 1-2 awns to ca 1.5 mm long).

*-*S. microcephala* var. *cordifolia* Eliass. - I (N. side); 400-1600m, apparently in mesic woodlands; dispersed by birds as in var. *microcephala*.

*-*S. pedunculata* Hook.f. - SaC, SaM, SC, SS; *Scalesia* Zone; 2n=68 (Ono, 1967a, 1971; Eliasson, 1974); dispersed by birds (external, mechanical attachment; achenes 4-6 mm long, pappus rarely forming a short awn).

*-*S. retroflexa* Hemsl. - SaC (SE part); Arid Zone; dispersed by birds (external, mechanical attachment; achenes 4 mm long, pappus absent).

*-*S. stewartii* Riley - Bar, SS 9E. side); Arid Zone; 2n=68 (Ono, 1971); dispersed by birds (external, mechanical attachment; achenes 3-4 mm long, pappus apparently absent).

*-*S. villosa* Stewart - Cal, Cha, Gar (SaM), O, SaM; on cinder soils in the Arid Zone; 2n=68 (Eliasson, 1974); dispersed by birds (external, mechanical attachment; achenes 3-4 mm long, pappus apparently absent).

-*Sonchus oleraceus* L. Introduced weed, pantropical distribution, originally from the Old World.

-*Spilanthes acmella* (L.) Murr. Introduced weed, pantropical distribution.

*-*Spilanthes darwinii* D. M. Porter - SaM, SC, SS; *Scalesia* Zone. *Spilanthes* is a tropical genus of about 60 species; *S. darwinii* is presumably related to one of the many tropical American species. It was listed by Cronquist (in Wiggins and Porter, 1971) as *S. diffusa*

Hook.f., a later homonym of S. *diffusa* Poepp. & Endl. Dispersed by birds (external, mechanical attachment; achenes 1.4-1.5 mm long, pappus absent or of 1 small awn).
-*Synedrella nodiflora* (L.) Gaertn. Introduced weed, pantropical distribution, originally from tropical America.
-*Tridax procumbens* L. (van der Werff 1977) Introduced weed, pantropical distribution, originally from Central America.

Appendix 1b: A current list from the CDRS database (A. Tye, personal communication) listing all members from of the Asteraceae in the Galápagos Islands and their conservation status:

Where:

En = Endemic
EnQ = Questionably Endemic
Na = Native (not endemic)
NaQ = Questionably Native (probablly introduced
Cu = Cultivated (introduced for cultivation, not naturalized)
Es = Escaped (introduced for cultivation, naturalized)
Ac = Accidental (accidentally introduced, naturalized)
AcQ = Doubtfully accidental (introduced, naturalized, but not known if introduced on purpose or not)
In = Introducida (not known if introduced on purpose or not, nor if it is naturalized)
CuE = Eradicated (Culivated species)
EsE = Eradicated (Escaped species)
NG = Species does not grow in the Galápagos

Genus	Species	Origen
Acanthospermum	*microcarpum*	NaQ
Acmella	*ciliata*	AcQ
Acmella	*darwinii*	En
Acmella	*sodiroi*	Ac
Adenostemma	*platyphyllum*	Ac
Ageratum	*conyzoides*	NaQ
Ambrosia	*peruviana*	Ac
Anthemis	*nobilis*	Cu
Baccharis	*gnidiifolia*	Na
Baccharis	*steetzii*	*En*
Bidens	*cynapiifolia*	Ac
Bidens	*pilosa*	NaQ
Bidens	*riparia*	Na
Blainvillea	*dichotoma*	Na
Brickellia	*diffusa*	NaQ
Centratherum	*punctatum*	Es
Chrysanthellum	*fagerlindii*	En
Chrysanthellum	*pusillum*	En
Chrysanthemum	*peggy*	Cu
Conyza	*bonariensis*	Ac
Conyza	*bonariensis*	Ac
Conyza	*canadensis*	Ac
Cosmos	*bipinnatus*	Cu
Dahlia	*pinnata*	Cu
Darwiniothamnus	*alternifolius*	En
Darwiniothamnus	*lancifolius*	En
Darwiniothamnus	*lancifolius*	En
Darwiniothamnus	*lancifolius*	En
Darwiniothamnus	*lancifolius*	En
Darwiniothamnus	*tenuifolius*	En

Darwiniothamnus	*tenuifolius*	En
Delilia	*biflora*	NaQ
Delilia	*inelegans*	En
Delilia	*repens*	En
Eclipta	*prostrata*	Na
Encelia	*hispida*	En
Enydra	*sessilifolia*	Na
Erechtites	*hieraciifolius*	Ac
Flaveria	*bidentis*	Ac
Fleischmannia	*pratensis*	Ac
Galinsoga	*quadriradiata*	Ac
Gamochaeta	*purpurea*	NaQ
Gazania	*splendens*	Cu
Gnaphalium	*viravira*	NaQ
Helianthus	*annuus*	Cu
Jaegeria	*gracilis*	En
Jungia	*hirsute*	Ac
Koanophyllon	*solidaginoides*	Na
Lactuca	*sativa*	Cu
Lecocarpus	*darwinii*	En
Lecocarpus	*lecocarpoides*	En
Lecocarpus	*pinnatifidus*	En
Macraea	*laricifolia*	En
Matricaria	*recutita*	Cu
Pectis	*linifolia*	NaQ
Pectis	*subsquarrosa*	En
Pectis	*tenuifolia*	En
Porophyllum	*ruderale*	Ac
Pseudelephantopus	*spicatus*	Ac
Pseudelephantopus	*spiralis*	Ac
Pseudogynoxys	*scabra*	Cu
Scalesia	*affinis*	En
Scalesia	*aspera*	En
Scalesia	*atractyloides*	En
Scalesia	*atractyloides/stewartii hybrids*	
Scalesia	*bauri*	En
Scalesia	*cordata*	En
Scalesia	*crockery*	En
Scalesia	*divisa*	En
Scalesia	*divisa/incisa*	En
Scalesia	*gordilloi*	En
Scalesia	*helleri*	En
Scalesia	*incisa*	En
Scalesia	*microcephala*	En
Scalesia	*pedunculata*	En
Scalesia	*retroflexa*	En
Scalesia	*stewartii*	En
Scalesia	*villosa*	EN
Smallanthus	*sonchifolius*	Cu

Soliv	*anthemifolia*	**Na**
Sonchus	*oleraceus*	**Ac**
Synedrella	*nodiflora*	**Ac**
Tagetes	*erecta*	**Cu**
Tanacetum	*cinerariifolium*	**Cu**
Taraxacum	*officinale*	**AcQ**
Tridax	*procumbens*	**Ac**
Zinnia	*peruviana*	**NaQ**

<u>APPENDIX 2:</u> A list of the current status of each population of *Darwiniothamnus* collected from at various sites throughout the archipelago. The order of the islands, and specific areas within each island listed trace the route I followed on my four separate collecting trips within the archipelago.Included are notes on different growth forms, the greatest biological dangers at each site and recommendations for future conservation work, where needed.

<u>Island</u>: Santa Cruz
<u>Location</u>: Los Gemellos
<u>Species present</u>: *D. tenuifolius* ssp. *santacruzianus*
<u>Additional remarks</u>: The population near los Gemellos is restricted to one small and very crowded population of exactly 7 plants. All plants are large and seemingly healthy, but unfortunately show the initial sign of *Icerya purchasi* (cottony cushion insect) infestation. A couple of the insects appeared to be ovigerous, thus I recommend that the population be monitered carefully over the next few years to ensure its protection. The leaves of this ssp.ecies are at least 2-4 times longer than other members from the same species and about half to a quarter as wide. In addition, the leaves are remotely hairy on both the ad and abaxial sides with several sharp teeth lining the margins.

<u>Island</u>: Santa Cruz
<u>Location</u>: area surrounding Cerro Crocker towards "los Picachos"
<u>Species Present</u>: *D. tenuifolius* ssp. *santacruzianus*
<u>Additional remarks</u>: This population was much more healthy than the one at los Gemellos, comprising of approx. 30 rather small plants; all of which share the similar leaf descriptions as those mentioned above. No presence of *I. purchasi* noticed and the only force apparently threatening the existence of this population is the large amount of *Pteridium aquilinum* (bracken fern) growing around, over and shading several members of the population; competition for light must be a factor. First sign of interesting, rhizomatous-like growth.

<u>Island</u>: Pinzón
<u>Location</u>: first stop on eastern side, second stop of western side of the island
<u>Species Present</u>: none
<u>Additional remarks</u>: *D. tenuifolius* previously inhabited this island, but after extensive searching, no extant populations were found...extinction probably due to foraging by goats.

<u>Island</u>: Isabela
<u>Location</u>: Cartago Bay (Bahia Cartago)
<u>Species Present</u>: *D. tenuifolius*
<u>Additional remarks</u>: Very large population found spanning ca 5 km^2 or more. Leaves surfaces (ad and abaxial) are completely glabrous in the entire population. *I. purchasi* present in abundance, several of which are ovigerous.

Island: Isabela
Location: trail up to Volcan Alcedo, started at Pta. Alfaro (no plants found at or around rim of the crater)
Species Present: *D. tenuifolius*
Additional remarks: several populations collected here. Several of the plants had leaves which were remotely denticulate, pubescent to densely pubescent, with hairs that were increasingly glandular with elevation.

Island: Isabela
Location: trail down from Volcan Alcedo (old trail facing NNE, which comes out near Pta. Garcia)
Species Present: *D. tenuifolius*
Additional remarks: several dead plants found along old river bed…only ca 10 plants found alive (presumably to *I. purchasi*, although none was found), whose leaves were much more linear than those found on the other trail leading up to the volcano. In addition, both surfaces of all leaves studied were completely glabrous and somewhat bullate; possibly a different variety (as are reproductively isolated) or just variation within the species.

Island:Isabela
Location:Volcan Wolff, (entered at "Piedras Blancas," half way between Pta. Albermarle and Pta. Flores).
Species Present: *D. lancifolius* ssp. *glandulosus*
Additional remarks: First sign of this species, fairly healthy populations; no sign of *I. purchasi* present. All leaves studied from this area were fairly coriaceous (sometimes with reddish margins and tips) with mucronate apices, and had glandular hairs covering both surfaces. A few of the new leaves from this population were oddly circinate, and some even had dead flowers and/or seeds inside.

Island: Isabela
Location: lower elevations of Volcan Ecuador (entered just south of Cabo Berkely)
Species Present: *D. lancifolius* ssp. *glandulosus*
Additional remarks: Again, fairly healthy plants, but very spread out and solitary. No sign of *I. purchasi.* Leaves showed all the same characteristics as from Volcan Wolff, except the glandular hairs were much finer on all specimens examined from this location.

Island: Fernandina
Location: Cabo Douglas
Species Present: *D. lancifolius* ssp. *glandulosus*
Additional remarks: Very healthy and large population found here – same remarks as for V. Ecuador and V. Wolff; this time, however, glandular hairs are much shorter & stubbier.

Island: Fernandina
Location: Lava stand in back of Roca Tarzan and base of Volcan Fernandina
Species Present: *D. lancifolius* ssp. *glandulosus*
Additional remarks: Healthiest population found in entire archipelago, the species forms huge stands and is definitely the most prolific plant on the island. No sign of *I. purchasi.* Same leaf description as found on Cabo Douglas, except there was greater leaf length and width variation found throughout the island. In addition, longer hair was found on the undersides of leaves and shorter & more stubby glands were found on top of all specimens studied from a variety of altitudinal gradients.

Island: Isabela
Location: Volcan Darwin (entered at Tagus Cove)
Species Present: *D. lancifolius* ssp. *glandulosus* and *D. tenuifolius*
Additional remarks: Several somewhat clustered populations were found ranging from the lava stand at the end of the tourist trail all the way up to the rim of the volcano. Leaves of both species were extremely densely covered with glandular hairs, which were more pannose than pilose. A possible population of hybrids was also found which was neither clearly *D. tenuifolius* nor *D. lancifolius* at first glance. Additional morphological studies should help clarify the taxonomic position of species from this area. Again, luckily no presence of *I. purchasi* was found.

Island: Isabela
Location: Pta. Tortuga Negra
Species Present: *D. lancifolius* ssp. *glandulosus* and *D. tenuifolius*
Additional remarks: Additional smaller and more scattered populations found here, again no presence of *I. purchasi* was found. First time *D. lancifolius* was found growing directly on the sand only a couple of meters from the ocean. Same leaf descriptions can be used here as for V. Darwin, except the glands and glandular hairs seemed to be smaller and finer on all specimens examined.

Island: Isabela
Location: Bahia Urvina
Species Present: *D. lanifolius* ssp. *glandulosus/glabriusculus*?
Additional remarks: Interesting population here – hair found on both sides of the leaves but only very rarely possessing glands. Population found growing only on the lava and not at all on the flat lands/savannah, and several plants found dead and/or dieing. *I. purchasi* unfortunately found on all plants (both live and dead) in abundance at this location. (Note: this site is a favorite among the tourist stops – thus the spread of *I. purchasi* to this location could be a direct correlation; and/or as a result of transportation by wind from Volcan Alcedo.)

Island: Isabela
Location: Bahia Elizabeth
Species Present: none
Additional remarks: not a single plant found from any species after extensive searching.

Island: Isabela
Location: Pta. Moreno
Species Present: *D. lancifolius* ssp. *glandulosus*
Additional remarks: Fairly large and scattered population found here. Oddly, no sign of *I. purchasi.* Plants seemingly healthy and match description of Pta. Tortuga Negra.

Island: Isabela
Location: Volcan Sierra Negra – Eastern edge of "El Alemania" in an area called "El Velasco" (savannah region, S-SSE slope of volcano)
Species Present: *D. lancifolius* ssp. *glabriusculus*, *D. tenuifolius*, *D. alternifolius*
Additional remarks:
-*D. l. glab*: very healthy populations, leaves of this ssp. are more quadrate than lanceolate (as in *D. l. glandulosus*) and extremely hairy underneath, seemingly manicate & somewhat glandular. Leaf surfaces are more or less glabrous and bullate. No presence of *I. purchasi* readily detected.
-*D. tenuifolius*: populations are rather small and restricted to only a few areas (*D. l. glab.* is definitely more abundant). Leaves of *D. ten.*at this location are more or less glabrous and bullate.
-*D. alternifolius*: only a very small population found here by sheer luck. Henning Adsersen (personal communication, 2002) has stated that the population(s) of *D. alternifolius* in this area suffered greatly from the 1985 fire in the area. The fire devastated most of the area *D. alternifolius* inhabited on Sierra Negra and most of the vegetation development after the fire would be unlikely to favor *D. alt.* The leaves of this third species have tiny gland-like dots on the adaxial surface and are rather pillose on the abaxial side.

Island: Isabela
Location: Volcan Sierra Negra – rim of crater, past the sulpher plumes
Species Present: *D. lancifolius* ssp. *glabriusculus* and *D. tenuifolius* only
Additional remarks: same description for both as was found in El Velasco. Another possible population of hybrids perhaps detected here as well, which are intermediate in leaf shape, hair type, and plant size. No presence of *I. purchasi* readily detected.

Island: Isabela
Location: Volcan Sierra Negra – trail to base VSN, west of El Velasco.
Species Present: *D. lancifolius* ssp. *glabriusculus* only
Additional remarks: same description as was found in El Velasco. No presence of *I. purchasi* readily detected.

Island: Isabela
Location: Volcan Cerro Azul
Species Present: *D. lancifolius* ssp. *glabriusculus* and *D. alternifolius* only

Additional remarks: Individual plants of *D. l. glab.* were scattered from Media Luna up to the rim and within the crater, rarely in clusters of 2 or 3. Same description as for those in El Velasco, with the plants very healthy and apparently unaffected by the feral pig and cattle population. Several plant of *D. alt.* were also found, clustered together in definite populations from approx. 1/2 km south of Media Luna to about half-way up the volcano. This seems to be the last remaining location where this species survives in relative abundance and although there was no presence of *I. purchasi* readily detected, I believe that these plants may be fed upon by any number of the feral animals present at this location.

Island: Santiago
Location: landed near Caleta Bucanero, Puerto Egas and at an unnamed area on the southeastern coast of the island.
Species Present: *D. tenuifolius* only at all three locations
Additional remarks: The plants of this species found at all three locations were scattered and relatively few. A large population of feral goats continue to live on this island which have been seen feeding on the plants on numerous occasions. This may explain why the largest and healthiest plants were found either within sink holes, behind protective fencing, and/or in huge lava stands, not often traversed by the animals. Some presence of *I. purchasi* was found, especially along the southern coast on those plants growing in the lava stands. An interesting morphological adaptation was found among all plants studied from this island in that they are pillose both on the ad and abaxial surfaces of the leaves. This is the first time a member of this species has been seen with such a degree of hairiness and across such a wide area. Stewart (1911) even considered giving plants from this area their own ssp.ecific epithet "*tomentosus*," and although I agree with his findings, I will wait for a careful morphological analysis to be completed before I formally say so.

Island: Marchena
Location: landed at Playa Negra and again between Pta. Mejia and Pta. Montalvo
Species Present: none
Additional remarks: after extensive searching by six of my colleagues from the CDRS, I am certain that no members of this genus reside on this island, from which it has never been recorded.

Island: Pinta
Location: arrived in between Cabo Ibbetson and Cabo Chalimers; and left the island on the other side in between Cabo Ibbetson and Rocas Nerus.
Species Present: *D. tenuifolius*
Additional remarks: Upon arrival it appeared that all members of this species had died out due to an extreme infestation of *I. purchasi*, which was perhaps the worst infestation seen so far and definitely comparable to that of Volcan Alcedo. However, upon summiting the solitary volcano on the island and continuing down the other side we found great stands of somewhat rather small plants of D. ten, all healthy and apparently not yet affected by *I. purchasi.* The leaves of the plants on this island share the same attributes as those on Santiago, and are even more odd in that they are extremely

tomentose on both sides of the leaf blade. I definitely feel that the representatives of this species on Pinta deserve at least a new ssp.ecific epithet, but again will wait to do so until I have completed a detailed morphological study of all species across the entire archipelago.

Island: Floreana
Location: I did not visit this island, but was sent material from it
Species Present: *D. tenuifolius*
Additional remarks (A. Tye, personal communication): Scattered bushes in the upper arid zone and transition zones of the western side of the island and western half of the central plateau, in amongst scrub and open *Scalesia pedunculata* woodland. The scrub habitat is dominated in places by the introduced *Lantana camara* but it is not known if the latter is adversely affecting the *Darwiniothamnus*.

APPENDIX 3: Notes on the soil analyses run for each sample collected within the Galápagos Islands. General information on the trends from location to location are also included and more specific information regarding these trends can be found in the text of Chapter 3.

SOIL pH. Soil pH levels have a direct influence over the availability of both macro and micro nutrients and their uptake by plants. The results of these analyses indicates that the soils have pH's ranging from very acidic to strongly alkaline (4.8 to 8.6); and the samples average was 7.15 collectively. The most acidic soils were found on Cerro Azul and Fernandina. The most alkaline soils were found on Volcán Ecuador and Volcán Wolf.

SOIL SALINITY. ECe levels were found to be within accepted agriculture limits for growing plants in most areas. For non-stressed plants, in general, a soil ECe of <1.5 mmho/cm is considered ideal. Most samples fell within this range except sample 13 from Fernandina in population 6, which was 3.4 and samples 1 and 2 which were extraordinarily high at 6.1 and 5.9. There is, as of yet, no explanation for the large variance.

SOLUBLE CALCIUM. The amount of soluble calcium within soil is very important in water infiltration for growing plants. Since there are vast differences in the climatic conditions and rainfall on each island, this subject has little bearing on the overall results except to note that Soluble Calcium levels of 8.0meq/liter are considered adequate for proper water infiltration. All but five of the 29 samples were well below this threshold.

NITROGEN (N). Nitrogen is a very important component in chlorophyll development. The broad range of available nitrogen as determined by dry soil and by Saturation Extract was all over the board. The Nitrate-Nitrogen ranged from a low of 3 ppm at site #23 on Marchena and only 2 ppm at site # 27 on Santíago to a high of 497 ppm at site 3 on Fernandina. The low level of Nitratre-Nitrogen in the soil on the island of Marchena may be a reason why no members of *Darwiniothamnus* have ever been known to inhabit this island, but this is only a rudimentary hypothesis and one which ought to be studied further.

PHOSPHOROUS (p). The phosphorous levels for all samples across the archipelago were all in the levels necessary for typical plant development and growth.

POTASSIUM (K). Soil levels of potassium were found to be, in large part, high . A base soil level of 125 ppm is considered to be adequate for most shrubs and vines. Potassium can become tightly bound upon clay particles and not be easily soluble however, no clay was observed in any of the soil samples. Potassium levels, expressed as ppm ranged from a low of 48 at site 27 on Santíago to a high of 2340 ppm at site 9 on Volcán Alcedo. The numerical average for K is 620 ppm, suggesting our results are very high indeed.

ZINC (ZN) AND BORON (B). The levels found of Zinc, and when possible Boron, are generally adequate for sustaining plant vigor and health. Since Zinc deficiencies are known to impact germination processes across several plant species, including some members of the Asteraceae, it would be interesting to see if the low levels found in some samples affected propagation. Future germination studies are therefore suggested with altering the levels of several different limiting nutrients, including Zinc and Boron.

CALCIUM/MAGNESIUM (CaMg). To provide proper nutrient uptake to plants, it is also important that soils contain higher percentages of calcium than magnesium. Soils that have less than two times the amount of calcium to magnesium will develop nutrient deficiencies. These deficiencies are due to the soils imbalance of calcium to magnesium which causes needed nutrients to be held tightly in the soil. The percentage of calcium to magnesium were found to be to a great degree below the minimum level considered desirable of 2.0. Samples number one and two were again out side the range of normal expectations, and should definitely be considered outliers. The Sodium Absorption Ratio (Ca/Mg) was 4.48 and the pH was 8.5.

TRACE MINERALS. Only samples 17, 18, 25, and 26 had statistically higher amounts of any of the trace elements. Iron (Fe) was high in all four. Sites 17 and 18 were taken from Volcan Sierra Negra, and samples 25 and 26 were taken from the island of Pinta. The high Iron content would lead one to believe that these were younger soils created by more recent Volcánoes, which could be the case for Volcan Sierra Negra, but not necessarily for the island of Pinta.

BIOMASS/ORGANIC MATERIAL AVAILABLE. It is readily known that an incredible diversity of organisms makes up the soil food web. These organisms can range in size from tinstone celled bacteria, algae, fungi, and protozoa; to more complex nematodes and micro-arthropods; to earthworms, insects, small vertebrates, and plants all readily seen by the human eye. As these organisms eat, grow, and move through the soil, they make it possible to have clean water, clean air, healthy plants, and moderated water flow. This typically normal, yet complex process however, probably only occurred at half of the sites where we collected soil. Several of the populations where I collected both plants and soil were located on vast stands of lava, where top soil (and the associated biomass and organic material) was either scant or absent altogether. In addition, many of the lava flows on Fernandina, Isabela and Santíago are so recent that vegetation has not yet colonized them and soil is practically nonexistent within their limits (Wiggens and Porter, 1971). This could be a reason for why *Darwiniothamnus* was found growing in great stands in some thick lava areas and was absent for miles in others; however it is more than likely that the reason has a lot to do with age, chance colonization and nearest source populations. The youngest flows with *Darwiniothamnus* present on seem to be more than 200 years old (e.g. SW Santiago) (A. Tye, personal communication).

Appendix 3 cont.: Results of Soil Analyses for all 29 sample sites.

Code	soil sample 1	soil sample 2	soil sample 3	soil sample 4
SATURATION EXTRACT				
Saturation percentage	150	155	189	138
pH	7.6	7.6	5.6	6.9
Ece (electrical conductivity)	6.1	5.9	2.0	2.6
Ca meq (calcium)	11.08	10.38	7.69	15.82
Mg meq (Magnesium)	17.93	16.61	2.88	6.33
Ca + Mg meq	29.01	26.99	10.57	22.15
Na meq (sodium)	32.19	27.84	7.83	4.35
K meq (Potassium)	6.14	7.39	2.81	2.15
CARB meq (carbonate + bicarbonate)	27.8	21.0	3.4	12.0
Cl meq (Chloride)	45.6	61.1	8.4	8.6
Na_ad (Sodium adsorption ratio)	8.45	7.58	3.41	1.31
Na_ex (exchangeable sodium percentage)	10.1	9.0	3.7	0.7
Nitrate-nitrogen, satuartion extract, ppm	31	30	62	50
Bo ppm (Boron)			1	0.89
NUTRIENTS- DRY SOIL ESTIMATE				
Nitrate-nitrogen, dry soil estimate, ppm	47	47	117	69
P ppm (Phosphorus)	39	42	27	6
K ppm (Potassium)	1890	2020	990	700
TRACE METALS				
Znppm	64.0	67.0	41.0	9.6
Mnppm	42.0	49.0	72.0	49.0
Feppm	12.0	15.0	29.0	14.0
Cuppm	3.0	3.8	3.0	2.0
EXCHANGABLE CATIONS:				
ppm = 1N Ammonium Acetate extraction				
meq/100 g = Atomic absporption /				
Flame Emission detection				
K ppm (Potassium)	1890	2020	990	700
K ppm (percentage only)	14.4	13.6	10.2	3.9
K meq (Potassium)	4.83	5.17	2.53	1.79
K meq (percentage only)	6.8	6.4	5.2	1.9
Ca ppm (Calcium)	5500	6170	7400	14650
Ca ppm (percentage only)	42.0	41.4	76.2	81.4
Ca meq (Calcium)	27.45	30.79	36.93	73.10
Ca meq (percentage only)	38.4	37.8	75.7	77.7
Mg ppm (Magnesium)	3700	4200	920	1990
Mg ppm (percentage only)	28.3	28.2	9.5	11.1
Mg meq (Magnesium)	30.43	34.54	7.57	16.37
Mg meq (percentage only)	42.6	42.4	15.5	17.4
Na ppm (Sodium)	2000	2500	400	650
Na ppm (percentage only)	15.3	16.8	4.1	3.6
Na meq (Sodium)	8.70	10.87	1.74	2.83
Na meq (percentage only)	12.2	13.4	3.6	3.0
NH4-N (amonium-nitrogen)- as nitrogen, ppm	2675	2595	2250	1225
Free Lime (Calcium Carbonate)	0	0	0	0
% organic matter (wt. loss by combustion)	57.1	66.7	88.0	76.4
texture				
Color			dk., charcoal black	dk., brown/black
Growers Testing Service sample number:	#2181	#2182	#2183	#2184

ppm (or mg/l) = equivalent weight X meq/l meq/l = ppm (or mg/l)/ eq.wt.

Appendix 3 cont: Results of Soil Analyses for all 29 sample sites

soil sample 5	soil sample 6	soil sample 7	soil sample 8	soil sample 9	soil sampl 10	soil sampl 11
73	50	40	50	94	34	29
7.4	7.3	8.6	8.2	7.4	8.2	6.6
2.0	0.3	1.1	3.1	2.5	1.3	2.5
6.39	1.60	4.83	14.52	13.22	5.34	11.83
2.63	0.68	2.55	7.16	3.78	2.06	7.57
9.02	2.28	7.38	21.68	17.00	7.40	19.40
6.53	0.61	3.39	10.00	4.78	4.31	7.40
4.19	0.20	0.15	1.92	4.54	1.13	0.56
4.9	0.9	3.2	8.7	2.4	4.3	1.2
9.8	0.8	5.9	17.9	3.5	4.4	19.8
3.08	0.57	1.77	3.04	1.64	2.24	2.38
3.2	0.1	1.4	3.1	1.2	2.0	2.2
39	18	4	71	156	9	26
0.82	0.33	0.27	0.48	0.45	1.41	0.3
28	9	2	36	147	3	8
18	29	27	100	29	16	68
2190	1990	148	1000	2340	1010	118
6.4	1.6	0.9	1.4	10.8	2.4	1.8
4.0	2.8	0.8	3.8	5.4	3.1	4.8
37.0	56.0	43.0	35.6	36.0	27.8	86.0
0.8	1.2	1.2	1.2	2.0	2.0	1.8
2190	1990	148	1000	2340	1010	118
34.9	19.9	5.4	18.6	27.2	26.4	6.2
5.60	5.09	0.38	2.56	5.98	2.58	0.30
20.8	10.5	2.7	10.0	15.5	15.1	3.1
3220	6720	2040	3380	5340	2140	1270
51.4	67.1	74.0	62.8	62.1	55.9	66.2
16.07	33.53	10.18	16.87	26.65	10.68	6.34
59.8	69.2	73.1	66.0	69.2	62.3	64.5
380	1070	230	460	490	240	230
6.1	10.7	8.3	8.6	5.7	6.3	12.0
3.13	8.80	1.89	3.78	4.03	1.97	1.89
11.6	18.2	13.6	14.8	10.5	11.5	19.2
480	240	340	540	430	440	300
7.7	2.4	12.3	10.0	5.0	11.5	15.6
2.09	1.04	1.48	2.35	1.87	1.91	1.30
7.8	2.1	10.6	9.2	4.9	11.1	13.2
1165	510	390	945	1090	430	375
0	0	med	0	0	0	0
13.6	10.9	4.2	9.4	19.2	5.3	3.0
		fine	fine	coarse	very fine	fine
lt brown	lt brown	med gray	med gray	med brown	brown gray	med dk. gray
#2185	#2186	#2187	#2188	#2189	#2190	#2191

Appendix 3 cont: Results of Soil Analyses for all 29 sample sites

soil sample 12	soil sample 13	soil sample 14	soil sample 15	soil sample 16	soil sample 17
33	50	45	80	39	100
6.9	7.0	6.6	8.1	8.5	4.8
0.8	3.4	0.3	0.9	0.3	0.5
2.85	27.69	1.74	3.18	0.40	1.78
2.63	6.33	1.05	0.82	0.28	0.94
5.48	34.02	2.79	4.00	0.68	2.72
2.18	1.74	0.53	3.92	2.61	1.70
0.56	2.33	0.08	1.15	0.15	0.63
0.3	1.9	0.3	4.1	0.7	0.2
0.3	0.6	0.6	2.5	2.2	0.2
1.32	0.42	0.45	2.77	4.48	1.46
0.7	0.1	0.1	2.8	5.1	0.9
81	497	31	47	2	3
0.27	0.3	0.3	0.48	0.24	0.27
27	249	14	38	1	3
15	32	7	15	2	32
108	510	128	2110	204	214
1.2	2.6	1.3	2.4	0.4	2.2
3.4	3.6	1.2	2.5	1.5	5.0
37.6	23.0	25.4	20.0	16.2	342.0
1.5	1.2	0.8	0.9	0.4	1.9
108	510	128	2110	204	214
10.1	13.7	25.5	40.1	18.7	24.4
0.28	1.30	0.33	5.40	0.52	0.55
4.9	7.2	15.0	24.9	10.0	14.0
600	2860	170	2420	445	396
56.0	76.7	33.9	46.0	40.7	45.2
2.99	14.27	0.85	12.08	2.22	1.98
52.4	79.2	38.6	55.8	42.5	50.3
220	230	34	260	144	66
20.5	6.2	6.8	4.9	13.2	7.5
1.81	1.89	0.28	2.14	1.18	0.54
31.7	10.5	12.7	9.9	22.6	13.7
144	128	170	470	300	200
13.4	3.4	33.9	8.9	27.4	22.8
0.63	0.56	0.74	2.04	1.30	0.87
11.0	3.1	33.6	9.4	24.9	22.1
280	435	280	760	305	490
0	0	0	0	0	0
1.7	10.4	2.0	10.5	4.6	18.8
fine, fibrous	medium	coarse chunky pumice	sandy, fibrous	sandy	fibrous chunky
dk. brown	very dk. brown	dk. black	lt. brown		dk. brown
#2192	#2193	#2194	#2195	#2196	#2197

Appendix 3 cont.: Results of Soil Analyses for all 29 sample sites

soil sample 18	soil sample 19	soil sample 20	soil sample 21	soil sample 22	soil sample 23	soil sample 24
109	109	103	90	66	40	75
5.4	5.4	6.1	5.0	6.7	7.9	7.3
0.3	1.1	1.4	0.4	1.2	0.2	0.8
0.77	8.33	3.22	1.09	3.61	0.78	4.10
0.81	1.10	5.92	1.32	3.29	0.54	2.72
1.58	9.43	9.14	2.41	6.90	1.32	6.82
1.17	0.91	2.09	1.52	2.26	0.96	1.13
0.68	0.39	2.81	0.20	2.51	0.15	0.39
0.2	0.2	0.3	0.2	3.1	0.7	2.7
1.7	0.9	0.7	0.5	1.3	0.6	3.2
1.32	0.42	0.98	1.39	1.22	1.18	0.61
0.7	0.1	0.2	0.8	0.5	0.5	0.1
39	102	195	44	46	3	20
0.24	0.22	0.22	0.13	0.22	0.22	0.22
43	111	201	40	30	1	15
6	35	16	4	31	5	20
306	222	1090	144	720	344	970
2.4	10.8	2.2	2.4	2.7	1.0	9.0
12.8	2.8	6.4	12.0	4.1	1.2	7.2
184.0	85.0	15.8	20.0	61.0	24.8	78.0
7.0	6.0	1.0	0.8	2.6	1.0	1.8
306	222	1090	144	720	344	970
24.9	15.2	22.1	13.7	25.0	18.4	9.3
0.78	0.57	2.79	0.37	1.84	0.88	2.48
13.3	8.3	10.9	6.5	13.7	10.0	4.5
512	1040	2390	462	1540	1120	7620
41.7	71.0	48.4	44.1	53.5	59.8	73.0
2.55	5.19	11.93	2.31	7.68	5.59	38.02
43.6	75.5	46.7	40.7	57.2	63.4	69.6
190	58	1160	280	310	148	1580
15.5	4.0	23.5	26.7	10.8	7.9	15.1
1.56	0.48	9.54	2.30	2.55	1.22	12.99
26.7	7.0	37.3	40.5	19.0	13.8	23.8
220	144	300	162	310	260	270
17.9	9.8	6.1	15.5	10.8	13.9	2.6
0.96	0.63	1.30	0.70	1.35	1.13	1.17
16.4	9.2	5.1	12.3	10.1	12.8	2.1
1850	1650	1430	1175	460	1120	1645
0	0	0	0	0	0	0
44.7	16.5	40.5	44.1	2.6	2.7	35.3
medium	medium		very fine,fibrous	fibrous	chunky	very fine
reddish brown	dk. brown	dk. brown/black	dk. brown	gray brown	med. brown gray	lt. gray brown
#2198	#2199	#2200	#2201	#2202	#2203	#2204

Appendix 3 cont.: Results of Soil Analyses for all 29 sample sites

soil sample 25	soil sample 26	soil sample 27	soil sample 28	soil sample 29
136	152	29	68	66
7.8	7.3	7.5	5.9	5.8
0.8	1.5	0.2	1.2	0.7
3.43	8.48	0.89	6.64	2.83
2.39	3.87	0.48	3.54	2.55
5.82	12.35	1.37	10.18	5.38
0.96	1.74	0.50	1.61	1.35
0.74	1.23	0.10	0.41	0.50
4.2	2.6	0.5	0.6	0.4
0.6	2.5	1.0	1.3	1.6
0.56	0.70	0.60	0.71	0.83
0.1	0.1	0.1	0.1	0.1
16	144	2	153	76
0.2	0.3	1	0.2	0.2
22	219	1	104	50
27	11	7	6	3
860	830	48	180	236
50.0	53.0	0.6	1.4	1.0
8.4	10.7	2.0	2.7	2.2
78.0	103.0	43.0	60.0	57.0
2.2	2.4	0.5	1.1	1.2
860	830	48	180	236
6.4	5.8	12.1	5.4	10.7
2.20	2.12	0.12	0.46	0.60
3.1	2.8	6.7	2.7	5.2
10270	11420	128	2470	1450
76.1	79.2	32.3	74.4	66.0
51.25	56.99	0.64	12.33	7.24
71.7	75.5	35.8	71.5	63.2
1990	1780	20	400	360
14.7	12.3	5.1	12.0	16.4
16.37	14.64	0.16	3.29	2.96
22.9	19.4	8.9	19.1	25.9
380	390	200	270	150
2.8	2.7	50.5	8.1	6.8
1.65	1.70	0.87	1.17	0.65
2.3	2.3	48.6	6.8	5.7
1710	2465	380	945	1120
0	0	0	0	0
59.2	60.3	0.9	13.8	12.5
fibrous	fibrous	very rocky pumice	moist	fibrous
very dk. brown	very dk. black brown	med. gray brown	very dk. moist black	med. gray black
#2205	#2206	#2207	#2208	#2209