

Summer 2011

A taxonomic revision of the endemic members of *Varronia* P. Br. (Cordiaceae) in the Galápagos Islands

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A taxonomic revision of the endemic members of
Varronia P. Br. (Cordiaceae) in the Galápagos Islands

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A thesis submitted to the Graduate Faculty of

JAMES MADISON UNIVERSITY

In

Partial Fulfillment of the Requirements

for the degree of

Master of Science

Biology

August 2011

ACKNOWLEDGMENTS

I would first like to thank Conley K. McMullen for accepting me as his first graduate student, and for allowing me to take on this project. His support and encouragement during the past two years have been invaluable, and I have been able to visit the remarkable Galápagos Islands because of his efforts. And a big thank you goes to Ed Lickey for helping both to formulate the new taxonomic keys developed for these species as well as navigate the sometimes confusing world of botanical nomenclature. Thanks also to Michael Renfroe and Heather Griscom for their constructive questions and comments while I have worked on this project. A special thanks also to Lance Kearns for his help in obtaining the incredible SEM images used in this paper that provide an excellent example of many of the characters used in the new taxonomic key.

The Earl Core Student Award, funded by the Southern Appalachian Botanical Society, the Norlyn L. Bodkin Scholarship for Arboretum and Botanical Field Studies, supported by Ronald and Edith Carrier, and the Peter T. Nielsen Annual Award for Botanical Studies, funded by Ann Nielson, have all been incredibly helpful in allowing me to complete this research and travel to the Galápagos Islands.

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ABSTRACT

The Galápagos Islands have long been an arena for biological diversity, scientific discovery, and conservation. Accurate identification and documentation of the flora of the Galápagos continue to aid conservation efforts. The purpose of this study was to conduct a taxonomic revision of the endemic members genus *Varronia* (Cordiaceae) on the Islands: *V. revoluta* (Hook. f.) Andersson, *V. leucophlyctis* (Hook. f.) Andersson, *V. canescens* Andersson, and *V. scouleri* (Hook. f.) Andersson. Taxonomic uncertainty among these species has resulted in difficult evaluation of their potential for conservation status by the International Union for the Conservation of Nature. The present taxonomic study concludes that there are four endemic species of *Varronia*: *V. revoluta* (Hook. f.) Andersson, *V. leucophlyctis* (Hook. f.) Andersson, *V. canescens* Andersson, and *V. scouleri* (Hook. f.) Andersson. Further, this study has resulted in a new dichotomous key for field identification, using hair types as the strongest characters for differentiation between species. A new distribution map also specifies on which islands each species has been found. Proper identification and distribution assessment adds valuable information for the evaluation of endemic *Varronia* populations on the Islands to determine the conservation status of each species.

INTRODUCTION

BACKGROUND

The Galápagos Islands are an archipelago comprising 13 major islands and over 100 smaller islands approximately 1000 km west of mainland Ecuador (Snell *et al.*, 1995). They have long been an arena for studying biological diversity, scientific discovery, and conservation. In particular, the need for conservation is the result of the establishment of non-indigenous species and an ever-increasing human population, both of which put pressure on the endemic species. These Galápagos endemics are a widely diverse group of species that deserve protection as unique examples of island evolution.

Human expansion and tourism can be devastating to the endemic and native flora and fauna of these oceanic islands. Conservation measures, such as protected areas or breeding programs, are required, and fortunately are underway for many species. The animals of the Galápagos, including giant tortoises, land and marine iguanas, frigate birds, and Darwin's finches, have a particularly strong charm in the conservation world. Plants may not have the same anthropomorphic charisma as the animals of the Galápagos, but their rich diversity is also threatened and equally deserving of protection. Plants are at the heart of ecosystem processes, and the loss of one plant species could mean the diminishment or loss of other species dependent upon it.

Accurate identification and documentation of the flora of the Galápagos is essential for conservation efforts. The purpose of this study was to review and update the characterization of the endemic members of the genus *Varronia* and to create an accurate taxonomic key for them. Taxonomic uncertainty between the species has resulted in the inability of several species to be evaluated for conservation status, some of which are

listed by the IUCN; this uncertainty may have discouraged research on these species of *Varronia*. This morphological study has determined how these species can be identified in the field, and a distribution map has also been created to specify on which islands a particular species has been found. This identification and distribution information will hopefully aid in an evaluation of endemic *Varronia* populations on the Islands and determine the conservation status of each species.

SITE DESCRIPTION

The Galápagos archipelago is composed of volcanic islands located in the Pacific Ocean with a total land area of 7880 km² within a geographical area of 45,000 km² (Neall and Trewick, 2008). The archipelago is approximately 1000 kilometers west of the nearest mainland and is the product of a stationary mantle hotspot (Morgan, 1971); the archipelago has never been in contact with any continental land mass. The ages of the individual islands increase with the eastward movement of the Nazca plate on which the Galápagos are located (Rassmann, 1997). From the velocity of the plate motion it is estimated that none of the islands are older than five million years, and radiometric data predict a younger origin of the present archipelago (White *et al.*, 1993). The older islands are estimated to be between three and four million years old, while the younger islands may be one to two million years old (Hickman and Lipps, 1985). The Islands were first discovered in 1535 by Tomás de Berlanga, Bishop of Panama (McMullen, 1999).

The flora and fauna that dispersed to the Galápagos originated in various regions around the Pacific basin, including North, Central, and South America, the Caribbean, and Asia/Australasia (Grehan, 2001; Jackson, 2003). The climate of the Galápagos is extremely arid compared to most tropical archipelagos. The Islands experience a warm

season from January to May, during which time lowland vegetation reaches its peak, and a cool season from June to December, where lowlands remain dry while highlands remain constantly wet from a mixture of light rain and mist (McMullen, 1999). Today, the Islands have a well-documented flora of 614 indigenous angiosperm species, 314 of which are native (62 questionably so) and 238 endemic; the islands also host 825 introduced species (McMullen, 2011). Of the introduced species, 324 are considered to be naturalized.

TAXONOMY OF *VARRONIA*

One of the plant families inhabiting the archipelago is Cordiaceae, comprising two genera (*Cordia* L. and *Varronia* P. Br.) and 7 species (Miller and Gottschling, 2007). *Varronia* is a New World tropical genus with approximately 100 species ranging from Arizona to Argentina (Miller and Gottschling, 2007). *Varronia* comprises five species in the Galápagos, the presence of which are likely due to long-distance dispersal by frugivorous birds (McMullen, 2009; Itow, 2003). The four endemic species of *Varronia* determined by this study to occupy the Islands include *V. revoluta* (Hook. f.) Andersson, *V. leucophlyctis* (Hook. f.) Andersson, *V. canescens* Andersson, and *V. scouleri* (Hook. f.) Andersson. These endemic species are likely related to Andean species, with *V. leucophlyctis*, *V. canescens*, and *V. scouleri* most closely related to *V. polyantha* Benth., a native of Columbia and Peru (Porter, 1983). It is estimated that all endemic Galápagos *Varronia* diverged from the mainland lineage 4.5 Myr ago, and that the four species last shared a common ancestor 1.12 Myr ago (Weeks *et al.*, 2010).

Until recently, the Galápagos *Varronia* were considered to be in the genus *Cordia*. However, Miller and Gottschling (2007), proposed a reevaluation of genus *Varronia* as distinct from *Cordia*, and provided the following descriptions of the genera:

Cordia: Plants usually single or few-stemmed trees; inflorescences cymose; leaf margins entire or irregularly sharply dentate on the apical half; pollen grains colpate.

Varronia: Plants usually multi-stemmed shrubs; inflorescences condensed, capitate, spicate, or if cymose, then small and few-flowered; leaf margins regularly serrate; pollen grains porate.

This morphological study follows the descriptions by Miller and Gottschling (2007) as accurate representations of the genera, and accepts the reinstatement of the genus *Varronia*, including the four endemic Galápagos species in this study.

Varronia revoluta is distinguishable by leaf shape, but the other three species are so morphologically similar that they are difficult to identify. A taxonomic key produced by Wiggins and Porter (1971) provides a description of leaf and calyx pubescence, which they used to distinguish these species:

Leaves lanceolate, margins not revolute; corolla funnelform, the tube less than twice as long as width of limb; upper surface of leaves with erect or ascending hairs, not appressed-pubescent:

Upper surface of leaves with both simple and stout, forked, or stellate and simple hairs with conspicuously pustulate bases; calyx lobes clothed with coarse simple and forked hairs much longer than those on lower part of cup.....*V. canescens*

Upper surface of leaves bearing only simple, erect or slightly curved, usually more slender hairs; calyx lobes with same-sized hairs as base of cup:

Stems and lower surface of leaves only stiff, erect, and simple hairs.....*V. leucophlyctis*

Stems and lower surface of leaves bearing scattered, erect, simple hairs and a close cover of minute, appressed, stellate hairs.....*V. scouleri*

However, these diagnoses do not cover the full range of *Varronia* variation and did not provide the necessary separation needed for accurate identification. This may have discouraged research on these species (C.K. McMullen, personal communication).

There has, however, been some research conducted by Andrea Weeks and Kristin Baird of George Mason University, in collaboration with Conley K. McMullen, on the genetic delimitation of these species based on sequence data of the nuclear ribosomal DNA internal transcribed spacer (ITS) regions 1 and 2 (Weeks *et al.*, 2010). According to this study, *V. revoluta*, the morphologically distinct species, is also genetically distinct, but there was apparently no ITS sequence divergence among the other three species. Weeks *et al.* (2010) suggest that given the young age of the clade (0.32-3.65 Myr), population genetic analyses might yield greater information than sequence-based comparisons. Because half of the sampled accessions had autapomorphic base pair changes in the ITS region, this suggests fingerprinting techniques that record nucleotide polymorphisms across the genome would be a better method for examining the relationship between these species in future studies (Weeks *et al.*, 2010).

RATIONALE

The difficulty in distinguishing these species may have conservation implications. Currently, the one endemic species easily identifiable, *V. revoluta*, is considered “Near Threatened” by the International Union for the Conservation of Nature (IUCN), whereas *V. scouleri* is considered “Vulnerable” (Tye, 2000c,d). A Vulnerable species is one that has been categorized by the IUCN as likely to become endangered unless the circumstances threatening its survival and reproduction improve. A status of Near

Threatened is assigned to a species that may be considered threatened with extinction in the near future, although it does not currently qualify for the Threatened status. Both *V. canescens* and *V. leucophlyctis* are classified as “Data Deficient” due to taxonomic uncertainty (Tye, 2000a,b). Data Deficient is a category applied to a species when the available information, including abundance and distribution, is not sufficient for a proper assessment of conservation status to be made. Because *V. scouleri* is so similar to *V. canescens* and *V. leucophlyctis*, it too suffers from taxonomic uncertainty. Removing uncertainty by distinguishing between closely related species will be useful in determining conservation priorities (Mortiz, 1994; Vane-Wright et al., 1991; Avise, 1989; Tye, 2002), and it may lead to the classification of additional species as stable, threatened, vulnerable, or potentially endangered.

Introduced species have become increasingly represented in the flora and fauna of the Galápagos Islands. The effects of these introduced species on the indigenous plants and animals of the archipelago must be monitored because so many of the species are endemic, such as the *Varronia* in this study. Because of the relatively unknown impact of introduced species on many endemic species, it is important to establish and maintain an accurately documented floral and faunal baseline for reference in future studies. Documentation of this sort, which includes updated nomenclature, taxonomic keys, and distribution maps, will provide useful information to Galápagos researchers, park personnel, and visiting researchers as they strive to develop sensible and effective conservation programs.

OBJECTIVES

To remedy this taxonomic ambiguity, morphological studies have been conducted on herbarium specimens of the Galápagos endemics in order to determine the defining characteristics that separate these species. Conley K. McMullen collected specimens from trips to the Galápagos in 2005 and 2007, and others were borrowed from national and international herbaria. In addition to the morphological study, an analysis of the island distributions of the species was completed. A map of the *Varronia* distribution will be helpful in evaluating the areas or islands most likely to be affected by introduced species, if their distributions are also known.

One objective of this study was to prepare a taxonomic key and distribution map for the endemic members of the *Varronia* in the Galapagos Islands. The information from this study will bring clarity to this genus as well as facilitate an informed and successful assessment of the conservation needs of these endemic species.

MATERIALS AND METHODS

The majority of research for this study took place from 2009 to 2011 at James Madison University, Harrisonburg, Virginia. A total of 348 herbarium specimens were examined: 133 specimens collected by Conley K. McMullen during trips to the Galápagos in 2005 and 2007 and an additional 215 loaned specimens collected between the years 1825 and 1983. A total of three specimens were obtained from the Brooklyn Botanic Garden (BKL), 49 from the California Academy of Sciences (CAS), eight from the New York Botanical Garden (NY), 56 from Harvard University (GH), 26 from the University of Copenhagen (C), 55 from the Swedish Museum of Natural History (S), and 18 from Kew Royal Botanic Gardens (K). All other specimens examined were from the James Madison University Herbarium (JMUH). Eight type specimens from Kew Royal Botanic Gardens and one type specimen from the Swedish Museum of Natural History, as well as photographs of three type specimens from the University of Cambridge Herbarium (CGE) were studied for a total of 11 type specimens included in this study. A total of 81 specimens of *Varronia canescens*, 95 specimens of *Varronia leucophlyctis*, 89 specimens of *Varronia scouleri*, and 83 specimens of *Varronia revoluta* were examined.

Specimens were examined with a dissecting microscope and sorted into piles according to morphological similarities in leaf shape and leaf pubescence regardless of the identification on the label. During this process, four distinct sets of morphological characteristics were observed, as described in the following species narratives. In addition, measurements of leaf length and width on two leaves per specimens were taken, and that information is also included in the species descriptions.

Endocarp structure of fruits from 17 different individuals was observed.

Preparation of the endocarp included boiling fruits in distilled water for 15 minutes, and then they were soaked in a room temperature water bath for a 24 hour period to help loosen the fleshy material surrounding the endocarp. Any remaining material was removed with tweezers before observing the endocarp under a dissecting scope.

Endocarp structure varied minimally between individuals observed, and was not useful in distinguishing species. This information is therefore not included in the new keys.

To obtain detailed images of the plants' leaf surface morphologies, a LEO 1340 VP Scanning Electron Microscope was used at the James Madison University SEM/EDS Regional Facility. The SEM operated with an acceleration voltage of 25 kV, a spot size of 300 (equivalent to a probe current of 102 picoamps), and a working distance of 25 mm. Samples of dried herbarium material were coated with gold from a sputter coater prior to imaging, and the images obtained are secondary electron images. The specimens selected to obtain SEM images were chosen as representative samples of the species based on observations with a dissecting microscope. In addition to work at James Madison University, a trip to the Galápagos Islands in February 2011 allowed direct observations of live specimens and field testing of the new taxonomic keys (Tables 1 and 2).

MORPHOLOGICAL CHARACTERIZATIONS

In the following species characterizations, all descriptions of leaf shape and size, leaf pubescence and color, and calyx pubescence and size at anthesis, are the result of this morphological study. All other descriptions are from Wiggins and Porter (1971), and are cited as such within each description.

1. *Varronia revoluta* (Hook. f.) Andersson, Kongl. Svenska. Vetenskapsakad. Handl. 1853: 204. 1855.
 - ≡ *Cordia revoluta* Hook. f., Trans. Linn. Soc. London 20: 199. 1847
 - Holotype: Ecuador, Galápagos Islands, Charles Island (Floreana Island): September 1835, Charles Darwin, s.n. (CGE 00287).
 - ≡ *Cordia revoluta* var. *nigricans* Hook. f., Trans. Linn. Soc. London 20: 199. 1847
 - Lectotype (Porter, 1980): Ecuador, Galápagos Islands, Albemarle Island (Isabela Island): no date, Macrae, s.n. (K 449166!).
 - Isolectotype (Porter, 1980): Ecuador, Galápagos Islands, Albemarle Island (Isabela Island): 1825, Macrae, s.n. (K 449167!).
 - ≡ *Lithocardium revolutum* (Hook. f.) Kuntze, Revis. Gen. Pl. 2: 977. 1891
 - ≡ *Sebestena revoluta* (Hook. f.) Friesen, Bull. Soc. Bot. Genève 2(24): 183. 1933, *nom. illeg.*
- = *Cordia linearis* Hook. f., Trans. Linn. Soc. London 20: 199. 1847
 - Lectotype (Porter, 1980): Ecuador, Galápagos Islands, James Island (Santiago Island): 1835, Charles Darwin, s.n. (CGE 00286).
 - Isolectotype (Porter, 1980): Ecuador, Galápagos Islands, James Island (Santiago Island): October 1835, Charles Darwin, s.n. (K 449161!).
 - Isolectotype (Porter, 1980): Ecuador, Galápagos Islands, James Island (Santiago Island): beginning of October 1835, Charles Darwin, s.n. (K 449162!).
 - ≡ *Varronia linearis* (Hook. f.) Andersson, Kongl. Svenska. Vetenskapsakad. Handl. 1853: 204. 1855
 - ≡ *Sebestena linearis* (Hook. f.) Friesen, Bull. Soc. Bot. Genève 2(24): 182. 1933
- = *Lithocardium hookerianum* Kuntze, Revis. Gen. Pl. 2: 976. 1891.
 - ≡ *Cordia hookeriana* (Kuntze) Gürke, Nat. Pflanzenfam. 4(3): 83. 1893.

Species description. – *Varronia revoluta* is a slenderly branched shrub 2-4 m in height, with dark gray-brown, shallowly fissured bark marked by transversely elliptic lenticels; young twigs are densely fine-pubescent with appressed simple hairs (Wiggins and Porter, 1971). Leaves are linear with strongly revolute margins, 2.5-11.0 cm long, 0.2-1.0 cm wide. Adaxial surfaces are dark green and densely pubescent; hairs are white,

simple, and appressed (Figure 1a). Abaxial surfaces are lighter green and densely villous pubescent, with more robust appressed hairs found on the veins; midrib is markedly elevated (Figure 2a). Inflorescence is globose-capitate on a slender, terminal peduncle 1.0-5.0 cm long with appressed-pubescent (Wiggins and Porter, 1971). Calyx is broadly cup-shaped to nearly globose, 2.5-3.5 mm long, about 3.0 mm wide, slightly contracted at apex, shallowly 5-lobed, only slightly turned outward in flower (Wiggins and Porter, 1971). Calyx lobes are much shorter than calyx tube at anthesis (Figure 3a). Calyx is densely villous pubescent with simple hairs; hairs are a uniform length throughout (Figure 3a). Corolla is white, usually 5-lobed (rarely 4), tubular, 7.0-12.0 mm long, 2.0-2.5 mm wide, with throat slightly narrowed, and lobes ascending-spreading to rotate (Wiggins and Porter, 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

Distribution and habitat. – Endemic to the Galápagos Islands. This species is found among other shrubs and in forests as an understory tree. It is also found on lava flows and rocky soil. It can be found at elevations from near sea level to 1300 m or more. Specimens have been collected from Fernandina, Floreana, Isabela, Santa Cruz, and Santiago Islands (Figure 4).

Specimens examined. – ECUADOR. GALÁPAGOS ISLANDS. FERNANDINA ISLAND: April 1899, R.E. Snodgrass and E. Heller, 327 (GH 244027). April 1906, Alban Stewart, 3177 (GH 244032). April 1906, Alban Stewart, 3177 (CAS 27260). February 1964, John R. Hendrickson, 56 (CAS 619244). February 1964, F.R. Fosberg, 45099 (CAS 749292). February 1965, D. Wiens, 3825 (CAS 516647). March, 1967, Inga Eliasson, 1700 (S s.n.). FLOREANA ISLAND: July 2005, Conley K. McMullen, 839 (JMUH 13707). July 2005, Conley K. McMullen, 838 (JMUH 13705). July 2005, Conley K. McMullen, 837 (JMUH 13703). June 1891, G. Baur, 214 (GH 233528). May 1932, John Thomas Howell, 9372 (CAS 468109). February 1964, Syuzo Itow, 189 (CAS 579308). October 1905, Alban Stewart, 664 (CAS 694469). February 1967, Ira L. Wiggins and Duncan M. Porter, 555 (CAS 526365). October 1932, H.J.F. Schimpff, 215 (NY s.n.). October 1932, H.J.F. Schimpff, 215 (BKL 81339). December 1966, Inga

Eliasson, 785 (S s.n.). May 1967, Inga Eliasson, 2099 (S s.n.). October 1932, H.J.F. Schimpff, 215 (S s.n.). December 1966, Inga Eliasson, 785 (K H2007/01159/13). ISABELA ISLAND: August 2005, Conley K. McMullen, 850 (JMUH 13729). August 2005, Conley K. McMullen, 851 (JMUH 13732). August 2005, Conley K. McMullen, 852 (JMUH 13734). August 2005, Conley K. McMullen, 853 (JMUH 13736). August 2005, Conley K. McMullen, 860 (JMUH 13750). August 2005, Conley K. McMullen, 861 (JMUH 13752). August 2005, Conley K. McMullen, 862 (JMUH 13754). August 2005, Conley K. McMullen, 863 (JMUH 13756). August 2005, Conley K. McMullen, 849 (JMUH 849). August 2005, Conley K. McMullen, 848 (JMUH 13725). July 1891, G. Baur, 213 (GH 233529). August 1905, Alban Stewart, 3170 (GH 244034). March 1932, John Thomas Howell, 9465 (GH 244020). January 1967, Ira L. Wiggins and Duncan M. Porter, 207 (GH 244021). January 1899, R.E. Snodgrass and E. Heller, 155 (GH 244022). March 1899, R.E. Snodgrass and E. Heller, 196 (GH 244023). February 1899, R.E. Snodgrass and E. Heller, 272 (GH 244028). August 1905, Alban Stewart, 3169 (GH 244025). March 1906, Alban Stewart, 3173 (GH 244031). July 1891, G. Baur, 213 (GH 244035). November 1905, Alban Stewart, 3172 (GH 244033). June 1899, R.E. Snodgrass and E. Heller, 897 (GH 244030). December 1898, R.E. Snodgrass and E. Heller, 28 (GH 244019). August 1905, Alban Stewart, 3170 (CAS 27261). April 1974, H.H. van der Werff, 1025 (CAS 606128). September 1975, H.H. van der Werff, 2332 (CAS 606129). June 1963, David Snow, 289 (CAS 579303). January 1967, Ira L. Wiggins and Duncan M. Porter, 207 (CAS 525322). January 1967, Ira L. Wiggins and Duncan M. Porter, 231 (CAS 525339). May 1967, Inga Eliasson, 2196 (S s.n.). May 1967, Inga Eliasson, 2173 (S s.n.). April 1967, Inga Eliasson, 2013 (S s.n.). March 1967, Inga Eliasson, 1711 (S s.n.). March 1967, Inga Eliasson, 1548 (S s.n.). February 1967, Inga Eliasson, 1305 (S s.n.). June 1959, Gunnar Harling, 5357 (S s.n.). June 1959, Gunnar Harling, 5385 (S s.n.). 1825, James Macrae, s.n. (K 449167). 1825, James Macrae, s.n. (K 449166). September 1975, H.H. van der Werff, 2332, (K H2007/01159/14). SANTA CRUZ ISLAND: May 1932, John Thomas Howell, 9465 (NY s.n.). SANTIAGO ISLAND: July 1905, Alban Stewart, 3176 (GH 244026). December 1905, Alban Stewart, 3175 (GH 244024). December 1905, Alban Stewart, 3175 (CAS 27257). October 1835, Charles Darwin, s.n. (K 449161). October 1835, Charles Darwin, s.n. (K 449162).

Nomenclatural history. – *Varronia revoluta* is the most distinct of the four *Varronia* species found on the Galápagos Islands. This species was first described by Hooker in 1847 as *Cordia revoluta* Hook. f. In the same publication, Hooker also described *Cordia revoluta* var. *nigricans* Hook. f. and *Cordia linearis* Hook. f., both of which have since been synonymized with *C. revoluta* Hook. f. Andersson (1855) transferred *C. revoluta* Hook. f., *Cordia revoluta* var. *nigricans* Hook. f., and *C. linearis* Hook. f. into *Varronia*. In 1891, Kuntze transferred *V. revoluta* (Hook. f.) Andersson into *Lithocardium*

revolutum (Hook. f.) Kuntze. At the same time, Kuntze (1891) also named a new species, *Lithocardium hookerianum* Kuntze, that is now considered to be the same species as *V. revoluta* (Hook. f.) Andersson. Gürke (1893) later renamed Kuntze's *L. hookerianum* as *Cordia hookeriana* (Kuntze) Gürke. In 1933 Friesen transferred *V. linearis* (Hook. f.) Andersson into *Sebestena linearis* (Hook. f.) Friesen and *C. revoluta* Hook. f. into *Sebestena revoluta* (Hook. f.) Friesen, either unaware of or ignoring Andersson's earlier renaming of *C. revoluta* Hook. f. as *V. revoluta* (Hook. f.) Andersson and Kuntze's later reclassification to *Lithocardium revolutum* (Hook. f.) Kuntze. Recently, genus *Varronia* was resurrected by Miller and Gottschling (2007) and because of this, the name *Varronia revoluta* (Hook. f.) Andersson has priority as the species name.

Contribution of this study. – After examining the types and a number of specimens, this species has distinctive linear leaves with revolute margins (Figure 5), separating it from the other three Galápagos *Varronia*. *Varronia revoluta* also has very consistent leaf hairs that do not vary among the specimens examined. Adaxial leaf surfaces are densely pubescent with distinctive white, simple hairs that are appressed with tips oriented towards the leaf apex and/or outer margins (Figure 6). Abaxial leaf surfaces also have simple, dense hairs. Margins are villous pubescent with simple hairs. More robust, appressed white hairs are found on the veins, which also bend towards the leaf apex/outer margins (Figure 7). Calyxes are densely villous with simple hairs which are a uniform length throughout the entirety of the calyx. Calyx lobes are much shorter than the calyx tube at anthesis. The characters observed in this study agree with the description reported by Wiggins and Porter (1971). However, this study provides a more complete

description of the leaf hairs which are deemed to be the distinguishing features among the other three Galápagos *Varronia* species.

2. *Varronia leucophlyctis* (Hook. f.) Andersson, Kongl. Svenska. Vetenskapsakad. Handl. 1853: 203. 1855
 ≡ *Cordia leucophlyctis* Hook. f., Trans. Linn. Soc. London 20: 199. 1847.
 Lectotype (Porter, 1980): Ecuador, Galápagos Islands, Albemarle Island (Isabela Island): 1835, Charles Darwin, s.n. (CGE 00285).
 Paralectotype (Porter, 1980): Ecuador, Galápagos Islands, Albemarle Island (Isabela Island): 1825, Macrae, s.n. (K 449164!).
 Paralectotype (Porter, 1980): Ecuador, Galápagos Islands, Albemarle Island (Isabela Island): no date, Macrae, s.n. (K 449163!).
 ≡ *Lithocardium leucophlyctis* (Hook. f.) Kuntze, Revis. Gen. Pl. 2: 977. 1891
 = *Varronia scaberrima* Andersson, Kongl. Svenska. Vetenskapsakad. Handl. 1853: 202. 1855
 = *Lithocardium galapagosenum* Kuntze, Revis. Gen. Pl. 2: 976. 1891.
 ≡ *Cordia galapagensis* (Kuntze) Gürke, Nat. Pflanzenfam. 4(3): 83. 1893.

Species description. – *Varronia leucophlyctis* is an open shrub 1.0-2.5 m tall, with one to several erect to ascending stems; bark is dark brownish gray, with scattered, reddish tan, almost circular lenticels; young twigs, petioles, and peduncles are densely pubescent with simple hairs (Wiggins and Porter, 1971). Leaves are broadly lanceolate, 2.0-11.0 cm long, 0.8-4.0 cm wide, with finely serrate to crenate margins. Adaxial leaf surfaces are dark green, pubescent with mostly erect and simple hairs (Figure 1b). Abaxial leaf surfaces are lighter green, often densely pubescent, with erect, mostly simple hairs; simple hairs on veins are commonly robust (Figure 2b). Inflorescence is capitate to short-spicate, on terminal peduncles 1.0-5.0 cm long (Wiggins and Porter, 1971). Calyx is broadly cup-shaped to narrowly campanulate, 6.0 mm long, 4.0 mm wide, 4- or 5-lobed (Wiggins and Porter, 1971). Calyx lobes are about as long as calyx tube at anthesis (Figure 3b). Calyx is pubescent with erect and simple hairs that are noticeably longer on calyx lobes than calyx tube (Figure 3b). Corolla is white, usually 5-lobed, funnelform,

tube 7.0-8.0 mm long, 7.0-8.0 mm wide; lobes are rotate-spreading to slightly reflexed (Wiggins and Porter, 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

Distribution and habitat. – Endemic to the Galápagos Islands. This species is found among lava boulders and in rocky soil among other shrubs. It is also sometimes found as an understory shrub in forested areas. Found from near sea level to 1500 m or more.

Specimens have been collected from Española, Fernandina, Floreana, Isabela, San Cristobal, Santa Cruz, and Santa Fe Islands (Figure 4).

Specimens examined. – ECUADOR. GALÁPAGOS ISLANDS. ESPAÑOLA ISLAND: February 1906, Alban Stewart, 3168 (GH 244016). February 1906, Alban Stewart, 3168 (CAS 27273). FERNANDINA ISLAND: March 1899, R.E. Snodgrass and E. Heller, 342 (GH 244008). April 1899, R.E. Snodgrass and E. Heller, 331 (GH 233533). March 1899, R.E. Snodgrass and E. Heller, 342 (CAS 9251). March 1967, Inga Eliasson, 1701 (S s.n.). September 1972, A.E.P. Schmidt, 2535 (C 24/2007/26). January 1972, Michelle and Ole Hamann, 222 (C 24/2007/22). FLOREANA ISLAND: July 2005, Conley K. McMullen, 840 (JMUH 13708). July 2005, Conley K. McMullen, 844 (JMUH 13716). December 1966, Inga Eliasson, 824 (S s.n.). December 1966, Inga Eliasson, 813 (S s.n.). December 1966, Inga Eliasson, 904 (S s.n.). December 1966, Inga Eliasson, 877 (S s.n.). ISABELA ISLAND: August 2005, Conley K. McMullen, 859 (JMUH 13748). August 2005, Conley K. McMullen, 857 (JMUH 13745). August 2005, Conley K. McMullen, 856 (JMUH 13743). August 2005, Conley K McMullen, 858 (JMUH 13747). August 2005, Conley K. McMullen, 854 (JMUH 13739). March 2007, Conley K McMullen and Michael Shane Woolf, 881 (JMUH 13797). March 2007, Conley K. McMullen and Michael Shane Woolf, 877 (JMUH 13788). March 2007, Conley K. McMullen and Michael Shane Woolf, 878 (JMUH 13790). March 2007, Conley K. McMullen and Michael Shane Woolf, 879 (JMUH 13792). March 2007, Conley K. McMullen and Michael Shane Woolf, 880 (JMUH 13794). March 1906, Alban Stewart, 3159 (GH 244014). March 1906, Alban Stewart, 3164 (GH 233526). March 1899, R.E. Snodgrass and E. Heller, 195 (GH 244007). February 1899, R.E. Snodgrass and E. Heller, 291 (GH 233534). June 1899, R.E. Snodgrass and E. Heller, 893 (GH 244011). June 1899, R.E. Snodgrass and E. Heller, 857 (GH 244013). June 1899, R.E. Snodgrass and E. Heller, 881 (GH 244012). August 1891, G. Baur, 212 (GH 233532). July 1891, G. Baur, 210 (GH 233530). No date, R.E. Snodgrass and E. Heller, 136 (GH 244009). December 1898, R.E. Snodgrass and E. Heller, 75 (GH 244010). June 1899, R.E. Snodgrass and E. Heller, 893 (CAS 9260). April 1932, John Thomas Howell, 8976 (CAS 468107). March 1906, Alban Stewart, 3161 (CAS 27270). January 1967, Ira L. Wiggins and Duncan M. Porter, 232 (CAS 525340). March 1906, Alban Stewart, 3160 (CAS 27272). May 1932, John Thomas Howell, s.n. (CAS 468103). May

1932, John Thomas Howell, 9431 (CAS 468111). April 1974, H.H. van der Werff, 1037 (CAS 606063). April 1974, H.H. van der Werff, 1033 (CAS 606062). June 1959, Gunnar Harling, 5622 (S s.n.). June 1959, Gunnar Harling, 5360 (S s.n.). June 1959, Gunnar Harling, 5312 (S s.n.). April 1967, Inga Eliasson, 2034 (S s.n.). March 1967, Inga Eliasson, 1713 (S s.n.). May 1967, Inga Eliasson, 2219 (S s.n.). May 1967, Inga Eliasson, 2208 (S s.n.). February 1967, Inga Eliasson, 1285 (S s.n.). February 1967, Inga Eliasson, 1303 (S s.n.). September 1972, Michelle and Ole Hamann, 2243 (C 24/2007/24). July 1972, Michelle and Ole Hamann, 1780 (C 24/2007/20). July 1972, Michelle and Ole Hamann, 1771 (C 24/2007/19). July 1972, Michelle and Ole Hamann, 1709 (C 24/2007/18). July 1972, Michelle and Ole Hamann, 1615 (C 24/2007/17). September 1972, Michelle and Ole Hamann, 2320 (C 24/2007/12). 1825, James Macrae, s.n. (K 449163). 1825, James Macrae, s.n. (K 449164). April 1932, John Thomas Howell, 8976 (K H2007/01159/15). January 1967, Ira L. Wiggins and Duncan M. Porter, 232 (K H2007/01159/9). SAN CRISTOBAL ISLAND: February 1967, Ira L. Wiggins and Duncan M. Porter, 379 (GH 233549). February 1967, Ira L. Wiggins and Duncan M. Porter, 379 (CAS 526675). SANTA CRUZ ISLAND: April 1930, H.K. Svenson, 7 (GH 233525-1). February 1964, Ira L. Wiggins, 18485 (GH 244006). August 1891, G. Baur, 211 (GH 233531). February 1964, Ira L. Wiggins, 184585 (CAS 619426). March 1938, C.M. Haggis, 21 (CAS 262726). March 1935, J.P. Chapin, 1125 (NY s.n.). May 1981, C. Grady Walker, 568 (NY s.n.). March 1935, J.P. Chapin, 1125 (BKL 81351). April 1967, Inga Eliasson, 1940 (S s.n.). April 1967, Inga Eliasson, 1919 (S s.n.). November 1966, Inga Eliasson, 514 (S s.n.). April 1972, P. Pritchard, 1197 (C 24/2007/13). March 1981, O. Hamann and O. Seberg, 1772b (C 24/2007/16). March 1981, O. Seberg, 1746 (C 24/2007/15). SANTA FE ISLAND: October 1905, Alban Stewart, 3164 (GH 244015). October 1905, Alban Stewart, 3164 (CAS 27266). February 1972, Michelle and Ole Hamann, 463 (C 24/2007/21).

Nomenclatural history. – This species was first described by Hooker (1847) as *Cordia leucophlyctis* Hook. f., and then later moved by Andersson (1855) to *Varronia leucophlyctis* (Hook. f.) Andersson. Kuntze (1891) then transferred *V. leucophlyctis* (Hook. f.) Andersson into *Lithocardium leucophlyctis* (Hook. f.) Kuntze. In 1855, Andersson also described a new species, *Varronia scaberrima* Andersson, which has since been recognized as a taxonomic synonym of *V. leucophlyctis*. In 1891, Kuntze also described a new species, *Lithocardium galapagosenum* Kuntze, later moved by Gürke (1893) to *Cordia galapagensis* (Kuntze) Gürke that is also considered taxonomically synonymous to *V. leucophlyctis*. Miller and Gottschling's (2007) resurrection of the

genus *Varronia* makes *Varronia leucophlyctis* (Hook. f.) Andersson the correctly recognized name for this species.

Contribution of this study. – The leaves of *V. leucophlyctis* tend to be distinct from those of either *V. canescens* or *V. scouleri*. The leaf shape tends to be broadly lanceolate with finely serrate to crenate margins, but this is not entirely consistent among the specimens examined (Figure 8). However, like *V. revoluta*, *V. leucophlyctis* has mostly consistent hair types across all of the examined specimens. Adaxial leaf surface hairs are mostly erect and simple (Figure 9). Abaxial leaf surfaces are often densely pubescent, with mostly simple, erect hairs; simple, larger hairs can be found on the veins (Figure 10). Very rarely, forked or stellate hairs may be found on either leaf surface of *V. leucophlyctis*. Calyx hairs are also erect and simple, and noticeably longer on the calyx lobes than on the calyx tube. The calyx lobes themselves are about as long as the calyx tube at anthesis.

Though leaf morphology of this species is often distinct, *V. leucophlyctis* can still be confused with both *V. canescens* and *V. scouleri*. In this situation, the hairs on the adaxial and abaxial leaf surfaces are the best character to use for identification. Neither *V. canescens* nor *V. scouleri* possesses predominately simple, erect hairs, on both leaf surfaces, and in the same abundance as found on *V. leucophlyctis*.

3. *Varronia canescens* Andersson, Kongl. Svenska. Vetenskapsakad. Handl. 1853: 203. 1855.

Holotype: Ecuador, Galápagos Islands, Charles Island (Floreana Island): 1853, Andersson, s.n. (S 04-1959!).

= *Lithocardium anderssonii* Kuntze, Revis. Gen. Pl. 2: 976. 1891.

≡ *Cordia anderssonii* (Kuntze) Gürke, Nat. Pflanzenfam. 4(3): 83. 1893.

≡ *Varronia anderssonii* (Kuntze) Borhidi, Acta Bot. Hung. 34: 383. 1988, *nom. illeg.*

Species description. – *Varronia canescens* is an erect, moderately branched shrub 1.0-3.0 m tall, with one to several stems from the base; bark is dark brown and thin (Wiggins and Porter, 1971). Young twigs are densely pubescent with appressed stellate, forked, and simple hairs. Leaves are lanceolate, 1.3-11.8 cm long, 0.5-4.3 cm wide, with finely serrate to crenate margins. Adaxial leaf surfaces are dark green, glabrous to sparsely pubescent with hairs typically appressed or sometimes weakly erect, stellate and forked, sometimes simple (Figure 1c). Abaxial leaf surfaces are lighter green, densely pubescent with appressed stellate, forked, and simple hairs (Figure 2c). Inflorescence is subcapitate to short-spicate, on slender peduncles, 1.5-10.0 cm long (Wiggins and Porter, 1971). Calyx is narrowly campanulate, 3.0-5.0 mm long, 4- or 5-lobed (Wiggins and Porter, 1971). Calyx lobes are as long as or shorter than calyx tube at anthesis (Figure 3c). Calyx is appressed pubescent with stellate, forked, and simple hairs, generally uniform length throughout (Figure 3c). Corolla is white, 5-lobed, funnelform, tube 5.0-8.0 mm at anthesis, lobes are rotate-spreading to reflexed (Wiggins and Porter, 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

Distribution and habitat. – Endemic to the Galápagos Islands. This species is found among lava boulders and in rocky soil among other shrubs. It is also sometimes found as an understory shrub in forested areas. Found from near sea level to 700 m or more. Specimens have been collected from Española, Floreana, Isabela, Pinta, Pinzón, San Cristobal, Santa Cruz, and Santiago Islands (Figure 4). This species is the most widely distributed of the endemic Galápagos *Varronia*.

Specimens examined. – ECUADOR. GALÁPAGOS ISLANDS. ESPAÑOLA ISLAND: February 1964, C.B. Koford, 24 (CAS 619350). April 1932, John Thomas

Howell, 8706 (CAS 468106). FLOREANA ISLAND: July 2005, Conley K. McMullen, 841 (JMUH 13710). July 2005, Conley K. McMullen, 842 (JMUH 13712). July 2005, Conley K. McMullen, 843 (JMUH 13714). 1853, Andersson, s.n. (GH 233538). April 1888, Leslie A. Lee, s.n. (GH 233547). 1853, Andersson, s.n. (S S04-1959). December 1966, Inga Eliasson, 826 (S s.n.). June 1972, Michelle and Ole Hamann, 1423 (C 24/2007/10). ISABELA ISLAND: August 1905, Alban Stewart, 3195 (GH 233543). August 1905, Alban Stewart, 3195 (CAS 27276). August 1905, Alban Stewart, 3195 (NY s.n.). PINTA ISLAND: September 1905, Alban Stewart, 3158 (GH 233542). September 1905, Alban Stewart, 3158 (CAS 27267). March 1972, Michelle and Ole Hamann, 869 (C 24/2007/6). March 1972, Michelle and Ole Hamann, 920 (C 24/2007/1). May 1964, David Snow, 589 (K H2007/01159/16). 1868, Habel, s.n. (K H2007/01159/17). PINZÓN ISLAND: August 1891, G. Baur, 215 (GH 244002). May 1970, Syuzo Itow, 51409-1 (CAS 623521). August 1905, Alban Stewart, 3167 (CAS 27274). January 1967, Inga Eliasson, 1046 (S s.n.). January 1967, Inga Eliasson, 1042 (S s.n.). May 1972, Michelle and Ole Hamann, 1250 (C 24/2007/5). SAN CRISTOBAL ISLAND: March 2007, Conley K. McMullen and Michael Shane Woolf, 882 (JMUH 13799). March 2007, Conley K. McMullen and Michael Shane Woolf, 883 (JMUH 13802). March 2007, Conley K. McMullen and Michael Shane Woolf, 884 (JMUH 13804). March 2007, Conley K. McMullen and Michael Shane Woolf, 885 (JMUH 13806). March 2007, Conley K. McMullen and Michael Shane Woolf, 886 (JMUH 13809). July 2005, Conley K. McMullen, 830 (JMUH 13688). July 2005, Conley K. McMullen, 824 (JMUH 13675). July 2005, Conley K. McMullen, 825 (JMUH 13677). July 2005, Conley K. McMullen, 826 (JMUH 13679). July 2005, Conley K. McMullen, 827 (JMUH 13681). July 2005, Conley K. McMullen, 828 (JMUH 13684). July 2005, Conley K. McMullen, 829 (JMUH 13685). June 1891, G. Baur, 216 (GH 233523). No date, Andersson, s.n. (GH 233539). February 1906, Alban Stewart, 3165 (GH 233540). February 1906, Alban Stewart, 3166 (GH 233541). February 1906, Alban Stewart, 3165 (CAS 27265). No date, F. Fagerlind and G. Wibom, s.n. (S s.n.). No date, F. Fagerlind and G. Wibom, 2753 (S s.n.). April 1967, Inga Eliasson, 1848 (S s.n.). No date, Andersson, s.n. (S s.n.). No date, Andersson, 222 (S s.n.). 1853, Andersson, s.n. (S s.n.). June 1959, Gunnar Harling, 5652 (S s.n.). SANTA CRUZ ISLAND: December 1966, Inga Eliasson, 1000 (S s.n.). March 1972, Michelle and Ole Hamann, 613 (C 24/2007/25). December 1974, H.H. van der Werff, 1722 (K H2007/01159/18). February 1939, T.W.J. Taylor, G21 (K H2007/01159/10). SANTIAGO ISLAND: January 1906, Alban Stewart, 3154 (GH 233544). January 1906, Alban Stewart, 3157 (CAS 27255). January 1967, Inga Eliasson, 1128 (S s.n.). August 1972, Michelle and Ole Hamann, 2053 (C 24/2007/23). August 2005, Conley K. McMullen, 870 (JMUH 13770). UNKNOWN ISLAND: No date, Andersson, 123 (C 24/2007/14). No date, Andersson, 123 (K 449160).

Nomenclatural history. – This species was first described by Andersson in 1855 as *Varronia canescens* Andersson. In 1891, Kuntze moved both *Varronia* P. Br. and *Cordia* L. into genus *Lithocardium* Kuntze. However, the epithet “*canescens*” was occupied by

Cordia canescens Kunth which had priority, so Kuntze (1891) renamed *V. canescens* Andersson as *Lithocardium anderssonii* Kuntze. Subsequently, Gürke (1893) later reclassified *L. anderssonii* Kuntze as *Cordia anderssonii* (Kuntze) Gürke. More recently Borhidi (1988) moved *C. anderssonii* (Kuntze) Gürke back into *Varronia* as *V. anderssonii* (Kuntze) Borhidi either ignoring or not knowing Andersson's (1855) original nomenclature for the species. Therefore, Borhidi's change is invalid. As such, *V. canescens* Andersson should be considered the correct name for this species based upon Miller and Gottschling's (2007) reinstatement of genus *Varronia*.

Contribution of this study. – Based on characters observed on the type specimen, this species has lanceolate leaves with finely serrate to crenate margins (Figure 11), but these characters can be variable when observing all herbarium specimens. *Varronia canescens* has a propensity to look most similar to *V. scouleri*, though the leaves of *V. canescens* do not tend to be as long as those found on *V. scouleri*, nor are the leaf margins on *V. canescens* as coarsely serrate as those generally found on *V. scouleri*. The pubescence on the adaxial surface of the leaves of *V. canescens*, when present, is typically appressed (Figure 12) or weakly erect (Figure 13) and composed mostly of stellate and forked, occasionally simple hairs. The abaxial leaf surfaces are densely pubescent, with appressed stellate, forked, and simple hairs (Figure 14). The abaxial pubescence of *V. canescens* is the densest of any of the four species, and the most obviously appressed. In addition, the hairs on the veins do not tend to be any larger than those found in the margins, providing another character that seems to distinguish *V. canescens* from the other three species. The pubescence on the calyx is composed of appressed stellate, forked, and simple hairs which are a uniform length through the length

of the calyx. In contrast to the other species, the hairs are generally very short. The calyx lobes are as long as or shorter than the calyx tube at anthesis.

4. *Varronia scouleri* (Hook. f.) Andersson, Kongl. Svenska. Vetenskapsakad. Handl. 1853: 204. 1855.
 ≡ *Cordia scouleri* Hook. f., Trans. Linn. Soc. London 20: 200. 1847.
 Holotype: (Porter, 1980): Ecuador, Galápagos Islands, James Island (Santiago Island): no date, John Scouler, s.n. (K 449165!).
 ≡ *Lithocardium scouleri* (Hook. f.) Kuntze, Revis. Gen. Pl. 2: 977. 1891.
 ≡ *Varronia scouleri* (Hook. f.) Borhidi. Acta Bot. Hung. 34: 387. 1988, *nom. illeg.*

Species description. – *Varronia scouleri* is an ascendingly branched shrub, with dullish dark gray bark with circular or transversely lenticular lenticels (Wiggins and Porter, 1971). Young twigs are sparsely pubescent with generally appressed stellate and forked, or sometimes simple hairs. Some noticeably larger, more robust hairs may also be observed. Leaves are lanceolate, 2.3-17.5 cm long, 0.5-5.0 cm wide, with coarsely serrate margins. Adaxial leaf surfaces are dark green and pubescent with erect simple, forked, and sometimes stellate hairs (Figure 1d). Abaxial leaf surfaces are lighter green and sparsely pubescent with weakly appressed stellate and forked, sometimes simple hairs which are noticeably more robust on elevated veins (Figure 2d). Inflorescence is globose-capitate, on peduncles 3.0-5.0 mm long (Wiggins and Porter, 1971). Calyx is globose in bud, campanulate after anthesis, 5-lobed; lobes are 4.0 mm long, excluding elongated slender lobe tips, and 3-4 mm wide (Wiggins and Porter, 1971). Elongated lobe tips may be as long as, or longer than the lobe, 4.0-8.0 mm. Calyx lobes are usually longer than calyx tube at anthesis (Figure 3d). Pubescence on the calyx is composed of erect and simple, sometimes forked or stellate hairs. Simple hairs are noticeably longer on the calyx lobes than on the calyx tube (Figure 3d). Corolla is white, 5-lobed, tubular-

funnelform, with a tube 6.0-8.0 mm long; lobes are short, crispate (Wiggins and Porter, 1971). See Wiggins and Porter (1971) for a more thorough description of the reproductive parts and fruits of this species.

Distribution and habitat. – Endemic to the Galápagos Islands. This species is found among lava boulders and in rocky soil among other shrubs. It is also sometimes found as an understory shrub in forested areas. *Varronia scouleri* on Santa Cruz Island near the Charles Darwin Research Station and town of Puerto Ayora are known to be found among *Bursera graveolens* (Burseraceae), *Opuntia echios* var. *gigantea* (J.T. Howell) D.M. Porter (Cactaceae), *Jasminocereus thouarsii* var. *delicatus* (Dawson) Anderson & Walkington (Cactaceae), *Parkinsonia aculeata* L. (Caesalpinaceae), *Croton scouleri* var. *scouleri* (Euphorbiaceae), *Waltheria ovata* Cav. (Sterculiaceae), *Castela galapageia* (Simaroubaceae), *Cordia lutea* Lam. (Boraginaceae), *Clerodendrum molle* (Verbenaceae), *Scutia spicata* var. *pauciflora* (Hook. f.) M.C. Johnst. (Rhamnaceae), *Passiflora foetida* L. (Passifloraceae), and *Acacia rorudiana* Christoph. (Mimosaceae). *Varronia scouleri* are found from near sea level to 1000 m or more. Specimens have been collected only from Floreana, Santa Cruz, and Santiago Islands (Figure 4). This species is the least distributed of the endemic Galápagos *Varronia*.

Specimens examined. – ECUADOR. GALÁPAGOS ISLANDS. FLOREANA ISLAND: December 1966, Inga Eliasson, 836 (S s.n.). February 1928, Borghild Rorud, 33 (S s.n.). SANTA CRUZ ISLAND: March 2007, Conley K. McMullen and Michael Shane Wolf, 876 (JMUH 13787). March 2007, Conley K. McMullen and Michael Shane Wolf, 875 (JMUH 13784). March 2007, Conley K. McMullen and Michael Shane Wolf, 874 (JMUH 13782). March 2007, Conley K. McMullen and Michael Shane Wolf, 873 (JMUH 13782). March 2007, Conley K. McMullen and Michael Shane Wolf, 872 (JMUH 13775). July 2005, Conley K. McMullen, 836 (JMUH 13701). July 2005, Conley K. McMullen, 835 (JMUH 13697). July 2005, Conley K. McMullen, 832 (JMUH 13692). July 2005, Conley K. McMullen, 833 (JMUH 13693). July 2005, Conley K. McMullen, 834 (13695). April 1930, H.K. Svenson, 7 (GH 233525). February 1967, Ira L. Wiggins and Duncan M. Porter, 610 (GH 244001).

February 1964, Ira L. Wiggins, 18472 (GH 244000). May 1932, John Thomas Howell, 9075 (GH 233550). January 1964, Syuzo Itow, 1 (CAS 579305). March 1970, Syuzo Itow, 30800-3 (CAS 623522). May 1970, Syuzo Itow, 52200-1 (CAS 623519). February 1964, Ira L. Wiggins, 18472 (CAS 619424). June 1970, Syuzo Itow, 62600-1 (CAS 623520). February 1964, Luis A. Fournier, 157 (CAS 705256). February 1967, Ira L. Wiggins and Duncan M. Porter, 610 (CAS 528171). February 1967, Ira L. Wiggins and Duncan M. Porter, 710 (CAS 528135). May 1932, John Thomas Howell, 9075 (CAS 468104). February 1964, Syuzo Itow, 45 (CAS 579313). June 1932, H.J.F. Schimpff, 40 (NY s.n.). May 1932, John Thomas Howell, 9075 (NY s.n.). 1939, T.W.J. Taylor, s.n. (NY s.n.). June 1932, H.J.F. Schimpff, 40 (BKL 81350). June 1932, H.J.F. Schimpff, 40 (S s.n.). May 1959, Gunnar Harling, 5194 (S s.n.). December 1966, Inga Eliasson, 986 (S s.n.). January 1967, Inga Eliasson, 1192 (S s.n.). December 1966, Inga Eliasson, 985 (S s.n.). December 1966, Inga Eliasson, 990 (S s.n.). December 1966, Inga Eliasson, 992 (S s.n.). December 1966, Inga Eliasson, 984 (S s.n.). January 1967, Inga Eliasson, 1200 (S s.n.). November 1966, Inga Eliasson, 515 (S s.n.). November 1966, Inga Eliasson, 513 (S s.n.). June 1972, Michelle and Ole Hamann, 1598 (C 24/2007/11). January 1972, Michelle and Ole Hamann, 155 (C 24/2007/9). January 1972, Michelle and Ole Hamann, 154 (C 24/2007/8). March 1981, O. Seberg, 1747 (C 24/2007/7). April 1972, Michelle and Ole Hamann, 1177 (C 24/2007/4). March 1972, Michelle and Ole Hamann, 726 (C 24/2007/2). April 1983, Phyllis S. Bentley, 318 (K H2007/01159/12). April 1930, H.K. Svenson, 7 (K H2007/01159/11). SANTIAGO ISLAND: August 2005, Conley K. McMullen, 864 (JMUH 13758). August 2005, Conley K. McMullen, 865 (JMUH 13761). August 2005, Conley K. McMullen, 866 (JMUH 13763). August 2005, Conley K. McMullen, 867 (JMUH 13764). August 2005, Conley K. McMullen, 868 (JMUH 13766). August 2005, Conley K. McMullen, 869 (JMUH 137869). March 2007, Conley K. McMullen and Michael Shane Woolf, 887 (JMUH 13811). March 2007, Conley K. McMullen and Michael Shane Woolf, 888 (JMUH 13813). March 2007, Conley K. McMullen and Michael Shane Woolf, 889 (JMUH 13815). March 2007, Conley K. McMullen and Michael Shane Woolf, 890 (JMUH 13817). August 1891, G. Baur, 209 (GH 233524). August 1972, Michelle and Ole Hamann, 2140 (C 24/2007/3). 1825, John Scouler, s.n. (K 449165).

Nomenclatural history. – This species was first described by Hooker in 1847 as *Cordia scouleri* Hook. f. Andersson (1855) transferred the species into *Varronia scouleri* (Hook. f.) Andersson. Kuntze (1891) later renamed the species *Lithocardium scouleri* (Hook. f.) Kuntze. Borhidi (1988) renamed the species *Varronia scouleri* (Hook. f.) Borhidi, without knowing or ignoring Andersson's (1855) designation. This renders Borhidi's name illegitimate, making the currently accepted name for this species

Varronia scouleri Andersson, based upon Miller and Gottschling's (2007) reinstatement of genus *Varronia*.

Contribution of this study. – Based on characters observed in the type specimen, this species typically has lanceolate leaves with coarsely serrate margins (Figure 15), but this can be variable when observing other herbarium specimens. As previously mentioned, *V. scouleri* tends to have longer leaves and more coarsely serrate margins than *V. canescens*, the most similar species. Adaxial leaf surface of *V. scouleri* is pubescent with erect and simple or forked (Figure 16) or sometimes stellate (Figure 17) hairs. Abaxial leaf surfaces are sparsely pubescent with appressed stellate and forked, sometimes simple, hairs (Figure 18). Much longer and more noticeably robust hairs can be found on the veins. These large hairs on the veins are very distinctive of this species. Pubescence of the calyx is composed of erect and simple, and sometimes forked or stellate hairs. Simple hairs on the calyx lobes are noticeably longer than the hairs on the calyx tube. The calyx lobes themselves are usually longer than the calyx tube at anthesis. *Varronia scouleri* is distinct in that its calyx lobes can be exceptionally long and outwardly splayed compared to the other three species.

DISCUSSION

All four species of *Varronia* endemic to the Galápagos Islands deserve recognition as distinct species. Based upon this morphological study, each species can be distinguished by a combination of characters. In addition, these characters appear to have remained constant over the 185 years these species have been collected. While this is not a substantially long period of time in terms of evolution, it does indicate that these species do not appear to be undergoing any rapid change. No obvious hybrids (plants with characteristics of more than one species) were observed during the morphological study, suggesting that there may be little if any hybridization between species. Based on personal observations, the individual species of *Varronia* do not generally appear to be found within close proximity to one another, further reducing the possibility of hybridization through shared pollinators. Additionally, these *Varronia* species are distylous, and initial research on *V. scouleri* indicates that almost all fruit set is the result of pin flowers that have been pollinated with pollen from thrum plants of the same species (C.K. McMullen and J.K. Stutzman, unpublished data). Thrum plants produce few, if any, fruits, indicating that only about 50% of a local plant population is capable of producing fruit. This initial research also indicates that only about 14% of flowers produce fruits. The limited ability of *Varronia* to effectively produce fruit further limits the possibility of established mature hybrid individuals. Future research on these species would include controlled pollination crosses between species to determine if hybridization is possible, and if so, the viability of the resulting hybrid individuals.

Due to the limited fruiting ability of these species, future recruitment may be cause for concern if the habitat of these species is disturbed. In 1959, the Ecuadorian

government created the Galápagos National Park, which comprises about 97% of the total landmass of the archipelago (Camancho, 2005). Because such a significant portion of the Islands are part of the National Park, the vast majority of *Varronia* populations are also likely to be in these protected areas. This existing protection decreases the risk of habitat destruction that could potentially reduce the survival of these species. Based on February 2011 observations on Santa Cruz Island near the Charles Darwin Research Station and the town of Puerto Ayora, few seedlings are visible among established populations, though mature adult plants appear to be relatively common and vigorous.

At this time, little is known about the abundance or complete distribution of *Varronia* in the Galápagos, and future field studies of these species would benefit from assessments of these populations. Data from herbarium collection labels has provided enough information to determine on which islands each species can be found (Figure 4), but specific collection locations were rarely, or only partially provided, apart from those specimens collected by Conley K. McMullen. Based on current information, it is evident that each species is distinct across multiple islands, with *V. canescens* found on eight islands, *V. leucophlyctis* on seven, *V. revoluta* on five, and *V. scouleri* on three islands (Figure 4). Several islands have all four species of *Varronia* present. It is possible that this is the result of collection intensity, and future studies may find that the least distributed species may in fact be present on other islands that have not previously undergone intensified collecting. Detailed GPS coordinates for *Varronia* populations in the Islands would provide the information needed to construct more complete distribution maps for each species. These species do not currently appear to be under any increased threat, and their conservation needs are unlikely to change in the near future; however,

the IUCN would benefit from updated information and distributions of these species in order to reevaluate, or evaluate for the first time, the status of each species.

This study supports the existence of four morphologically distinct endemic *Varronia* species in the Galápagos Islands. While Weeks *et al.* (2010), did not find *V. leucophlyctis*, *V. canescens*, and *V. scouleri* to be genetically distinct from one another, this may have been due to the ITS regions that were used in the study. These regions may not have been significantly variable if these species have diverged relatively recently. Weeks *et al.* (2010) suggest that fingerprinting techniques that record nucleotide polymorphisms, such as microsatellites or amplified fragment length polymorphisms, would be a better method for use in the future. Future molecular studies may find that genetic variation exists in now-unexamined regions, but until that time, these populations deserve recognition as morphologically different species based on this study.

CONCLUSIONS

Morphological characterization indicates the existence of four endemic species of *Varronia* in the Galápagos Islands that are distinct across both time and location. The results from this study will be helpful in evaluating these species for their conservation statuses. Over 100 misidentified specimens are now correctly identified through the course of this study, and the diagnostic information provided here in the new taxonomic keys will help provide the information necessary for other specimens to be reevaluated, or new collections to be correctly identified. In addition, an effort must be made to assess the size and stability of the populations of each endemic *Varronia* species in order to evaluate how these species should be managed. Protecting the endemic species of the Galápagos is important both for the survival of the individual species as well as the continuation of the Galápagos Islands as a unique example of island evolution and diversity. Effective conservation programs to protect this exceptional diversity can only result from research that strives to document the flora and fauna of these islands. Accurate descriptions of the distinctive species of the Galápagos, such as those accomplished in this study, are the first step towards protecting and ensuring their future on the islands.

APPENDIX A

Table 1. A diagnostic key to the four species of endemic *Varronia* in the Galápagos Islands.

	<i>V. revoluta</i>	<i>V. leucophlyctis</i>	<i>V. canescens</i>	<i>V. scouleri</i>
leaf shape	linear	broadly lanceolate	lanceolate	lanceolate
leaf margins	revolute	finely serrate to crenate	finely serrate to crenate	coarsely serrate
adaxial leaf surface	hairs white and all simple appressed; densely pubescent	hairs mostly erect and simple	hairs typically appressed or sometimes weakly erect, stellate and forked, sometimes simple; hairs almost completely absent on some leaves	hairs erect simple, forked, sometimes stellate
abaxial leaf surface	hairs simple; densely villous pubescent; more robust, appressed white hairs on veins	hairs mostly simple and erect; often densely pubescent; simple, robust hairs common on veins	hairs appressed stellate, forked, and simple; densely pubescent	hairs appressed stellate and forked, sometimes simple; sparsely pubescent; noticeably more robust hairs on veins
calyx hairs	hairs simple; densely villous, uniform length throughout	hairs erect and simple; noticeably longer on calyx lobes than on calyx tube	hairs appressed stellate, forked, and simple, uniform length throughout	hairs erect and simple, sometimes forked or stellate; simple hairs noticeably longer on calyx lobes than on calyx tube
calyx lobes	much shorter than calyx tube at anthesis	about as long as calyx tube at anthesis	as long as or shorter than calyx tube at anthesis	usually longer than calyx tube at anthesis

Table 2. A dichotomous key to the four species of endemic *Varronia* in the Galápagos Islands.

- 1a. Leaves linear.
2. Leaf margins revolute; adaxial leaf hairs white and all simple appressed, densely pubescent; abaxial leaf hairs simple, densely villous pubescent, with more robust, appressed white hairs on veins; calyx hairs simple, densely villous, and uniform length throughout; calyx lobes much shorter than calyx tube at anthesis.....*V. revoluta*
- 1b. Leaves lanceolate.
- 3a. Adaxial leaf hairs almost entirely erect and simple; abaxial leaf hairs mostly simple and erect, with robust, simple hairs found on veins.
4. Leaf margins finely serrate to crenate; calyx hairs erect and simple, noticeably longer on calyx lobes than on calyx tube; calyx lobes about as long as calyx tube at anthesis;*V. leucophlyctis*
- 3b. Adaxial leaf hairs simple, forked, or stellate; abaxial leaf hairs simple, forked, or stellate.
- 5a. Leaf margins finely serrate to crenate; adaxial leaf hairs typically appressed or sometimes weakly erect, stellate and forked, sometimes simple; adaxial leaf hairs almost completely absent on some leaves; abaxial leaf hairs appressed stellate, forked, and simple, densely pubescent; calyx hairs appressed stellate, forked, and simple, uniform length throughout; calyx lobes as long as or shorter than calyx tube at anthesis.....*V. canescens*
- 5b. Leaf margins generally coarsely serrate; adaxial leaf hairs erect simple, forked, sometimes stellate; abaxial leaf hairs appressed stellate and forked, sometimes simple, sparsely pubescent, with noticeably more robust hairs on veins; calyx hairs erect and simple, sometimes forked or stellate, with simple hairs noticeably longer on calyx lobes than on calyx tube; calyx lobes usually longer than calyx tube at anthesis.....*V. scouleri*

APPENDIX B

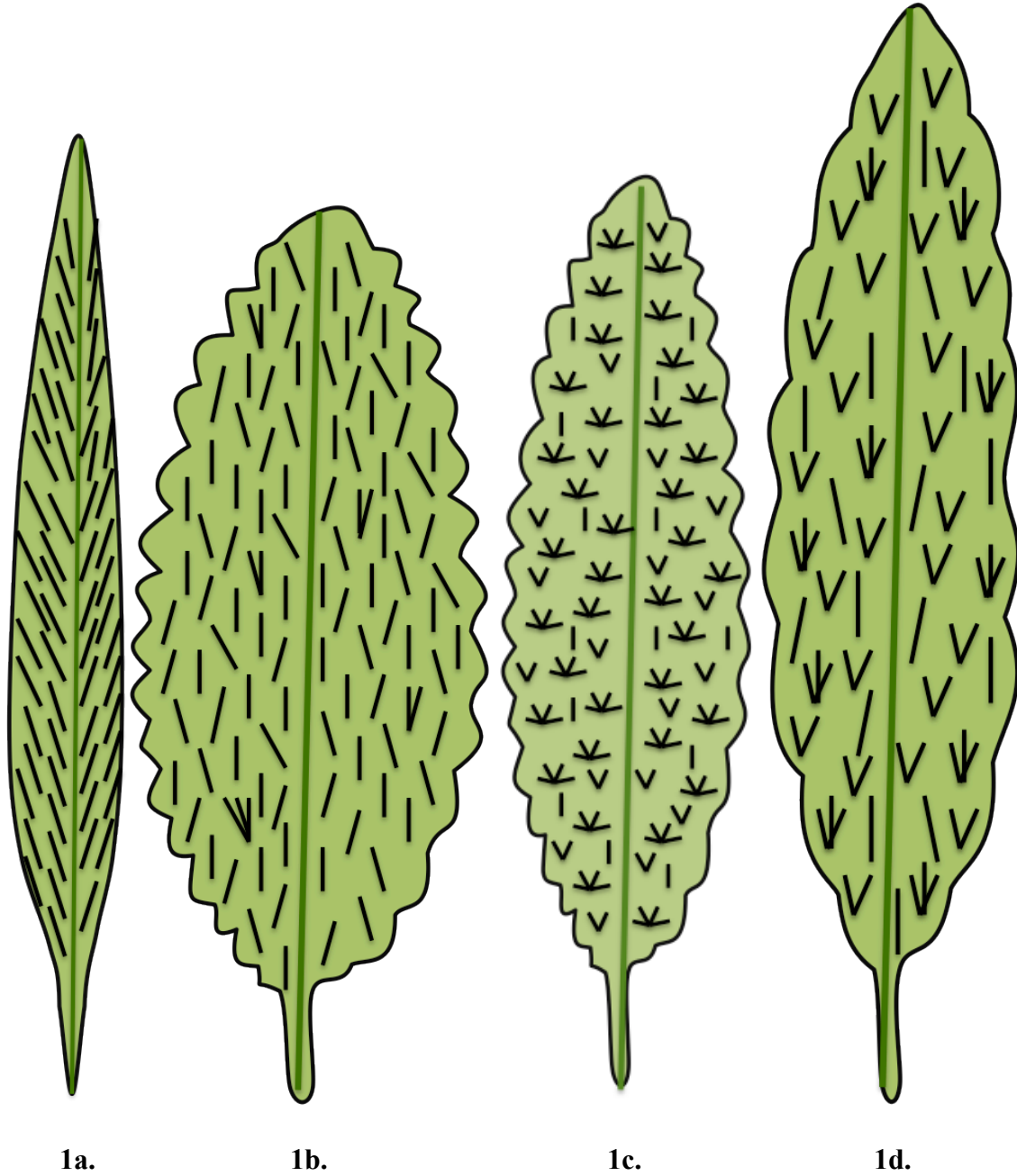


Figure 1. Graphic representation of the variation in adaxial leaf surface hair types. 1a represents *Varronia revoluta*, 1b represents *Varronia leucophlyctis*, 1c represents *Varronia canescens*, and 1d represents *Varronia scouleri*.

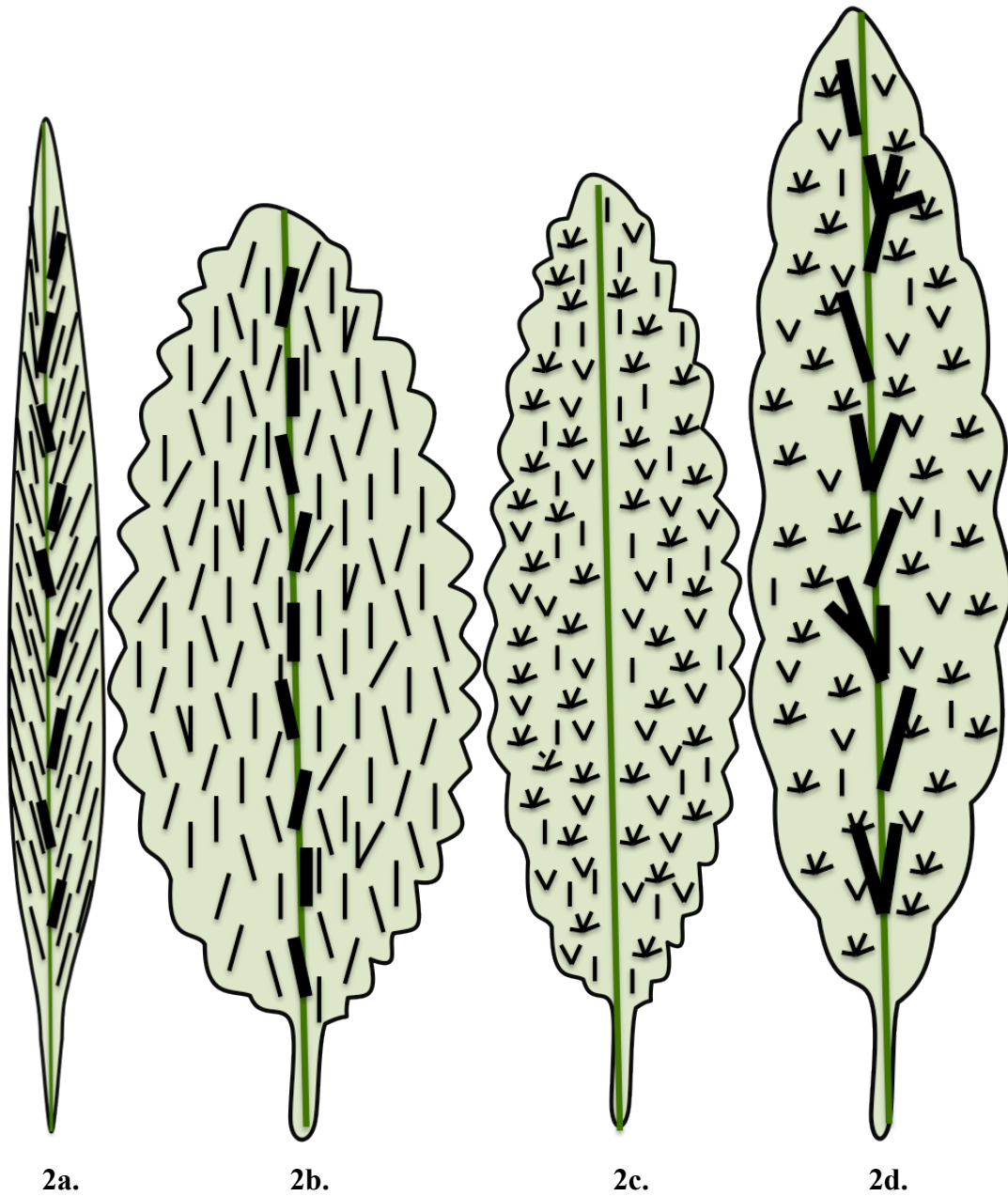
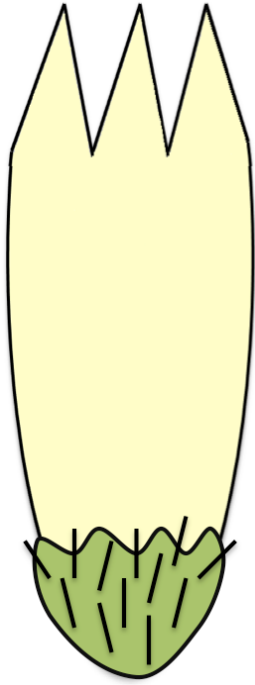
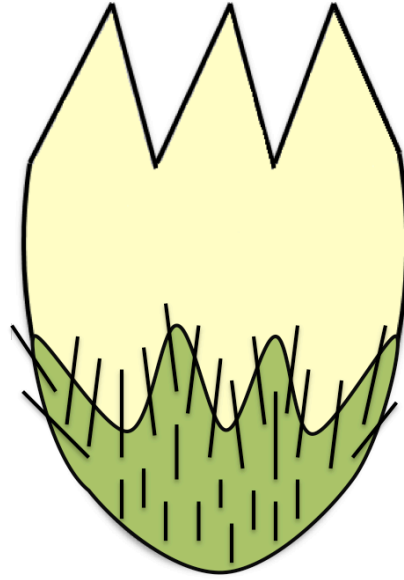


Figure 2. Graphic representation of the variation in abaxial leaf surface hair types and positioning. 2a represents *Varronia revoluta*, 2b represents *Varronia leucophlyctis*, 2c represents *Varronia canescens*, and 2d represents *Varronia scouleri*.

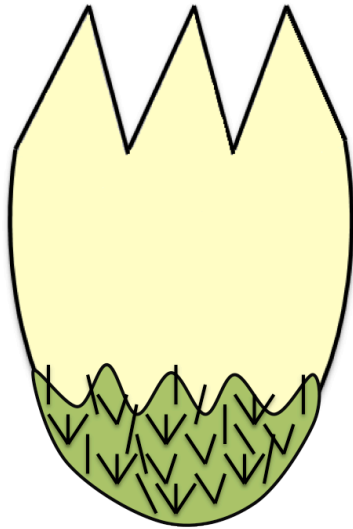
3a.



3b.



3c.



3d.

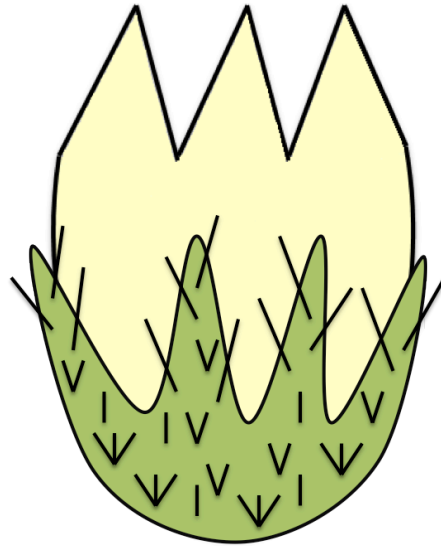


Figure 3. Graphic representation of the variation in calyx lobe length in comparison to calyx tube length, and variation in calyx hair types. 3a represents *Varronia revoluta*, 3b represents *Varronia leucophlyctis*, 3c represents *Varronia canescens*, and 3d represents *Varronia scouleri*.

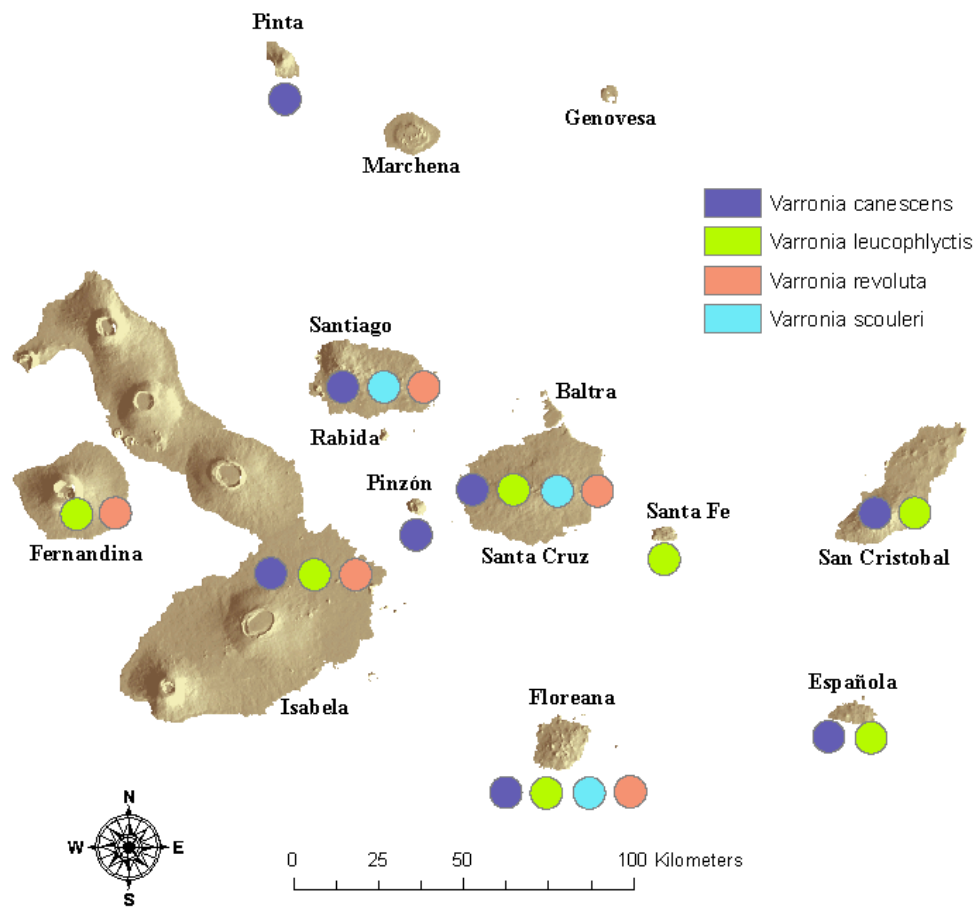


Figure 4. Distribution of the four endemic *Varronia* species on the Galápagos Islands. The dots represent on which islands an individual species can be found, rather than a specific distribution on each island. No collections have been recorded for Marchena or Genovesa Islands.



Figure 5. Photograph of a typical *Varronia revoluta* shrub displaying characteristic linear leaves and tubular flowers. Photograph courtesy of Conley K. McMullen. Specimen: August 2005, Conley K. McMullen, 848 (JMUH 13725).

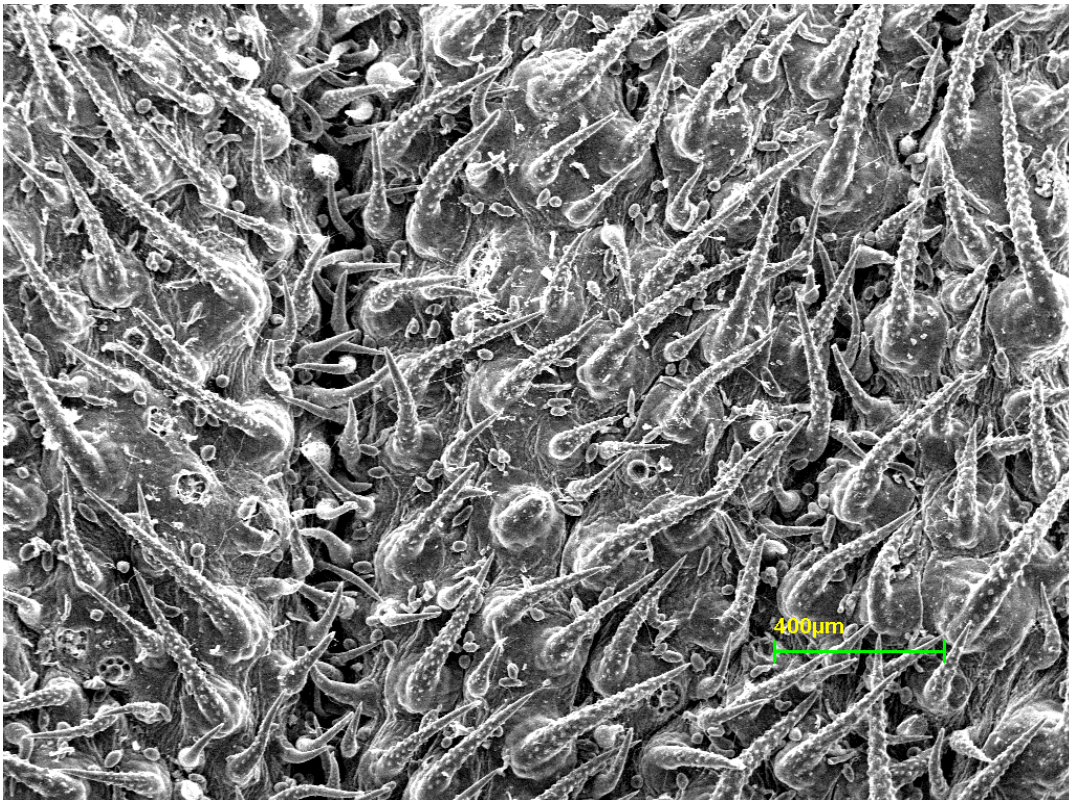


Figure 6. *Varronia revoluta* adaxial leaf surface displaying typical large, appressed simple hairs. Scale represents 400 μm . Specimen: July 2005, Conley K. McMullen, 838 (JMUH 13705).

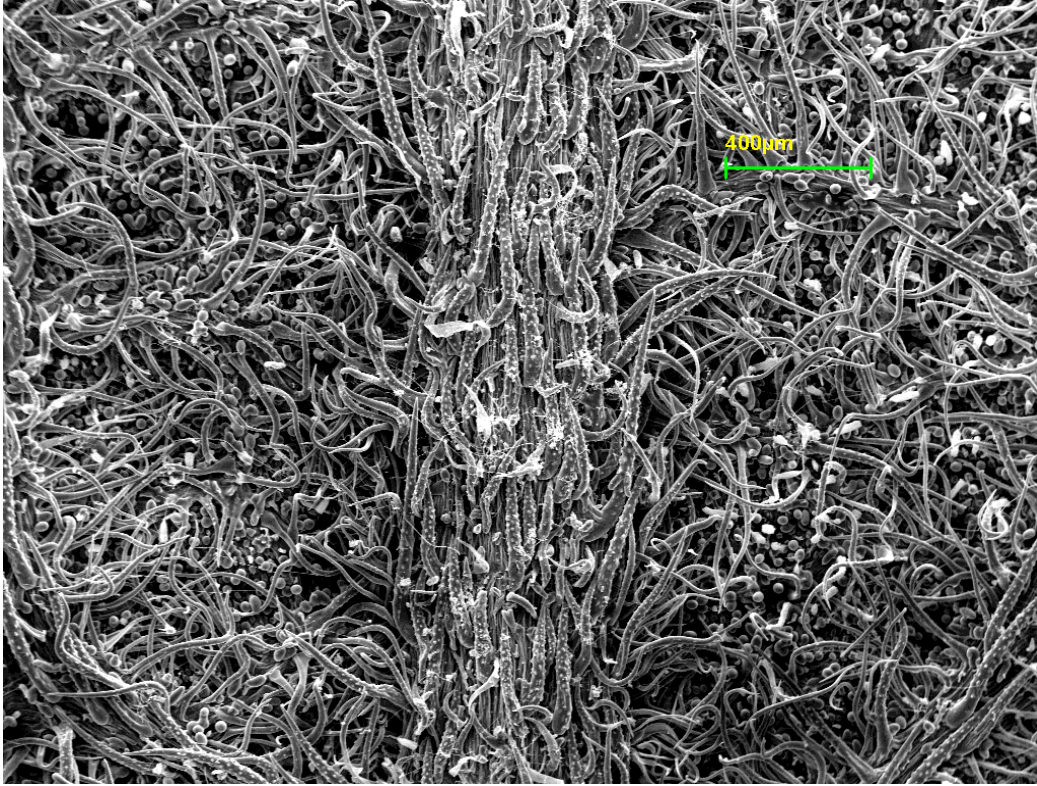


Figure 7. *Varronia revoluta* abaxial leaf surface displaying robust appressed simple hairs on veins, and densely villous simple hairs in margins. Scale represents 400 μm . Specimen: July 2005, Conley K. McMullen, 838 (JMUH 13705).



Figure 8. Photograph of a typical *Varronia leucophlyctis* lanceolate leaf with crenate margins. Photograph courtesy of Conley K. McMullen. Specimen: March 2007, Conley K McMullen and Michael Shane Woolf, 881 (JMUH 13797).

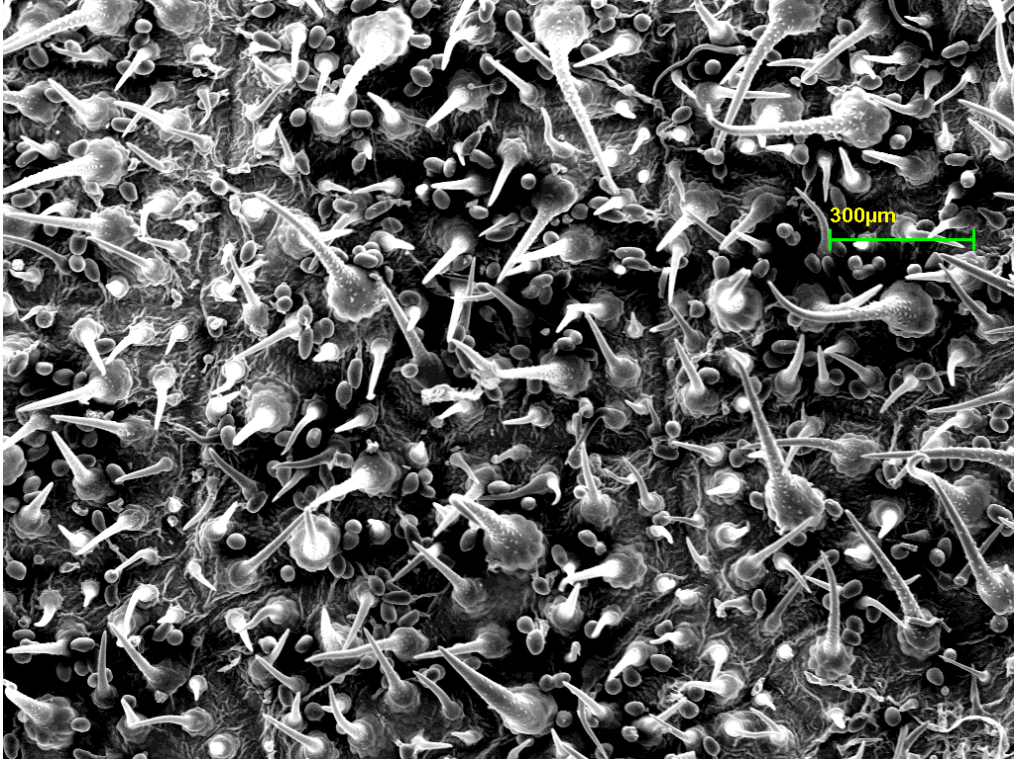


Figure 9. *Varronia leucophlyctis* adaxial leaf surface displaying erect, simple hairs. Scale represents 300 μm . Specimen: July 2005, Conley K. McMullen, 844 (JMUH 13716).

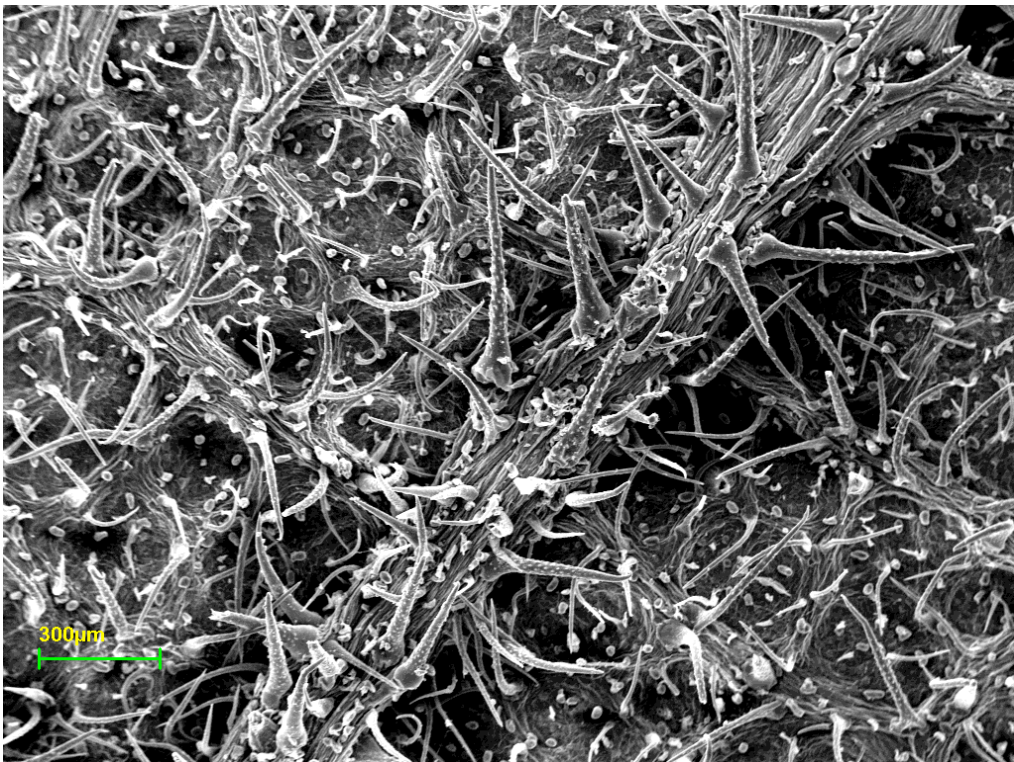


Figure 10. *Varronia leucophlyctis* abaxial leaf surface displaying robust, erect simple hairs on veins, and simple hairs in margins. Scale represents 300 μm . Specimen: March 2007, Conley K. McMullen and Michael Shane Woolf, 880 (JMUH 13794).



Figure 11. Photograph of typical *Varronia canescens* lanceolate leaves with crenate margins. Photograph courtesy of Conley K. McMullen. Specimen: March 2007, Conley K. McMullen and Michael Shane Woolf, 884 (JMUH 13804).

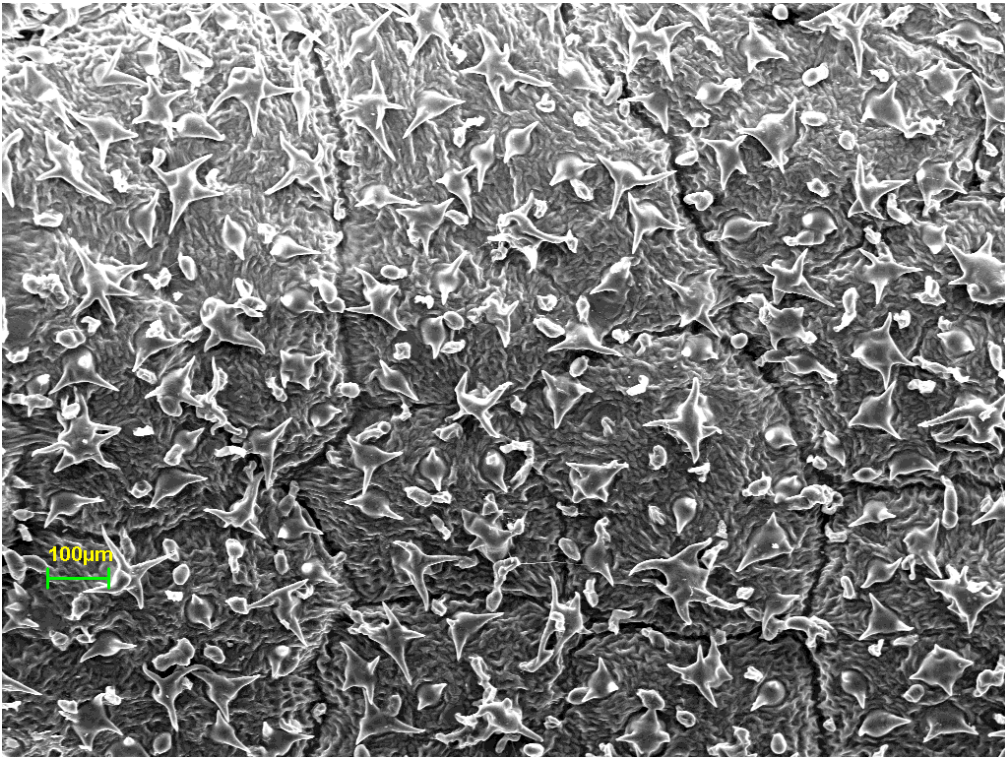


Figure 12. *Varronia canescens* adaxial leaf surface displaying appressed stellate and forked hairs. Scale represents 100 μm. Specimen: 2005, Conley K. McMullen, 824 (JMUH 13675).

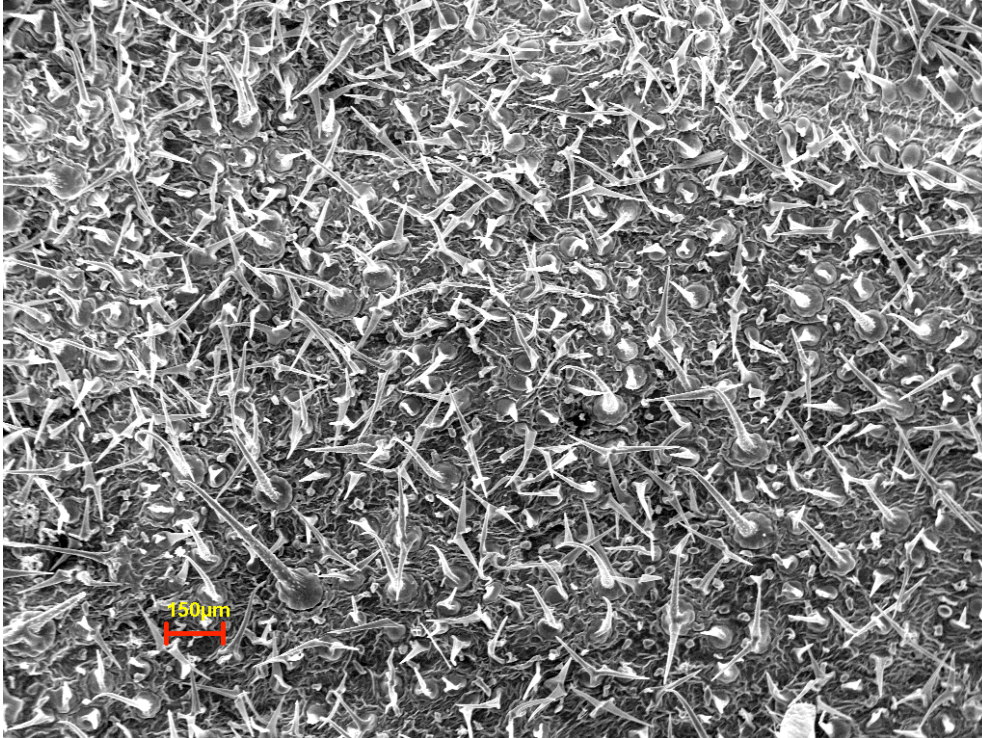


Figure 13. *Varronia canescens* adaxial leaf surface displaying weakly erect stellate, forked, and simple hairs. Scale represents 150 μm . Specimen: March 2007, Conley K. McMullen and Michael Shane Woolf, 884 (JMUH 13804).

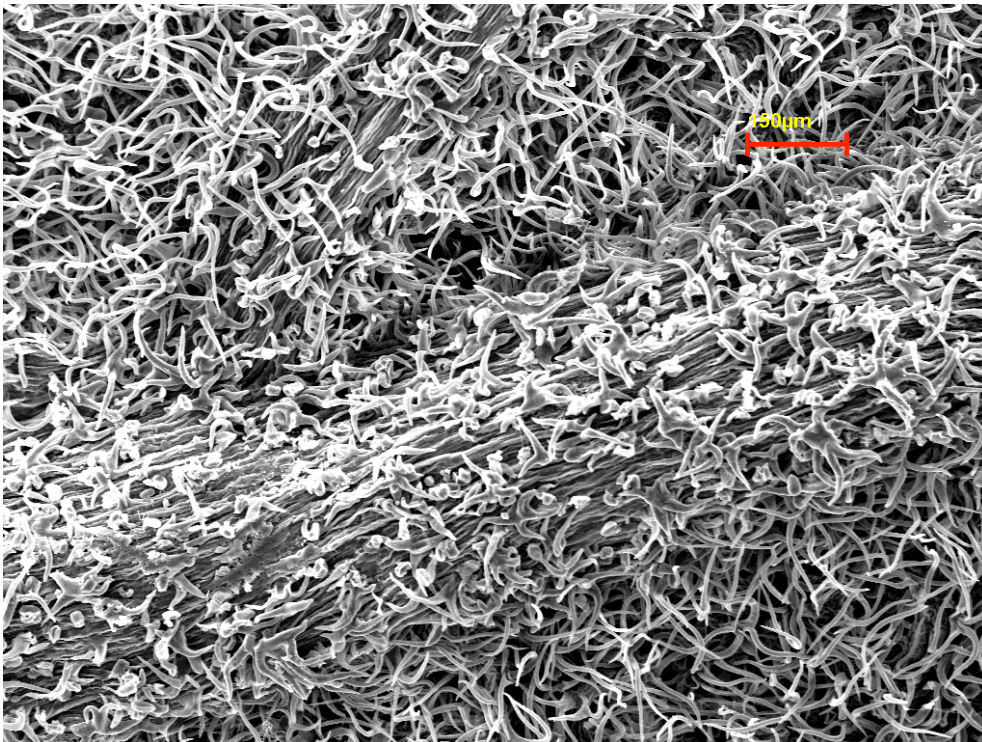


Figure 14. *Varronia canescens* abaxial leaf surface displaying densely pubescent stellate, simple and forked hairs. Hairs on veins are generally the same size as found in margins. Scale represents 150 μm . Specimen: 2005, Conley K. McMullen, 824 (JMUH 13675).



Figure 15. Photograph of typical *Varronia scouleri* lanceolate leaves with serrate margins. Photograph courtesy of Conley K. McMullen. Specimen: March 2007, Conley K. McMullen and Michael Shane Woolf, 889 (JMUH 13815).

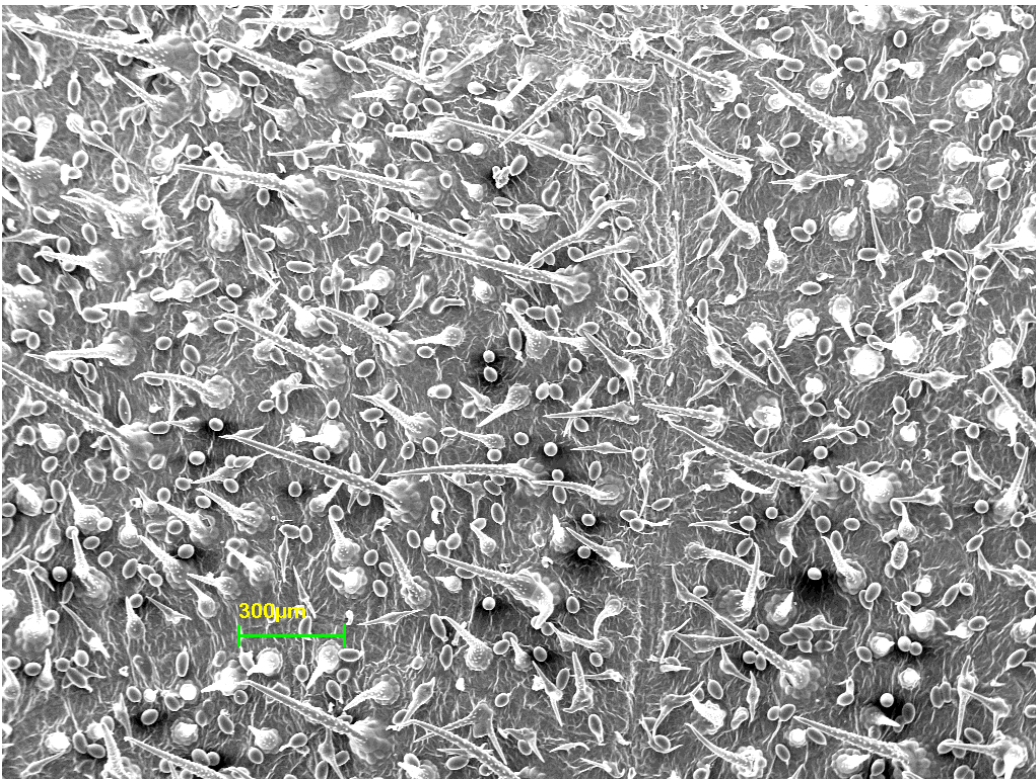


Figure 16. *Varronia scouleri* adaxial leaf surface displaying erect simple and forked hairs. Scale represents 300 μm . Specimen: March 2007, Conley K. McMullen and Michael Shane Woolf, 876 (JMUH 13787).

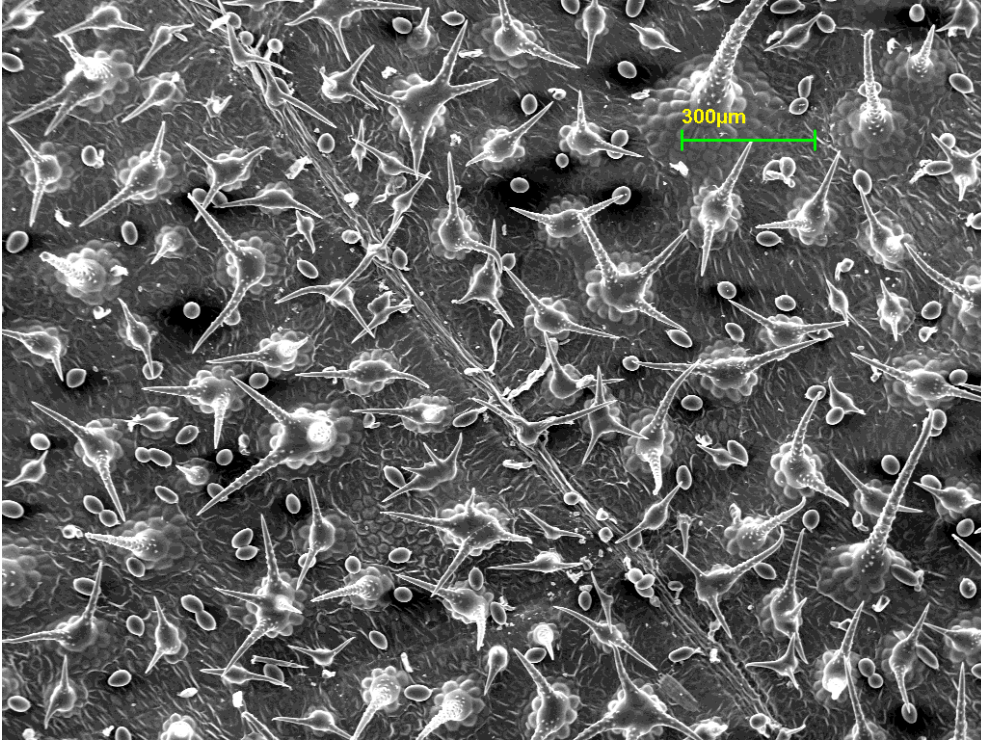


Figure 17. *Varronia scouleri* adaxial leaf surface displaying erect simple, forked, and stellate hairs. Scale represents 300 μm . Specimen: March 2007, Conley K. McMullen and Michael Shane Woolf, 873 (JMUH 13782).

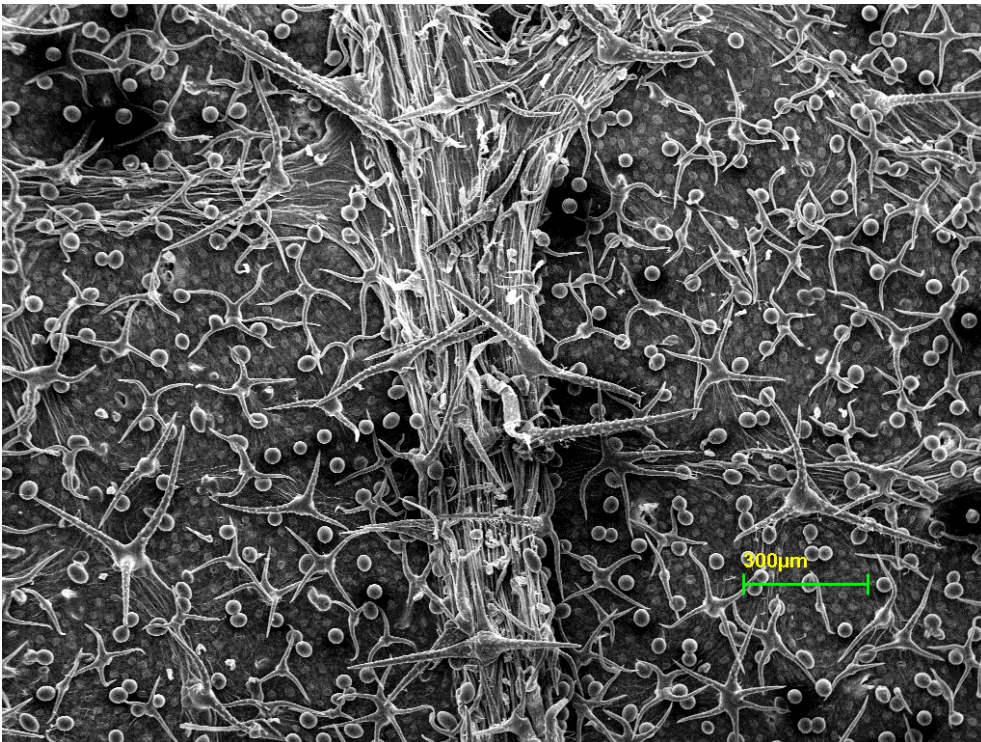


Figure 18. *Varronia scouleri* abaxial leaf surface displaying robust simple, forked and stellate hairs on veins, and smaller, appressed stellate hairs in margins. Scale represents 300 μm . Specimen: March 2007, Conley K. McMullen and Michael Shane Woolf, 873 (JMUH 13782).

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